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Species Redescriptions and New Species of the *Onthophagus mexicanus* Species Group (Coleoptera: Scarabaeidae), with Notes on Distribution and Rodent-dung Beetle Associations

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The *Onthophagus mexicanus* species group includes at least 18 species: *O. anewtoni* Howden and Génier, *O. arnetti* Howden and Cartwright, *O. browni* Howden, *O. cartwrighti* Howden, *O. championi* Bates, *O. concinnus* Castelnau, *O. cynomysi* Brown, *O. eulophus* Bates, *O. guatemalensis* Bates, *O. hecate* (Panzer), *O. mcclevei* Howden and Génier, *O. medorensis* Brown, *O. mexicanus* Bates, *O. orpheus* (Panzer), *O. polyphemi* Hubbard, *O. pseudoguatemalensis* sp. n., *O. totonacus* sp. n. and *O. velutinus* Howden and Cartwright. *Onthophagus pseudoguatemalensis* sp. n. and *O. totonacus* sp. n. are described from Mexico (Jalisco and Veracruz, respectively). *Onthophagus cartwrighti*, *O. championi*, *O. eulophus* and *O. guatemalensis* are redescribed, while lectotypes are designated herein for *O. championi* and *O. eulophus*. The distribution of *O. cartwrighti* is clarified; a new country record is provided for *O. championi* (Honduras); new state records are reported for *O. championi* (Oaxaca and Veracruz, Mexico) and *O. guatemalensis* (Oaxaca, Mexico). The accurate distribution of *O. eulophus* remains unknown since its original description. Updated distribution maps are included for all the species within the group. An updated determination key to species of the *O. mexicanus* species group is provided. The rarity of *O. eulophus* and *O. totonacus* in the entomological collections is thought to be a consequence of their trophic habits; both species are suggested to be inquilines of rodent nests or burrows.

Key words: Scarabaeinae, Onthophagini, *Neotoma*, *Cynomys*, Coevolution.

BACKGROUND

The genus *Onthophagus* Latreille (Coleoptera: Scarabaeidae) includes at least 190 described species in the New World (Pulido-Herrera and Zunino 2007; Kohlmann and Solís 2012; Solís and Kohlmann 2012; Delgado and Curoe 2014; Génier and Howden 2014; Arriaga-Jiménez et al. 2016 2019; Moctezuma et al. 2016a 2020; Rossini and Vaz-de-Mello 2016; Génier 2017; Gasca-Álvarez et al. 2018; Sánchez-Huerta et al. 2018; Rossini et al. 2018a b; Delgado and Mora-Aguilar 2019; Halffter et al. 2019; Joaqui et al. 2019; Kohlmann et al. 2019; Moctezuma and Halffter 2019a b 2020a b c), with 21 undescribed species (Creedy and Mann 2011; Rossini et al. 2018b) and a dubious synonymy (*Onthophagus mesoamericanus* Zunino and Halffter = *O. cyanellus* Bates) that has been provisionally maintained (Pulido-Herrera and Zunino 2007; Halffter

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et al. 2019; Moctezuma and Halffter 2020b). The New World *Onthophagus* are widely distributed from southern Canada to central Argentina (Howden and Cartwright 1963; Zunino and Halffter 1997; Rossini et al. 2018b). We recognize the organization of New World *Onthophagus* into seven species groups: *O. chevrolati*, *O. clypeatus*, *O. dicranius*, *O. gazellinus*, *O. hircus*, *O. landolti* and *O. mexicanus* (Génier 2017; Rossini et al. 2018b; Joaqui et al. 2019; Moctezuma and Halffter 2019a). However, these species groups were established intuitively and thus lack a comprehensive phylogenetic background (Delgado 1995; Delgado and Curoe 2014; Delgado and Mora-Aguilar 2019; Joaqui et al. 2019), while preliminary phylogenetic analysis suggests that most are non-monophyletic groups (Moctezuma 2019).

The *O. mexicanus* species group is studied here. This group includes at least 16 species (Zunino and Halffter 1988 1997 2007; Howden and Génier 2004; Moctezuma and Halffter 2019a) and is distributed from southern Canada to Costa Rica (Howden and Cartwright 1963; Zunino and Halffter 1997; Kohlmann and Solís 2001). Several species of the *O. mexicanus* species group are thought to be inquilines of rodents (*e.g.*, *Cynomys* Rafinesque, *Marmota* Blumenbach, and *Neotoma* Say and Ord), but particularly those of North America (Howden et al. 1956; Howden and Cartwright 1963; Halffter and Matthews 1966; Anduaga 2007; Edmonds 2018).

The first species of the *O. mexicanus* species group to be described were *O. hecate* (Panzer) and *O. orpheus* (Panzer) by Panzer (1794). Subsequently, *O. concinnus* Castelnau was described (Castelnau 1840). The first reference to the *O. mexicanus* species group was made by Bates (1887), who described *O. championi* Bates from Guatemala, *O. guatemalensis* Bates from Belize and Guatemala, and *O. eulophus* Bates and *O. mexicanus* Bates from Mexico (Bates 1887). Later, *O. polyphemi* Hubbard was described from the United States (Hubbard 1894), and *O. cynomysi* Brown and *O. medorensis* Brown were described from North America, while a relationship was suggested among *O. cynomysi*, *O. medorensis*, *O. hecate* and *O. orpheus* (Brown 1925 1927 1929). Boucomont (1932) included *O. championi*, *O. cynomysi*, *O. eulophus*, *O. guatemalensis*, *O. hecate*, *O. medorensis*, *O. mexicanus*, *O. mirabilis* Bates and *O. orpheus* within his 7th group, while *O. arnetti* Howden and Cartwright, *O. velutinus* Howden and Cartwright, and *O. cartwrighti* Howden were described from the United States, and *O. browni* Howden and Cartwright was described from the United States and Mexico (Howden and Cartwright 1963; Howden 1973).

Zunino (1981) examined the type material of *O. eulophus* and additional specimens and suggested a close relationship between that species and *O. arnetti* and *O. championi*. Zunino and Halffter (1988) preliminarily considered the *O. mexicanus* species group to include 11 species (*O. arnetti*, *O. browni*, *O. championi*, *O. concinnus*, *O. cynomysi*, *O. eulophus*, *O. guatemalensis*, *O. hecate*, *O. medorensis*, *O. mexicanus* and *O. orpheus*); Zunino and Halffter (1997) subsequently redefined this species group to include *O. velutinus*. Later, *O. championi* and *O. mexicanus* were redescribed (Kohlmann and Solís 2001; Zunino 2003), while Howden and Génier (2004) described two additional species from Mexico: *O. anewtoni* Howden and Génier and *O. mcclevei* Howden and Génier. *Onthophagus polyphemi* was then included within the group (Zunino and Halffter 2007) and, finally, Moctezuma and Halffter (2019a) suggested that *O. cartwrighti* should be included within the *O. mexicanus* species group due to its close relationship to *O. velutinus* (Howden 1973).

Several issues remain unsolved for the taxonomy of the *O. mexicanus* species group. The location of the type series of *O. orpheus* and *O. hecate* is unknown (Howden and Cartwright 1963), while lectotypes for *O. championi*, *O. eulophus*, *O. guatemalensis* and *O. mexicanus* have not yet been designated. The biology of *O. arnetti*, *O. cartwrighti*, *O. eulophus*, *O. guatemalensis* and *O. velutinus* has remained poorly known since they were described, and the morphology of the male genitalia has not been illustrated and remains unknown in several species of the *O. mexicanus* species group. Moreover, the subspecies of *O. hecate* (*O. h. hecate* and *O. h. blatchleyi* Brown), *O. orpheus* (*O. o. orpheus*, *O. o. canadensis* (Fabr.) and *O. o. pseudorpheus* Howden and Cartwright), and *O. polyphemi* (*O. p. polyphemi* and *O. p. sparsisetosus* Howden and Cartwright) may represent sibling species rather than subspecies and thus require further revision (Howden and Cartwright 1963). The aim of this study is therefore to contribute to the knowledge of the *O. mexicanus* species group. Some previously described species (*O. cartwrighti*, *O. championi*, *O. eulophus* and *O. guatemalensis*) are redescribed and two new species are described from Mexico. The lectotypes for *O. championi* and *O. eulophus* are designated, and the determination key to species within the *O. mexicanus* species group is updated. In addition, the distribution of some species is updated.

MATERIALS AND METHODS

Studied specimens are deposited in the following entomological collections: CNC, The Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa Research and Development Centre, Ottawa,

Ontario, Canada. CZUG, Colección Entomológica, Centro de Estudios en Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Guadalajara, Jalisco, Mexico. GHC, Gonzalo Halffter Collection, Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico. IEXA, Colección Entomológica Dr. Miguel Angel Morón Ríos, Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico. JLSHC, José Luis Sánchez Huerta Collection, Xalapa, Veracruz, Mexico. MNHN, Muséum National d'Histoire Naturelle, Paris, France. UVGC, Colección de Artrópodos de la Universidad del Valle de Guatemala, Guatemala. VMC, Victor Moctezuma Collection, Puebla, Puebla, Mexico.

The morphological species concept was used for this work, which defines species as the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means (Cronquist 1978). This remains the most widely accepted species concept in taxonomy to date (Zachos 2016). The nomenclature proposed by Howden and Cartwright (1963), Harris (1979) and Cristóvão and Vaz-de-Mello (2020) was followed for external morphology and that of Tarasov and Solodovnikov (2011) modified by Génier (2019) for male genital morphology. Type specimens bear determination labels indicating the specimen's sex, and whether they are the holotypes or paratypes. Label data are given verbatim. The genital structures were soaked with a 10% KOH solution for 24 hours at room temperature, then rinsed with 96% ethanol and later with water. These structures were permanently stored in 15 mm glass microvials (BioQuip Products, Inc., Rancho Dominguez, California, United States) with glycerol. These microvials were pinned under the dissected specimens.

Specimen measurements and photographs were taken using a Leica Z16APOA stereomicroscope equipped with a Leica Smart Touch and a Leica DMC2900 camera (Leica, Wetzlar, Germany), using the manufacturer's software (Leica Application Suite version 4.7) and the z-stack image capture method (except for Figs. 2–3, 7–10, 11E, 12B). The stereomicroscope lightning was substituted (except for Figs. 11–12) as follows: a cylinder made of matt drafting acetate functioned as a light diffuser, while a cylinder made of a rolled LED light strip (300 LEDs / 5 m, 12 Vcc, white 6000–7000k, LED 3528, 13 W/h; Steren, Mexico City, Mexico) was used as light source. The final photographs were edited using a Wacom Intuos PEN tablet CTL-6100WL (Wacom Co., Ltd., Toyonodai Kazo-shi, Saitama, Japan) with Adobe Photoshop CC version 2015 (Adobe Systems Incorporated, San José, California, United States) and CorelDRAW X7 version 17.0.0.491 (Corel Corporation, Ottawa, Canada). Locality data was taken from specimen labels, literature and databases.

RESULTS

TAXONOMY

Family Scarabaeidae Latreille
Subfamily Scarabaeinae Latreille
Genus *Onthophagus* Latreille

Onthophagus mexicanus species group

Diagnosis: The *O. mexicanus* species group is diagnosed by the following characters. Length from the apex of clypeus to tergite VIII 3.9–10.3 mm. Males with clypeus strongly sinuate laterally; apical border of clypeus frequently projected upwardly, medially sinuate or complete; frontal carina laterally produced into two cephalic tubercles or horns; pronotum frequently protruded frontally into a flattened process, this process usually bilobed or bifid apically; apex of parameres well developed; ventral angle of parameres obtuse; endophallite copulatrix concave and large; inferior left lobe of the endophallite copulatrix strongly developed longitudinally; inferior right lobe of the endophallite copulatrix laterally bent, and additional medial endophallite poorly ornamented but strongly developed. Females with frontal and clypeal carinae well developed; pronotal process flattened, reduced into two tubercles or obsolete; and medial sclerozation of the vagina H shaped. Both males and females frequently show the pronotal punctures accompanied by a conspicuous tubercle, and dorsal integument alutaceous and scabriculous.

Onthophagus cartwrighti Howden
(Figs. 1, 11C, 12D, 16)

Diagnosis: *Onthophagus cartwrighti* is related to *O. velutinus*, but major males differ by the cephalic horns with an inner basal swelling (cephalic horns without swelling in *O. velutinus*). Additionally, the pronotal process is distinctly developed in both males and females of *O. cartwrighti* (pronotal process less evident, lower, broad, and slightly arcuate in females of *O. velutinus*).

Redescription: Major male. Dark blue alutaceous dorsally (Fig. 1A–B).

Head: Dorsal surface coarsely punctatorugose, some punctures bearing a setae. Clypeus concave, transverse, slightly reflexed apically. Clypeogenal suture superficially indicate. Genae flat, laterally triangular. Clypeal carina distinctly developed or almost

completely effaced. Frontal carina effaced medially. Two nearly vertical cephalic horns, strongly developed behind the eyes, with inner basal swellings.

Pronotum: Tegument scabriculous. Pronotal surface evenly punctate, each puncture bearing a setae and accompanied by a tubercle. Pronotal process rounded, weakly projected frontally, not extending over the head.

Elytra: Striae coarsely impressed; with evenly spaced, coarsely impressed punctures. Interstriae surface scabriculous; minutely, sparsely punctate; each puncture bearing a setae and accompanied by a tubercle.

Tergite VIII: Distinctly punctate with coarse punctures, each puncture bearing a setae. Tegument scabriculous.

Legs: Protibia elongate, quadridentate, slender.

Genitalia. Apex of parameres well developed and defined; ventral angle of parameres obtuse; apical teeth of the parameres distinctly triangular and not projected ventrally (Fig. 11C–D).

Minor male: Similar to major male, except for the reduction of secondary sexual characters (pronotal process, cephalic horns) and body size.

Female: Differs of the male by the frontal carina distinctly developed; cephalic horns absent; pronotal process widened and strongly reduced; and widened protibiae (Fig. 1C).

Variation: Mean length from the apex of clypeus to tergite VIII 8.9 mm (8.2–9.4 mm).

Non-type material examined: 2 males, 3 females. MEXICO. Baja California Sur: 1 male: "La Paz. 790 m. 15-VIII-2007. G. Nogueira Col." (VMC); 1 male, 1 female: "San José del Cabo. 820 m. 10-IX-2005. G. Nogueira Col." (GHC); 1 female: "San Pedro de la Soledad. Fecha: 25-Nov-87. Colecta: Nido-huevo. Altitud: 700 msnm. Fecha emergencia: 2-marzo-87. Fecha montaje: 7-abril-88. Colecto: A. T. R." (VMC); 1 female: "Todos Santos. Cañón de la Burrera. Sierra de la Laguna. Fecha: 30-sept-87. Boñiga de coyote. Col. A. T. R." (GHC).

Type locality: Mexico, Baja California Sur, Comondú.

Distribution and ecology: From southern California, United States to Baja California Sur, Mexico

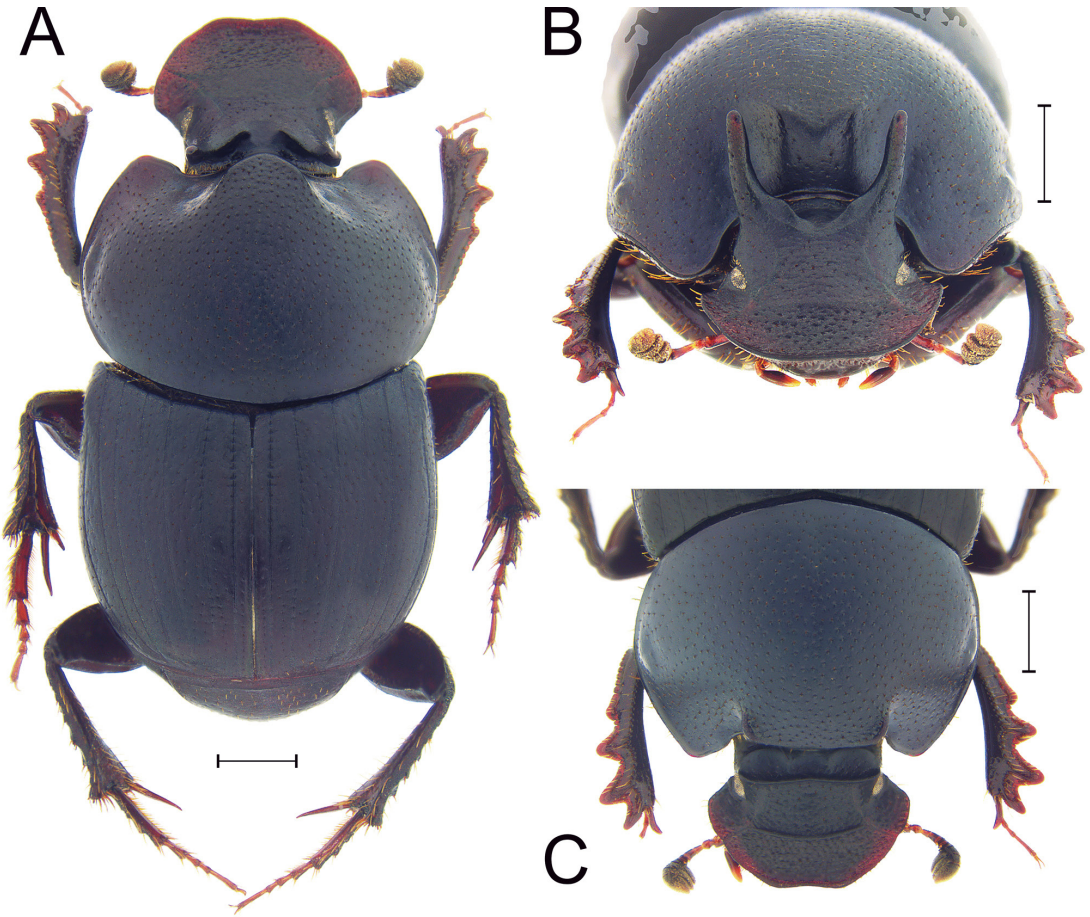

Fig. 1. *Onthophagus cartwrighti*. A, male dorsal view. B, male frontal view. C, female. Scale bar = 1 mm.

