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***Dichotomius woodruffi*, a new *Dichotomius* species of the *agenor* group from Costa Rica and Nicaragua (Coleoptera: Scarabaeidae: Scarabaeinae)**

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Dichotomius woodruffi, a new *Dichotomius* species
of the *agenor* group from Costa Rica and Nicaragua
(Coleoptera: Scarabaeidae: Scarabaeinae)

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Abstract. We describe a new species of *Dichotomius* Hope, 1838, from the *D. agenor* species-group from Costa Rica and Nicaragua: *D. woodruffi* Solís and Kohlmann, **new species** (Coleoptera: Scarabaeidae: Scarabaeinae). Based on this discovery, we confirm that *Dichotomius enioi* Montoya-Molina and Vaz-de-Mello, 2021 and *D. agenor* (Harold, 1869) are not currently distributed in Costa Rica. Instead, the only species of *Dichotomius* that are currently distributed in Costa Rica from the *D. agenor* species-group are *D. centralis* (Harold, 1869) and *D. woodruffi*. We discuss the distribution of the *Dichotomius agenor* species-group in Central America.

Key words. Dichotomiini, *D. agenor*, *D. centralis*, *D. enioi*, dung beetles, Neotropics, new species.

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Introduction

In this paper, we intend to better understand the Costa Rican biodiversity by clarifying the taxonomy of the *D. agenor* species-group. To achieve this goal, we use comparative morphology (external morphology and male genitalia), collection specimens, electronic databases (National Museum of Costa Rica, MNCR; Escuela Agrícola Panamericana, Honduras, EAPZ), and a literature revision. The present taxonomic analysis includes the description of a new species, an illustrated key for species-group identification for all Central America, and a map indicating the distribution of the species-group in Nicaragua, Costa Rica, and Panama.

Montoya-Molina and Vaz-de-Mello (2021) taxonomically reviewed the *Dichotomius agenor* species-group and considered it part of the subgenus *Luederwaldtinia* Martínez, 1951. However, Nunes and Vaz-de-Mello (2019) had previously synonymized *Luederwaldtinia* with *Selenocopriss* Burmeister, 1846. Nunes and Vaz-de-Mello (2019) fused the species-groups of both subgenera into eleven species-groups and three isolated species as part of the subgenus *Selenocopriss*. Nunes and Vaz-de-Mello (2019) diagnosed the subgenus *Selenocopriss* by the following combined characters: clypeal teeth present, strong; lacking clypeo-genal angle; clypeal and genal margin curved; ventral clypeal process bifurcated and female sixth ventrite three to four times larger than the fifth ventrite, not modified medially. Pardo-Díaz et al. (2019) undertook a phylogenetic analysis of the genus *Dichotomius* and found support for the existence of a *D. agenor* species-group and considered it also to be a member of the subgenus *Selenocopriss*. We follow here the last two taxonomic suggestions and consider the *D. agenor* species-group as a member of the subgenus *Selenocopriss*.

In their work, Montoya-Molina and Vaz-de-Mello (2021: 4) diagnosed the *D. agenor* species-group using the following morphological characters: head of males bearing a transverse trituberculate carina, medial tubercle higher than lateral ones; in females head carina generally bituberculate or quadrituberculate, except in two species (*D. fornicatus* Luederwaldt, 1931 and *D. rafanunezi* Montoya-Molina and Vaz-de-Mello, 2021), where they are trituberculate; pronotum without ornamentation, displaying at most a truncate declivity or knob; pronotum

convex in females. The *D. agenor* species-group is distributed from the north Pacific coast of Mexico (Sonora) to Argentina (Santiago del Estero) and Brazil (Mato Grosso), and it includes seventeen described species so far (Montoya-Molina and Vaz-de-Mello 2021). Pardo-Díaz et al. (2019) suggest, based on their molecular analysis, that *D. belus* (Harold, 1880) is not a part of the *D. agenor* species-group.

Among other new species, Montoya-Molina and Vaz-de-Mello (2021) described a new species from the *D. agenor* species-group from Mexico, Guatemala, and Costa Rica: *D. enioi* Montoya-Molina and Vaz-de-Mello, 2021. The report of this new species in Costa Rica prompted our reanalysis of the *Dichotomius* Hope, 1838 fauna for Costa Rica, as originally published by Kohlmann and Solís (1997).

Montoya-Molina and Vaz-de-Mello (2021: 25) diagnosed *D. enioi* by combining the following characters: male interocular space microsculpture shagreened, with flat, well-defined punctures resembling rugosity. Median tubercle conical, twice as high as lateral, with fine apical emargination; lateral tubercles with acute apex. Row of dense uninterrupted ocellate punctures arranged along anterior and posterior margin of pronotum. Anterior disc declivity with weak anteromedian lobe subemargination. Interstriae microsculpture shagreened.

Materials and Methods

Collections studied. Specimens used in this work are deposited in the following collections:

ASC Ángel Solís Collection, Zarcero, Alajuela, Costa Rica

EAPZ Escuela Agrícola Panamericana, Tegucigalpa, Honduras

FSCA Florida State Collection of Arthropods, Gainesville, FL, USA

MNCR Museo Nacional de Costa Rica, San José, Costa Rica.

Measurements. Length of specimens used in this work was measured from the anterior margin of the clypeus to the pygidial disc in resting position. Widths were measured at either the pronotum or the elytra at the widest point.

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

Label data from type specimens are separated by a slash “/”. Square brackets “[]” were used to describe characteristics of each type label (e.g., [red]). For locality data, country names are indicated in capital letters and provinces, or departments are indicated in bold (e.g., **Heredia**) followed by geographic coordinates (when available) and other complementary information, data, and collector. Our description follows the style used by Montoya-Molina and Vaz-de-Mello (2021) to facilitate comparisons between both papers. The key includes all the *D. agenor* group species known from Central America. Although we used the term ‘species-group’ in this work, we agree that it does not constitute a valid species-group name, according to Article 11.9 of The Code (ICZN 1999).

