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An annotated checklist of the dung beetles (Coleoptera: Geotrupidae and Scarabaeidae, subfamilies Aphodiinae and Scarabaeinae) of Oaxaca, Mexico

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An annotated checklist of the dung beetles (Coleoptera: Geotrupidae and Scarabaeidae, subfamilies Aphodiinae and Scarabaeinae) of Oaxaca, Mexico

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Abstract. A checklist of the dung beetles (Coleoptera: Geotrupidae; Scarabaeidae: Aphodiinae and Scarabaeinae) of Oaxaca, Mexico, is presented for the first time. The checklist contains 252 taxa, 15 Geotrupidae, 77 Aphodiinae, and 160 Scarabaeinae. The state includes 58 genera and 15 tribes, where *Onthophagus* is the most species-rich genus with 49 taxa, followed by *Ataenius* with 22, *Canthon* with 17 and *Phanaeus* with 15 taxa. Valid names, as well as synonyms, are provided. First records, notes on presently recognized species, nomenclatural problems, and biodiversity comparisons are included. *Phanaeus dionysius* Kohlmann, Arriaga-Jiménez and Rös, 2018 (Coleoptera: Scarabaeidae: Scarabaeinae) is **re-established as a valid species**.

Keywords. Faunistics, distribution, first records, endemicity, invasive species, species revalidation.

Resumen. Se presenta por primera vez una lista verificada de los escabajos coprófagos (Coleoptera: Geotrupidae; Scarabaeidae: Aphodiinae y Scarabaeinae) del estado de Oaxaca, Mexico. El listado contiene 252 taxa, 15 de Geotrupidae, 77 de Aphodiinae y 160 de Scarabaeinae. El estado registra 58 géneros y 15 tribus, donde *Onthophagus* es el género más diverso con 49 taxa, seguido por *Ataenius* con 22, *Canthon* con 17 y *Phanaeus* con 15 taxa cada uno. Se presentan nombres válidos, así como sinónimos. Se incluyen nuevos registros, notas sobre especies reconocidas, problemas nomenclatoriales y comparaciones de la biodiversidad. Una extensa lista de referencias es proporcionada. *Phanaeus dionysius* Kohlmann, Arriaga-Jiménez y Rös es **reestablecido como especie válida.**

Palabras clave. Faunística, distribución, primeros registros, endemismo, especies invasoras, revalidación de especies.

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"What's in a name? Everything."
— English proverb

Introduction

Dung beetles (Coleoptera: Geotrupidae; Scarabaeidae, subfamilies Scarabaeinae and Aphodiinae) occur worldwide, except in Antarctica (Scholtz et al. 2009; Schoolmeesters 2023) and number more than 10,000 species (Cabrero-Sañudo et al. 2007). Schoolmeesters (2023) lists 6,838 species for Scarabaeinae, 1,105 for Geotrupidae, and 3,558 for Aphodiinae. Dung beetles are essential ecosystem service providers; they feed not only on dung but also on carrion, rotting fruit, fungi, seeds, decomposing plant matter, and some of them are even carnivores (Scholtz et al. 2009). Dung beetles are of paramount importance for recycling dung in cattle ranching areas. Slade et al. (2016) have stressed the importance of this guild in reducing greenhouse gas (GHG) emissions (methane

and nitrous oxide), especially for tropical grassland areas, through manure removal, thereby increasing grass growth and soil fertilization. However, Fowler et al. (2020) believe dung beetles cannot adequately reduce GHG.

The state of Oaxaca has a surface area of 93,952 km^2, representing 4.8% of the Mexican territory. It has a highly complex orography (Fig. 1) with two principal mountain chains. Sierra Norte (SN) is in the north of the state, with a northwest-southeast extension and is limited to the north by the lowlands of the Gulf of Mexico coast; Sierra Sur (SS) has a west-east extension, limited to the south by the Pacific coast (Centeno-García, 2004). Both Sierras have peaks higher than 3,000 m (around 3,300 m SN and 3,750 m in SS). Montane highlands separate them in the west, the Mixteca Shield (between 1,500 m and 3,000 m), a valley plain in the central part, the Central Valleys of Oaxaca (at 1,500 m), a mix of smaller valleys and hills in the east (1,000–1,500 m), and the isolated Sierra Atravesada (or Sierra de Niltepec) of Chimalapas in the East (2,250 m), surrounded by lowlands. Current geomorphological and landscape forms originated during the Cenozoic era but were probably molded locally (in the higher mountains) by the last glaciation process (Centeno-García, 2004). Oaxaca is perhaps the most biodiverse state in Mexico (8,431 plant species, 1,103 butterfly species, 736 bird species, 378 amphibian and reptile species, and 190 mammal species (García-Mendoza et al. 2004). This Mexican state represents a rich mix of Nearctic and Neotropical elements, with a critical mountain-generated endemic component (Kohlmann 2022). It is thought that its high biodiversity is a product of a very complex orography (García-Mendoza et al. 2004). A comprehensive study of its flora and fauna is underway by the Oaxaca state government and the National Biodiversity Commission (CONABIO).