(Fig. 16). This species is apparently coprophagous and inhabits arid and tropical environments close to sea level and is seemingly associated with xeric shrublands over sandy soils. Zunino and Halffter (2007) commented that this species might be associated with *Neotoma* nests. Howden (1973) commented that the type locality of *O. cartwrighti* was found in Baja California. However, we discovered that the type locality Comondú is actually in the Mexican state of Baja California Sur.

Remarks: The genital morphology of males was overlooked in the original description of the species and is illustrated herein for the first time (Figs. 11C, 12D). Some specimens from Baja California Sur were used by us to redescribe the species.

Onthophagus championi **Bates**

(Figs. 2, 11D, 12E, 17)

Diagnosis: Major males of *O. championi* are distinguished of related species (*i.e.*, *O. eulophus*, *O. guatemalensis*, *O. mexicanus*, *O. eulophus*) by the pronotum and head alutaceous black with green metallic sheen; clypeal carina distinctly developed; frontal carina effaced medially and raised laterally by two cephalic tubercles; pronotal process widened, bifid apically, extending over the frons (Fig. 2).

Redescription: Lectotype male. Length from the apex of the clypeus to tergite VIII ≈ 8 mm. Alutaceous black, with dark metallic green sheen. Dorsal surface superficially punctate, with some punctures bearing a setae (Fig. 2A–B).

Head: Clypeus distinctly reflexed apically. Clypeogenal suture superficially indicate. Genae lightly concave, rounded laterally. Clypeal carina distinctly developed. Frontal carina completely effaced medially, raised laterally by two weakly developed and triangular cephalic tubercles.

Pronotum: Alutaceous black, with dark metallic green sheen. Tegument scabriculous. Pronotal surface densely punctate with superficial punctures, each puncture bearing a setae and accompanied by a tubercle; except for the almost smooth and impunctate anterolateral concavities. Pronotal process widened, strongly projected frontally, extending over the frons, with apex strongly bifurcate.

Elytra: Striae coarsely impressed; with evenly spaced, rounded, coarsely impressed punctures. Interstriae surface alutaceous black, scabriculous, densely punctate; with each puncture bearing a setae and accompanied by a tubercle.

Tergite VIII: Distinctly punctate with coarse punctures, each puncture bearing a setae. Tegument scabriculous.

Legs: Protibia elongate, quadridentate, slender.

Genitalia: Apex of parameres well developed and defined; ventral angle of parameres obtuse; apical teeth of the parameres distinctly triangular, distinctly projected ventrally (Figs. 11D, 12E).

Minor male: Similar to major male, except for the frontal carina distinctly developed; clypeus rounded, not reflexed; and reduction of the pronotal process and body size.

Female: Differing of male by the head coarsely punctatorugose; clypeus rounded, not reflexed; frontal carina distinctly developed; cephalic tubercles reduced to two lateral small bumps; pronotal process widened and strongly reduced; and widened protibiae (Fig. 1C).

Variation: Mean length from the apex of clypeus to tergite VIII 8.8 mm (8.4–9.3 mm). The colouration was uniform in all the revised specimens.

Type material examined: 1 male, 2 females. *Lectotype male* (present designation; Fig. 2A–B). GUATEMALA: "Paraiso, 300 ft. Champion / *Ontho. championi* Bates ♂ / Ex-Musæo H.W.BATES 1892 / *championi* Bates / Muséum Paris 1952 Coll. R. Oberthur / Syntype (illegible data) / SYNTYPE / SYNTYPE *Onthophagus championi* Bates, 1887 / MNHN EC10854" (MNHN). Paralectotypes. GUATEMALA: 2 females, same data as the lectotype, except for: "MNHN EC10855" (MNHN); "MNHN EC10856" (MNHN).

Non-type material examined: 6 males, 2 females. GUATEMALA. Zacapa: 1 male: "Camino de San Lorenzo a Santa Rosalia. 930 a 1540 msnm" (UVGC). HONDURAS. Francisco Morazán: 2 males: "El Loarque. VII.30 1968. B. K. Dozier" (GHC: 1 male; VMC: 1 male). MEXICO. Oaxaca: 2 males, 2 females: "San Miguel Chimalapa. San Miguel Chimalapa. 100 m. VII-2018. Bosque tropical seco. J. L. Sánchez-Huerta, V. Moctezuma Col." (JLSHC: 1 male, 1 female; VMC: 1 male, 1 female). Veracruz: 1 male: "Dos Amates (Catemaco). IX-63. col. G. Halffter (GHC).

Type locality: Guatemala, Paraíso.

Distribution and ecology: From Mexico (Oaxaca and Veracruz) to Costa Rica (Fig. 17). The first occurrence records for *O. championi* from Honduras (Francisco Morazán) and Veracruz, Mexico are reported herein. The records from Puebla and Morelos, Mexico (Deloya 1992; Deloya et al. 1993; Zunino 2003), have not been confirmed by us because the current location of the reported specimens is unknown (Deloya pers. comm.) and these specimens could pertain to *O. anewtoni* (Fig. 13). Previous distribution records of *O. championi* from Guerrero, Mexico (Delgado-Castillo 1989; Zunino 2003) pertained to *O. anewtoni* (Fig. 13). *Onthophagus championi* is a coprophagous species that inhabits tropical rainforests and tropical dry forests.

Remarks: The lectotype of *O. championi* (Fig. 2A–B) is designated herein in order to fix the name

of the species on a single specimen for nomenclatural stability (ICZN 1999) and to provide accurate future identifications. The specimen under consideration was the only male that was unambiguously traced in the MNHN to the original type series (unknown number of specimens). Additional paralectotypes should be deposited at the Natural History Museum in London (Kohlmann and Solís 2001).

***Onthophagus eulophus* Bates**

(Figs. 3, 11E)

Diagnosis: *Onthophagus eulophus* and *O. championi* seem to be related species, both distinguished by the head and pronotum alutaceous black, with green metallic sheen, punctate with dense punctures, and pronotal process widened. However, major males of *O. eulophus* are easily recognized by the pronotal process bilobed (bifid in *O. championi*), extending over the posterior portion of the frontal carina (extending over the frons in *O. championi*).

Redescription: Lectotype male. Length from the apex of the clypeus to tergite VIII ≈ 9.3 mm (Fig. 3).

Head: Alutaceous black, with dark metallic green sheen. Dorsal surface coarsely punctatorugose, some punctures bearing a setae. Clypeus concave, transverse, not reflexed apically. Clypeogenal suture superficially indicate. Genae flattened, rounded laterally. Clypeal

Fig. 2. *Onthophagus championi*. Lectotype male (present designation): A, dorsal view and labels. B, frontal view (by Christophe Rivier, MNHN). C, paralectotype female (by Christophe Rivier, MNHN). Scale bar = 1 mm.

carina distinctly developed. Frontal carina distinctly developed, raised laterally by two triangular tubercles.

Pronotum: Alutaceous black, with dark metallic green sheen. Tegument scabriculous. Pronotal surface densely punctate with superficial punctures, each puncture bearing a setae and accompanied by a tubercle; except for the almost smooth and impunctate anterolateral concavities. Pronotal process widened, distinctly projected frontally, extending over the posterior portion of the frontal carina, with the apex strongly bilobed.

Elytra: Striae coarsely impressed; with evenly spaced and coarsely impressed punctures. Interstriae surface alutaceous black, scabriculous; densely punctate, each puncture bearing a setae and accompanied by a tubercle.

Tergite VIII: Distinctly punctate with coarse punctures, each puncture bearing a setae. Tegument scabriculous.

Legs: Protibia elongate, quadridentate, slender.

Genitalia. Apex of parameres well developed and defined; ventral angle of parameres obtuse; apical teeth of the parameres distinctly triangular, strongly acute and projected ventrally (Fig. 11E).

Minor male: Unknown.

Female: Unknown.

Type material examined: 1 male. *Lectotype male* (present designation; Figs. 3, 11E). MEXICO: "*eulophus*

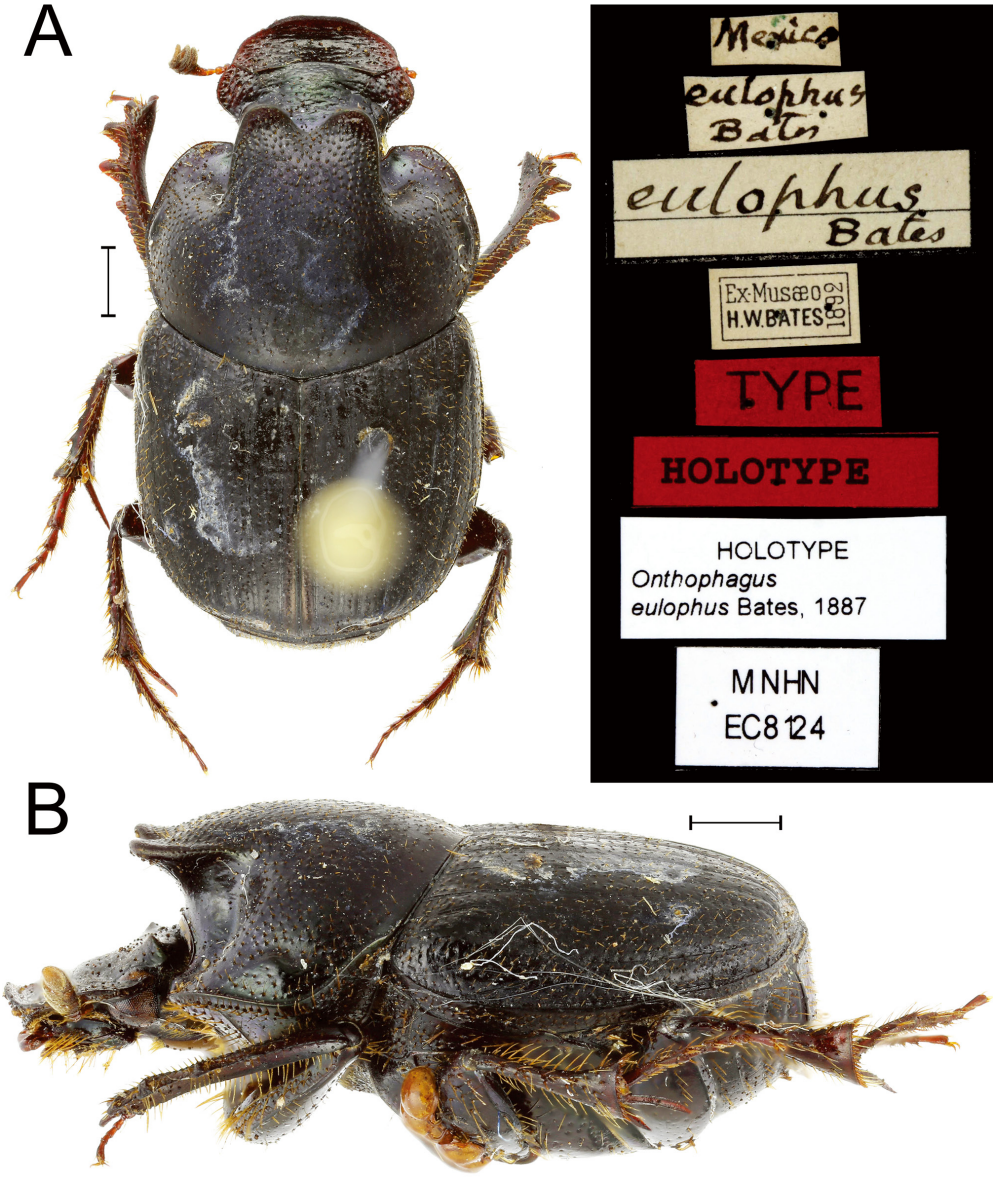

Fig. 3. *Onthophagus eulophus*. Lectotype male (present designation): A, dorsal view and labels. B, lateral view (by Christophe Rivier, MNHN). Scale bar = 1 mm.

Bates / *eulophus* Bates / Ex-Musæo H.W.BATES 1892 / TYPE / HOLOTYPE / HOLOTYPE *Onthophagus eulophus* Bates, 1887 / MNHN EC8124" (MNHN).

Type locality: Mexico.

Distribution and ecology: Nothing is known regarding the distribution and ecology of this species, except that the lectotype was collected from Mexico. This species might be a specialist of rodent nests.

Remarks: A syntype specimen of *O. eulophus* was assumed to be the holotype by Zunino (1981). However, Bates (1887) did not provide information on the number of individuals in the type series. Article 73 of the International Code of Zoological Nomenclature recommends that the assumption of holotype be avoided. Consequently, the lectotype (Figs. 3, 11E) of *O. eulophus* is designated herein in order to fix the name of the species on a single specimen for purposes of nomenclatural stability (ICZN 1999) and to provide accurate future identifications. The specimen under consideration was the only one that could be unambiguously traced in the MNHN to the original type series.

Onthophagus guatemalensis Bates

(Figs. 4, 11F, 12F, 20)

Diagnosis: Major males of *O. guatemalensis* are distinguished within the *O. mexicanus* species group by the metallic green pronotum and head; cephalic horns distinctly developed behind the eyes, projected laterally; and pronotal process slender, strongly projected frontally, extending over the posterior portion of clypeus. *Onthophagus guatemalensis* and *O. pseudoguatemalensis* are distinguished by the genital (apex of parameres triangular in *O. pseudoguatemalensis*, trapezoidal in *O. guatemalensis*) and external morphology (the apex of pronotal process distinctly bifid in *O. guatemalensis*; medially straight, weakly protruded laterally in *O. pseudoguatemalensis*).

Redescription: Major male (Fig. 4A–B).

Head: Dull metallic green. Dorsal surface superficially punctate, with rounded punctures; frons and clypeus roughened laterally. Clypeus strongly projected and reflexed apically. Clypeal process dentiform, rounded apically. Clypeogenal suture distinctly indicate. Genae concave, rounded laterally. Clypeal carina distinctly developed rarely. Frontal carina completely effaced medially. Cephalic horns distinctly developed behind the eyes, projected laterally. Pronotum. Dull metallic green. Tegument scabriculous.

Pronotum: Pronotal punctation superficially impressed, each puncture bearing a setae and accompanied by a tubercle; except for the almost smooth and impunctate anterolateral concavities. Anterior pronotal process slender, strongly projected frontally, extending over the frons, with the apex distinctly bifid. Tegument scabriculous.

Elytra: Striae distinctly impressed; with evenly spaced, rounded, distinctly impressed punctures. Interstriae surface black, scabriculous, distinctly punctate; each puncture bearing a setae and accompanied by a tubercle.

Tergite VIII: Distinctly punctate with rounded punctures, each puncture bearing a setae. Tegument scabriculous.

Legs: Protibia elongate, quadridentate, slender.

Genitalia: Apex of parameres trapezoidal, well developed and defined; ventral angle of parameres obtuse; apical teeth of the parameres distinctly triangular and not projected ventrally (Figs. 11F, 12F).