Illustrations. Photographs of specific characters (Fig. 5–18) were taken 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. Photographs of the whole/partial body (Fig. 1–4) were taken using a Nikon d7000 digital camera using the WeMacro automatic focus stacking rail with a 40–60 μ step length. These photos were stacked using the Zerene stacker program.

Results

At present, Montoya-Molina and Vaz-de-Mello (2021) consider seventeen species in the *D. agenor* species-group. Type specimens of *D. enioi* were not studied, but we did not consider this necessary because the description and the excellent photos published by Montoya-Molina and Vaz-de-Mello (2021) allow precise identifications. We also used our own *D. enioi* material for making the necessary morphological comparisons. The characters that separate *D. enioi* from *D. woodruffi* **new species** are contrasted in the remarks section.

Regarding the *D. enioi* that Montoya-Molina and Vaz-de-Mello (2021) cited from Costa Rica, we obtained photographs through the kind agency of Fernando Vaz-de-Mello and Jorge Arias, of four of the paratypes (2♀, 2♂) housed at the Coleção Zoológica da Universidade Federal de Mato Grosso, that were cited from Santa Rosa.

From our comparisons, we concluded that the specimens are *D. centralis* (Harold, 1869) and that they were most probably confused with *D. enioi*. *Dichotomius centralis* is a very common species in Santa Rosa.

The following number of specimens were studied: *D. agenor* (Harold, 1869) (6 specimens from Panama, 6 specimens from Colombia), *D. centralis* (261 specimens from Costa Rica, 22 specimens from Nicaragua, 1 specimen from El Salvador, 2 specimens from Guatemala), *D. enioi* (2 specimens from Guatemala, 2 specimens from Mexico), *D. woodruffi* **new species** (218 specimens from Costa Rica, 6 specimens from Nicaragua, 106 specimens in alcohol from Costa Rica). Our analysis confirms that *D. enioi* is not present in Costa Rica. We expand the known distribution of *D. enioi* into the Mexican state of Chiapas. Additionally, Montoya-Molina and Vaz-de-Mello (2021) suggested that Kohlmann and Solís (1997) might have reported this species for Costa Rica as *D. agenor* (Harold, 1869). Under closer inspection, the *D. agenor* that had been initially reported for Costa Rica by Kohlmann and Solís (1997) turned out to be a new species, which is described in the present work. We confirm that *D. agenor* is present in Panama but not in Costa Rica.

New distributional records for the *Dichotomius agenor* species-group in Central America

To better understand the biodiversity of the *D. agenor* species-group in Central America, we report new distributional records for two species.

First record of *D. centralis* (Harold, 1869) for Honduras at El Paraíso state: HONDURAS: **El Paraíso**. 8.3 km SE Capire. 675 m. 1 Junio 2000. R. Cave & J. Torres. 13°58'54"N 85°49'25"W (1 specimen) (EAPZ).

First record of *D. enioi* for the Mexican state of Chiapas: MEXICO: **Chiapas**. Lacanjá-Chansayab, 300 m. 23-VII-1977. En excremento humano en selva. M. Lamotte & B. Kohlmann cols. (1♀, 1♂) (ASC).

Montoya-Molina and Vaz-de-Mello cite *D. sagittarius* (Harold, 1869) (a member of the *D. agenor* species-group) from Chiapas at Boca de Chajul. This report requires reconfirmation because *D. enioi* has been collected only 70 km away from this location (at Lacanjá-Chansayab).

Systematic Zoology

Dichotomius (Selenocpris) woodruffi Solís and Kohlmann, new species

(Fig. 1–11, 19)

Dichotomius agenor (Harold, 1869) – Kohlmann and Solís 1997: 345; Kohlmann et al. 2007: 30; Solís and Kohlmann 2012: 6.

Dichotomius enioi Montoya-Molina and Vaz-de-Mello, 2021 (in part): 25.

Type depository. Holotype male, allotype female and 210 (88♀, 122♂) paratypes in MNCR, 2 (1♀, 1♂) paratypes in FSCA, and 4 (3♀, 1♂) paratypes in ASC.

Type status. Holotype male, *type labels*: “COSTA RICA: **Puntarenas Prov.** Est. Q. Bonita. 50 m, agos 1993, R. M. Guzmán. L N 194500_469850 #2297. INBIO CRI001 969440”. “HOLOTYPE / *Dichotomius* / *woodruffi* n. sp. / Solís & Kohlmann ded. 2022 [printed, red]”.

Paratypes (89♀, 122♂). Allotype, female, *type labels*. “COSTA RICA: **Puntarenas Prov.** Est. Q. Bonita. 50 m, Res. Biol. Carara. May 1992. J.C. Saborío. L-N194500-469850. INBIO CRI000 796048”. “ALLOTYPE / *Dichotomius* / *woodruffi* n. sp. / Solís & Kohlmann ded. 2022 [printed, red]”. **Puntarenas Prov.** Est. Q. Bonita. 50 m, Res. Biol. Carara. May 1992. J.C. Saborío. L-N194500-469850. INBIO CRI000 796048”. “ALLOTYPE / *Dichotomius* / *woodruffi* n. sp. / Solís & Kohlmann ded. 2022 [printed, red]”. “COSTA RICA: **Guanacaste Prov.** Area de cons. Arenal. Río San Lorenzo, Tierras Morenas. 10.610459 N, –84.994969 W. 01 jul 1994. Col. Rodríguez, G.” (1 ♀); with same data as previous but “Tierras Morenas. 10.5710619 N, –85.025949 W. 01 may 1994. Col. Rodríguez, G.” (4 ♀, 2♂); with same data as previous but “Río San Lorenzo, Tierras Morenas. 10.610459 N, –84.994969 W. 01 jul 1994. Col. Rodríguez, G.” (10 ♂); with same data as previous but “Área de cons. Guanacaste. La Cruz, La Garita, Est Los Almendros. 11.033856 N, –85.524789 W. 28 jul 1992. Col. López, E.” (1 ♂); with same data as previous but “**Puntarenas Prov.** Area de cons. Osa. Golfito, Pque Nal Corcovado, Est Agujas, Las Quebraditas. 8.5226319 N, –83.48411 W. 03 may 2002. Col. Azofeifa A.” (2♀, 1♂); with same data as previous but “La Bonanza, entre Agujas y Cerro Rincón. 8.5304219 N, –83.449049 W. 17 jun 2008. Col. Hernández, B.” (2♀, 3♂); with same data as previous but “Osa. P.N. Corcovado. Est. Agujas. 8.536614 N, –83.42551 W. 12 abr 2000. Col. Azofeifa A.” (1 ♀); with

