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Two new species of the *Onthophagus clypeatus* species group (Coleoptera: Scarabaeidae: Scarabaeinae)

Victor Moctezuma^{1,*}, José Luis Sánchez-Huerta², and Gonzalo Halffter¹

Abstract

Two new species of *Onthophagus* from Oaxaca, Mexico, are described and illustrated: *Onthophagus istmenus* **new species**, and *Onthophagus santamariensis* **new species**. Keys for separating major males of the new and allied species are presented. Taxonomic remarks are commented for the new and closely related species.

Key Words: dung beetles; Onthophagini; Chimalapas

Resumen

Describimos e ilustramos dos especies nuevas de *Onthophagus* provenientes de Oaxaca, México: *Onthophagus istmenus* **nueva especie**, y *Onthophagus santamariensis* **nueva especie**. Presentamos una clave para separar a los machos mayor de las nuevas especies y de los taxa cercanamente relacionados. Comentamos algunos aspectos taxonómicos de las nuevas especies.

Palabras Clave: escarabajos del estiércol; Onthophagini; Chimalapas

New World *Onthophagus* Latreille are divided into supraspecific units, considered as species groups and complexes. Howden & Gill (1993) defined the *Onthophagus dicranus* and the *Onthophagus mirabilis* (both Coleoptera: Scarabaeidae) species groups to include some Mesoamerican species. Zunino & Halffter (1997) proposed the *Onthophagus clypeatus* (Coleoptera: Scarabaeidae) species group, with 28 species distributed from Mexico to South America, including those of the species groups defined by Howden & Gill (1993). Génier & Howden (1999) redefined the *O. mirabilis* and *O. dicranus* species groups, but Kohlmann & Solís (2001) merged the species of both groups into the *O. dicranus* species group. The structure of the *O. dicranus* species group was redefined by Génier (2017), who split it into the *O. dicranus* and *O. mirabilis* species complexes. In this context, we accept the grouping of the *O. clypeatus* and the *O. dicranus* species groups. This study aims to describe 2 new species of the *O. clypeatus* species group. Keys for separating the major males of the new and closely related species are presented. We also comment upon the relevance for systematics of the discovery of these new species.

Material and Methods

Abbreviations for collections cited in this work are as follows:

CEMT = Colección Entomológica, Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil.

CMNC = Canadian Museum of Nature, Ottawa, Ontario, Canada.

GHC = Gonzalo Halffter Collection, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico.

IEXA = Colección Entomológica Miguel Ángel Morón, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico.

JLSHC = José Luis Sánchez-Huerta Collection, Xalapa, Veracruz, Mexico.

TAMU = Texas A&M University Insect Collection, College Station, Texas, USA.

VMC = Victor Moctezuma Collection, Xalapa, Veracruz, Mexico.

For this study, we used the phylogenetic species concept sensu Wheeler & Platnick (2000), which defines the species as the smallest aggregation of populations or lineages that is diagnosable by a unique combination of character states. Type specimens bear determination labels printed on red acid-free paper, indicating specimen sex, and which one is holotype and which are paratypes. A second label printed on white acid-free paper contains the collection data. Label data is given verbatim. Genital structures were prepared with a 10% KOH solution, soaked 24 h at room temperature, rinsed with 96% ethanol, then with water, and stored in microvials (BioQuip Products, Inc., Rancho Dominguez, California, USA) with glycerol. These microvials were pinned under the dissected specimens. Measurements and pictures were taken with a Leica Z16APOA stereomicroscope (Leica Microsystems, Wetzlar, Germany) using the manufacturer's software (z-stack image capture method). Climate data was taken from INEGI (2019).

Taxonomy

Onthophagus istmenus Moctezuma, Sánchez-Huerta & Halffter **new species** (Fig. 1).

TYPE LOCALITY

Benito Juárez, municipality of San Miguel Chimalapa, state of Oaxaca, Mexico.