Among essential checklists and synoptic studies of dung beetles for Mesoamerica, are the following: Bates 1886–1890; Ratcliffe 2002; Morón 2003a, Solís and Kohlmann 2012. Guzmán-Vásquez et al. (2021) have published a checklist of the Oaxaca Dynastinae. No checklist or catalogue covering dung beetles has heretofore been published for Oaxaca. There is a need for such a checklist among researchers, curators, and entomologists. This state has attracted much taxonomic work recently (Kohlmann 2022), and many new species belonging to these groups have been published lately. The purpose of the present study is to list all known species of dung beetles for Oaxaca.

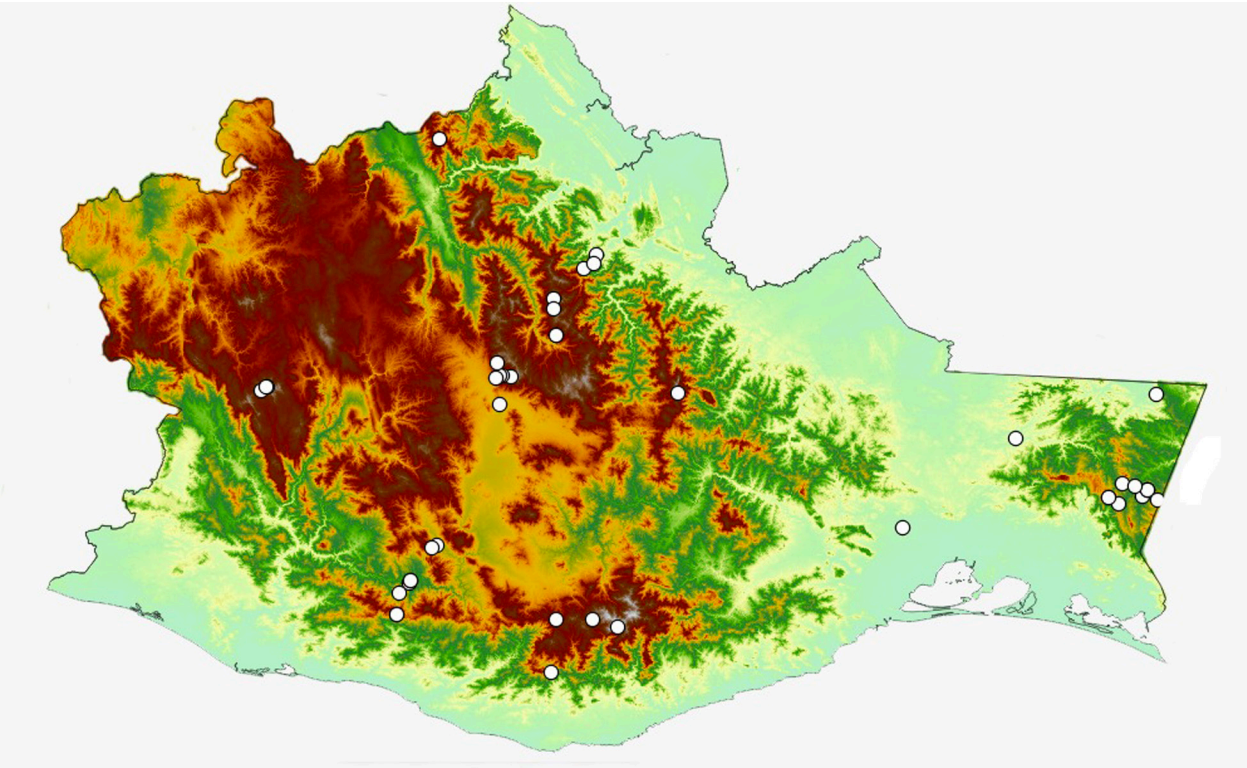

Figure 1. Distribution of the endemic species from the state of Oaxaca, Mexico.