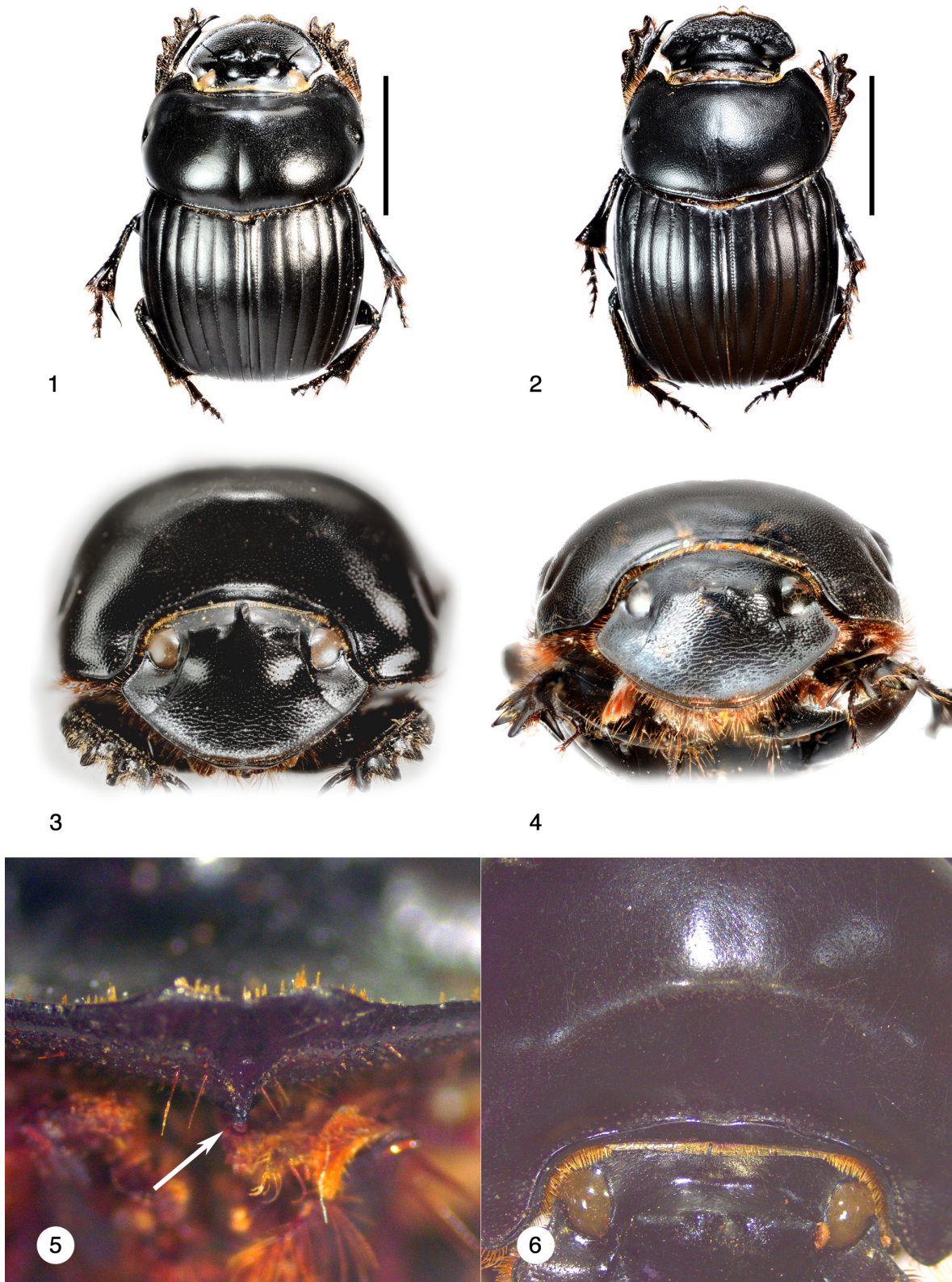
same data as previous but “Area de cons. Pacifico Central. Garabito, Reserva Biol. Carara, Est. Quebrada Bonita. 9.7674529 N, –84.608119 W. 01 jul 1990. Col. Bello, E.” (1♀, 2♂); with same data as previous but “01 may 1992. Col. Saborío, J.C.” (15♀, 15♂); with same data as previous but “01 jun 1992. Col. Saborío, J.C.” (4♀, 8♂); with same data as previous but “01 jul 1992.” (6♀, 5♂); with same data as previous but “01 jul 1992. Col. Guzmán, R.” (6♀, 6♂); with same data as previous but “10 ago 1992.” (1♀, 2♂); with same data as previous but “01 set 1992. Col. Saborío, J.C.” (1♂); with same data as previous but “02 set 1992. Col. Guzmán, R.” (4♀, 3♂); with same data as previous but “18 oct 1992.” (3♀); with same data as previous but “01 nov 1992. Col. Saborío, J.C.” (3♀, 1♂); with same data as previous but “01 may 1993. Col. Saborío, J.C.” (3♀, 17♂); with same data as previous but “01 jun 1993.” (2♂); with same data as previous but “01 jun 1993. Col. Guzmán, R.” (4♂); with same data as previous but “01 jul 1993. Col. Saborío, J.C.” (2♀); with same data as previous but “01 jul 1993. Col. Guzmán, R.” (1♀); with same data as previous but “01 ago 1993. Col. Saborío, J.C.” (2♀, 4♂); with same data as previous but “01 ago 1993. Col. Guzmán, R.” (2♀, 9♂); with same data as previous but “01 set 1993.” (2♀, 2♂); with same data as previous but “01 abr 1994.” (1♂); with same data as previous but “01 set 1994.” (2♀, 1♂); with same data as previous but “01 oct 1994. Col. Saborío, J.C.” (1♀); with same data as previous but “01 oct 1994. Col. Guzmán, R.” (8♀); with same data as previous but “01 nov 1994. Col. Saborío, J.C.” 1♀); with same data as previous but “01 jul 1995. Col. Guzmán, R.” (1♀, 1♂); with same data as previous but “01 ago 1995.” (1♀, 2♂); with same data as previous but “01 may 1996.” (1♂); with same data as previous but “Area de cons. Tempisque. Lepanto, Karen Morgensen, Sendero Principal. 9.8670949 N, –85.05995 W. 20 set 2003. Col. Cárdenas, Yow.” (1♀, 2♂); with same data as previous but “23 jun 2003. Col. Briceño, Duvalier.” (1♀); with same data as previous but “22 jun 2003. Col. Porras Vega, Wendy.” (3♂); with same data as previous but “Send. Central. Est. San Miguel. 9.5839859 N, –85.11212 W. 22 abr 1997. Col. Alvarado, F.” (1♂); with same data as previous but “Area de cons. La Amistad Pacifico. Parcelas IDA. 8.958083 N, –83.05217 W. 10 jun 2008. Col. Pulido, A.” (2♂); with same data as previous but “**San José Prov.** Area de cons. Pacifico Central. Est. Bijagual, 600 m. N de Bijagualito. 9.7430889 N, –84.544759 W. 01 jul 1995. Col. Saborío, J.C.” (6♀, 4♂); with same data as previous but “P. N. La Cangreja, Puriscal, Chires. 9.690711 N, –84.377529 W. 28 jun 2005. Col. Hernández, B.” (2♀, 3♂); with same data as previous but “800 m al N. de Bajo La Palma. 9.7630379 N, –84.244929 W. 22 may 1995. Col. Solis, A.” (3♂). All paratypes deposited in MNCR. “NICARAGUA: **Managua Dep.** El Crucero, Reserva privada El Bajo, Sendero Quebrada, 730–597 m. 11.991915 N, –86.322757 W. 26–27 nov 2019. Col. Hernández, B.” (4♀, 2♂, paratypes deposited in ASC and FSAC).