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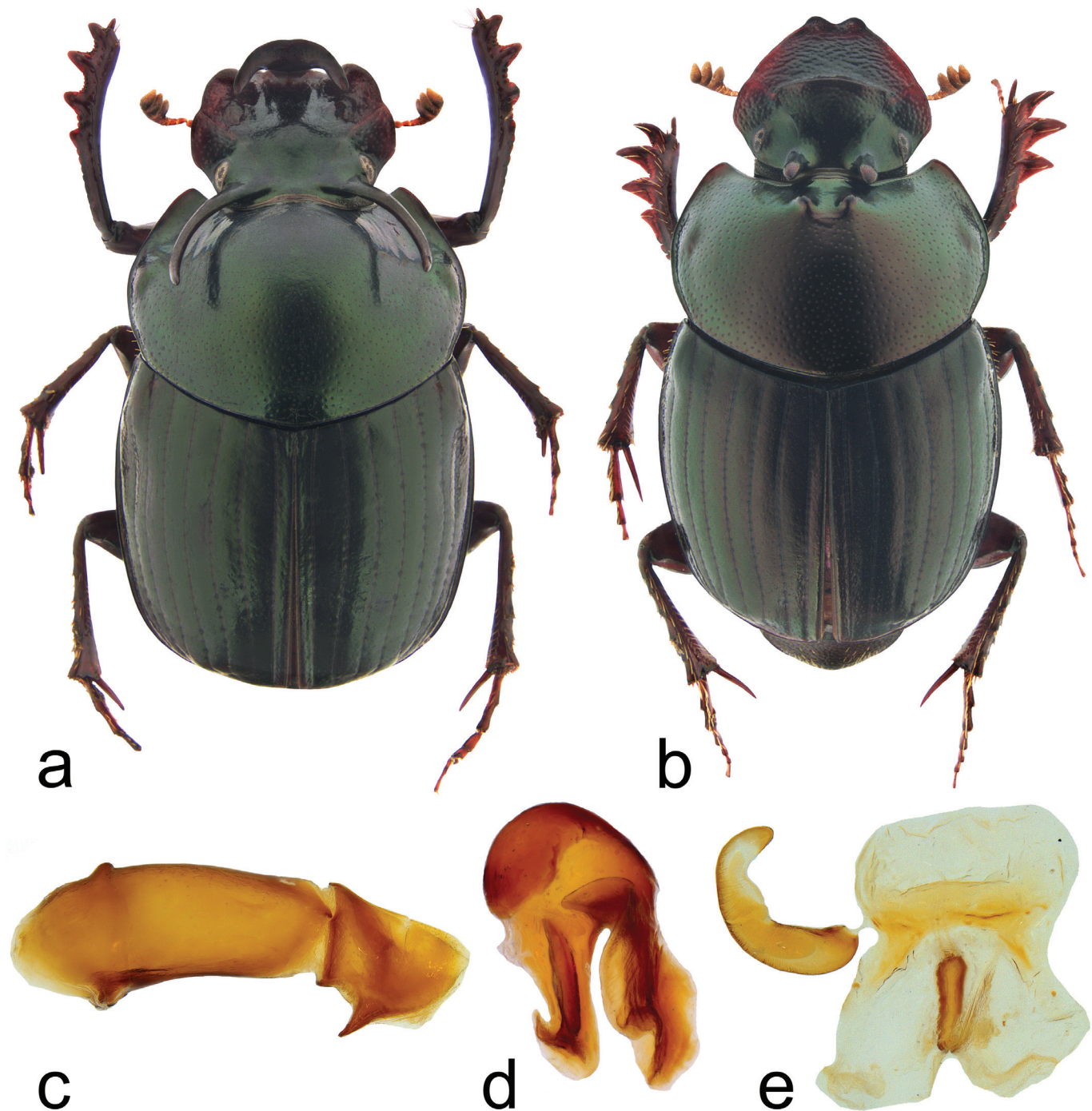


Fig. 1. *Onthophagus istmenus* new species: (a) male dorsal habitus; (b) female dorsal habitus; (c) aedeagus; (d) lamella copulatrix; (e) vagina.