Minor male: Similar to major male, except for the clypeal and frontal carinas sometimes developed, and the reduction of secondary sexual characters (pronotal process, cephalic horns, clypeal process) and body size.

Female: Differing of male by the head coarsely punctatorugose; clypeus rounded, not reflexed; clypeal and frontal carinas distinctly developed; cephalic horns and clypeal process absent; pronotal process widened and strongly reduced; and widened protibiae (Fig. 4C).

Variation: Mean length from the apex of clypeus to tergite VIII 8.9 mm (7.2–10.3 mm).

Non-type material examined: 35 males, 37 females. MEXICO. Oaxaca: 32 males, 32 females: "San Miguel Chimalapa. San Antonio, Benito Juárez. Bosque de pino, pino-encino. 900–1500 m. Victor Moctezuma Col." (GHC: 2 males, 2 females; IEXA: 5 males, 5 females; VMC: 25 males, 25 females). Chiapas: 3 males, 5 females: "Sta. Rosa. VIII-1962. G. Halffter leg." (GHC: 2 males, 4 females, VMC: 1 male, 1 female).

Type locality: Belize, R. Sarstoon; and Guatemala, Capetillo and San Joaquín.

Distribution and ecology: From Mexico (Oaxaca) to Belize and Guatemala (Fig. 20). This is a coprophagous species that inhabits pine-oak forests. This is the first record for *O. guatemalensis* from Oaxaca, Mexico. Erroneous records from Costa Rica, Honduras, Nicaragua and Panama (GBIF 2020c) pertain to *Ateuchus guatemalensis* (Bates).

Onthophagus pseudoguatemalensis sp. n. Moctezuma and Halffter

(Figs. 5, 11K, 12K, 27)

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Diagnosis: Major males of *O. pseudoguatemalensis* are distinguished within the *O. mexicanus* species

group by the green pronotum and head; cephalic horns distinctly developed behind the eyes, projected laterally; and pronotal process slender, strongly projected frontally, extending over the posterior portion of clypeus. *Onthophagus guatemalensis* is probably the sister species of *O. pseudoguatemalensis*, but they are easily separate by the morphology of the apex of pronotal process (straight medially, weakly protruded laterally in *O. pseudoguatemalensis*; distinctly bifid in *O. guatemalensis*) and male genitalia.

Description: Holotype male. Length from the apex of the clypeus to tergite VIII 9.8 mm (Fig. 5A–B).

Head: Dull metallic green, apparently glabrous. Dorsal surface superficially punctate, with rounded punctures; frons and clypeus roughened laterally. Clypeus strongly projected and reflexed apically. Clypeal process dentiform, rounded apically. Clypeogenal suture distinctly indicate. Genae concave, rounded laterally. Clypeal and frontal carinas effaced. Cephalic horns distinctly developed behind the eyes, projected laterally.

Pronotum: Dull metallic green. Tegument scabriculous. Pronotal punctation superficially impressed, each puncture bearing a setae and accompanied by a tubercle; except for the almost smooth and impunctate anterolateral concavities. Pronotal process slender, strongly projected frontally, extending over the posterior portion of clypeus, with apex straight medially, weakly protruded laterally. Tegument scabriculous.

Elytra: Striae distinctly impressed; with evenly spaced, rounded, distinctly impressed punctures. Interstriae surface black, scabriculous, distinctly punctate; each puncture bearing a setae and accompanied by a tubercle.

Tergite VIII: Distinctly punctate with rounded punctures, each puncture bearing a setae. Tegument scabriculous.

Legs: Protibia elongate, quadridentate, slender.

Genitalia: Apex of parameres well developed and defined; ventral angle of parameres obtuse; apical teeth of the parameres distinctly triangular and barely projected ventrally (Figs. 11K, 12K).

Minor male: Similar to major male, except for the clypeal and frontal carinas sometimes developed, and the reduction of secondary sexual characters (pronotal

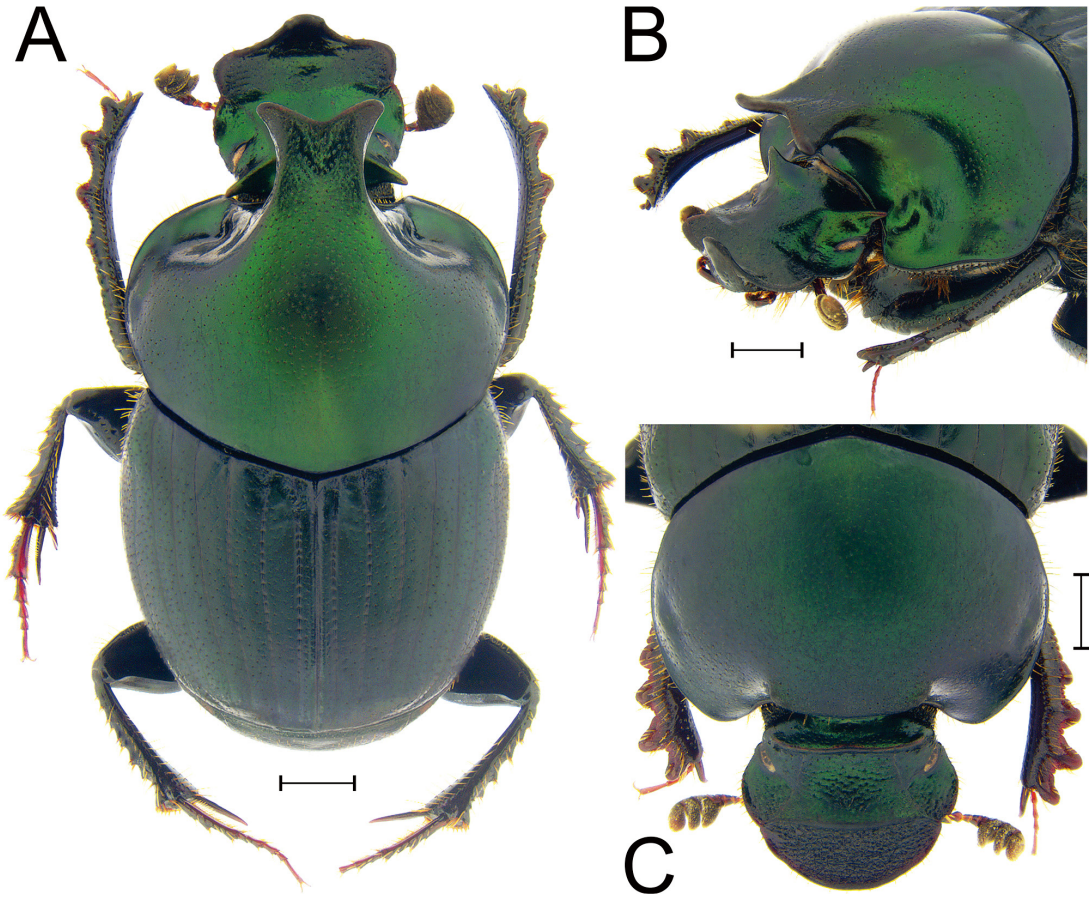

Fig. 4. *Onthophagus guatemalensis*. A, male dorsal view. B, male lateral view. C, female. Scale bar = 1 mm.

process, cephalic horns, clypeal process) and body size.

Female: Differing of male by the head coarsely punctatorugose; clypeus rounded, not reflexed; clypeal and frontal carinas distinctly developed; cephalic horns reduced to two lateral, small bumps in the frontal carina; clypeal process absent; pronotal process widened and strongly reduced; and widened protibiae (Fig. 5C).

Variation: Mean length from the apex of clypeus to tergite VIII 8.9 mm (7.2–10.3 mm). Rare specimens are blue, or green with red sheen.

Etymology: The specific epithet refers to the confusion between the new species and *O. guatemalensis*.

Type material examined: 25 males, 27 females. *Holotype male* (Fig. 5A–B). MEXICO. Jalisco: "Sierr. Manantlán. 1400 msnm. 18/20–1995. G. Nogueira Col." (IEXA). *Paratypes*. MEXICO. Jalisco: 11 males, 15 females: same data as holotype (IEXA); 2 males, 2 females: "Casimiro Carrillo. La Calera. 700 m. 21/24-VII-1995. G. Nogueira Col" (IEXA); 1 male, 1 female: "Telcome, Yolostla. 02-VII-2017. 1,845 m. G. Nogueira Col." (GHC); 1 male: "Sierra de Manantlán. 20-XI-1985. V. Bedoy Col. Los Asoleaderos del Tlacuache. En hoja de milp. Spad Agave." (GHC); 1 female: "Sierra de Manantlán. 11-II-1989. E. García, Col. El Tigre. Municipio Casimiro castillo. Bosque Tropical Subcaducifolio. Alt. 700 m." (GHC); 1 female: "Mascota. J. L. Sánchez-Huerta Col." (JLSHC); 6 males, 4 females: "Talpa de Allende. 03-III-08-IV-2016. (MZO). Bosque mesófilo. NTP6" (CZUG: 4 males, 2 females; VMC: 2 males, 2 females); 3 males, 3 females: Talpa de Allende. 03VII-30VII-2015 (JUL). Bosque pino. NTP1" (CZUG).

Type locality: Mexico, Jalisco, Sierra de Manantlán.

Distribution and ecology: Jalisco, Mexico (Fig. 27). This is apparently a copro-necrophagous species that inhabits montane cloud forests dominated by *Acer binzayedii* Vargas-Rodriguez, temperate pine-oak forests and subtropical dry forests.

Remarks: This species was previously considered as part of *O. guatemalensis* (García-Real 1995; Quiroz-Rocha et al. 2008; Naranjo-López and Navarrete-Heredia 2011; Escobar et al. 2015; Martínez-Rodríguez 2018). Nevertheless, there is a distributional gap of ≈1000 km between both species (Figs. 20, 27). Furthermore, *O. guatemalensis* seems to be mainly coprophagous, while *O. pseudoguatemalensis* is

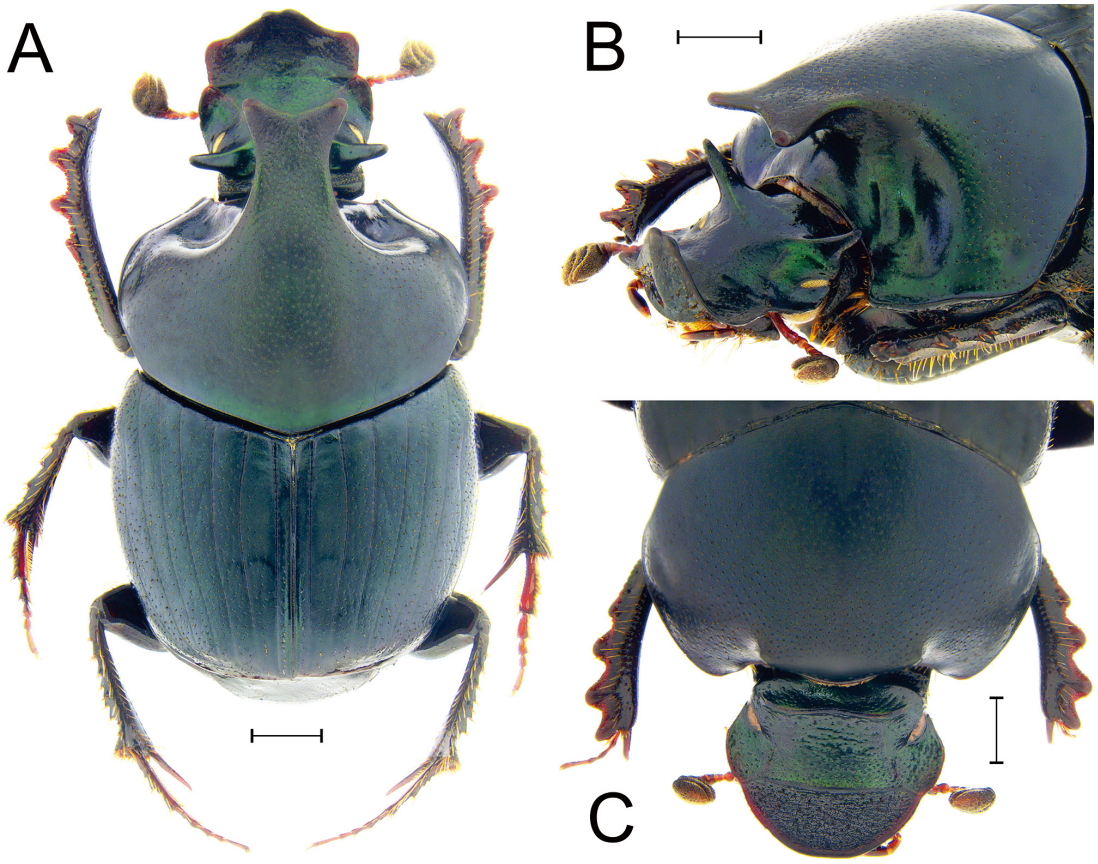

Fig. 5. *Onthophagus pseudoguatemalensis* sp. n. Holotype male: A, dorsal view. B, lateral view. C, paratype female. Scale bar = 1 mm.

considered to be copro-necrophagous.

Onthophagus totonacus sp. n. Moctezuma and Halffter

(Figs. 6, 11L, 12L, 28)

urn:lsid:zoobank.org:act:DD9E641C-4A63-4A2D-AA0F-662B5F5C307B

Diagnosis: Major males of *O. totonacus* are easily recognized by the pronotal process reflexed laterally, widened and extending over the posterior portion of the frontal carina; and apical teeth of the parameres distinctly acute and projected ventrally.

Description: Holotype male. Length from the apex of the clypeus to tergite VIII 9.8 mm (Fig. 6).

Head: Alutaceous black, with dark metallic green sheen. Dorsal surface coarsely punctatorugose, some punctures bearing a setae. Clypeus concave, transverse, not reflexed apically. Clypeogenal suture superficially indicate. Genae flattened, rounded laterally. Clypeal carina distinctly developed. Frontal carina distinctly developed, raised laterally by two distinctly developed, flattened and triangular cephalic horns.

Pronotum: Alutaceous black, with dark metallic green sheen. Tegument scabriculous. Pronotal surface densely punctate with superficial punctures, each puncture bearing a setae and accompanied by a tubercle; except for the almost smooth and impunctate anterolateral concavities. Pronotal process widened, distinctly projected frontally, extending over the posterior portion of the frontal carina, with apex reflexed laterally.

Elytra: Striae coarsely impressed; with evenly spaced and coarsely impressed punctures. Interstriae surface alutaceous black, scabriculous; densely punctate, each puncture bearing a setae and accompanied by a tubercle.

Tergite VIII: Distinctly punctate with coarse punctures, each puncture bearing a setae. Tegument scabriculous.

Legs: Protibia elongate, quadridentate, slender.

Genitalia: Apex of parameres well developed and defined; ventral angle of parameres obtuse; apical teeth of the parameres distinctly triangular, strongly acute and projected ventrally (Figs. 11L, 12L).

Minor male: Unknown.

Female: Unknown.

Variation: Mean length from the apex of clypeus to tergite VIII 9.4 mm (8.9–9.8 mm).

Etymology: The new species is dedicated to the ancient Totonac civilization that developed in the central Veracruz. In the Totonac language the term "totonaco" means "three hearts" and it represents the three main urban centers of their culture.

Type material examined: 3 males. *Holotype male* (Fig. 6). MEXICO. Veracruz: "Comapa, Dos caminos, 4-6/VIII/2016, tran1trap4, 19°11'50.90"N, 96°40'12.33"O, coprotrap, Selva mediana, 452 m, T. Suarez-Joaqui Col." (IEXA). *Paratypes*. MEXICO. Veracruz: 1 male: "Palma Sola, 400–450 m, pastizal rodeado de *Quercus* spp., cebo: excremento humano, C. Huerta, S. Anduaga Col. 21/27-VII-1979, det. Zunino 1981" (GHC); 1 male: "Jalcomulco, Jalcomulco, 13-15/IX/2016 tran2trap6, 19°19'16.09"N, 96°44'43.94"O, coprotrap, selva mediana, 508 m, T. Suarez-Joaqui Col." (VMC).

Type locality: Mexico, Veracruz, Comapa.

Distribution and ecology: Central Veracruz, Mexico (Fig. 28). This is a coprophagous species that inhabits subtropical forests and pastures. The new species could be associated with *Neotoma* nests.

