Revista Mexicana de Biodiversidad

Revista Mexicana de Biodiversidad 94 (2023): e945081

Taxonomy and systematics

A new species of the *Onthophagus mirabilis* species complex (Coleoptera: Scarabaeidae: Scarabaeinae) from the Chimalapas region, Oaxaca, Mexico

Una especie nueva del complejo de especies Onthophagus mirabilis *(Coleoptera: Scarabaeidae: Scarabaeinae) de la región de Los Chimalapas, Oaxaca, México*

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Received: 15 July 2022; accepted: 28 April 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:9AA4C72B-329F-423F-8280-4F0454DBB964

Abstract

Onthophagus zoquecornis, new species of the *O. mirabilis* species complex is described and illustrated. Keys to separate adult males, and females of the *O. mirabilis* species complex are updated. An updated distribution map of the *O. mirabilis* species complex is presented. A brief discussion on species richness of the New World *Onthophagus*, and distribution and ecology of the new species is provided.

Keywords: Dung beetles; Onthophagini; Mountain Cloud Forest; Frugivory; Coprophagy

Resumen

Onthophagus zoquecornis, nueva especie del complejo de especies *O. mirabilis* es descrito e ilustrado. Las claves para separar a los machos adultos y hembras del complejo de especies *O. mirabilis* son actualizadas. Se presenta un mapa de distribución actualizado del complejo de especies *O. mirabilis*. Se incluye una discusión breve sobre la riqueza de especies de los *Onthophagus* del Nuevo Mundo, la distribución y ecología de la especie nueva.

Palabras clave: Escarabajos del estiércol; Onthophagini; Bosque de niebla; Frugivoría; Coprofagia

ISSN versión electrónica: 2007-8706; Universidad Nacional Autónoma de México, Instituto de Biología. https://doi.org/10.22201/ib.20078706e.2023.94.5081

Introduction

The *Onthophagus mirabilis* species group was originally proposed by Howden and Gill (1993) and it was initially composed by 4 species: *O. mirabilis* Bates, 1887 from Ecuador, *O. neomirabilis* Howden, 1973 from Mexico and Guatemala, *O. quetzalis* Howden and Gill, 1993 from Costa Rica and Panama, and *O. solisi* Howden and Gill, 1993 from Costa Rica. Génier and Howden (1999) revised the *O. mirabilis* species group some years later and 3 additional species were included by them within this group: *O. barretti* Génier and Howden, 1999 from Panama; *O. breviconus* Génier and Howden, 1999 from Guatemala and Honduras; and *O. orphnoides* Bates, 1887 from Costa Rica, which was removed from previous synonymy with *O. mirabilis*. In the same work *O. quetzalis* was transferred to the *O. dicranius* species group.

Kohlmann and Solís (2001) considered the species within the *O. dicranius* and *O. mirabilis* species groups to be part of a unique supraspecific unit referred to as *O. dicranius* species group. Kohlmann and Solís (2012) described *O. turgidus* Kohlmann and Solís, 2012 from Panama. Finally, Génier (2017) redefined the *O. dicranius* species group by splitting it into the *O. dicranius* and *O. mirabilis* species complexes, and described *O. contrapositus* Génier, 2017 from Guatemala as a new species within the *O. mirabilis* species complex.

For this work, the classification proposed by Génier (2017) is followed. Currently, the *O. mirabilis* species complex is made up by 8 species, all of them restricted to the tropical humid mountains from Mexico to northern South America, where environmental conditions allow the cloud forests to occur (Halffter et al., 2019). The external morphology of males within the *O. mirabilis* species complex is occasionally homogeneous: some of them may be easily misidentified and the examination of the medial endophallite is frequently required to confirm taxonomical determinations, but females usually show informative characters on head and pronotum to separate species (Howden & Gill, 1993; Génier, 2017; Génier & Howden, 1999). In recent expeditions to the eastern Oaxaca state of Mexico, some specimens of the *O. mirabilis* species complex were found, and they are described herein as a new species.