TYPE MATERIAL (8 MALES, 13 FEMALES)

HOLOTYPE, 1 male: "México, Oaxaca, San Miguel Chimalapa, Benito Juárez. 8/X/2015, Coprotrap t12c03, 16.7414722°N, 94.2055583°W, Bosque de niebla, 1,275 m, Victor Moctezuma Col" (Colección Entomológica Miguel Ángel Morón, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico). **PARATYPES**: 1 female, same data as holotype (Colección Entomológica Miguel Ángel Morón, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico); 2 males, same data except: "8/X/2015, t12c19, 16.736055°N, 94.204944°W, 1,384 m" (Canadian Museum of Nature, Ottawa, Ontario, Canada; Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 male, 1 female, same data except: "t12c7, 16.740111°N, 94.205500°W, 1,275 m" (Colección Entomológica, Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil); 2 males, same data except: "t12c21, 16.735583°N, 94.205305°W, 1,362 m" (José Luis Sánchez-Huerta Collection, Xalapa, Veracruz, Mexico; Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "9/X/2015, t13c16, 16.740500°N, 94.217055°W, 1,127 m" (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 male, same data except: "t13c14, 16.739861°N, 94.216722°W, 1,131 m"

uma Collection, Xalapa, Veracruz, Mexico); 1 male, 1 female, same data except: "t12c7, 16.740111°N, 94.205500°W, 1,275 m" (Colección Entomológica, Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil); 2 males, same data except: "t12c21, 16.735583°N, 94.205305°W, 1,362 m" (José Luis Sánchez-Huerta Collection, Xalapa, Veracruz, Mexico; Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "9/X/2015, t13c16, 16.740500°N, 94.217055°W, 1,127 m" (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 male, same data except: "t13c14, 16.739861°N, 94.216722°W, 1,131 m"

(Texas A&M University Insect Collection, College Station, Texas, USA); 2 females, labeled: "México, Oaxaca, Sta. María Chimalapa, SnFco La Paz, 12/VI/2016, t22c26, 17.103083°N, 94.065833°W, 314 m, Selva alta, 314 m, Victor Moctezuma Col." (José Luis Sánchez-Huerta Collection, Xalapa, Veracruz, Mexico; Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "12/VI/2016, t22c33, 17.102083°N, 94.063805°W, 361 m" (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "t22c34, 17.102083°N, 95.110000°W, 370 m" (Texas A&M University Insect Collection, College Station, Texas, USA); 1 female, same data except: "t22c36, 17.101722°N, 94.063055°W, 387 m" (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "t22c38, 17.101638°N, 94.062472°W, 397 m" (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "t22c27, 17.102944°N, 94.065555°W, 321 m" (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "t22c31, 17.085722°N, 94.064388°W, 348 m" (Canadian Museum of Nature, Ottawa, Ontario, Canada); 1 female, labeled: "México, Oaxaca, San Miguel Chimalapas, San Antonio, 14/X/2015, t14c15, 16.660194°N, 94.225361°W, bosque de niebla, 1,647 m, Victor Moctezuma Col." (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 male, 1 female, labeled: "México, Finca San Carlos (Palomares), Oaxaca, 25-V-59, G. y V. Halffter leg" (Gonzalo Halffter Collection, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico).

ETYMOLOGY

The specific epithet derives from "Istmeño," the demonym for inhabitants of the Tehuantepec Isthmus, Oaxaca, Mexico.

MALE

Holotype major male (Fig. 1a). Length 8.5 mm, pronotal width 4.3 mm, elytral width 4.6 mm. Dorsal surface dark-metallic green in color with a reddish cast, glabrous, reticulate microsculpture. Head: hexagonal shape. Clypeal projection trapezoidal and bent upwards in frontal view, broadly bifurcate and u-shaped in dorsal view. Clypeal punctures weakly marked. Frons concave with weakly marked and irregularly sized punctures. Clypeal and frontal carinae lacking. Clypeogenital sutures well marked. Genae obtusely oval with large, coarse punctures. Two strongly elongate, inwardly curved, slender cephalic horns behind the eyes. Pronotum: lacking projections. Anterior midline not marked. Anterior half of pronotum with 2 concavities. Weakly marked, minute, sparse punctures in the anterior-central portion of the pronotal disc; becoming ocellate, large and dense in the rest of the pronotum. Lateral fovea inconspicuous, irregular in shape. Elytra: dark matte-green in color. Elytral striae well marked, with well defined, variably sized and regularly spaced punctures. Interstriae with minute punctures. Pygidium: coarse, confluent, dense punctures, becoming smaller and less dense towards the apex. Setae sparse. Protibia: quadridentate on external border, lacking projections on internal border and apex. Apex with a long setal brush (some setae are lost by abrasion). Parameres: apical teeth acute, well developed (Fig. 1c). Lamella copulatrix: inferior right lobe much longer than the left lobe (Fig. 1d).