Other examined material (106 specimens, non-paratypes, material identified by AS, not mounted, and preserved in alcohol at MNCR). Their locality data is the following: “COSTA RICA: **Guanacaste Prov.** Area de cons. Guanacaste. Camino del Aguacate, Est. La Perla, 375 m, Pitfall T. 28 al 30 junio de 2017, A. Solís, E Cantillano, J. Cortez, Coord. 10.771236, –85.428981” (25 unverified sex); with same data as previous but “Bosque Húmedo en Sector Santa Rosa, ACG, 300 m, Pitfall T. 8 al 10 de junio 2016, A. Solís, Coord. 10.851171, –85.606955” (35 unverified sex); with same data as previous but “Área de cons. Tempisque. Bagaces, Est. Palo Verde. 10.35 N, –85.352779 W. 14 nov 2004. Col. Gamboa R. B.” (1♂); with same data as previous but “**Puntarenas Prov.** Bosque de Asentamiento de INDER en Sansi, SINAC, 500 m, Pitfall T. 13 al 15 junio 2013, A. Solís y C Godínez, Coord. 8.959002, –83.052355” (20 unverified sex); with same data as previous but “La Bonanza, sendero entre Agujas y Cerro Rincón, Parque Nacional Corcovado, 400 a 600 m, Pitfall T. 17 al 19 junio 2008, B. Hernández y M. Moraga, Coord. 8.530277, –83.4488” (14 unverified sex); with same data as previous but “La Cangreja, Zona Protectora Cerro de La Cangreja, 600 m. 9.69916 N, –84.37750 W. Pitfall T. 29 jun 2005, Col. B. Hernández” (11 unverified sex).

Distribution. Costa Rica (Guanacaste, Puntarenas, and San José provinces) and Nicaragua (Managua department) (Fig. 19).

Etymology. *Dichotomius woodruffi* **new species** is an eponym after the late Robert Woodruff, a scarabaeologist, known for his work on Florida Scarabaeidae, especially dung beetles and the melolonthine genus *Phyllophaga*. He was also interested in collecting postage stamps with scarabs depicted on them.

Diagnosis. *Dichotomius woodruffi* **new species** is separated from other species in the *D. agenor* species-group by the following combination of characters: Male interocular surface with lightly shagreened microsculpture (small, lightly impressed punctures) (Fig. 1). Anterior pronotal border medially sinuate in major males (Fig. 6); anterior pronotal declivity with a medial sulcus (Fig. 7); male median tubercle conical, without apical emargination, twice



Figures 1–6. *Dichotomius woodruffi*, new species. 1) Dorsal habitus, holotype, male. Scale bar equals 1 cm. 2) Dorsal habitus, allotype, female. Scale bar equals 1 cm. 3) Frontal view, holotype, male. 4) Frontal view, allotype, female. 5) Ventral clypeal process spiniform, holotype male. 6) Anterior pronotal border (frontal view), holotype male.

as high as lateral tubercle; lateral tubercles with acute apex (Fig. 3). Female fronto-clypeal carina quadrituberculate (Fig. 4). Ventral clypeal process spiniform (Fig. 5). Row of dense uninterrupted ocellate punctures arranged along anterior and posterior margin of pronotum (Fig. 6). Interstriae with surface shagreened (Fig. 1–2). Pygidium twice as wide as long (Fig. 8). Setigerous lateral areas on the anterior and lateral lobes of metasternum interrupted at the posteromedial mesocoxal margins. Ventral surface of profemur covered with well-impressed punctures, setigerous setae near the medial edge. Ventral surface of metafemur without setose punctures.