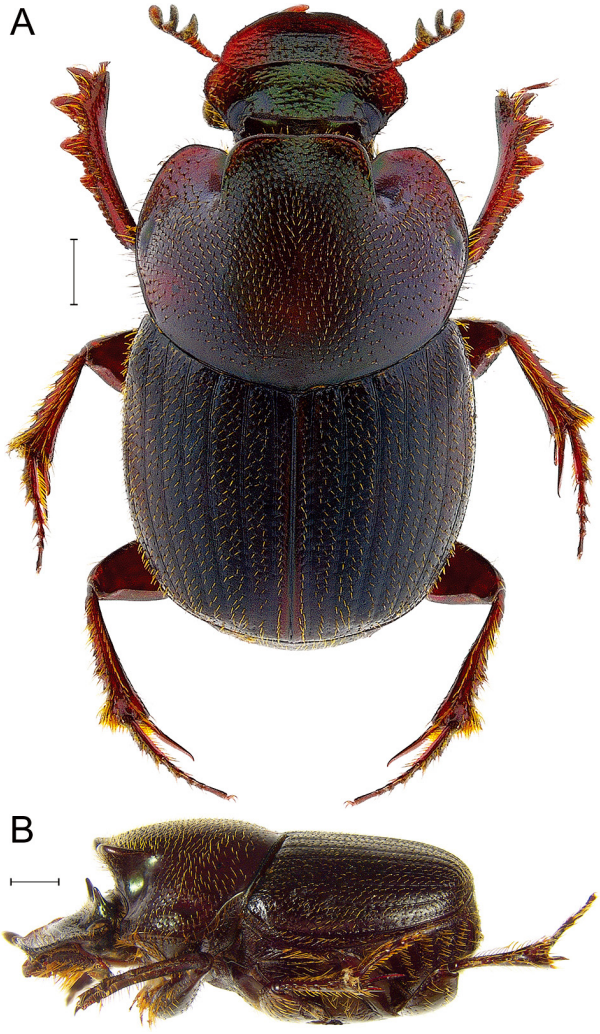

Fig. 6. *Onthophagus totonacus* sp. n. Holotype male: A, dorsal view (by José Luis Sánchez-Huerta). B, lateral view. Scale bar = 1 mm.

Remarks: This new and rare species was previously referred to as *O. eulophus* (Zunino 1981 2003; Joaqui et al. 2021). The revision of the lectotype of *O. eulophus* (designated herein, Fig. 3) allowed us to conclude that the former and *O. totonacus* are not conspecifics.

Key to species of the *Onthophagus mexicanus* species group (modified from Howden and Cartwright 1963)

1. Disc of pronotum smooth or distinctly punctate, tubercles obsolete on disc or if present, less than one-half of the diameter of nearest puncture in basal area 2
- Disc of pronotum distinctly tuberculate; punctures, if present, vague with diameters approximately equal to that of the tubercles 7

2 (1). Disc of pronotum virtually impunctate, shiny black or brownish black; males without cephalic horns or pronotal process; found in burrows of gopher tortoise 3
- Disc of pronotum distinctly punctate, males with cephalic horns of pronotal process 4

3 (2). Elytral intervals with one or two rows of setigerous punctures, punctures often with a tubercle at anterior margin. The east coast from Florida to South Carolina, United States (Fig. 26) ..... *O. p. polyphemi* Hubbard
- Elytral intervals II and IV with only a few scattered setae, nearly impunctate. Florida west of Apalachicola River to Mississippi, United States (Fig. 26) .... *O. p. sparsisetosus* Howden & Cartwright

4 (2). Dorsally metallic. Pronotal process of male distinctly bifurcate, with slender bifurcations 5
- Dorsally dull, alutaceous. Pronotal process of male dorsally flattened, each side curved outwardly and anteriorly to rounded acute angle, transverse anterior edge shallowly, broadly emarginate. Sonora, Mexico (Fig. 22) .... *O. mcclevei* Howden & Génier

5 (4). Elytral intervals with small tubercles anterior to each indistinct puncture; pronotal punctures usually large and close, often anteriorly tuberculate; body commonly green above, the head and pronotum rarely with slight coppery cast, elytra often blackish 6
- Elytral intervals, particularly the fifth, distinctly punctate, the anterior tubercles lacking or barely indicated; pronotal punctures more widely spaced, usually shallow, lacking anterior tubercles; body above shining green to distinctly coppery red. From Ontario, Canada and Appalachian Mountains to Georgia and northeastern United States (Fig. 25) ..... *O. o. canadensis* (Fabr.)

6 (5). Male major lacking a distinct clypeal carina; female with frontal carina evenly elevated or highest at middle; setae of pronotum and elytra not conspicuous. In forested areas of eastern United States (Figs. 11J, 12J, 25) ....*O. o. orpheus* (Panzer)
- Male major with a distinct clypeal carina, often elevated medially; females with frontal carina highest near eyes; setae of pronotum and elytra conspicuous. The Great Plains from Manitoba, Canada to Arkansas and Ohio, United States (Fig. 25) ..... *O. o. pseudorpheus* Howden & Cartwright

7 (1). Clypeus of either sex broadly rounded or slightly emarginate 8
- Clypeus of males triangularly produced upwardly at middle, clypeus of females evenly rounded; if not, elytra bicolored 11

8 (7). Surface of pronotum and (or) elytra finely alutaceous 9
- Surface of pronotum and elytra between tubercles smooth and shining; in prairie dog burrows. From Oklahoma to New Mexico, United States (Figs. 9, 19) ..... *O. cynomysi* Brown

9 (8). Uniformly brown or black dorsally 10
- Pronotum greenish, elytra black 17

10 (9). Pronotum of male with flat projecting protuberance, its wide shallow, usually angular emarginate anterior edge wider than base, and its external angles rounded; females with carina of vertex distinctly bent posteriorly at middle; female pronotal protuberance distinct, sharply defined. From western Texas and Arizona, United States to Durango, Mexico (Figs. 8, 11B, 12C, 15) ..... *O. browni* Howden & Cartwright
- Pronotum of male with a pronounced median swelling; head with two upright diverging slender horns in front of the high angulate anterior margin of pronotum; females with carina of vertex nearly straight 16

11 (7). Pronotum bright shiny green or bluish; elytra usually bicoloured, green with yellow base and apex. From Pennsylvania to Florida and Louisiana, United States (Fig. 18) ..... *O. concinnus* Castelnau
- Color feebly shining to dull uniform dark green, blue, or black; elytra dull, sometimes with brown spots at apex 12

12 (11). Male without basal cephalic horns 13
- Male with basal cephalic horns 14

13 (12). Pronotal setae fine and long, length much greater than distance between elongate oval tubercles. East of Rockies, Canada and United States (Figs. 11G, 12G, 21) .... *O. h. hecate* (Panzer)
- Pronotal setae short, inconspicuous, scarcely longer than distance between small round tubercles; usually brown spots at apex of elytra. From Florida to South Carolina, United States (Fig. 21) ..... *O. h. blatchleyi* Brown

14 (12). Pronotal process of males broad, slightly wider than the distance between the eyes, with anterior margin flared, acutely angled, and deeply emarginated. From Kansas to Texas and Louisiana, United States (Figs. 10, 11H, 12H, 23) . ..... *O. medorensis* Brown
- Pronotal process of males slender, slightly wider than the distance between the eyes, with anterior margin bifid 15

15 (14). Apex of pronotal process of males distinctly marginate medially. From Oaxaca, Mexico to Guatemala and Belize (Figs. 4, 11F, 12F, 20) ..... *O. guatemalensis* Bates
- Apex of pronotal process of males medially straight, weakly protruded laterally. Jalisco, Mexico (Figs. 5, 11K, 12K, 27) .. .. *O. pseudoguatemalensis* sp. n. Moctezuma and Halffter

16 (10). Pronotal swelling of female very weak, poorly defined; cephalic horns of males without an inner basal swelling. From Colorado and Kansas to Texas and Arizona, United States (Fig. 29) ..... *O. velutinus* Horn
- Pronotal swelling distinct in both sexes; cephalic horns of males with and inner basal swelling. From southwestern California, United States to Baja California Sur, Mexico (Figs. 1, 11C, 12D, 16) ..... *Onthophagus cartwrighti* Howden

17 (9). Cephalic horns of males distinctly developed upwards 18
- Cephalic horns of males reduced to small triangular tubercles, projected laterally 20

18 (17). Pronotal process of male forming a wide, shell-like projection over the head, the sides of the process parallel, anterior margin terminating over the eyes, broadly marginate and somewhat depressed medially. Arizona, United States (Figs. 7, 12b, 14) ..... *O. arnetti* Howden & Cartwright
- Pronotal process of male forming a wide, shell-like over the

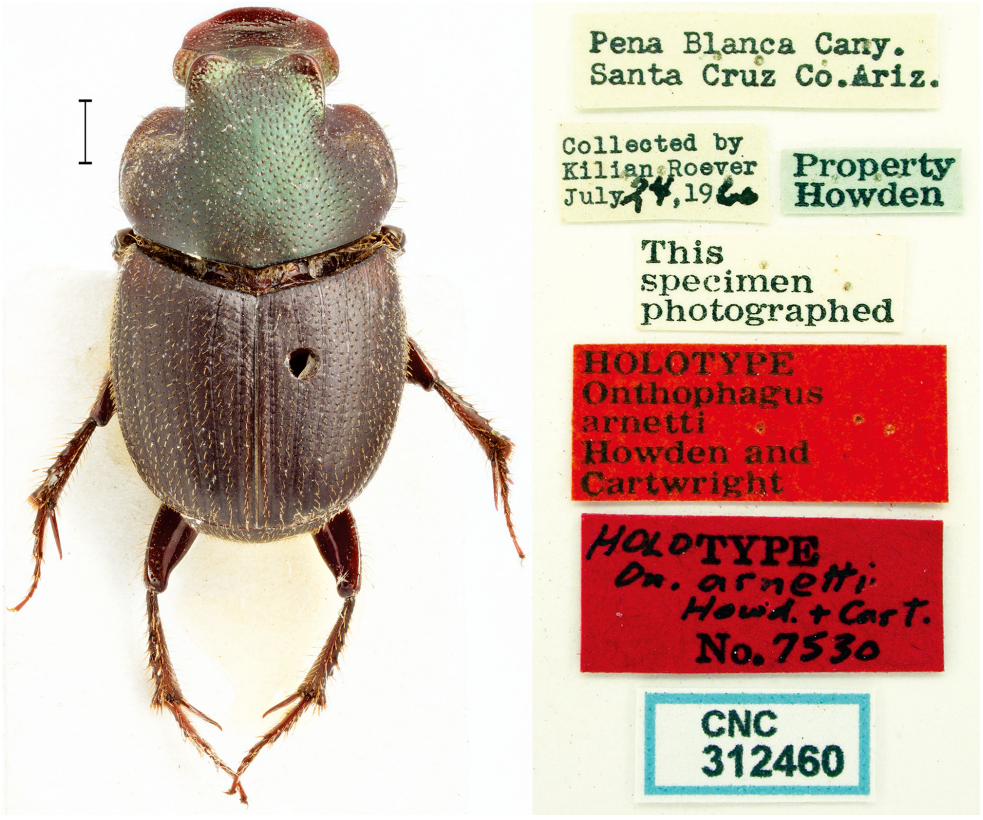

Fig. 7. *Onthophagus arnetti*. Holotype male and labels (by Serge Laplante, CNC). Scale bar = 1 mm.

Fig. 8. *Onthophagus browni*. Holotype male and labels (by Serge Laplante, CNC). Scale bar = 1 mm.

Fig. 9. *Onthophagus cynomysi*. Holotype male and labels (by Serge Laplante, CNC).

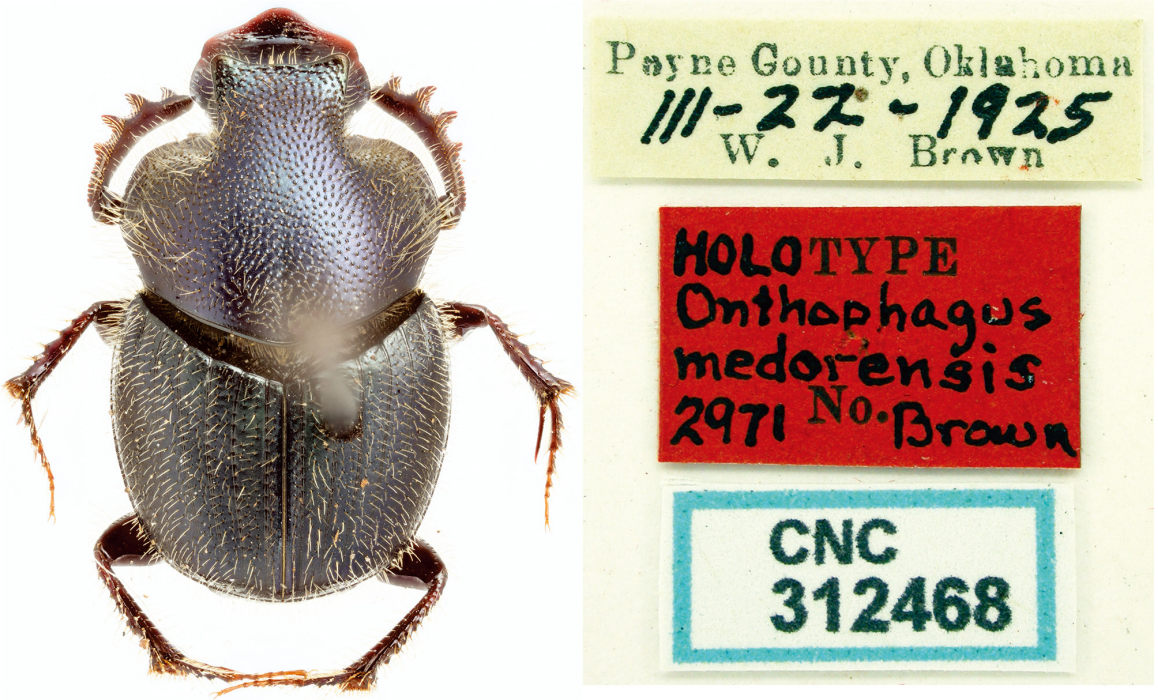

Fig. 10. *Onthophagus medorensis*. Holotype male and labels (by Serge Laplante, CNC).

head, the sides of the process parallel, with anterior slightly thickened edge as wide as distance between eyes, almost truncate 19

19 (18). Pronotal surface densely tuberculate and roughened; robust species, with pronotum frequently wider than 4.5 mm. From Jalisco to Chiapas, Mexico (Figs. 11A, 12A, 13) .... *O. anewtoni* Howden & Génier

- Pronotal surface moderately tuberculate, not roughened; slender species, with pronotum frequently narrower than 4.5 mm. Central Veracruz, Mexico (Figs. 6, 11L, 12L, 28) .... *O. totonacus* sp. n. Moctezuma and Halffter

20 (17). Pronotal protuberance of male distinctly bifid. Mexican High Plateau, Mexico (Figs. 11I, 12I, 24) ..... *O. mexicanus* Bates

- Pronotal protuberance of male forming a wide, shell-like projection over the head 21

21 (20). Pronotal process with apex strongly bifurcate. From Oaxaca and Veracruz, Mexico to Costa Rica (Figs. 2, 11D, 12E, 17) .. .. *O. championi* Bates

- Pronotal process with apex distinctly bilobed. Mexico (Figs. 3, 11E) ..... *O. eulophus* Bates

DISCUSSION

This study contributes to the knowledge of the New World *Onthophagus* by redescribing some poorly known species (*i.e.*, *O. cartwrighti*, *O. championi*, *O. eulophus* and *O. guatemalensis*), describing two new species (*O. pseudoguatemalensis* and *O. totonacus*), designating two lectotypes (*O. championi* and *O. eulophus*), and presenting new records for species distributions, as well as an updated key to the *O. mexicanus* species group. *Onthophagus guatemalensis* and *O. eulophus* had not been redescribed or illustrated since their original description (Bates 1887). The redescription of these species was pivotal to allowing description of the new *O. pseudoguatemalensis* and *O. totonacus*. The populations of *O. pseudoguatemalensis* were previously considered as part of *O. guatemalensis* (García-Real 1995; Quiroz-Rocha et al. 2008; Naranjo-