MINOR MALE

Differs from the major male by the parabolic clypeal apex, cephalic horns reduced to small conical tubercles, pronotum with 2 small pro-

tuberances on the anterior half, pronotal punctures uniform in shape and size, and widened protibia.

FEMALE

Differs from the male by the head pentagonal in shape, bidentate clypeus, well-marked clypeal carina, small, straight cephalic horns, projected upwards and placed in the center of the frons, 2 small tubercles in the anterior half of the pronotum (Fig. 1b). The ventral portion of the vagina is well sclerotized (Fig. 1e).

VARIATION

Mean length: 8.5 mm (7.2–8.8 mm), mean pronotal width: 4 (3.7–4.8 mm), mean elytral width: 4.5 mm (4.1–5.1 mm). Some paratypes are completely dark metallic red in color.

DISTRIBUTION AND ECOLOGY

Onthophagus istmenus was collected in the Mountain Cloud Forest and the Tropical Rainforest between an elevation range of 150 to 1,700 m, a mean temperature of 16 to 26 °C, and an annual rainfall of 1,500 to 3,000 mm, from the Tehuantepec Isthmus, eastern Oaxaca, Mexico (Fig. 2). The new species follows the Typical Neotropical distributional pattern (Halffter & Morrone 2017), and may occur in Veracruz and Chiapas. *Onthophagus istmenus* was attracted to and captured with pitfall traps baited with human dung. Pereira & Halffter (1961) collected this species on horse dung. Species in the *Onthophagus belorhinus* Bates (Coleoptera: Scarabaeidae) species complex are frequently attracted to dung, carrion, and rotten fruits (Howden & Young 1981; Kohlmann & Solís 2001; Halffter & Halffter 2009).

DIAGNOSIS

Onthophagus belorhinus and *O. istmenus* seem to be closely related species. The major males of the new species can be distinguished easily by the obsolete anterior midline of the pronotum, whereas the midline in *O. belorhinus* is strongly impressed. The minor males and females can be confused, but both species differ in dorsal coloring (dark metallic green with a reddish cast or dark metallic red in *O. istmenus*; dark brown, brownish black, glossy with a cupreous cast in *O. belorhinus*) and elytral interstitial punctures (coarsely marked in *O. istmenus*, obsolete in *O. belorhinus*).

REMARKS

The *O. belorhinus* species complex was defined by Howden & Gill (1987) to include *O. belorhinus* and the closely related *Onthophagus andersoni* Howden & Gill (Coleoptera: Scarabaeidae). *Onthophagus andersoni*, *O. belorhinus*, *O. istmenus*, and *Onthophagus grataehelenae* Kohlmann & Solís (Coleoptera: Scarabaeidae) are proposed by us in a preliminary manner to conform the *O. belorhinus* species complex. The major males of these species share the trapezoidal clypeal horn that is bent upwards in frontal view, with a u-shaped apical bifurcation; elongate, inwardly curved, slender cephalic horns rising behind the eyes; clypeal and frontal carinas absent; pronotum lacking well developed tubercles and projections, and occasionally with the midline strongly impressed in the frontal portion. Pereira & Halffter (1961) collected *O. istmenus* several decades ago, but they confused it with *O. belorhinus*.