Description. Holotype male. Length 23.0 mm. Width 13.5 mm. Dorsal surface black and shagreened (Fig. 1).

Head and pronotum shiny, elytra and pygidium dull. Head with the anterior dorsal surface crosswise rugose, rugosity irregular. Transverse tubercle wide and flattened fronto-posteriorly (Fig. 3), with a simple conical central process or horn and two lateral carinae whose profile in frontal view is acute at the lateral angles and sinuous in the upper part (Fig. 3). Punctures decrease in size and depth as one advances from the clypeus up the slope and the upper part of the transverse forehead, where they almost disappear. Vertical posterior area of the transverse tubercle shows punctures in the form of small transverse lines. Horizontal posterior area of the head shows small transverse punctures in the lateral area, central area devoid of punctures. Anterior clypeal border with two teeth separated by an obtuse indentation. Ventral clypeal process spiniform (Fig. 5).

Pronotum wider than long with a pronounced slope in the anterior area and with a slight central concavity, a slight elevation on each side and another slight bilobed elevation in the upper part of the concavity. The surface of the pronotum possesses fine, small, simple punctures in the central disc area than in the lateral area. Punctures near the anterior and posterior margin are ocellate. Anterior pronotal border medially sinuate (Fig. 6); anterior pronotal declivity with a fine sulcus in its upper part (Fig. 7).

Elytral striae with ocellate punctures. Interstriae with very small, almost imperceptible punctures.

Pygidium twice as wide as long (Fig. 8); with very small punctures throughout most of its surface except for a row of strongly impressed ocellate punctures bordering the basal margin.

Ventral area. The entire ventral surface, as well as the dorsal surface, with shagreened micro-sculpture. Area of the hypomeron with the anterior and posterior third covered with setigerous punctures strongly impressed with long setae, central area smooth without setigerous punctures except for one, two or three rows of setigerous punctures near the lateral border (4 or 5 rows in *D. enioi*).

Prosternal surface lacking obvious punctures. Mesosternum with setaceous, ocellate punctures; setae minute. Mesepimeron and metepisternum densely covered with setigerous, ocellate punctures. Metasternum with lateral lobes covered with setigerous punctures, anterior central lobe with ocellate setigerous punctures strongly impressed in the anterolateral areas. Central and posterior area of metasternum, including the area adjacent to the posterior border of the mesocoxa, without setigerous punctures.

Abdominal ventrites with one (more frequently two) row of ocellate punctures in the area near the anterior border.

Ventral surface of profemora with small and shallow punctures medially (surface appearing rugose), with large setigerous punctures very strongly impressed in the posterior distal region. Ventral area of the meso- and metafemora smooth, with minute punctures (almost invisible) except in the most distal region.

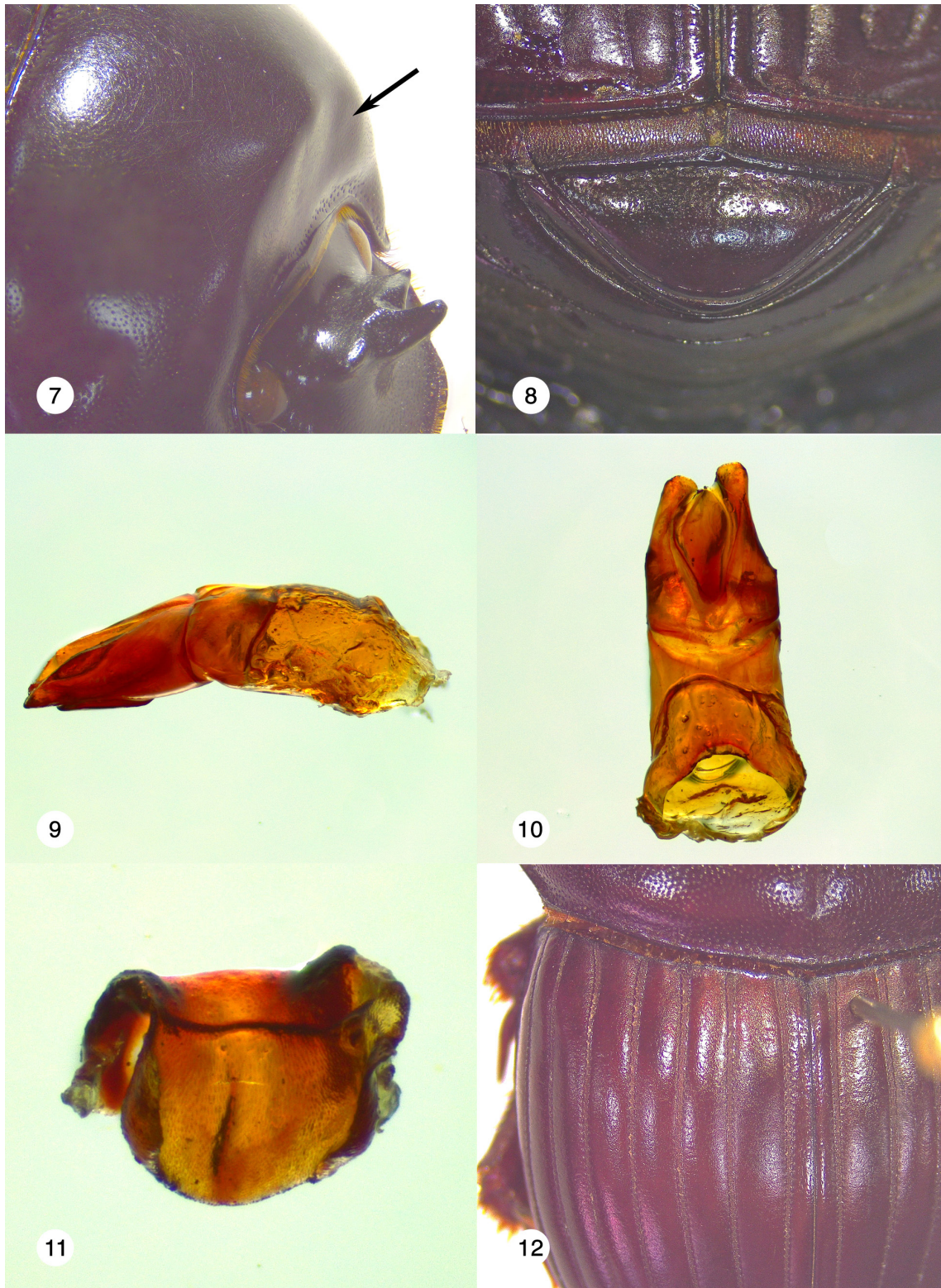
Posterior coxa with a row of setigerous annular punctures along the entire length and contiguous to the posterior border.