Materials and Methods

Classifications used here are those of Bouchard et al. (2011), Tarasov and Génier (2015), and Tarasov and Dimitrov (2016). The list presents each species' distribution (by country), the author(s), and the page where each species was described. Families, tribes, genera, and species are listed alphabetically. It was compiled from the literature, personal collecting, records from the Database of the National Biodiversity Commission of Mexico (CONABIO), databases of Federico Escobar from the Institute of Ecology (INECOL, Xalapa, Veracruz), the Institute of Ecology Collection (IEXA, Xalapa, Veracruz), the National Insect Collection of the National Autonomous University of Mexico (CNIN, Mexico City), the National Insect Collection of the Natural History Museum of Mexico City (MCMC), the insect collection of the Interdisciplinary Center for Research and Integral Regional Development (CIIDIR, Oaxaca City), the private collection of Julián Blackaller (JBBC, La Paz, Baja California Sur), and the private collection of Eder Mora-Aguilar (EMAC, Coatepec, Veracruz).

Regarding the taxonomic positioning and status of the different genera of Ateuchini and the transfer of the genus *Canthidium* to Coprini, we follow the results published by Vaz-de-Mello (2008). We also follow Bouchard et al. (2011) regarding the latest family-group names, especially the name change of Canthonini to Deltochilini. We have followed Vaz-de-Mello et al. (2011) regarding many generic and subgeneric placements. Regarding the treatment of the genus *Canthon* and its subgenera, we reported here provisionally *Canthon* and *Glaphyrocanthon*, although the subgeneric taxonomy of *Canthon* needs to be reworked. Kohlmann (1984b) and Medina et al. (2003) have indicated that *Canthon* is polyphyletic and that its systematics should be restructured. Regarding the taxonomic delimitation of *Copris*, we follow Marchisio and Zunino (2012).

Morphological structures were studied using a Zeiss Stemi SV-6 stereomicroscope. Photographs and measurements of *Phanaeus dionysius* Kohlmann, Arriaga-Jiménez and Rös, 2018 were taken with a Nikon SMZ25 stereomicroscope and DS-Fi2 camera, and image processing using the NIS-Elements software. The distribution map was made in Quantum GIS 3.2 software (QGIS Development Team 2018). Digital Elevation Model Layers have been taken from SRTM project (NASA 2022).

Results

We record 252 dung-beetle taxa for the state of Oaxaca (Table 1): 15 taxa belong to the Geotrupidae, 77 to the Aphodiinae, and 160 to the Scarabaeinae. Of this total, one genus is endemic to Oaxaca, 112 taxa are endemic to Mexico, 46 are endemic to Oaxaca, seven flightless, and two are introduced. All these taxa are distributed in 58 genera and 15 tribes. *Onthophagus* is the most biodiverse genus with 49 species, followed by *Ataenius* with 22, closing with *Canthon* and *Phanaeus* with 17 and 15 taxa, respectively.

Table 1. Richness and endemicity from Oaxaca State.

Taxa	Genera richness	Species richness	Species endemic to Mexico	Species endemic	Genera endemic	Flightless species	Introduced species
Geotrupidae	5	15	8	5	0	0	0
Aphodiinae	29	77	28	11	1	2	0
Scarabaeinae	24	160	76	30	0	5	2
Total	58	252	112	46	1	7	2

In the following list, the following marks are used as appropriate: * = species endemic to Oaxaca; ** = introduced species; *** = flightless species; **** = endemic genus of Oaxaca.

SCARABAEOIDEA Latreille, 1802

GEOTRUPIDAE Latreille, 1802

BOLBOCERATINAE Mulsant, 1842

ATHYREINI Lynch Arribálzaga, 1878

NEOATHYREUS Howden and Martínez, 1963

Synopsis. Howden 1985

Neoathyreus (*Neoathyreus*) *excavatus* (Laporte, 1840: 103) Mexico Panama Colombia Venezuela Trinidad Guyana Surinam French Guiana Brazil
Neoathyreus (*Neoathyreus*) *fissicornis* (Harold, 1880: 45) Mexico Guatemala Costa Rica
Neoathyreus (*Neoathyreus*) *granulicollis* Howden, 1964: 29 Mexico
Neoathyreus (*Neoathyreus*) *interruptus* Howden, 1964: 22 Mexico Guatemala El Salvador
Neoathyreus (*Neoathyreus*) *mexicanus* (Klug, 1845: 29) Mexico Guatemala El Salvador Nicaragua Costa Rica Panama