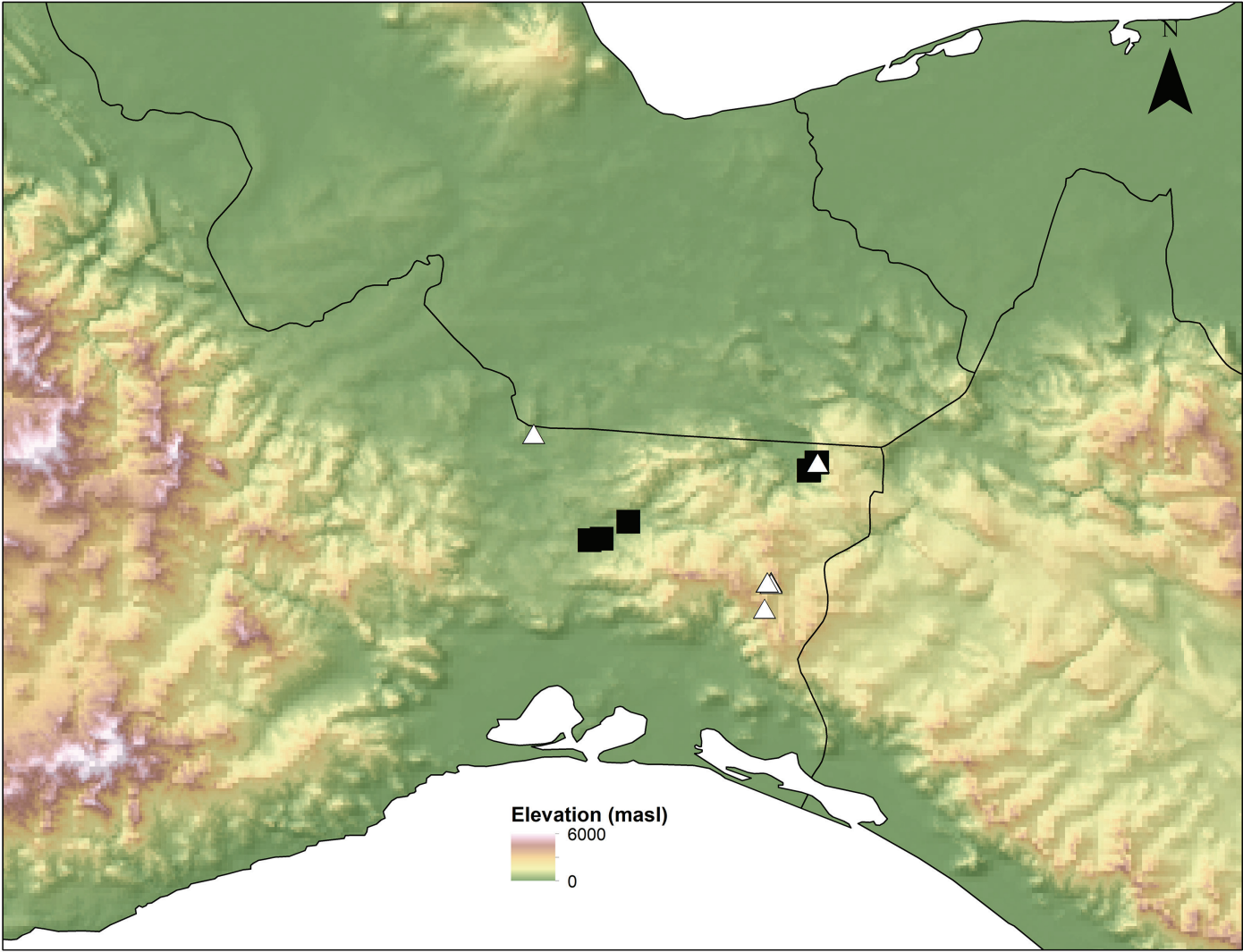


Fig. 2. Distribution of *Onthophagus istmenus* (white triangles) and *Onthophagus santamariensis* (black squares).

Key to the species of the *Onthophagus belorhinus* species complex, based on major males

- 1. Anterior mid-line of the pronotum strongly impressed 2
- 1'. Anterior mid-line of the pronotum obsolete *O. istmenus* **new species**
- 2. Bifurcation of clypeal horn v-shaped *O. grataehelena* Kohlmann & Solís
- 2'. Bifurcation of clypeal horn broadly u-shaped 3
- 3. Bifurcation of clypeal horn strongly elongate over the genae, with an indentation in the apex *O. andersoni* Howden & Gill
- 3'. Bifurcation of clypeal horn elongate over the clypeus, without indentations *O. belorhinus* Bates

Onthophagus santamariensis Moctezuma, Sánchez-Huerta & Halffter **new species** (Fig. 3).

TYPE LOCALITY

Santa María Chimalapa, municipality of Santa María Chimalapa, state of Oaxaca, Mexico.