Parameres and lamella copulatrix as in Figures 9–11.

Allotype female. Length 19.0 mm. Width 13.0 mm. As male except for the following characters: Head with the entire dorsal surface crosswise rugose, the rugosity is irregular and most strongly impressed on the clypeus (Fig. 2). Transverse, quadrate elevation in the surface of the forehead. Two central tubercles a little higher and connected to each other by a small, curved carina forming a concavity posteriorly (Fig. 4). Less developed males are like females in the characteristics of the dorsal area of the head.

Pronotum without declivity as in the holotype but with a slight elevation in the anterior discal area, like intermediately developed males and nearly absent in less-developed females. Punctures always more strongly impressed in less developed females.

Morphological variation (paratypes). Length 17.0–23.0 mm. Width 10.5–13.5 mm. Anterior edge of the pronotum of males varies from very wide (majors) to less wide (minors). The anterior declivity of the pronotum



Figures 7–12. *Dichotomius woodruffi*, new species, and *D. centralis*. 7–11) *D. woodruffi*. 7) Anterior pronotal sulcus (lateral-oblique view), holotype male. 8) Male pygidium twice as broad as long, slightly convex, holotype male. 9) Lateral view of the aedeagus, holotype male. 10) Ventral view of the aedeagus, holotype male. 11) Lamella copulatrix, holotype male. 12) *D. centralis*, elytral stria crenulate.

is wider in major males and decreases in amplitude until it is lacking in intermediate males (like females). Pronotum may vary from finely to coarsely punctate; females have coarser punctures. Minor males have the anterior pronotal border parallel and not sinuate. Minor males resemble females, especially regarding the cephalic carina. Male forms vary from minors to intermediates to majors.

The hypomeron in the central area may lack punctures or possess a few ring-like punctures without setae. Intermediately developed males with apex of the central process bituberculate and in less developed males the transverse elevation of the forehead like that of females. Ventral profemur surface varies from finely to coarsely punctate; females tend to possess coarser punctures. On its left side, one very well-developed female specimen was found to have setigerous punctures of the medial and lateral edges of the metasternum continuous at the inner mesocoxal area, but not on its right-side specimen possessed a convex pygidium.

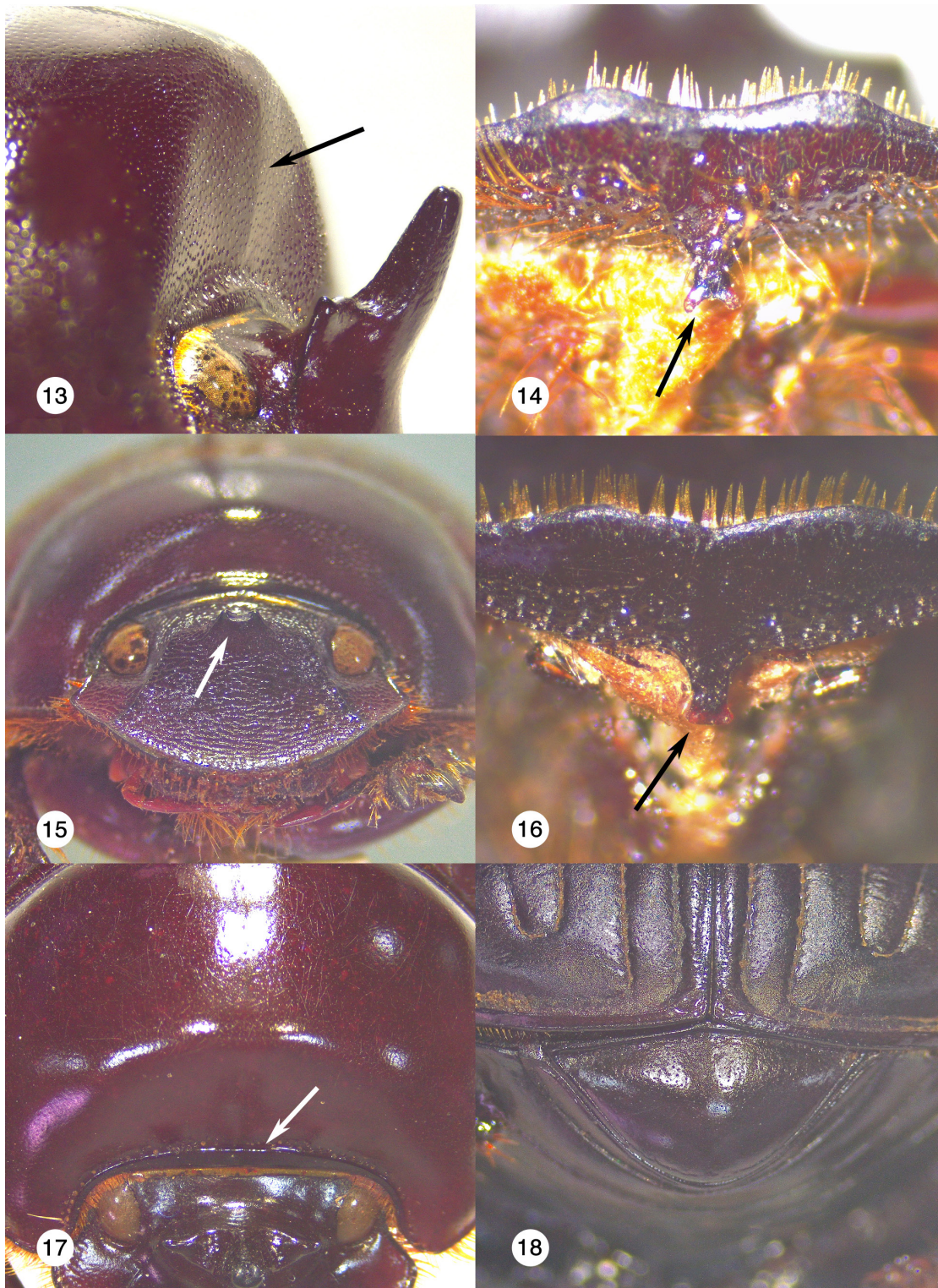
Ecology. We collected this species in traps baited with human, pig, and horse dung. It is distributed in humid forests and piedmont forest areas along the Pacific slope in Costa Rica and southern Nicaragua. The species has been collected from April to November, from 0 to 800 m altitude.