BOLBOCERATINI Mulsant, 1842

BOLBELASMUS Boucomont, 1911

Synopsis. Howden 1964, 2003

Bolbelasmus arcuatus (Bates, 1887: 111) Mexico Guatemala El Salvador Honduras Nicaragua Costa Rica Panama
Bolbelasmus variabilis Howden, 1964: 41 USA Mexico

BOLBORHOMBUS Cartwright, 1953

Synopsis. Howden 1964, 2003

Bolborhombus sallei sallei (Bates, 1887: 111) Mexico

GEOTRUPINAE Latreille, 1802

CERATOTRUPINI Zunino, 1984

CERATOTRUPES Jekel, 1865

Synopsis. Halffter and Martínez 1962

Ceratotrupes sturmi (Jekel, 1865: 543) Mexico*

GEOTRUPINI Latreille, 1802

GEOTRUPES Latreille, 1796

Synopsis. Howden 1964, 2003

Geotrupes (*Onthotrupes*) *lobatus* Howden, 1974: 573 Mexico*
Geotrupes (*Onthotrupes*) *nebularum* Howden, 1964: 53 Mexico
Geotrupes (*Onthotrupes*) *nuntiatus* Kohlmann and Arriaga-Jiménez, 2020: 494 Mexico*
Geotrupes (*Onthotrupes*) *pecki* Howden, 1974: 572 Mexico*
Geotrupes (*Onthotrupes*) *sallei* Jekel, 1865: 596 Mexico
Geotrupes (*Onthotrupes*) *viridiobscurus* Jekel, 1865: 599 Mexico*

SCARABAEIDAE Latreille, 1802

APHODIINAE Leach, 1815

APHODIINI Leach, 1815

APHODIINA Leach, 1815

AGRILINELLUS Dellacasa, Dellacasa, and Gordon, 2008

Synopsis. Dellacasa, Dellacasa, and Gordon 2008

Agrilinellus azteca (Harold, 1863b: 381) Mexico Guatemala
= *Aphodius euprosopus* Bates, 1887
= *Aphodius multimaculosus* Hinton, 1934
Agrilinellus oaxacaensis Dellacasa, Dellacasa, and Gordon, 2008: 12 Mexico*

BLACKBURNEUS Schmidt, 1913

Blackburneus charmionus (Bates, 1887: 89) Mexico El Salvador Costa Rica Panama
Blackburneus guatemalensis (Bates, 1887: 88) Mexico Guatemala El Salvador Costa Rica Honduras Panama
= *Aphodius striatipennis* Petrovitz, 1962
Blackburneus saylorea (Robinson, 1940: 147) USA Mexico
Blackburneus teposcolulaensis Dellacasa, Dellacasa and Gordon, 2011: 32 Mexico

CEPHALOCYCLUS Dellacasa, Gordon and Dellacasa, 1998

Cephalocyclus durangoensis (Bates, 1887: 91) Mexico
= *Aphodius pugil* Balthasar, 1946
Cephalocyclus fuliginosus (Harold, 1863b: 333) Mexico Guatemala
Cephalocyclus hogei (Bates, 1887: 90) USA? Mexico Guatemala
= *Aphodius transversus* Robinson, 1940
Cephalocyclus iohannisgabrielis Dellacasa and Arriaga-Jiménez, 2020: 144 Mexico*
Cephalocyclus luridiventris (Harold, 1862: 385) Mexico
Cephalocyclus mexicanus (Harold, 1862: 380) Mexico Guatemala
= *Aphodius omiltemius* Bates, 1889
Cephalocyclus pseudofuliginosus Dellacasa, Dellacasa and Gordon, 2011: 31 Mexico*
Cephalocyclus villosipes (Harold, 1862: 384) Mexico

DELLACASIELLUS Gordon and Skelley, 2007

Dellacasiellus claudus (Fall, 1932: 188) USA Mexico

DIAPTERNA Horn, 1887

Diapterna dugesi (Bates, 1887: 83) Mexico

GONAPHODIELLUS Schmidt, 1913

Synopsis. Dellacasa, Dellacasa and Gordon 2012

Gonaphodiellus bimaculosus (Schmidt, 1909: 19) Mexico El Salvador
= *Aphodius (Gonaphodiellus) xalapensis* Galante, Stebnicka and Verdú 2003
Gonaphodiellus hoffmanni (Islas, 1945: 451) Mexico
Gonaphodiellus opisthius (Bates, 1887: 92) Mexico Guatemala Honduras Nicaragua Costa Rica
= *Aphodius duplex* Bates, 1887