Materials and methods

Institution-based collections cited in this work are: Setor de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil (CEMT); Canadian Museum of Nature, Ottawa, Ontario, Canada (CMNC), Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico (CNIN); Colección Entomológica "Dr. Miguel Ángel Morón", Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico (IEXA); Texas A&M University Insect Collection, College Station, Texas, USA (TAMU). The following personal collections are cited: Daniel J. Curoe Collection, Ciudad de México, Mexico (DJCC); Leonardo Delgado Collection, Xalapa, Veracruz, Mexico (LLDC); Eder Mora-Aguilar Collection, Coatepec, Veracruz, Mexico (EMAC); Victor Moctezuma Collection, Puebla, Puebla, Mexico (VMC).

For external morphology, the nomenclature proposed by Génier and Howden (1999) modified by us was followed, and Tarasov and Solodovnikov (2011) modified by Génier (2019) for genital morphology. Label data is given verbatim. Climate data were taken from INEGI (2019). The distribution records were taken from specimen labels, literature (Bates, 1887; Génier, 2017; Génier & Howden, 1999; Génier & Medina, 2004; Howden & Gill, 1993; Kohlmann & Solís, 2001, 2012). Databases (GBIF, 2019) were consulted and compared with previous literature for *O. mirabilis*, *O. barretti*, *O. breviconus*, *O. contrapositus*, and *O. orphnoides*; while *O. neomirabilis* was omitted because its distribution was not correct.

Genital structures, measurements and photographs were prepared with the methods suggested by Moctezuma and Halffter (2021), except for figures 5 and 9, that where provided by François Génier (CMNC): genital structures were soaked with a 10% KOH solution for 24 hours at room temperature, then rinsed with 96% ethanol and later rinsed with water. These structures were stored in 15 mm glass microvials with glycerol. These microvials were pinned under the dissected specimens. By using the manufacturer's software (Leica Application Suite version 4.7) and the z-stack image capture method, specimen measurements (all of these are expressed in mm through this manuscript) and photographs were taken with a Leica Z16APOA stereomicroscope (Red de Ecoetología, Instituto de Ecología, A. C.) equipped with a Leica Smart Touch and a Leica DMC2900 camera. The stereomicroscope lightning was substituted by 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 6,000-7,000k, LED 3528, 13 W/h).

Description

Family Scarabaeidae Latreille, 1802
Subfamily Scarabaeinae Latreille, 1802
Genus *Onthophagus* Latreille, 1802

Onthophagus zoquecornis Moctezuma, Halffter and Mora-Aguilar, new species
(Figs. 1-4, 6, 7)
http://zoobank.org/urn:lsid:zoobank.org:act:27C82E94-F85A-4551-BC12-039955DED890

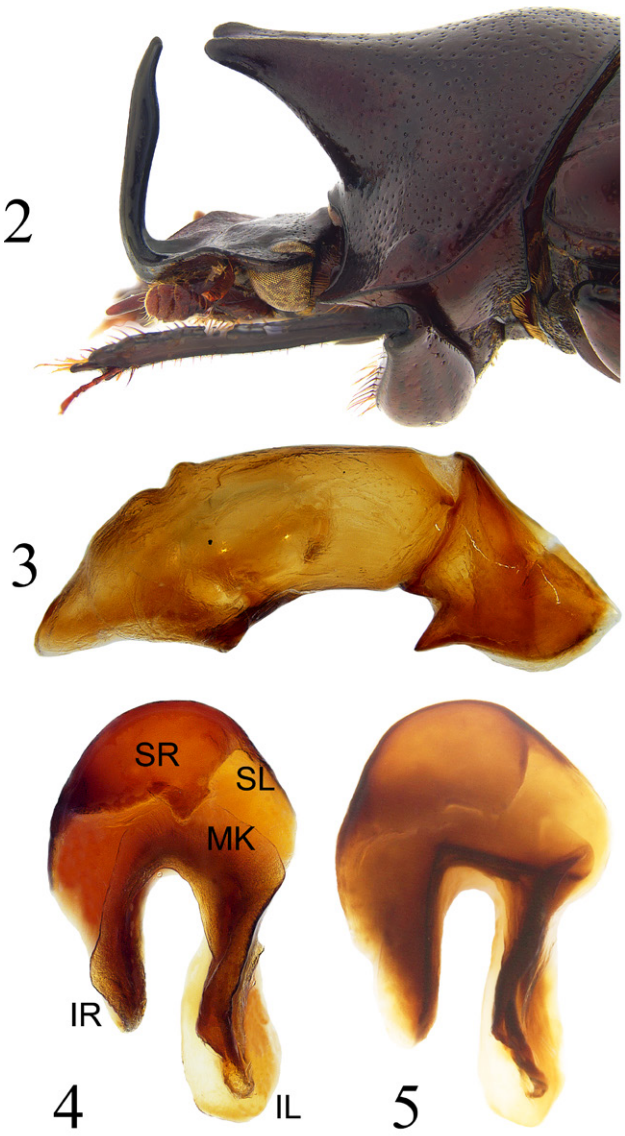
Diagnosis. *Onthophagus zoquecornis* (Figs. 1, 2) may only be confused with *O. neomirabilis* (Fig. 9), but males of *O. zoquecornis* are separated by the frontoclypeal area convex, with a tubercle in major specimens (convex, without tubercle in *O. neomirabilis*); basal portion of the medial keel of medial endophallite distinctly rounded as in Figure 4 (distinctly straight in *O. neomirabilis*; Fig. 5); superior right lobe of medial endophallite distinctly protruded into a triangular dent (rounded in *O. neomirabilis*); females of *O. zoquecornis* show the vertex of clypeus almost flat and frons with 2 triangular dents as in Figure 6 (vertex of clypeus concave in and frons with 2 widened tubercles in *O. neomirabilis*; see Figure 12 in Génier, 2017).