TYPE MATERIAL (1 male, 6 females)

HOLOTYPE, male: “México, Oaxaca, Santa María Chimalapa, 15/VII/2016, coprotrap t24c19, 16.923944°N, 94.636638°W, potrero, 264 m, Victor Moctezuma Col” (Colección Entomológica Miguel Ángel Morón, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico). PARATYPES: 1 female, same data as holotype except: “Cerro Azul, c5, 12/

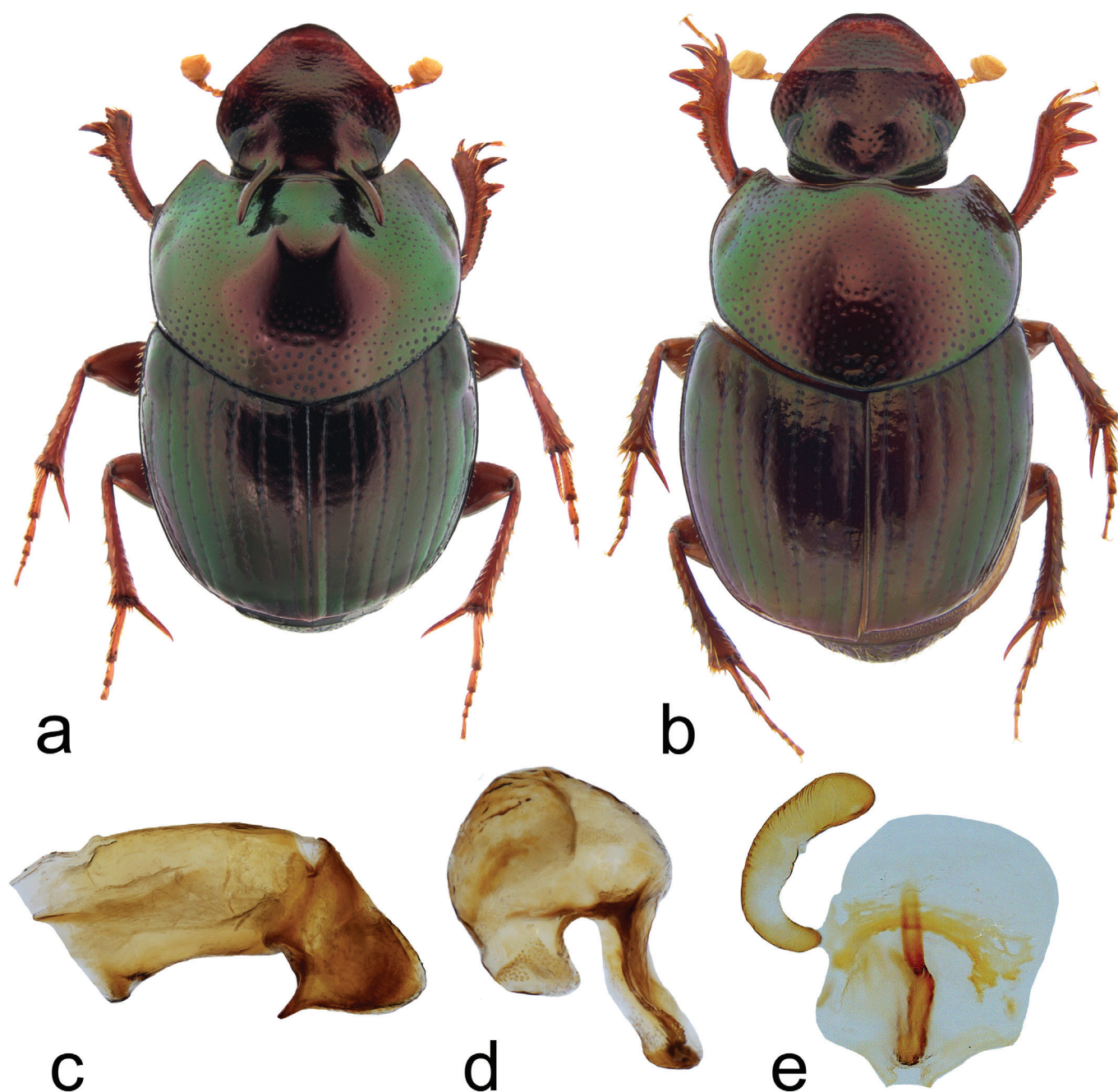


Fig. 3. *Onthophagus santamariensis* new species: (a) male dorsal habitus; (b) female dorsal habitus; (c) aedeagus; (d) lamella copulatrix; (e) vagina.