GONAPHODIOIDES Dellacasa, Dellacasa and Gordon, 2012

Synopsis. Dellacasa, Dellacasa and Gordon 2012

Gonaphodioides chapini (Hinton, 1934: 189) Mexico Costa Rica Panama Peru Ecuador Venezuela Brazil
= *Aphodius ataenioides* Hinton, 1938 = *Aphodius* (*Blackburneus*) *castanescens* Petrovitz, 1973
Gonaphodioides ratcliffei Dellacasa, Dellacasa, Gordon, 2012: 20 Mexico*
Gonaphodioides zempoaltepetlensis Dellacasa, Dellacasa, Arriaga-Jiménez, 2018: 587 Mexico*

GONAPHODIOPSIS Dellacasa, Dellacasa and Gordon, 2012

Gonaphodiopsis deloyai Dellacasa, Dellacasa and Gordon, 2012: 23 Mexico

HAROLDIELLUS Gordon and Skelley, 2007

Haroldiellus lansbergei (Harold, 1874: 179) Mexico
Haroldiellus sallei (Harold, 1863b: 336) North and Central America Caribbean Colombia
= *Aphodius freyi* Balthasar, 1941

LABARRUS Mulsant and Rey, 1870

Labarrus cincticulus (Hope, 1847: 284) North Central and South America Oceania Central and Southern Africa
= *Aphodius spilopterus* Germar, 1848 = *Aphodius pseudolividus* Balthasar, 1941: 148

LIOTHORAX Motschulsky, 1859

Liothorax innexus (Say, 1835: 177) Mexico Virgin Islands
= *Aphodius flavocinctus* Harold, 1860
Liothorax levatus (Schmidt, 1907: 568) Mexico
= *Aphodius nigroclavus* Hinton, 1934

NIALAPHODIUS Kolbe, 1908

Nialaphodius nigrita (Fabricius, 1801: 73) USA Mexico Belize Honduras Panama Venezuela Ecuador Peru Chile Brazil Paraguay Puerto Rico Grenadines Center and Southwest Africa Madagascar Cape Verde Seychelles
= *Aphodius cuniculus* Chevrolat, 1864 = *Aphodius paivanus* Wollaston, 1867 = *Aphodius vestiarus* Horn 1870 = *Aphodius expertus* Harold, 1871 = *Aphodius granarius* var. *guadeloupensis* Fleutiaux and Sallé, 1889

OSCARINUS Gordon and Skelley, 2007

Oscarinus indutilis (Harold, 1874: 178) Mexico Guatemala Costa Rica

OXYOMUS Dejean, 1833

Oxyomus mariateresae Dellacasa, Dellacasa and Gordon, 2014: 2 Mexico*
Oxyomus setosopunctatus Schmidt, 1911b: 15 Mexico

PLANOLINELLUS Dellacasa and Dellacasa, 2005

Planolinellus vittatus (Say, 1825: 191) Old World Canada USA Mexico
= *Aphodius cruentatus* Dejean, 1833 = *Aphodius mundus* Reitter, 1892 = *Aphodius* (*Agrilinus*) *mundus* subsp. *vitiosus* Reitter, 1892 = *Aphodius niger* Cockerell, 1888 = *Aphodius rufoplagiatus* Reitter, 1892 = *Aphodius sellatus* Mannerheim, 1852 = *Aphodius semiruber* Motschulsky, 1860 = *Aphodius tjanshanicus* Balthasar, 1956 =*Aphodius vitiosus* Reitter, 1892 = *Aphodius vittatus* Say, 1825 = *Planolinus vittatus* (Say, 1825)

PSEUDAGOLIUS Schmidt, 1913

Pseudagolius coloradensis (Horn, 1870: 130) Canada USA Mexico
= *Aphodius flohri* Bates, 1887

PSEUDOCOELOTRACHELUS Dellacasa, Dellacasa and Gordon 2013

Pseudocoelotrachelus tristaobrancoi Dellacasa, Dellacasa and Gordon, 2013: 2 Mexico*

PSEUDOGONAPHODIELLUS Dellacasa, Gordon and Dellacasa, 2007

Pseudogonaphodiellus zdzislawae Dellacasa, Gordon and Dellacasa, 2007: 140 Mexico