Holotype major male. Measurements: length from the apex of clypeus to tergite VIII 11.8, pronotal width 6.3, elytral width 6.5. Dorsal habitus (Fig. 1): dorsal surface dark brown in color, lateral margins of head, antennae damaged (club are missing), outer side of protibiae, anterolateral margins of pronotum, lateral margins and apex of elytra, legs, and venter reddish brown; surface glabrous and microreticulate. Head (Figs. 1, 2, 10): clypeal projection with an upright horn on anterior edge medially, basal portion of horn tapering on basal fourth in frontal view, apical edge rounded. Clypeal surface is deeply concave posteriorly to base of horn, with weakly marked punctuation at vertex, rugopunctate at base. Frontoclypeal area convex, frons with distinctly marked and irregularly sized punctation. Clypeal and frontal carinae obsolete. Clypeogenal sutures superficially marked. Genae obtusely triangular with large and coarse punctation. Pronotum (Figs. 1, 2, 10): frontally projected with a large conical horn extending over the head. Apex of pronotal horn bilobed and flattened dorsoventrally. Low callosity on each side near margin at anterior 2/5. Lateral fovea inconspicuous, irregular in shape. Elytra (Fig. 1): striae distinctly impressed, with medium sized and umbilicate punctures, separated by 2-3 puncture diameters. Interstriae with minute punctation. Venter: prosternum laterally smooth lacking punctures. Metasternum gradually descending to mesosternum, almost smooth at middle and with fine and moderate-sized punctures, denser and larger to the margins, separate less than 1 puncture diameter. Abdominal segments with a transverse row of coarse punctures near anterior margin. Tergite VIII rugopunctate, with coarse, confluent and dense punctures. Legs (Figs. 1, 10): protibiae quadridentate

Figure 1. *Onthophagus zoquecornis* male dorsal habitus.

on external border, lacking projections on internal border and apex. Protibial apex with a long setal brush. Middle and hind femora with outer surfaces smooth, with a few fine punctures superficially impressed. Genitalia (Fig. 4): parameres with apical teeth triangular, not acute. Inferior left lobe of medial endophallite more developed than the right lobe and spatulate in shape; superior left lobe of medial endophallite distinctly concave; superior right lobe of medial endophallite distinctly protruded; medial keel of medial endophallite distinctly rounded.

Variation. Mean length from the apex of clypeus to tergite VIII 10.1 (8.8-11.3). Minor males differ from major males by clypeal and pronotal horns reduced, tubercle



Figures 2-5. *Onthophagus zoquecornis* male. 2, Lateral view of pronotum; 3, aedeagus; 4, lateral view of medial endophallite (SR: superior right lobe, SL: superior left lobe, MK: medial keel, IR: inferior right lobe, IL: inferior left lobe); 5, *O. neomirabilis* lateral view of medial endophallite.

of the frons reduced or lacking, and widened protibiae. Females differ from males by the clypeus with anterior margin bidentate, clypeal teeth reflexed, separated by a V-shaped emargination; clypeus flat, surface transversely wrinkled; clypeofrontal suture carinated and reaching clypeogenal suture; vertex of clypeus with 2 short, compact, trapezoidal tubercles, and obliquely directed to the apex of eyes; pronotal small tubercle on the middle of the posterior border of depression (Figs. 6, 10). The ventral portion of the vagina is well sclerotized (Fig. 7).