VI/2015, 16.872611°N, 94.717472°W, selva mediana, 243 m" (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "San Francisco La Paz, 12/VI/2016, t22c27, 17.102944°N, 94.065555°W, selva alta, 321 m" (Colección Entomológica Miguel Ángel Morón, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico); 1 female, same data except: "t22c24, 17.103444°N, 94.066361°W, 297 m" (José Luis Sánchez-Huerta Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "t22c19, 17.103194°N, 94.067916°W, 269 m" (Victor Moctezuma Collection, Xalapa, Veracruz, Mexico); 1 female, same data except: "14/VI/2016, t19c01, 17.079638°N, 94.090000°W, 113 m" (Texas A&M University Insect Collection, College Station, Texas, USA); 1 female, same data except: "t19c06, 17.078305°N, 94.091333°W, 132

m" (Gonzalo Halffter Collection, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico).

ETYMOLOGY

The specific epithet derives from Santa María Chimalapa, the municipality where the type series was collected.

MALE

Holotype major male (Fig. 3a). Length: 5.5 mm, pronotal width: 3 mm, elytral width: 2.8 mm. Dorsal surface dark metallic red in color

with a greenish cast, glabrous, reticulate microsculpture. Head: hexagonal in shape. Clypeus narrowly rounded anteriorly, distinctly reflexed. Clypeal punctures weakly marked. Frons concave with weakly marked punctures variable in size. Clypeal and frontal carinae lacking. Clypeogenae sutures well marked. Genae obtusely triangular with coarse punctures. Two elongate, slightly inwardly curve, slender cephalic horns rising behind the eyes. Pronotum: 2 longitudinal, dorsally acute, well defined tubercles in front of disc; tubercles well separated by a shallow concavity. Anterior half of pronotum with 2 concavities. Weakly marked, minute, sparse punctures in the antero-central portion of the pronotal disc, becoming coarse, dense, large and ocellate in the rest of the pronotum. Lateral fovea inconspicuous, irregular in shape. Elytra: elytral striae well marked; with coarse, ocellate, variably sized and regularly spaced punctures. Interstriae with minute punctures. Pygidium: coarse, dense, ocellate punctures, becoming smaller and less dense towards the apex, with dense, short, thick setae. Protibia: quadridentate on external border, lacking projections on internal border and apex. Apex with a dull, short setal brush. Parameres: apex strongly projected frontwards, obtusely triangular; apical teeth acute, well developed (Fig. 3c). Lamella copulatrix: inferior right lobe much longer than the left lobe (Fig. 3d).

FEMALE

Differs from male by the head pentagonal in shape, clypeus reflexed and weakly sinuate, clypeal carina well marked, frons with 2 rounded transversal tubercles, pronotum uniformly punctate with coarse and ocellate punctures, anterior margin of pronotum with 2 almost indistinct concavities, and last abdominal sternite widened (Fig. 3b). The ventral portion of the vagina is well sclerotized (Fig. 3e).

VARIATION

Mean length: 4.9 mm (5.5–4.6 mm), mean pronotal width: 2.9 (3.1–2.5 mm), mean elytral width: 2.5 mm (2.8–2.1 mm). Some paratypes are completely dark metallic red in color, lacking the greenish shine.

Key to the species of the *Onthophagus luismargaritorum* species complex, based on major males

1. Tubercles of the pronotum separated by a deep longitudinal concavity *O. luismargaritorum* Delgado
- 1'. Tubercles of the pronotum separated by a shallow concavity 2
2. Dorsal color dark metallic green or blue, with a cupreous sheen; tubercles of pronotum obtuse *O. yucatanus* Delgado, Peraza & Deloya
- 2'. Dorsal color dark metallic red, with a greenish sheen; tubercles of pronotum dorsally acute *O. santamariensis* new species

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DISTRIBUTION AND ECOLOGY

Onthophagus santamariensis was collected in Subtropical Oak Forest fragments surrounded by pastures, and Tropical and Subtropical Rainforests between an elevation range of 100 to 400 m, a mean temperature of 22 to 24 °C, and an annual rainfall of 1,500 to 3,000 mm, from Los Chimalapas region, eastern Oaxaca, Mexico (Fig. 2). The new species follows a Typical Neotropical distributional pattern (Halffter & Morrone 2017), and may occur in Veracruz and Chiapas. *Onthophagus santamariensis* was collected with pitfall traps baited with human dung. Species in the *Onthophagus luismargaritorum* Delgado (Coleoptera: Scarabaeidae) species complex are frequently attracted to dung and carrion (Delgado 1995; Delgado et al. 2006).