TRICHONOTULOIDES Balthasar, 1945

Trichonotuloides glyptus (Bates, 1887: 66) Mexico

EUPARIINI Schmidt, 1910

ATAENIOPSIS Petrovitz, 1973

Ataeniopsis jaltipani Stebnicka, 2003: 109 Mexico

ATAENIUS Harold, 1867

Ataenius aequalis Harold, 1880: 40 North to South America West Indies
= *Ataenius insulicola* Chapin, 1940 = *Ataenius titschacki* Balthasar, 1941
Ataenius apicalis Hinton, 1937: 195 USA Mexico Honduras
Ataenius castaniellus Bates, 1887: 95 Mexico Guatemala El Salvador Honduras
= *Ataenius liogaster castaniellus* Bates, 1887
Ataenius communis Hinton, 1936: 461 Mexico to South America
Ataenius complicatus Harold, 1869: 102 Mexico to Argentina
= *Ataenius loretti* Martinez 1952
Ataenius crenulatus Schmidt, 1910: 359 Mexico Belize Honduras Barbados Bolivia Brazil Paraguay Argentina
Ataenius cribrithorax Bates, 1887: 95 Mexico Guatemala El Salvador Honduras Nicaragua Costa Rica Panama Cuba Jamaica St. Thomas
Ataenius glabriventris Schmidt, 1911a: 52 Mexico Guatemala El Salvador Honduras Costa Rica Panama Venezuela
Ataenius gracilis (Melsheimer, 1845: 137) USA Mexico Belize Guatemala Honduras El Salvador Costa Rica Panama Colombia Suriname Peru Brazil Argentina Chile Cuba Puerto Rico Guadeloupe St. Vincent Granada Galapagos Thailand Vietnam Indonesia Micronesia
= *Ataenius nocturnus* (Nomura, 1943)
Ataenius hirsutus Horn, 1871: 288 USA Mexico
Ataenius imbricatus (Melsheimer, 1845: 136) USA Mexico Guatemala Honduras Nicaragua Cuba Puerto Rico Dominican Republic Bahamas St. Croix Brazil Argentina
Ataenius jalapensis Bates, 1887: 99 Mexico Belize Guatemala Honduras Panama
Ataenius languidus Schmidt, 1911a: 31 USA Mexico Guatemala Honduras Nicaragua Costa Rica West Indies Venezuela
= *Ataenius linelli* Cartwright 1944 = *Ataenius orbicularis* Schmidt 1914 = *Ataenius edwardsi* Chapin 1940 =*Ataenius nitidulus* Nomura 1943 = *Ataenius kelatianus* Balthasar 1965 = *Ataenius hoguei* Cartwright and Spangler 1981
Ataenius nugator Harold, 1880: 41 Mexico Guatemala El Salvador Honduras Nicaragua Costa Rica Panama Cuba Jamaica Virgin Islands Colombia Venezuela Bolivia Peru Brazil
= *Ataenius duplex* Hinton, 1936 = *Ataenius bolivianus* Hinton, 1937
Ataenius oaxacaensis Stebnicka and Lago, 2005: 78 Mexico*
Ataenius peregrinator Harold 1887: 96 USA Mexico Guatemala Belize Honduras Panama Colombia Ecuador Vietnam Indonesia Philippines Micronesia
= *Ataenius hieronymi* Bates, 1887 = *Ataenius nunenmacheri* Cartwright, 1974 = *Ataenius polyglyptus* Bates, 1887 = *Ataenius stroheckeri* Cartwright, 1974 = *Ataenius sumatrensis* Balthasar, 1941
Ataenius platensis (Blanchard, 1846: 185) USA Mexico

= *Ataenius integer* Harold 1868 = *Ataenius anticus* Fall 1930 = *Ataenius granchacoensis* Balthasar 1939 = *Ataenius histrionicus* Balthasar 1947 = *Ataenius heyrovskyi* Balthasar 1960 = *Ataenius degallieri* Chalumeau 1990

Ataenius pseudousingeri Galante, Stebnicka and Verdú, 2003: 295 Mexico Guatemala

Ataenius scalptifrons Bates 1887: 100 México Guatemala, Belize, El Salvador, Honduras, Costa Rica Panama

Ataenius setiger Bates, 1887: 98 USA Mexico

= *Ataenius pseudohirsutus* Cartwright 1974

Ataenius texanus Harold, 1874: 23 USA Mexico Guatemala West Indies

= *Ataenius punctifrons* Cartwright 1974

Ataenius usingeri Hinton, 1937: 191 Mexico Guatemala Belize El Salvador Honduras Nicaragua Costa Rica Panama