Chorology. The known southern distribution limit of *D. woodruffi* **new species** is in Costa Rica near the border with Panama (8.9520000 –83.0345000), and the known northernmost distribution limit is at El Bajo Private Reserve near Managua, Nicaragua (11.991928 –86.322666). It is an uncommon species in the northern portion of its range, whereas it is prevalent in the southern portion and is allopatric with *D. centralis*. The known northern range limit for *D. agenor* is Veraguas, Panama (8.1996830 –81.2343500), thus separating populations of *D. agenor* and *D. woodruffi* **new species** by approximately 200 km.

Taxonomic remarks. Montoya-Molina and Vaz-de-Mello (2021) reported six specimens of *D. enioi* in Santa Rosa, Guanacaste Province and in the Quebrada Bonita Station in the Carara Biological Reserve in Puntarenas Province along the Pacific coast of Costa Rica. We examined specimens from these same localities, but we recorded the presence only of *D. woodruffi* **new species**. (35 specimens from Santa Rosa and 152 specimens from Quebrada Bonita). We have recorded no specimens of *D. enioi* in Costa Rica or Nicaragua. Instead, we have recorded only *D. centralis* and *D. woodruffi* **new species** in Costa Rica and Nicaragua (Fig. 19). Substantial evidence is here presented for the species concept (*D. woodruffi* **new species**). As indicated earlier, Montoya-Molina and Vaz-de-Mello (2021) seem to have confused *D. enioi* specimens with *D. centralis*. These species are separated based on the following characteristics, in the case of *D. enioi*: Ventral clypeal process truncate (Fig. 16); male anterior pronotal border simple, not medially sinuate (Fig. 17); setigerous lateral areas on the anterior and lateral lobes of metasternum continuous at the posteromedial mesocoxal margins; male pygidium less than twice as long as width, strongly convex (Fig. 18); it is distributed in Guatemala and Mexico. Whereas *D. woodruffi* **new species** is characterized by: Ventral clypeal process spiniform (Fig. 5); male anterior pronotal border medially sinuate (Fig. 6); setigerous lateral areas on the anterior and lateral lobes of metasternum interrupted at the posteromedial mesocoxal margins; male pygidium more than twice as long as width, slightly convex (Fig. 8); it is distributed in Costa Rica and Nicaragua.

Key for the *Dichotomius agenor* species-group in Central America

1. Elytral striae crenulate (Fig. 12); pronotal surface subrugose (Fig. 13), male pronotal anterior declivity with a medial carina (Fig. 13); elytral surface matt (Costa Rica, Nicaragua, El Salvador, Honduras, Guatemala, Belize, Mexico) ***D. centralis* (Harold)**
- Elytral striae punctate, not crenulate (Figs. 1, 2); pronotal surface punctate (Fig. 7), male pronotal anterior declivity with weakly impressed to moderately impressed medial sulcus (Fig. 7); elytral surface shiny **2**
- 2(1). Ventral clypeal process bifurcate to cordate (Fig. 14); female cephalic carina bituberculate (Fig. 15) (Panama, Colombia, Venezuela) ***D. agenor* (Harold)**
- Ventral clypeal process spiniform or truncate (Figs. 5, 16); female cephalic carina quadrituberculate (Fig. 4) **3**
- 3(2). Ventral clypeal process truncate (Fig. 16); male anterior pronotal border simple, not medially sinuate (Fig. 17); setigerous lateral areas on the anterior and lateral lobes of metasternum continuous at the



Figures 13–18. Comparative structures of *Dichotomius* spp. **13)** *D. centralis* anterior pronotal surface (lateral-oblique view) subrugose, male pronotal anterior declivity with a medial carina. **14)** *D. agenor* ventral clypeal process bilobed. **15)** *D. agenor* female cephalic carina bituberculate. **16)** *D. enioi* ventral clypeal process truncate. **17)** *D. enioi* male anterior pronotal border simple, not medially sinuate. **18)** *D. enioi* male pygidium less than twice as long as wide, convex.