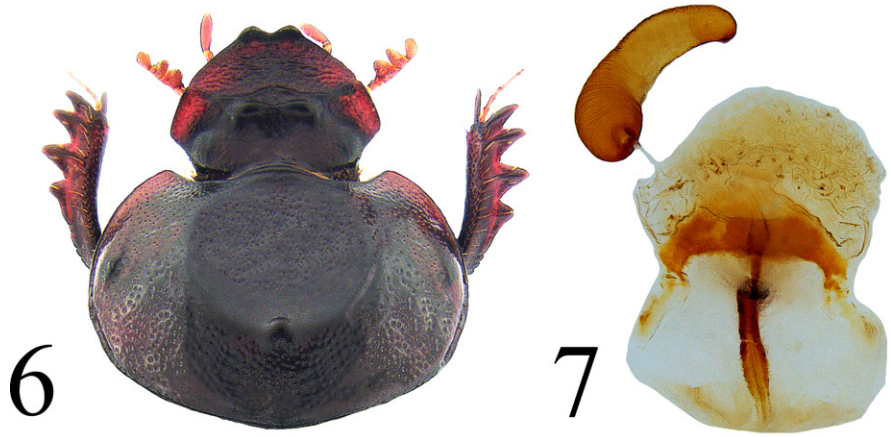
Taxonomic summary

Type locality. Voluntary Conservation Area El Cordón del Retén (Reserva Ecológica Campesina de Los Chimalapas), San Antonio, San Miguel Chimalapa, State of Oaxaca, Mexico (Fig. 8).

Type material. Holotype male, labeled: "México, Oaxaca, San Miguel Chimalapa, San Antonio, El Retén, El Gringo, 18/VI/2017, trampa de intercepción, 16.6836º N, -94.2623º W, 1,600m, Bosque mesófilo, A. Ramírez-Ponce, E. Mora, D. Curoe cols." (IEXA). Paratypes. 6 males and 4 females, same data as holotype (CEMT, CNIN, DJCC, IEXA, EMAC, LLDC). 1 male, same data except: "VI-VII-2013, E. Mora, L. Delgado cols." (EMAC). 1 male and 2 females, same data except: "23-VII-2017, BMM, 16.6787º N, -94.2629º W, D. Curoe, E. Mora-A., A. Ramírez cols." (IEXA, EMAC). 1 male: "México, Oaxaca, San Miguel Chimalapa, Benito Juárez. 8/X/2015, coprotrap t12c35, 16°43'54.4" N, 94°12'22.3" W, bosque de niebla, 1,329 m, Victor Moctezuma Col." (VMC). One female, same data except: "t12c03, 16°44'29.3" N, 94°12'20.1" W, 1,275 m" (VMC); 1 female, labeled: "México, Oaxaca, San Miguel Chimalapa, San Antonio. 14-X-2015, coprotrap t14c04, 16°39'41.1" N, 94°13'16.9" W, bosque de niebla, 1,573 m, Victor Moctezuma Col." (VMC); 1 female, same data except: "t14c11, 16°39'37.7" N, 94°13'25.8" W, 1,616 m" (IEXA); 1 female, same data except: "t14c15, 16°39'36.7" N, 94°13'31.1" W, 1,647 m" (TAMU); 1 male, same data except: "t14c21, 16°39'38.3" N, 94°13'39.8" W, 1,702 m" (TAMU); 1 female, same data except: "t14c26, 16°39'36" N, 94°13'45.5" W, 1,741 m" (VMC); 5 males, 4 females: "MEX. Oaxaca, Chimalapas, Sn Antonio. El Retén. Mesófilo 1,796 m 13-20/vii/2018. Intercepción. 16°39'50.9" N, 94°14'0.2" W. Ramírez-Ponce, Curoe & Avendaño cols."; 7 males, 5 females: "MEX. Oax. Chimalapas, Sn Antonio. Boca de montaña. 16°39.2'97" N, 94°13.2'3.2" W, 1,444 m. Mesófilo, 24-VII-18. Ramírez-Ponce and Curoe, col." (CNIN, IEXA).