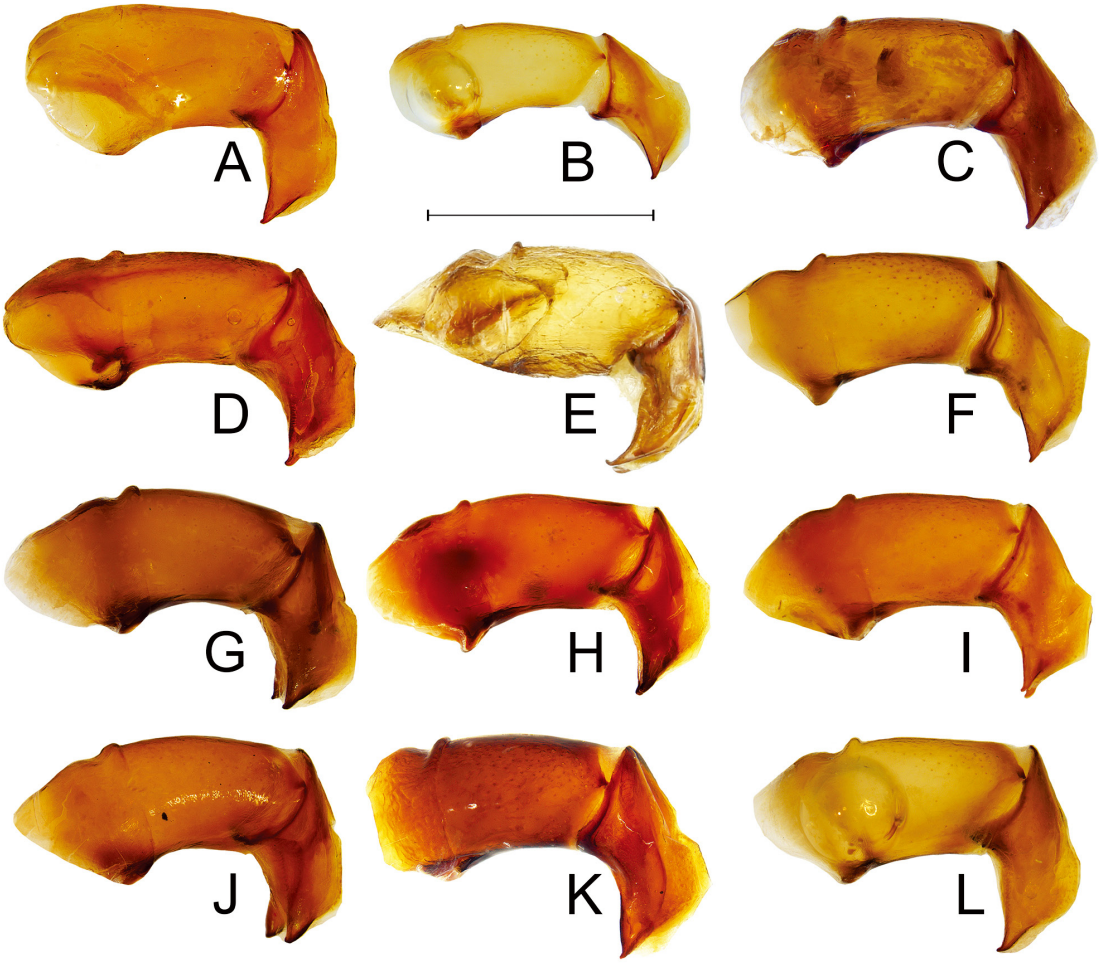

Fig. 11. Aedeagi within the *O. mexicanus* species group. A, *O. anewtoni*. B, *O. browni*. C, *O. cartwrighti*. D, *O. championi*. E, *O. eulophus* (by Christophe Rivier, MNHN). F, *O. guatemalensis*. G, *O. h. hecate*. H, *O. medorensis*. I, *O. mexicanus*. J, *O. o. orpheus*. K, *O. pseudoguatemalensis* sp. n. L, *O. totonacus* sp. n. Scale bar = 1 mm.

López and Navarrete-Heredia 2011; Escobar et al. 2015; Martínez-Rodríguez 2018; GBIF 2020c). Nevertheless, the comparison of the specimens from Jalisco to those collected from Oaxaca, Chiapas and Guatemala allowed us to conclude that they are not conspecifics.

In the case of *O. eulophus*, this is a rare species for which only the lectotype is known by us. We hope that the redescription of *O. eulophus* will lead to the discovery of additional specimens through the revision of previously collected specimens and future collections. *Onthophagus totonacus* is also a rare species that was previously confused with *O. eulophus*. Zunino (1981) suggested that two male specimens from central Veracruz, misidentified by that author, pertained to *O. eulophus*. Nevertheless, the morphological revision of one of these specimens and two recently collected males lead us to confirm that the "*O. eulophus*" specimens from Veracruz actually pertain to the new *O. totonacus*.

The distribution of the species group in the Mexican states of Puebla and Morelos requires revision, since some specimens referred to as *O. championi* (Deloya 1992; Deloya et al. 1993; Zunino 2003) could actually pertain to *O. anewtoni*. These specimens and several individuals from Jalisco and Guerrero were erroneously referred to as *O. championi* (Delgado-Castillo 1989; Zunino 2003; Quiroz-Rocha et al. 2008). The specimens from Jalisco and Guerrero were subsequently used for the description of *O. anewtoni* (Howden and Génier 2004), but the populations from Puebla and Morelos remained unrevised. Exploration of northern Mexico is necessary in order to improve the knowledge of the *O. mexicanus* species group. Interestingly, the distributional areas of some species (*e.g.*, *O. arnetti*, *O cynomysi*, *O. medorensis* and *O. velutinus*) seem to be limited by the border between the United States and Mexico. Future entomological

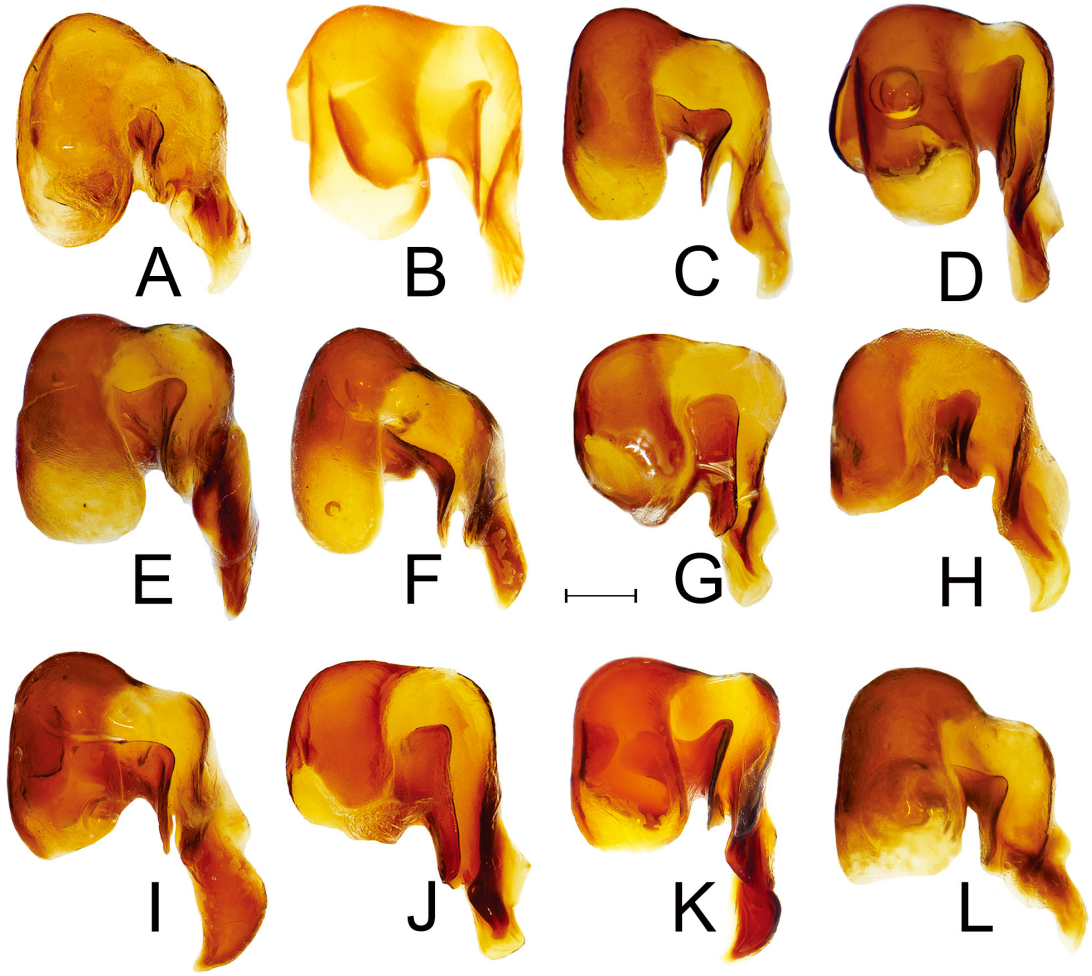

Fig. 12. Endophallites within the *O. mexicanus* species group (only the endophallite copulatrix is figured). A, *O. anewtoni*. B, *O. arnetti* (by Serge Laplante, CNC). C, *O. browni*. D, O. *cartwrighti*. E, *O. championi*. F, *O. guatemalensis*. G, *O. h. hecate*. H, *O. medorensis*. I, *O. mexicanus*. J, *O. o. orpheus*. K, *O. pseudoguatemalensis* sp. n. L, *O. totonacus* sp. n. Scale bar = 0.1 mm.

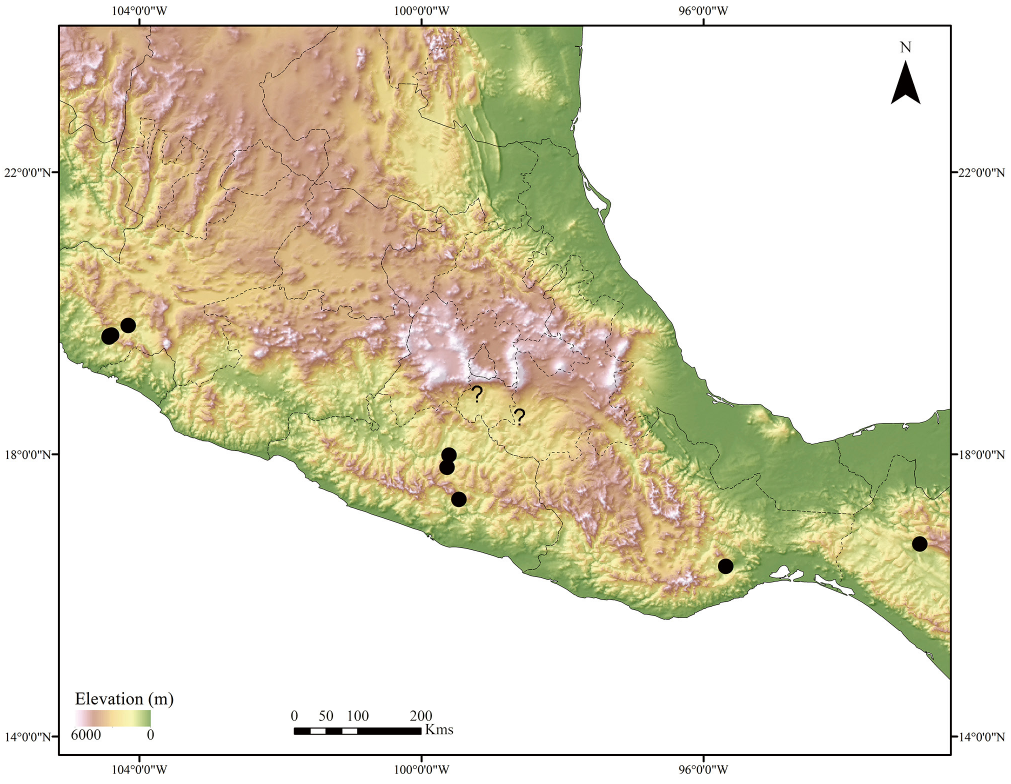

Fig. 13. Distribution of *O. anewtoni* (Howden and Génier 2004; Deloya et al. 2014; Sánchez-Hernández and Gómez 2018). ? - doubtful localities (Deloya 1992; Deloya et al. 1993).

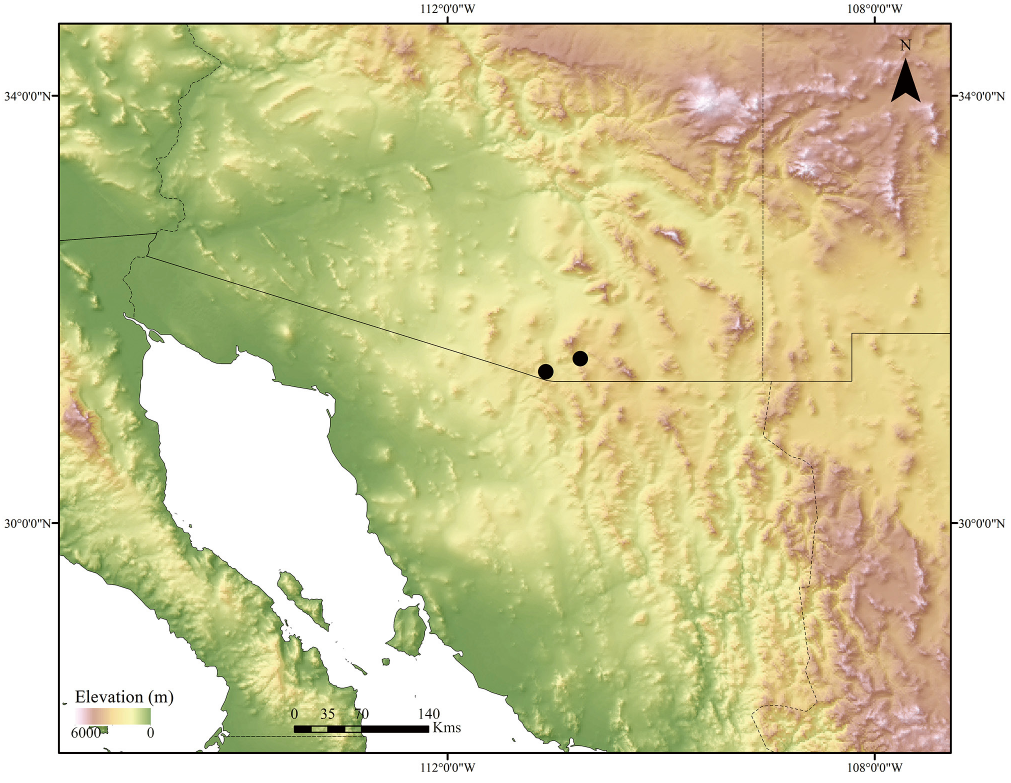

Fig. 14. Distribution of *O. arnetti* (Howden and Cartwright 1963).

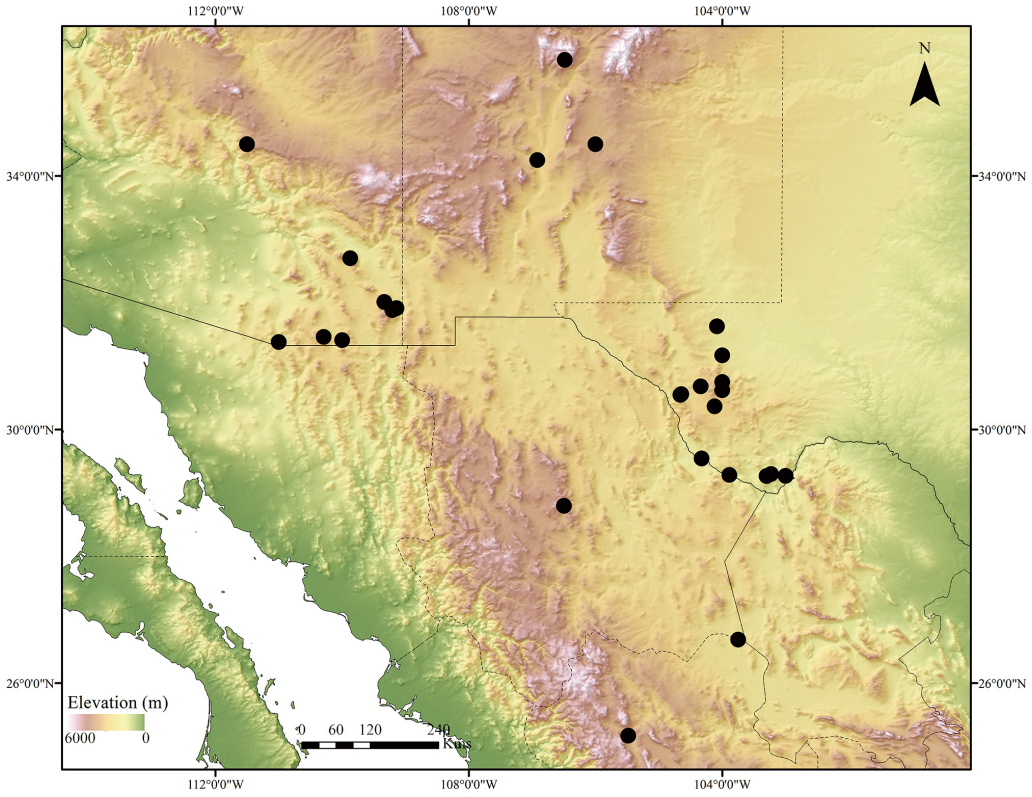

Fig. 15. Distribution of *O. browni* (Howden and Cartwright 1963; Anduaga 2007; Edmonds 2018).