DIAGNOSIS

Onthophagus santamariensis and *O. luismargaritorum* seem to be closely related species. The new species may be distinguished easily by the acute longitudinal tubercles of the pronotum, separated by a shallow concavity in major males (rounded longitudinal tubercles, separated by a deep longitudinal concavity in major males of *O. luismargaritorum*), and the apex of parameres strongly projected anteriorly and obtusely triangular (dorsally concave, not strongly projected anteriorly, irregular in shape in *O. luismargaritorum*).

REMARKS

Onthophagus luismargaritorum, *O. santamariensis*, and *Onthophagus yucatanus* Delgado, Peraza & Deloya (Coleoptera: Scarabaeidae) share several characters that distinguish them from the remaining taxa of the *O. clypeatus* species group: the reduced size; clypeus obliquely reflexed and narrowly rounded; not strongly elongate, cephalic horns rising between the eyes; protibia short and wide; and female pronotum without tubercles (Delgado et al. 2006). These 3 species are proposed by us in a preliminary manner to conform to the *O. luismargaritorum* species complex.

References Cited

- Delgado L. 1995. *Onthophagus luismargaritorum*, nueva especie mexicana del grupo *clypeatus* (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana* 94: 57–61.
- Delgado L, Peraza LN, Deloya C. 2006. *Onthophagus yucatanus*, a new species of the *clypeatus* group from Mexico and Guatemala (Coleoptera: Scarabaeidae). *Florida Entomologist* 89: 6–9.
- Génier F. 2017. A new Guatemalan cloud forest endemic *Onthophagus* Latreille, 1802 (Coleoptera: Scarabaeidae: Scarabaeinae). *The Canadian Entomologist* 149: 574–580. <https://doi.org/10.4039/tce.2017.32> (last accessed 13 Aug 2019).
- Génier F, Howden HF. 1999. Two new Central American *Onthophagus* Latreille of the *mirabilis* species group (Coleoptera: Scarabaeidae, Scarabaeinae). *The Coleopterists Bulletin* 53: 130–144.

- Halffter G, Halffter V. 2009. Why and where coprophagous beetles (Coleoptera: Scarabaeinae) eat seeds, fruits or vegetable detritus. *Boletín de la Sociedad Entomológica Aragonesa* 45: 1–22.
- Halffter G, Morrone JJ. 2017. An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. *Zootaxa* 4226: 1–46. <https://doi.org/10.11646/zootaxa.4226.1.1> (last accessed 13 Aug 2019).
- Howden HF, Young OP. 1981. Panamanian Scarabaeinae: taxonomy, distribution, and habits (Coleoptera, Scarabaeidae). *Contributions of the American Entomological Institute* 18: 1–204.
- Howden HF, Gill BD. 1987. New species and new records of Panamanian and Costa Rican Scarabaeinae (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin* 41: 201–224.
- Howden HF, Gill BD. 1993. Mesoamerican *Onthophagus* Latreille in the *dicranus* and *mirabilis* species groups (Coleoptera: Scarabaeidae). *The Canadian Entomologist* 125: 1091–1114.
- INEGI – Instituto Nacional de Geografía y Estadística. 2019. Datos. Mapas. Climatología. <https://www.inegi.org.mx/temas/climatologia/> (last accessed 13 Aug 2019).
- Kohlmann B, Solís A. 2001. El género *Onthophagus* (Coleoptera: Scarabaeidae) en Costa Rica. *Giornale Italiano di Entomologia* 9: 159–261.
- Pereira FS, Halffter G. 1961. Nuevos datos sobre Lamellicornia mexicanos con algunas observaciones sobre saprofagia. *Revista Brasileira de Entomologia* 10: 53–66.
- Wheeler QD, Platnick NI. 2000. The phylogenetic species concept (sensu Wheeler and Platnick), pp. 55–69 *In* Wheeler QD, Meier R [eds.], *Species Concepts and Phylogenetic Theory. A Debate*. Columbia University Press, New York, USA.
- Zunino M, Halffter G. 1997. Sobre *Onthophagus* Latreille, 1802 americanos (Coleoptera: Scarabaeidae: Scarabaeinae). *Elytron* 11: 57–178.