Etymology. The specific epithet derives from the "Zoque" forest, the indigenous region where the type series was collected; and "*cornis*", referring the protrusion of the apex of clypeus of this new species.

Distribution and ecology. *Onthophagus zoquecornis* is endemic to the Mountain Cloud Forest from Los Chimalapas, eastern Oaxaca, Mexico. This forest occurs between an elevation range of 1,200-1,800 m, a mean temperature of 18-22 °C, and an annual rainfall of 1,500-2,000 mm (Fig. 8).



Figures 6-7. *Onthophagus zoquecornis* female. 6, Dorsal habitus; 7, vagina.

In the Génier and Howden's (1999) key for major males of the *O. mirabilis* species complex, *O. zoquecornis* keys to *O. neomirabilis*. We propose the following modification to identify the males of both species:

6 (5'). Frontoclypeal area flat, without tubercles (Fig. 9). Basal portion of the medial keel of medial endophallite distinctly straight; superior right lobe of medial endophallite rounded (Fig. 5). Northern Oaxaca (Fig. 8) ..... *O. neomirabilis* Howden, 1973

6 (5''). Frontoclypeal area convex, sometimes with a small tubercle (Fig. 2). Basal portion of the medial keel of medial endophallite distinctly rounded; superior right lobe of medial endophallite distinctly protruded into a triangular dent (Fig. 4). Eastern Oaxaca (Fig. 8)..... *O. zoquecornis* Moctezuma, Halffter and Mora-Aguilar new species

In the Génier's (2017) key for females of the *O. mirabilis* species complex, *O. zoquecornis* keys with *O. neomirabilis*. We propose the following modifications to include our new species:

5. Vertex of moderate to large individuals with tubercles low, transverse and always set closer to the frontoclypeal carina than anterior edge of the eyes; pronotum as in Figure 13 in Génier (2017); Mexico (Oaxaca; Fig. 8) 5a

– Vertex of moderate to large individuals with tubercles conical and set more or less in line with anterior edge of the eyes 6

5a. Vertex of moderate to large individuals with 2 wide transversal tubercles almost reaching lateral suture, equally in high (obtusely trapezoidal in shape), and with concave surface posterior to the tubercles (Fig. 12 in Génier, 2017) ..... *O. neomirabilis* Howden, 1973

– Vertex of moderate to large individuals with 2 wide transversal tubercles far of lateral suture, higher near middle (dentiform in shape), and with flat surface posterior to the tubercles (Fig. 6 in this work) .... *O. zoquecornis* Moctezuma, Halffter and Mora-Aguilar, new species.

Discussion

Scarabaeinae dung beetles are a very important indicator group for studies on ecology, biomonitoring and conservation (Carvalho et al., 2019; Favila & Halffter, 1997; Halffter & Favila, 1993; Nichols et al., 2008). In this regard, contributions dealing with the Linnean (species taxonomy), Wallacean (species distribution) and Raunkiaeran (functional traits and ecological functions) shortfalls of diversity knowledge in dung beetles are of great heuristic value (Favila & Halffter, 1997; Halffter & Favila, 1993; Hortal et al., 2015). Particularly, the genus *Onthophagus* is an outstanding component of the American dung beetle fauna with more than 190 described species in the continent (Moctezuma, 2021a). Despite that some supraspecific groups of *Onthophagus* are relatively well studied in the New World, a number of species remain undescribed, the distribution of many species is poorly known (Moctezuma, 2021a; Moctezuma & Halffter, 2021; Rossini et al., 2018), and the ecological functions