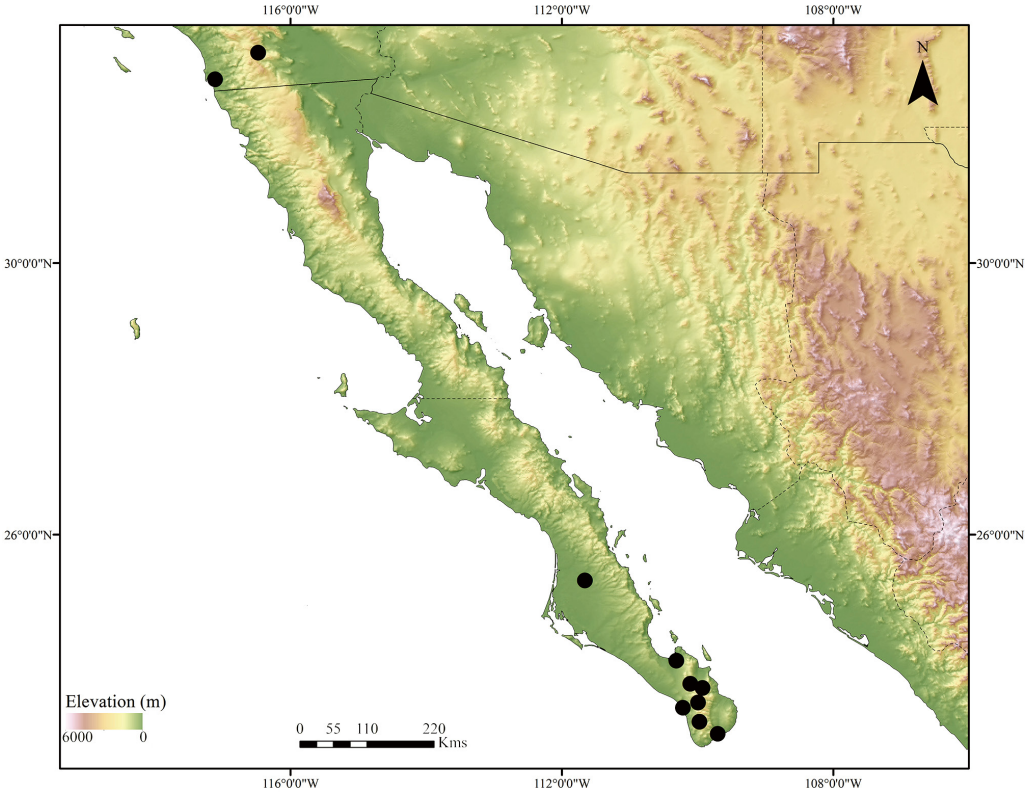

Fig. 16. Distribution of *O. cartwrighti* (Howden 1973).

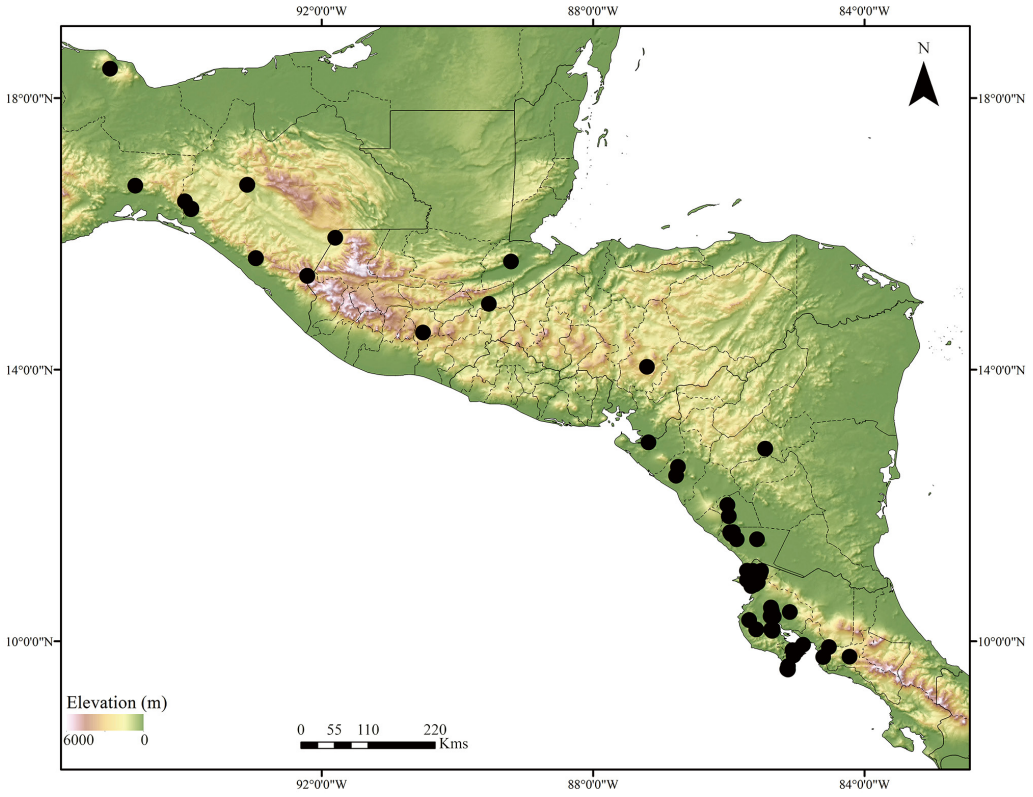

Fig. 17. Distribution of *O. championi* (Kohlmann and Solís 2001; Escobar et al. 2015; GBIF 2020a).

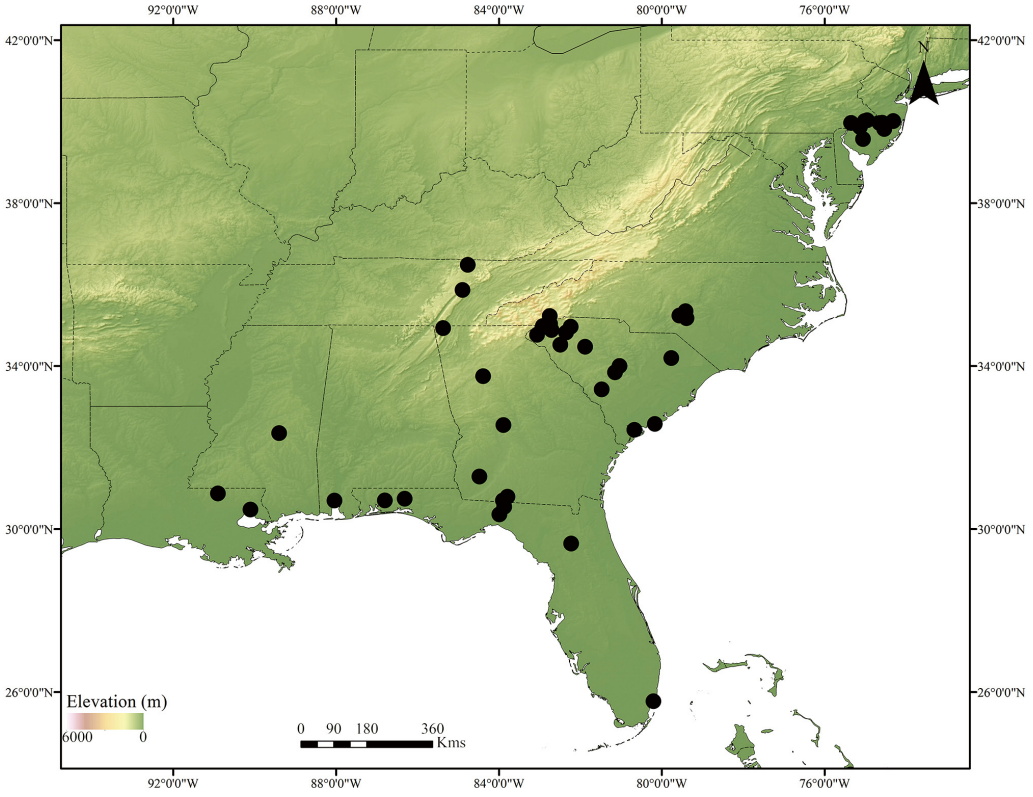

Fig. 18. Distribution of *O. concinnus* (Howden and Cartwright 1963; GBIF 2020b).

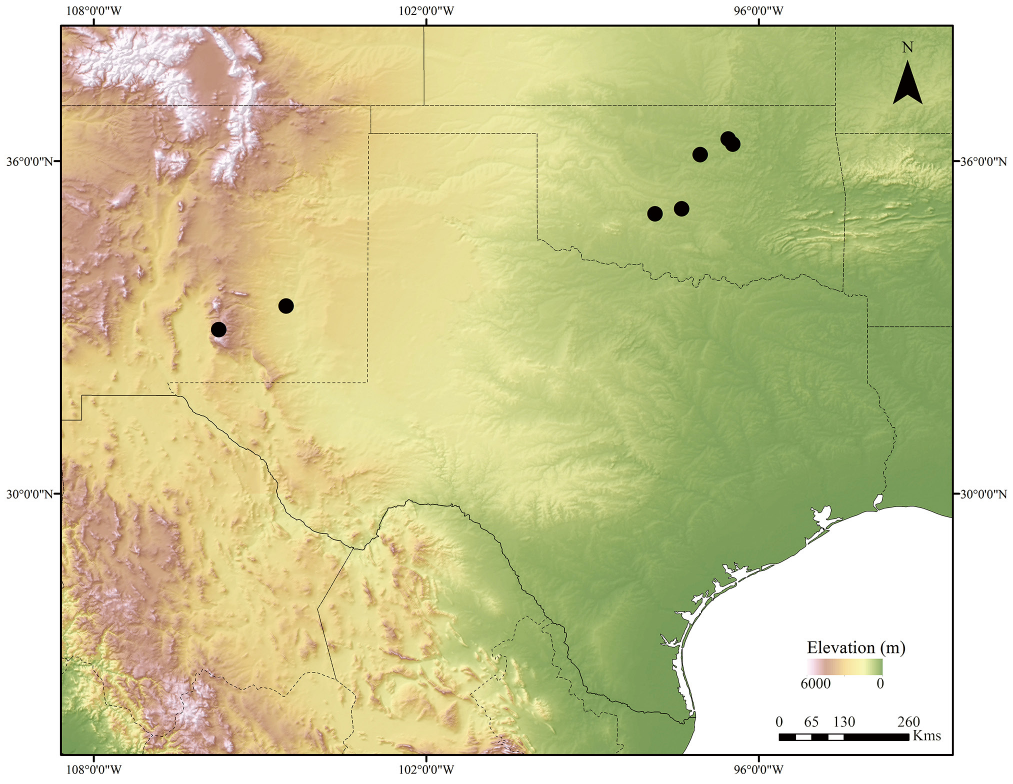

Fig. 19. Distribution of *O. cynomysi* (Howden and Cartwright 1963).

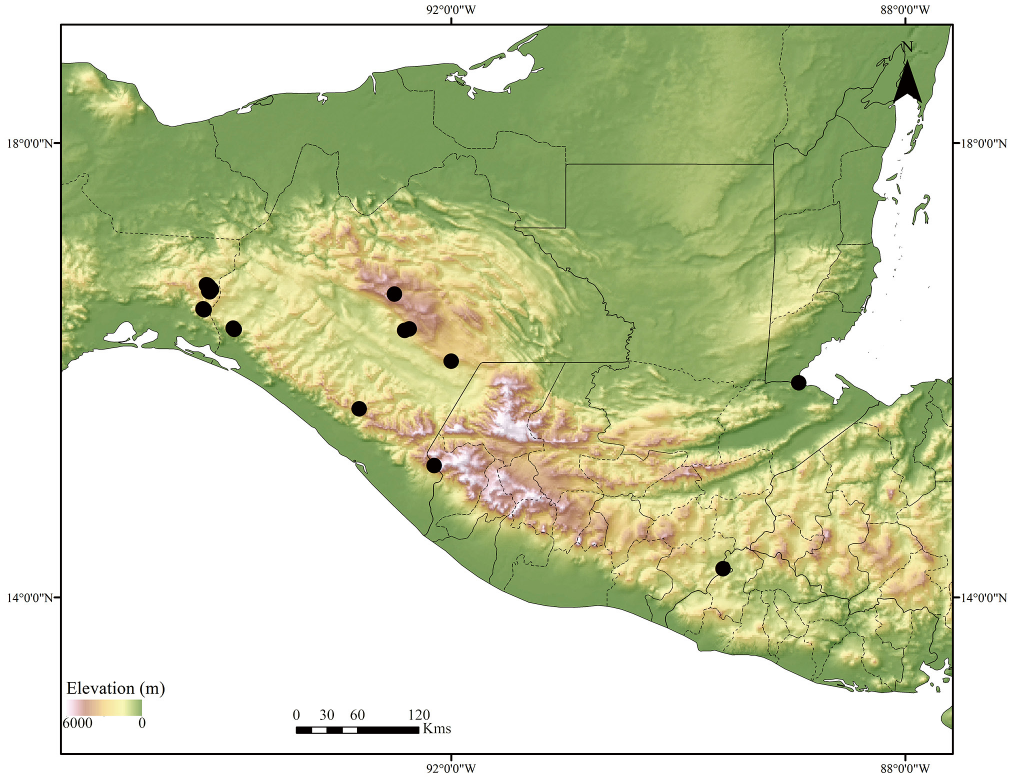

Fig. 20. Distribution of *O. guatemalensis* (Bates 1887; Escobar et al. 2015; GBIF 2020c). Erroneous localities from Costa Rica, Honduras, Nicaragua, Panamá and the United States (GBIF 2020c) were omitted.

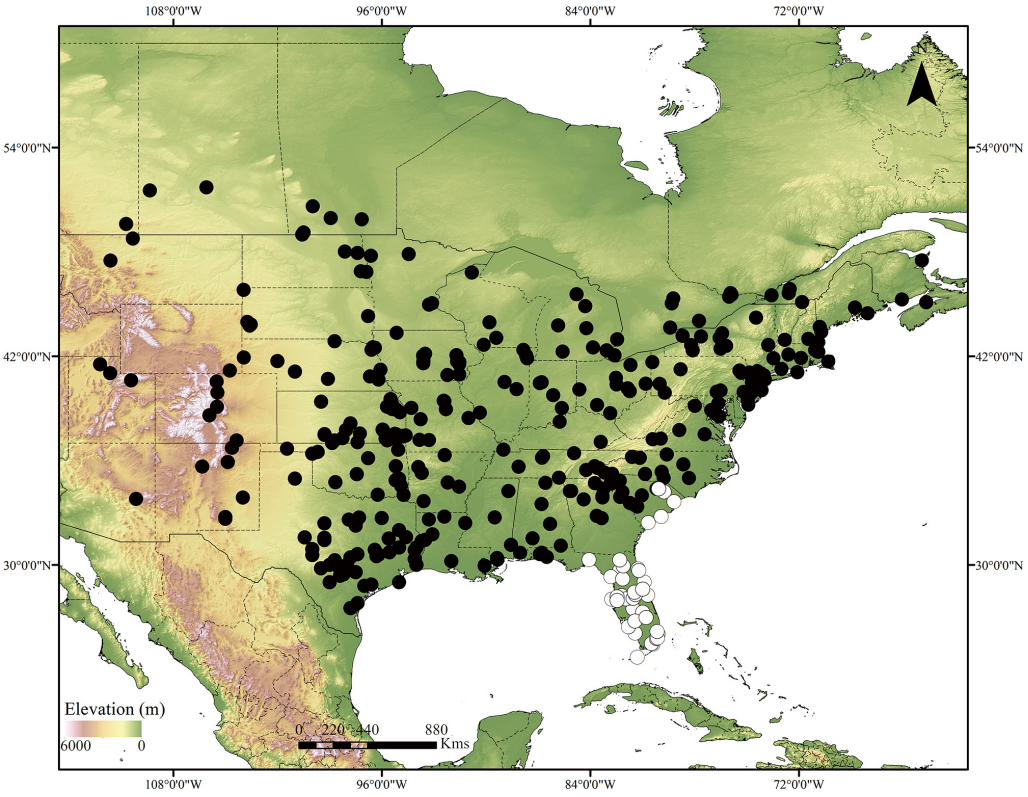

Fig. 21. Distribution of *O. hecate* (Howden and Cartwright 1963; GBIF 2020d). Black dots - *O. h. hecate*, white dots - *O. h. blatchleyi*.