EUPARIA Le Peletier de Saint-Fargeau and Audinet-Serville, 1828

= *Auperia* Jacquelin-Duval 1857

Synopsis. Chalumeau and Howden 1984

Euparia castanea Le Peletier de Saint-Fargeau and Audinet-Serville, 1828: 357 USA Mexico Guatemala El Salvador Honduras Nicaragua Costa Rica Panama Ecuador

HAROLDATAENIUS Chalumeau, 1981

Haroldataenius limbatus (Bates, 1887: 159) Mexico Guatemala El Salvador Honduras

Haroldataenius mariarum (Bates, 1887: 102) Mexico Panama

ODONTOLYTES Kozhantshikov, 1916

= *Phalangochaeta* Martínez 1952 = *Auperia* sensu Stebnicka 2002, nec *Auperia* Chevrolat 1864, nec *Auperia* Jacquelin-Duval 1857

Synopsis. Stebnicka 2002

Odontolytes capitosus (Harold, 1867: 83) Mexico Guatemala El Salvador Costa Rica Panama Colombia Ecuador Bolivia Peru Brazil

Odontolytes denominatus (Chevrolat, 1864: 413) USA Mexico Guatemala Belize Honduras Panama Colombia Venezuela Ecuador French Guiana Brazil Bolivia Cuba

= *Auperia denominatus* Chevrolat, 1864 = *Ataenius arator* Harold, 1869 = *Ataenius brevinotus* Chapin, 1940 = *Ataenius benjaminbanderai* Islas, 1955 = *Ataenius sciurus* Cartwrght, 1974 = *Phalangochaete grandis* Petrovitz, 1973 = *Ataenius euglyptus* Bates, 1887

Odontolytes landai (Balthasar, 1963: 286) Mexico Guatemala Honduras Panama Colombia Ecuador Venezuela Trinidad and Tobago Bolivia Paraguay

= *Phalangochaeta squamosa* Petrovitz 1976

PARATAENIUS Balthasar, 1961

Parataenius simulator (Harold, 1868: 85) USA Mexico Argentina Chile, Uruguay Brazil Portugal Australia New Zealand Africa

= *Ataenius lusitanicus* Paulian, 1979 = *Euparia simulatrix* Burmeister, 1877

= *Parataenius granuliceps* Petrovitz, 1971= *Psammodius schwarzi* Linell, 1896

PSAMMODIINI Mulsant, 1842

PSAMMODIINA Mulsant, 1842

NEOPSAMMODIUS Rakovič, 1986

Synopsis. Rakovič 1986

Neopsammodius culminatus (Bates, 1887: 103) Mexico

Neopsammodius quinqueplicatus (Horn, 1871: 292) USA Mexico
Neopsammodius veraecrucis (Bates, 1887: 103) Mexico
Neopsammodius werneri (Cartwright, 1955: 429) USA Mexico Honduras

***PARAPSAMMODIUS* Verdú, Stebnicka and Galante, 2006**

Synopsis. Verdú, Stebnicka and Galante 2006

Parapsammodius puncticollis (LeConte, 1858: 66) USA Mexico

RHYPARINI Schmidt, 1910

***RHYPARUS* Westwood, 1843**

Synopsis. Mora-Aguilar and Delgado 2019a

Rhyparus chimalapensis Mora-Aguilar and Delgado, 2019a: 196 Mexico*
Rhyparus opacus Cartwright and Woodruff, 1969: 6 Mexico

NANOTERMITODIUS* Howden 2003***

Synopsis. Skelley, Smith and Mora-Aguilar 2022

Nanotermitodius peckorum Howden, 2003a: 396 Mexico*, ****
Nanotermitodius andersoni Skelley, Smith and Mora-Aguilar, 2022: 356 Mexico *, ****

SCARABAEINAE Latreille, 1802

ATEUCHINI Perty, 1830

ATEUCHINA Perty, 1830

***ATEUCHUS* Weber, 1801**

= *Choeridium* Le Peletier de Saint-Fargeau and Audinet-Serville, 1828
Synopsis. Kohlmann 1984a