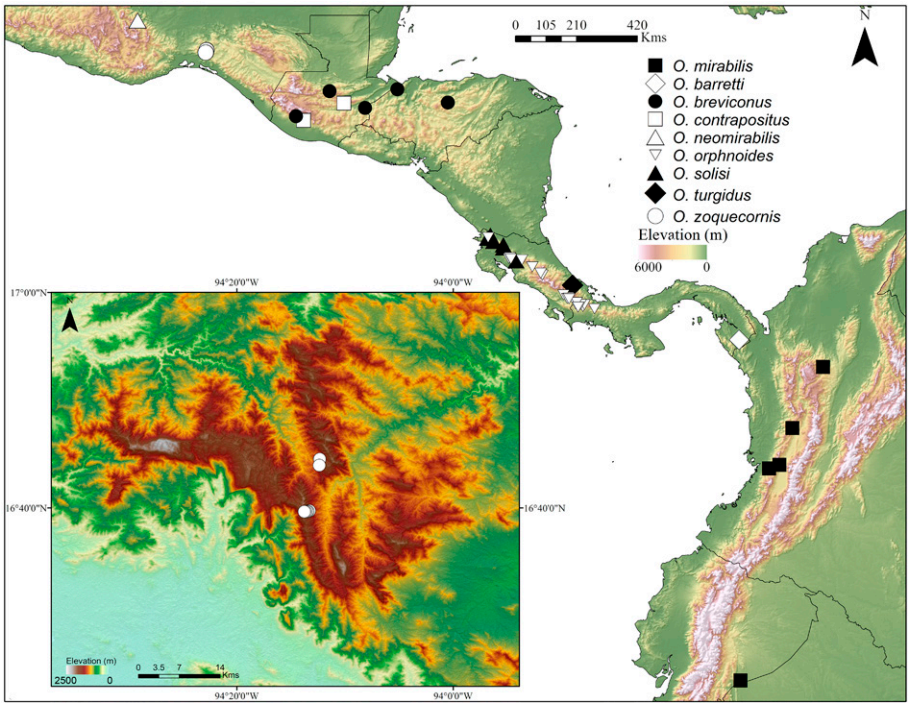


Figure 8. Continental distribution of the *O. mirabilis* species complex (large rectangle) and regional distribution of *O. zoquecornis* (small rectangle).

Figure 9. *Onthophagus neomirabilis* male lateral view.

of several species are poorly understood (Arellano et al., 2017; Moctezuma, 2021b; Moctezuma & Halffter, 2021). Our work contributes to reduce the aforementioned biodiversity shortfalls by describing a new species of *Onthophagus* and updating determination keys, presenting a distribution map, and providing ecological data of the newly described species.

Mexico is considered as the main center of diversification for the genus *Onthophagus* in the New World with at least 120 described species and 85 endemics (Moctezuma, 2021a). With the addition of *O. zoquecornis* and 2 new species from Jalisco (Moctezuma et al., 2022), the Mexican fauna of *Onthophagus* reaches at least 123 species and 88 endemics while Mexico is considered as the richest country in the Americas to date. Despite that the knowledge of the *Onthophagus* from Central and South America is fairly incomplete (Moctezuma, 2021a; Rossini et al., 2018), other countries from the New World are not expected to host a comparable number of species, because Mexico exhibits unique biogeographic conditions that allow the co-occurrence of several species of *Onthophagus* adapted to fairly varied ecosystems from the lowlands to the mountains (Halffter et al., 2019; Moctezuma, 2021a; Zunino & Halffter, 1988, 1997).

As previously stated, the knowledge of the New World *Onthophagus* is not geographically even (Moctezuma, 2021a; Rossini et al., 2018). *Onthophagus* has been divided into different species groups in the Americas, but the split into species groups is controversial. The following species groups have been fairly accepted in recent works: *O. chevrolati*, *O. clypeatus*, *O. dicranius*, *O. gazellinus*, *O. hircus*, *O. landolti* and *O. mexicanus* (Moctezuma

Figure 10. Pronotal and cephalic comparison of *O. zoquecornis* male (left) and female (right).

& Halffter, 2021). Particularly, the best studied species groups are *O. chevrolati* (Halffter et al., 2019; Joaqui et al., 2019; Moctezuma & Halffter, 2020a, b; Zunino & Halffter, 1988), *O. dicranius* (Delgado & Mora-Aguilar, 2019; Génier, 2017; Génier & Howden, 1999; Howden & Gill, 1993; Kohlmann & Solís, 2001; Zunino & Halffter, 1981) and *O. mexicanus* (Moctezuma & Halffter, 2021; Zunino & Halffter, 1997). In this regard, *Onthophagus zoquecornis* is preliminarily included in the *O. dicranius* species group, but particularly within the *O. mirabilis* species complex. External morphology of *O. zoquecornis* is similar to that of *O. neomiramilis*, but the morphology of the medial endophallite fairly supports our taxonomic hypothesis: the morphology of this structure is proven to have high levels of interspecific variation within the *O. mirabilis* species complex (Howden & Gill, 1993).