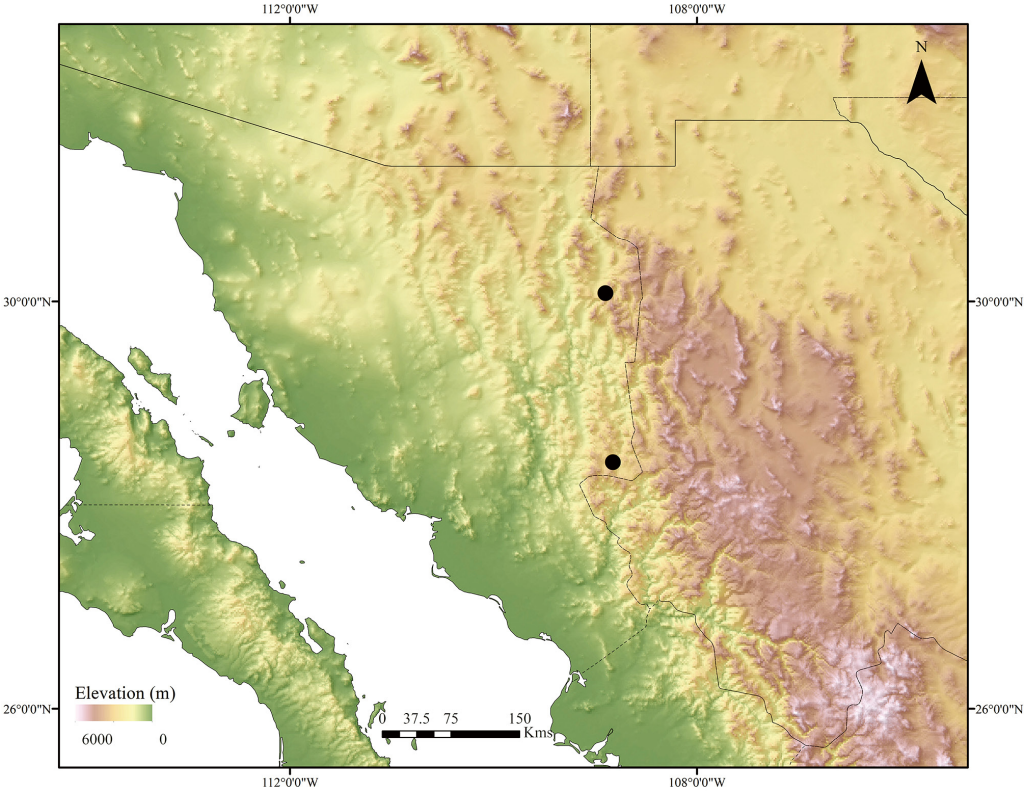

Fig. 22. Distribution of *O. mcclevei* (Howden and Génier 2004).

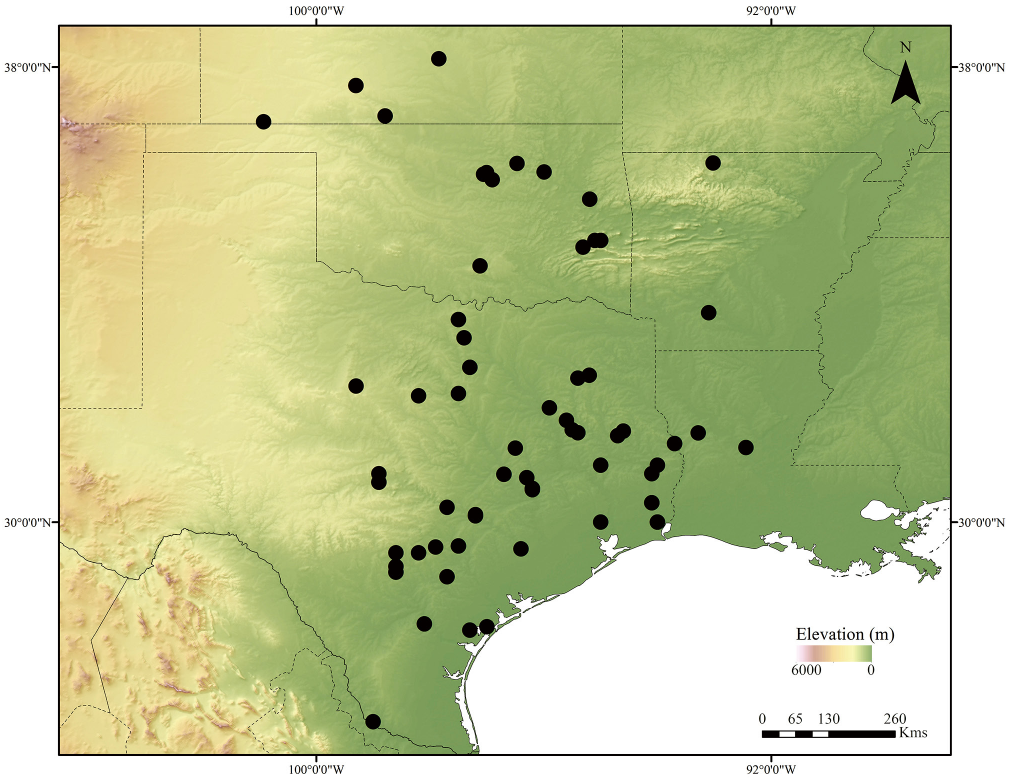

Fig. 23. Distribution of *O. medorensis* (Howden and Cartwright 1963, GBIF 2020e).

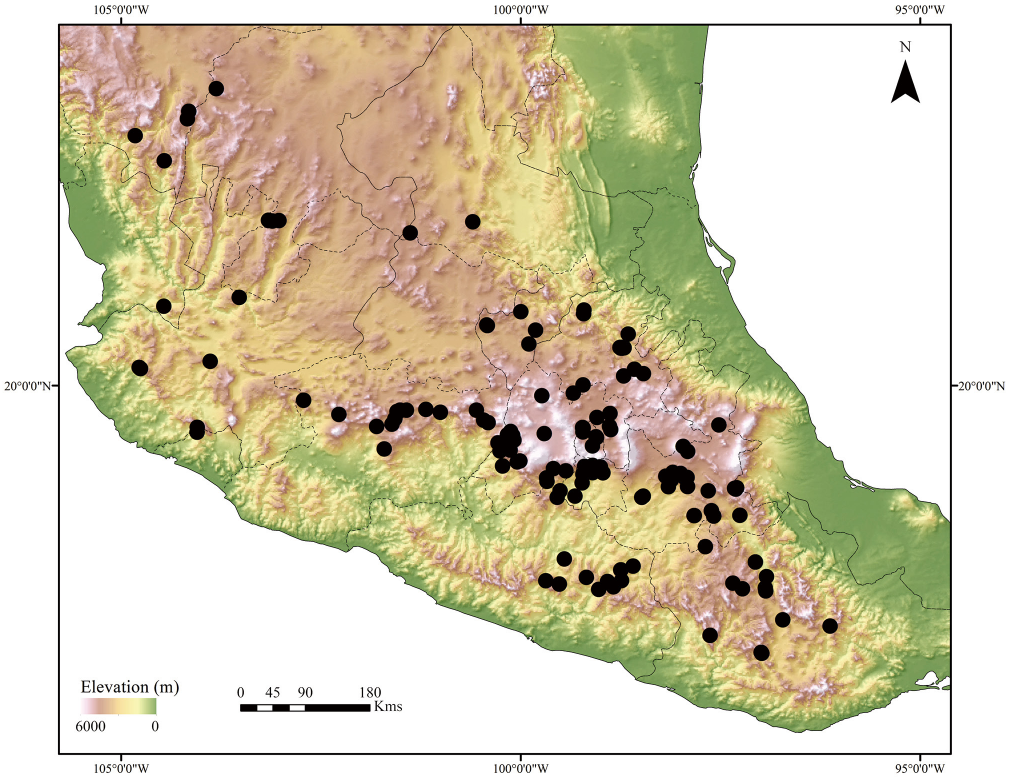

Fig. 24. Distribution of *O. mexicanus* (García de Jesús et al. 2013; Escobar et al. 2015; Moctezuma et al. 2016a b; GBIF 2020f). Erroneous localities from the Gulf of Mexico lowlands (Escobar et al. 2015; GBIF 2020f) were omitted.

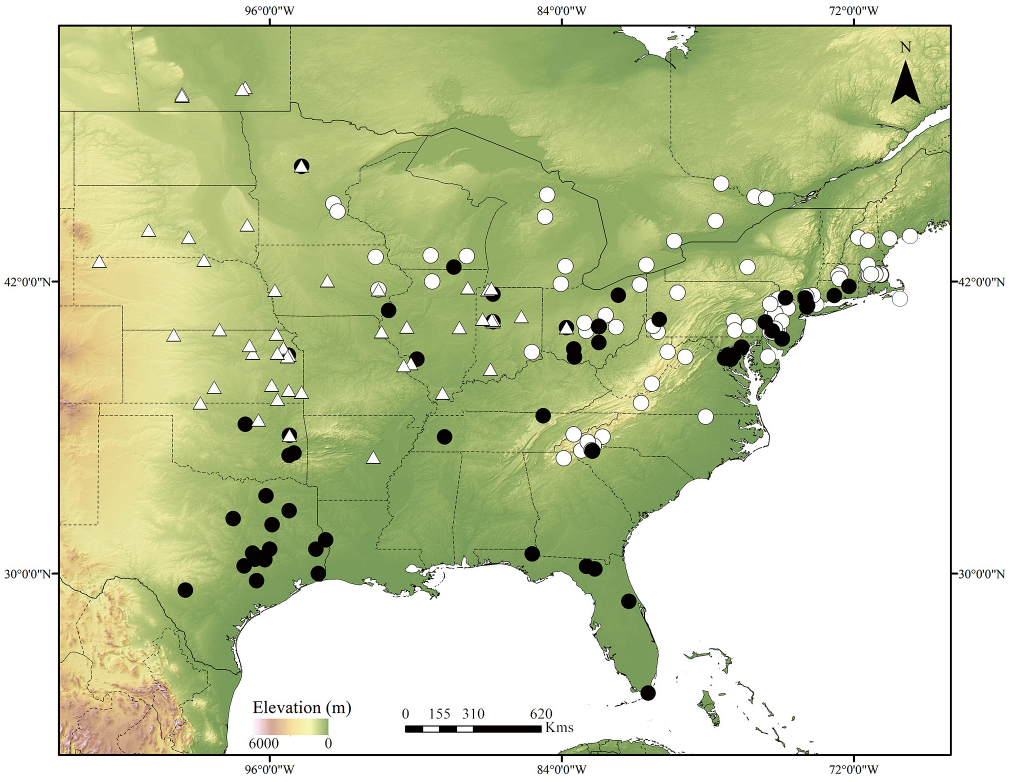

Fig. 25. Distribution of *O. orpheus* (Howden and Cartwright 1963; GBIF 2020g). Black dots - *O. o. canadensis*, white dots - *O. o. orpheus*, white triangles- *O. o. pseudorpheus*.

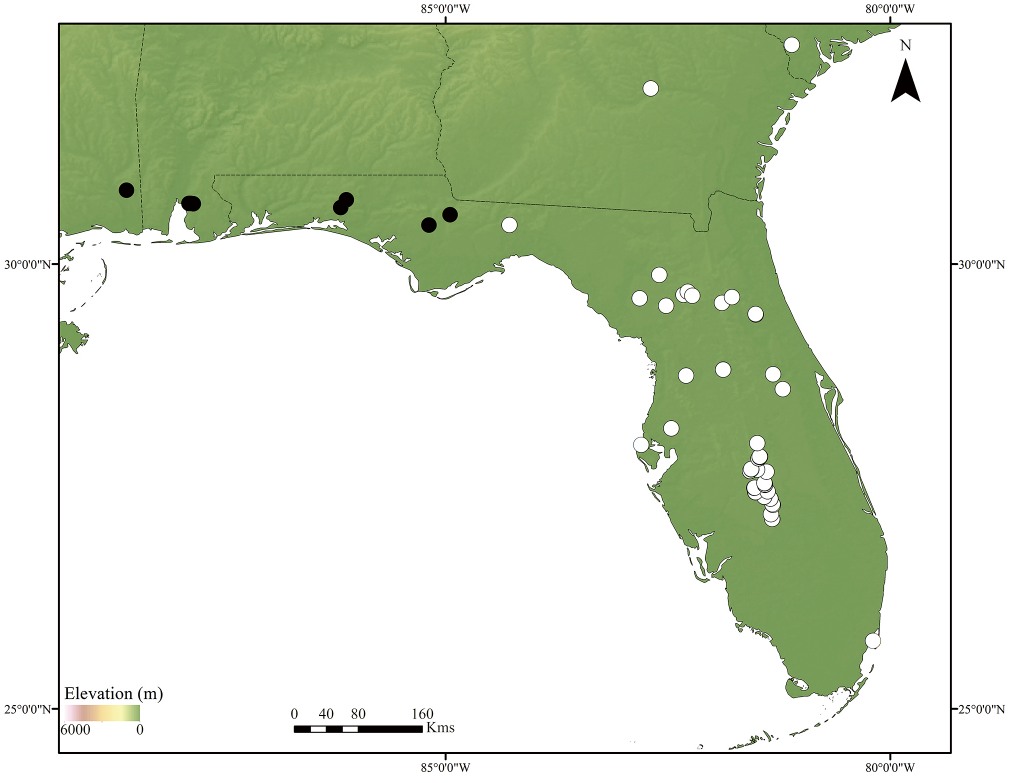

Fig. 26. Distribution of *O. polyphemi* (Howden and Cartwright 1963; GBIF 2020h). Black dots - *O. p. polyphemi*, white dots - *O. p. sparsisetosus*.

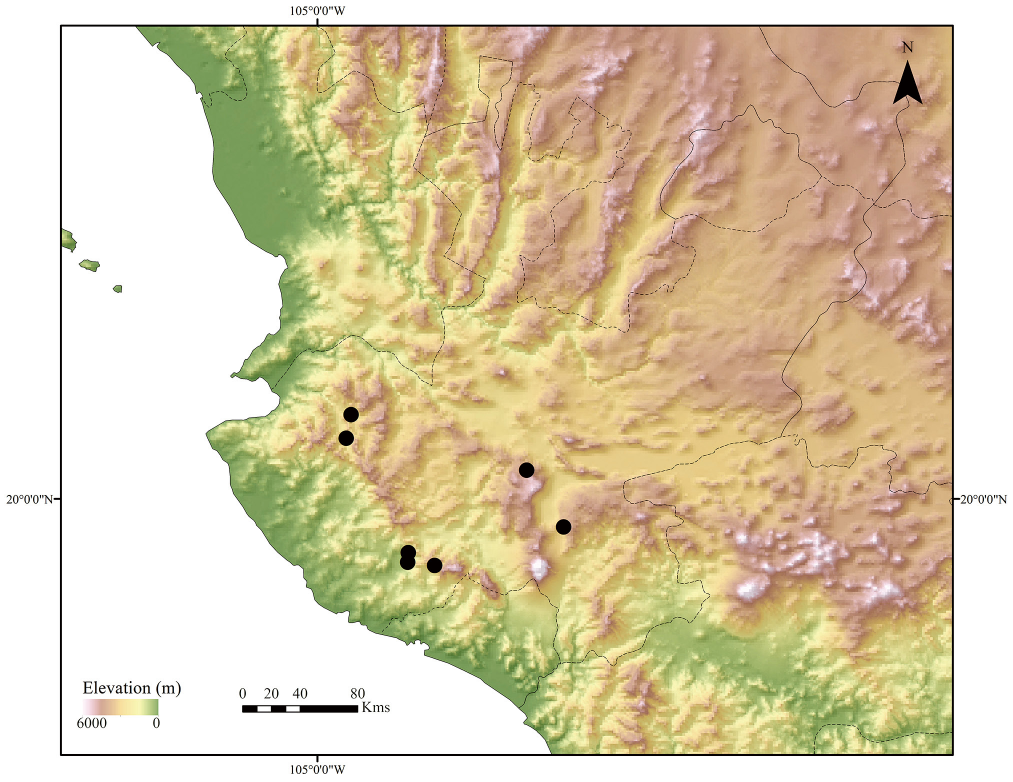

Fig. 27. Distribution of *O. pseudoguatemalensis* sp. n. (García-Real 1995; Quiroz-Rocha et al. 2008; Naranjo-López and Navarrete-Heredia 2011; Escobar et al. 2015; Martínez-Rodríguez 2018; GBIF 2020c).