- posteromedial mesocoxal margins; male pygidium less than twice as long as width, strongly convex (Fig. 18) (Guatemala, Mexico) ***D. enioi* Montoya-Molina and Vaz-de-Mello**
- Ventral clypeal process spiniform (Fig. 5); male anterior pronotal border medially sinuate (Fig. 6); setigerous lateral areas on the anterior and lateral lobes of the metasternum interrupted at the posteromedial mesocoxal margins; male pygidium more than twice as long as width, slightly convex (Fig. 8) (Costa Rica, Nicaragua) ***D. woodruffi* Solís and Kohlmann, new species**

Discussion

With the description of *D. woodruffi* **new species**, the *D. agenor* species-group now includes eighteen species. Four species in this species-group are distributed in Central America (*D. agenor*, *D. centralis*, *D. enioi*, and *D. woodruffi* **new species**). *Dichotomius agenor* is distributed from Venezuela to Panama. This last species may represent a recent expansion from South America into Panama, following the formation of a Panama Isthmus *sensu stricto* around 2.8 Ma according to the latest research (O’Dea et al. 2016). *Dichotomius centralis* and *D. enioi* are also distributed in southern Mexico.

Variation has always been a complex subject to tackle in taxonomy. Some groups seem to vary more than others, and it is always difficult to fully comprehend even if adequate samples are available. The *D. agenor* species-group seems to be such a problematic and variable group, as Montoya-Molina and Vaz-de-Mello (2021) recognized. Montoya-Molina and Vaz-de-Mello (2021, fig. 2A) reported in *D. agenor* the ventral clypeal process as cordate. However, Panamanian specimens that we examined possess a bifurcate ventral clypeal process (Fig. 14). This bifurcate ventral clypeal process in Panamanian populations can vary from an open to a close divergent process, perhaps resembling a cordate structure.

It is interesting to note that according to a molecular analysis done by Pardo-Díaz et al. (2019), the analysis recovers the *D. agenor* species-group as a sister clade to one formed by the *D. inachus*, *batesi*, and *carolinus*



Figure 19. Known distribution of *Dichotomius agenor*, *D. centralis*, and *D. woodruffi* **new species** in Nicaragua, Costa Rica, and Panama.

species-groups. All these species-groups belong to the subgenus *Selenocopris*. Contrary to the *D. inachus* and *D. batesi* species-groups that are mainly Amazonian and expand their distribution to Central America (Vaz-de-Mello and Nunes 2016), the *D. agenor* and *D. carolinus* species-groups expand their distribution from South America to Mexico and the USA, respectively.

In the specific case of the *D. agenor* species-group, the fact that several species are distributed in dry tropical forest (*D. agenor*, *D. amplicollis* (Harold, 1869), *D. centralis*, *D. sagittarius*) in Central and North America suggests that following similar distribution patterns presented by the *Phanaeus endymion* species-group (Coleoptera: Scarabaeinae), this species-group most probably invaded and speciated from South to North America during the Miocene, if not earlier, coeval with the origin of this type of forest (Axelrod 1975; Kohlmann et al. 2018; Gillet and Toussaint 2020). On the other hand, *D. enioi* and *D. woodruffi* **new species** live in humid tropical forests. The area where *D. enioi* is distributed is known as the Selva Lacandona. Toledo (1982) suggested that this area acted as a refuge for the humid tropical forest during the last glacial period of the Pleistocene. The area has a high species diversity and endemism, with as much as 25% of Mexico's animal species (Harcourt and Sayer 1996; Weinberg 2003). The monotypic plant genus *Chiangiodendron* Wendt (Achariaceae) lives in this area and, interestingly, also in the humid forests of the Costa Rican Pacific at the foot of the Talamanca Range (Sosa et al. 2003). The fact that *D. woodruffi* **new species** is distributed in the same area as the abovementioned plant genus, plus the case that this area is also one of the most biodiverse and rich areas of endemics in Costa Rica (Kohlmann et al. 2010), suggests that the southern Pacific tropical humid forest area of Costa Rica probably acted as a Pleistocene glacial refuge too. This area represents a biogeographic region isolated from the rest of Central America by topographic and climatic factors.

Lastly, according to Halffter and Matthews (1966), Culot et al. (2013), and Nunes and Vaz-de-Mello (2019), species in the genus *Dichotomius* feed primarily on dung and sometimes on carrion, rotten fruits, and organic garbage. In addition, we report here that *D. amplicollis* (a member of the *D. agenor* species-group) was observed feeding on macromycete fungi of the genus *Boletus* L. (Boletaceae) in the Sierra Madre del Sur in the vicinity of San José del Pacífico, Oaxaca, Mexico, in a pine-oak forest (observation by BK, June 1980). This case seems to be the first report of mycetophagy in a *Dichotomius*. Philips (2016) considers mycetophagy rare within the oniticellines and onthophagines (Coleoptera: Scarabaeinae), perhaps being a recently evolved behavior with several independent origins. This rarity in *Dichotomius* would seem to support Philips' thesis (2016).

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On Discovering a Butterfly

I found it in a legendary land
all rocks and lavender and tufted grass,
where it was settled on some sodden sand
hard by the torrent of a mountain pass.

The features it combines mark it as new
to science shape and shade—the special tinge,
akin to moonlight, tempering its blue,
the dingy underside, the checkered fringe.

My needles have teased out its sculptured sex;
corroded tissues could no longer hide
that priceless mote now dimpling the convex
and limpid teardrop on a lighted slide.

Smoothly a screw is turned; out of the mist
two ambered hooks symmetrically slope,
or scales like battledores of amethyst
cross the charmed circle of the microscope.

I found it and I named it, being versed
in taxonomic Latin; thus became
godfather to an insect and its first
describer—and I want no other fame.

Wide open on its pin (though fast asleep)
and safe from creeping relatives and rust,
in the secluded stronghold where we keep
type specimens it will transcend its dust.

Dark pictures, thrones, the stones that pilgrims kiss,
poems that take a thousand years to die
but ape the immortality of this
red label on a little butterfly.

—Vladimir Nabokov, 1943