Despite that the species groups of *Onthophagus* from the New World provide a taxonomic background and these are fairly accepted (Halffter et al., 2019; Zunino & Halffter, 1988, 1997), some studies have suggested that these might not be monophyletic units, and that future phylogenetic analyses are needed to adequately conform the supraspecific classification of the American *Onthophagus* (Delgado & Curoe, 2014; Delgado & Mora-Aguilar, 2019; Delgado et al., 2006; Moctezuma, 2021a; Moctezuma et al., 2021).

The distribution of the new *O. zoquecornis* fits well with the Paleoamerican Mesoamerican cenocron. This cenocron was proposed to include Holarctic taxa that successfully diversified in the tropical mountain forests of Central America and Mexico during the Miocene (Halffter & Morrone, 2017; Halffter et al., 2019; Morrone, 2020). *Onthophagus zoquecornis* and all the species within the *O. mirabilis* species complex are recognized to be inhabitants of the humid tropical mountains from Mexico (Oaxaca) to Ecuador (Génier, 2017; Génier & Howden, 1999; Howden & Gill, 1993; Halffter & Morrone, 2017; Halffter et al., 2019; Kohlmann & Solís, 2001; Zunino & Halffter, 1981). The tropical mountain cloud forest from Los Chimalapas, where *O. zoquecornis* was discovered, is a region recognized by its high values of diversity and endemism for various groups of insects. Several new species of scarab beetles have been discovered there and many more await to be discovered and described (Moctezuma et al., 2019; Mora-Aguilar & Delgado, 2019).

Feeding preferences of *O. zoquecornis* are poorly understood because it was collected with unbaited flight interception traps (14/21 specimens) and pitfall traps baited with human feces (7/21 specimens). Despite that a reduced number of specimens of *O. zoquecornis* was apparently attracted to human feces, it won't be adequate to suggest that this is a coprophagous species. Indeed, the records of *O. zoquecornis* obtained by pitfall traps might be a consequence of accidental captures promoted by intensive sampling: 120 pitfall traps were set-up in the tropical mountain cloud forest from Los Chimalapas, but just 7 traps obtained specimens of *O. zoquecornis* (Moctezuma, 2021b). On the other hand, flight interception traps were more effective than pitfall traps for the capture of *O. zoquecornis*, because only 3 of these traps helped to collect a majority of the type series.

Species within the *O. dicranius* species group are recognized to be trophic specialists that mainly feed on rotten fruits (Halffter & Halffter, 2009). The taxonomically related *O. orphnoides*, *O. solisi* and *O. mirabilis* have been documented to exploit rotten fruits and seeds of *Persea* sp. (Halffter & Halffter, 2009; Kohlmann & Solís, 2001), but future studies are needed to determine if this might be the case of *O. zoquecornis*. The *O. dicranius* species group almost exclusively inhabits conserved tropical forests

and is dependent of fruits associated with these forests. Consequently, this group might be highly vulnerable to habitat modification and climate change, and an appropriate indicator to assess the impact of human disturbance.

Acknowledgments

The residents from Los Chimalapas supported this work, particularly those of the communities of Santa María, Benito Juarez, San Antonio and San Francisco La Paz. This work was partly funded by the Dirección General of the Instituto de Ecología, A. C. (No. 20,035/30,916), the Fondo Sectorial de Investigación para la Educación SEP-CONACyT Mexico (No. 257,039) and the Organization for Tropical Studies (Hovore-Horn Fellowship No. 3,116). CONACYT-Mexico awarded support for postgraduate studies, research assistant activities and postdoctoral fellowship to V. Moctezuma (CVU 486,765). The first author thanks José Luis Sánchez-Huerta for his help in the fieldwork of postgraduate studies. We thank the generosity of the CMNC, particularly to F. Génier, who kindly shared the photographs of *O. neomirabilis*. The last author thanks Leonardo Delgado, Andrés Ramírez-Ponce and Daniel Curoe for the loan of specimens and collaboration in fieldwork. We thank to K. Philips for English language edition. Unfortunately, professor Gonzalo Halffter passed away before the final version of this work was complete, this work is dedicated to him. The commentaries by an anonymous reviewer helped to improve this work.

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