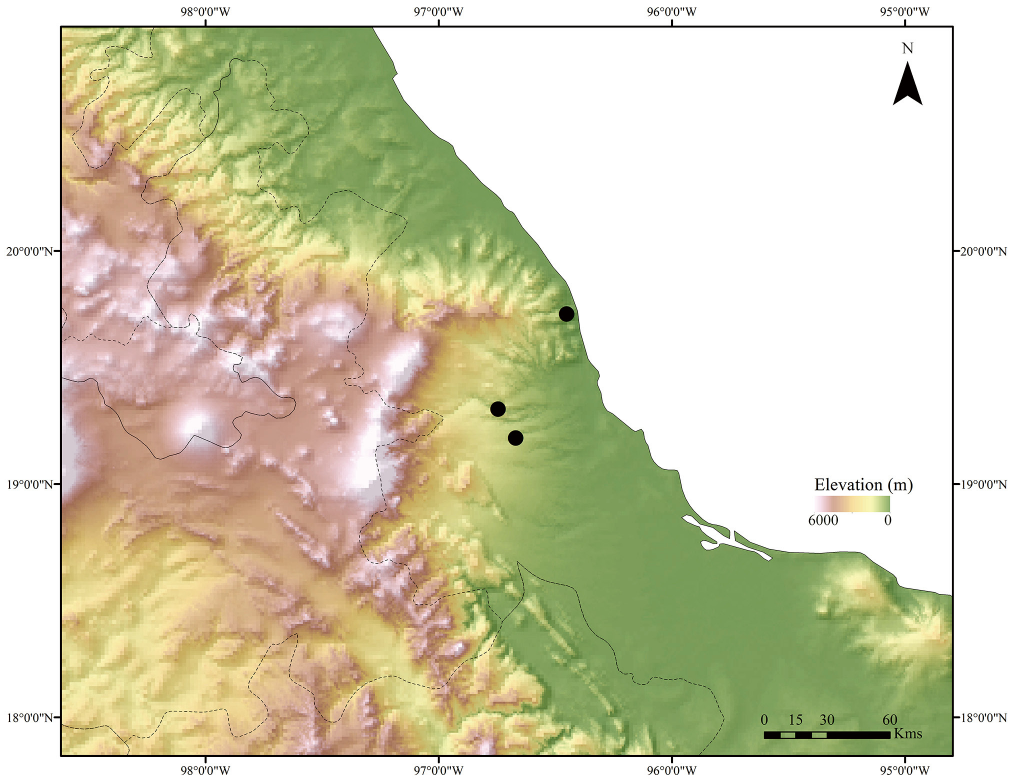

Fig. 28. Distribution of *O. totonacus* sp. n.

surveys on the Mexican side of this border will probably lead to the discovery of these species.

The rarity of *O. eulophus* and *O. totonacus* in entomological collections might be a consequence of their trophic habits. Several cases of association with rodents have been reported within the *O. mexicanus* species group, including *O. arnetti*, *O. browni*, *O. cynomysi*, *O. orpheus* and *O. velutinus* (Brown 1927; Howden et al. 1956; Howden and Cartwright 1963; Halffter and Matthews 1966; Woodruff 1973; Anduaga 2007; Zunino and Halffter 2007; Edmonds 2018). Some Mexican species are found within the nests of the *Neotoma* woodrats (Anduaga 2007; Zunino and Halffter 2007) and this might also be the case with *O. eulophus* and *O. totonacus*. The example of *O. browni* is particularly well documented. This species seems to be an obligate inquiline of woodrats since adults, larvae and nidification brood masses are found within the nest debris of the white-throated woodrat *Neotoma albigula* Hartley (Halffter and Matthews 1966; Anduaga 2007; Edmonds 2018). Individuals of *O. browni* are occasionally attracted to human feces, but they are always collected in larger numbers from the nests of the woodrats (Edmonds 2018).

The Mexican woodrat *N. mexicana* Baird, which is found in the tropical lowlands of central Veracruz (Zarza and Ceballos 2014), might be a potential host for *O. totonacus*. The Bryant's woodrat *N. bryanti* Merriam, the big-eared woodrat *N. macrotis* Thomas and the desert woodrat *N. lepida* Thomas might be the hosts of *O. cartwrighti*, since the distribution areas of these species overlap with that of *O. cartwrighti* (Howden 1973; Luévano and Mellink 2014a b; Mellink et al. 2014). Further research is required in order to study the association between Mexican dung beetles and rodents. *Neotoma* nests could be a major source for discoveries since at least 16 species of woodrats are reported for Mexico (Ceballos and Arroyo-Cabrales 2014). Nevertheless, such an exploration of the *Neotoma*-dung beetle association is an urgent task considering the current demise of the woodrats, with two probably extinct species and at least six species included in conservation categories (Ceballos and Arroyo-Cabrales 2014; Ceballos et al. 2014). Since insular woodrats are particularly threatened with extinction, or have gone extinct (Ceballos and Arroyo-Cabrales 2014; Ceballos et al. 2014), the study of insular environments is particularly critical. Loss of the insular woodrats might promote a cascade effect, driving their inquiline arthropods to extinction. Consequently, study of the effects of insularity on the ecology and evolution of rodent-arthropod associations might be irreversibly hampered.

Knowledge of the Mexican dung beetles

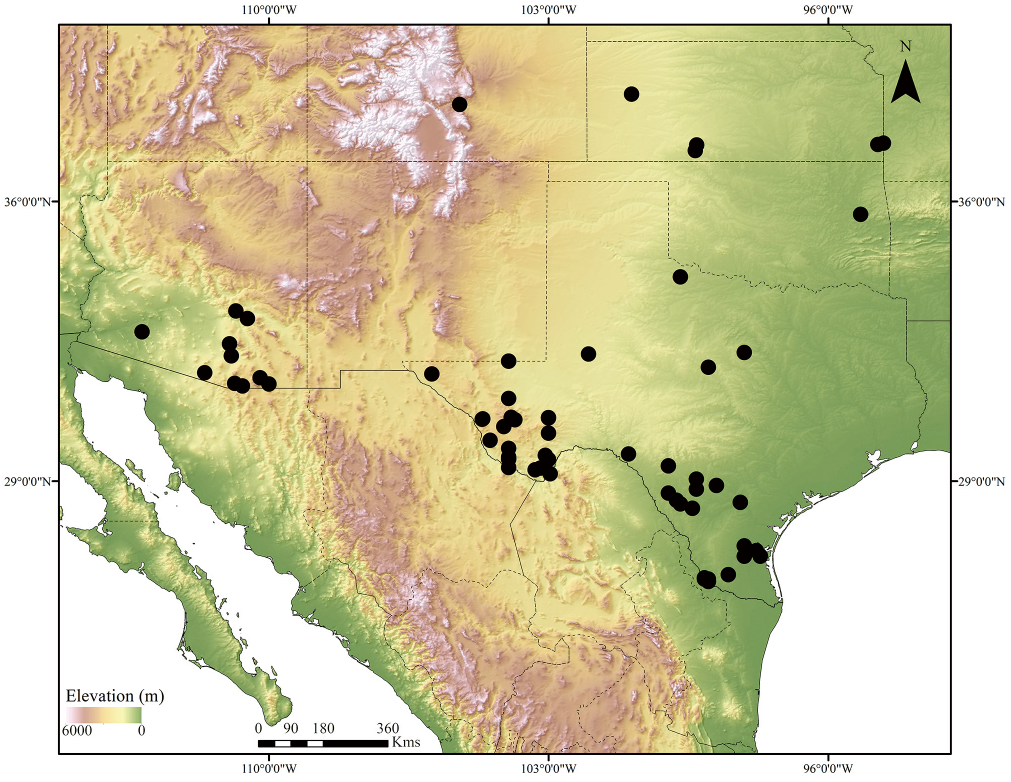

Fig. 29. Distribution of *O. velutinus* (Howden and Cartwright 1963; Edmonds 2018; GBIF 2020i)

associated with burrows of the prairie dogs *Cynomys ludovicianus* (Ord) and *C. mexicanus* Merriam remains limited. *Onthophagus cynomysi* has been reported from the United States as an obligate inquiline of the black-tailed prairie dog *C. ludovicianus* (Brown 1927; Howden et al. 1956; Howden and Cartwright 1963; Halffter and Matthews 1966; Zunino and Halffter 2007). Consequently, *O. cynomysi* could be expected to occur within the burrows of the Mexican populations of the black-tailed prairie dogs. The Mexican prairie dog *C. mexicanus* is an endemic species closely related to *C. ludovicianus* (Ceballos et al. 2014; Pacheco and Ceballos 2014), which is thought to have originated as a consequence of isolation caused by Pleistocenic climate changes (Hoffman and Jones 1970; Ceballos et al. 2014). It would therefore be interesting to determine whether *O. cynomysi* is associated with *C. mexicanus*, or if a hitherto unknown species in the *O. mexicanus* species group coevolved with the Mexican prairie dog during the Pleistocene climatic fluctuations. The search for dung beetles (and other arthropods) associated with burrows of prairie dogs is also urgent, since *C. mexicanus* is considered to be an endangered species and *C. ludovicianus* is threatened in Mexico due to reductions in its historic distributional areas (Ceballos and Arroyo-Cabrales 2014; Pacheco and Ceballos 2014). Since the accurate distribution of *O. eulophus* in Mexico remains unknown, we are unable to discount the possibility that this species might be associated with *Cynomys* or *Neotoma*.

Despite the fact that the association between the *O. mexicanus* species group and rodents is known, evident morphological adaptations to exploit the dung/burrows of rodents have not been recognized within this grouping of dung beetles. The North American *O. hippopotamus* species complex is also recognized for its strong association with rodent burrows (Howden et al. 1956; Halffter and Matthews 1966; Zunino and Halffter 1988 2007; Sánchez-Huerta et al. 2015 2018; Halffter et al. 2019). Some apparent adaptations to exploit rodent dung/burrows have been recognized within *O. hippopotamus* Harold and allies, including the protibiae with an apical spur strongly curved inwardly and with obsolete secondary teeth (Zunino and Halffter 1988; Sánchez-Huerta et al. 2015 2018). Future studies are required in order to understand the mechanisms (olfactory, physiological, ethological, mandible morphology evolution, gut microbiota, among others) that allowed dung beetles to exploit the sources provided by fossorial mammals.

Traditionally, species within the *O. mexicanus* species group have been believed to follow the Mexican Plateau Paleoamerican distribution pattern (Zunino and Halffter 1988 1997; Halffter et al. 2008; Arriaga et al. 2012; Barragán et al. 2014; Moctezuma et al. 2016a b; Halffter and Morrone 2017; Halffter 2019; Moctezuma and Halffter 2019a; Morrone 2020). The Mexican Plateau Paleoamerican distribution corresponds to Holarctic taxa that diversified into endemic lineages of the southern United States and northern Mexico, which subsequently dispersed to the Balsas basin and the highlands of Chiapas and Guatemala (Halffter et al. 2008; Halffter and Morrone 2017; Morrone 2020). Species following this distribution pattern are usually associated with xeric habitats and are occasionally found at lower elevations of adjacent mountains (Halffter et al. 2008; Moctezuma et al. 2016a b; Halffter 2019). Nevertheless, some inconsistences have arisen with the assumption that all of the species within the *O. mexicanus* species group fit the Mexican Plateau Paleoamerican distribution.

Only nine species of the *O. mexicanus* species group are typical of the xeric environments of the southern United States, northern Mexico and the Balsas basin (*O. anewtoni*, *O. arnetti*, *O. browni*, *O. cartwrighti*, *O. cynomysi*, *O. mcclevei*, *O. medorensis*, *O. mexicanus* and *O. velutinus*), while some species apparently fit the Tropical Paleoamerican (*O. championi*, *O. concinnus*, *O. polyphemi* and *O. totonacus*) and the Mountain Paleoamerican (*O. guatemalensis* and *O. pseudoguatemalensis*) patterns. Furthermore, no species have been found to date in the Mesoamerican high plateaus. Some taxa do not fit with any of the previously proposed distributional patterns, because they are associated with several environments and are widely distributed in America north of Mexico (*O. hecate* and *O. orpheus*). A new distributional pattern should probably be established to accommodate *O. hecate* and *O. orpheus*, but their taxonomy must be reassessed. A similar case is that of the *O. chevrolati* species group, which was considered to exclusively include Mountain Paleoamerican taxa (Zunino and Halffter 1988 1997; Gasca-Álvarez et al. 2018) until recent studies suggested that the group also includes different distributional patterns, such as the Mesoamerican Paleoamerican, Tropical Paleoamerican and Baja Californian Paleoamerican (Halffter et al. 2019; Moctezuma and Halffter 2019a 2020a b c).

Apparently, there is no evidence to argue that the *O. mexicanus* species group is a monophyletic unit that diversified in the xeric environments of the southern United States and northern Mexico, and subsequently colonized new environments and regions (Zunino and Halffter 1988 1997). Phylogenetic analysis based on four molecular markers (*COI*, COII, 16S and ITS2) suggested that the xerophytic environments of northern Mexico and southern United States were colonized by Tropical Paleoamerican lineages (Moctezuma

2019). Previous studies (Zunino and Halffter 1988 1997; Kohlmann and Solís 2001; Rossini et al. 2018a b; Halffter et al. 2019) have assumed that the species groups proposed for the New World *Onthophagus* are natural units. However, it has been suggested that the majority of the species groups recognized for the New World *Onthophagus* are non-monophyletic (Moctezuma 2019). According to Moctezuma (2019), *O. orpheus*, *O. hecate* and *O. anthracinus* form a monophyletic clade, while *O. championi* is the sister taxon to the clade including *O. hecate* + *O. orpheus* + *O. anthracinus* Harold, *O. haematopus* Harold + *O. marginicollis* Harold, and *O. sharpi* Harold. Supplementary evidence that supports the fact that the *O. mexicanus* species group might be a non-monophyletic unit is provided by the morphology of *O. polyphemi*. Males of this species show obsolete pronotal projections or protuberances on the pronotum (Howden and Cartwright 1963), while the *O. mexicanus* species group is characterized by males with the pronotum distinctly protruded frontally into a flattened projection, this projection usually bilobed or bifid apically (Zunino and Halffter 1988 1997). In addition, *O. cambrai* Delgado and Curoe is thought to share characters with both the *O. mexicanus* and *O. dicranius* species groups.

Further studies are required in order to propose monophyletic units within the New World *Onthophagus*, to adequately understand the biogeography of this group, and to determine whether the morphological differences that exist between the subspecies of *O. hecate*, *O. polyphemi* and *O. orpheus* merit full species status or should be considered as intraspecific variation. When these subspecies were proposed (Howden and Cartwright 1963), comparison of their genital structures was overlooked, and there is now a need to study the aedeagus, endophallites and sclerozation of the vagina in particular, since these have been demonstrated to be crucial for species determination and delimitation within the New World *Onthophagus* (Zunino and Halffter 1988; Rossini et al. 2018b; Joaqui et al. 2019; Moctezuma and Halffter 2019a b 2020a b c).

CONCLUSIONS

With the addition of the new species described herein, the New World *Onthophagus* and the *O. mexicanus* species group include at least 192 and 18 species, respectively. The redescriptions and lectotype designations for some previously described species will help to stabilize the nomenclature of the *O. mexicanus* species group, and are likely to lead to the discovery of new taxa. Taking into consideration the fact that several species of the *O. mexicanus* species group are strongly associated with rodents, exploration of rodent nests and burrows (such as those of *Neotoma* and *Cynomys*) should lead to the discovery of new species, including ones of poorly known dung beetles. The study of dung beetle-rodent associations is urgently required as a result of the decline in burrowing rodents. The demise of burrowing rodents and their inquilines could obscure the study of the ecological and evolutionary processes of the ecosystems that they inhabit. Further studies are required in order to adequately understand the phylogenetic relationships and biogeography of the New World dung beetles, and to propose monophyletic infrageneric units.

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