Ateuchus candezei (Harold, 1868: 82) Mexico Guatemala Belize Nicaragua Costa Rica Panama Colombia
= *Choeridium poropyge* Bates, 1887
Ateuchus carolinae Kohlmann, 1981: 78 Mexico
Ateuchus colossus Moctezuma, Sánchez-Huerta and Halffter, 2018: 78 Mexico*
Ateuchus guatemalensis (Bates, 1887: 45) Mexico Guatemala Honduras Nicaragua
= *Ateuchus benitojuarezi* Moctezuma, Sánchez-Huerta and Halffter, 2018
Ateuchus illaesum (Harold, 1868: 53) Mexico
Ateuchus perezvelai Kohlmann, 2000: 238 Mexico
Ateuchus rodriguezi (Preudhomme de Borre, 1886: 107) Mexico Guatemala Honduras El Salvador Costa Rica
= *Choeridium ampliatum* Bates, 1887
Ateuchus tuza Kohlmann and Vaz-de-Mello, 2018: 132 Mexico

***BDELYROPSIS* Pereira, Vulcano and Martínez, 1960**

Synopsis. Howden 1971

Bdelyropsis newtoni Howden, 1971: 1475 Mexico Guatemala

***UROXYS* Westwood, 1842**

= *Pseuduroxys* Balthasar, 1938
Synopsis. Delgado and Kohlmann 2007

Uroxys boneti Pereira and Halffter, 1961: 55 Mexico Guatemala El Salvador Costa Rica Panama Colombia

= *Uroxys bidentis* Howden and Young 1981
Uroxys chichanich Delgado and Kohlmann, 2007: 8 Mexico
Uroxys deavilai Delgado and Kohlmann, 2007: 10 Mexico Guatemala El Salvador Nicaragua Costa Rica
Uroxys microcularis Howden and Young, 1981: 59 Mexico Guatemala El Salvador Costa Rica Panamá
Uroxys micros Bates, 1887: 43 Mexico Guatemala Nicaragua Costa Rica Colombia
Uroxys platypyga Howden and Young 1981: 60 Mexico Guatemala Costa Rica Panama Colombia
Uroxys transversifrons Howden and Gill, 1987: 212 Mexico Guatemala El Salvador Honduras Nicaragua

COPRINI Leach, 1815

SCATIMINA Vaz-de-Mello, 2008

SCATIMUS Erichson, 1847

Synopsis. Génier and Kohlmann 2003

Scatimus ovatus Harold, 1862: 101 Mexico Guatemala Nicaragua Costa Rica Panama Colombia

CANTHIDIUM Erichson, 1847

= *Pleronyx* Lansberge, 1874 = *Eucanthidium* Martínez and Halffter, 1986
Synopsis. Cupello 2018

Canthidium (*Canthidium*) *ardens* Bates, 1887: 48 Mexico Guatemala Honduras Nicaragua Costa Rica Panama
Canthidium (*Neocanthidium*) *centrale* Boucomont, 1928: 203 Mexico Guatemala Honduras Costa Rica Panama Colombia Suriname French Guiana Ecuador
= *C. martinezi* Edmonds and Halffter, 1978
Canthidium (*Canthidium*) *chimalapense* Moctezuma, Sánchez-Huerta and Halffter, 2019: 435 Mexico*
Canthidium (*Canthidium*) *hespenheidei* Howden and Young, 1981: 92 Mexico Costa Rica Panama Ecuador
Canthidium (*Canthidium*) *howdeni* Kohlmann and Solís, 2006: 251 Mexico*, ***
Canthidium (*Canthidium*) *kohlmanni* Mora-Aguilar and Delgado, 2019b: 1068 Mexico*
Canthidium (Canthidium) laetum Harold, 1867: 53 Mexico Guatemala El Salvador Honduras Nicaragua Costa Rica
= *C. granivorum* Halffter and Halffter, 1978
Canthidium (*Canthidium*) *macclevei* Kohlmann and Solís, 2006: 257 Mexico
Canthidium (Canthidium) moroni Kohlmann and Solis 2006: 260 Mexico Guatemala Honduras
Canthidium (*Canthidium*) *nebularum* Moctezuma, Sánchez-Huerta and Halffter, 2019b: 433 Mexico*
Canthidium (*Canthidium*) *pseudoperceptibile* Kohlmann and Solís, 2006: 261 Mexico Belize Guatemala El Salvador
Canthidium (*Canthidium*) *pseudopuncticolle* Solís and Kohlmann, 2004: 61 USA Mexico Guatemala El Salvador Costa Rica.
Canthidium (*Canthidium*) *quercetorum* Kohlmann, Arriaga-Jiménez and Rös, 2018b: 273 Mexico*
Canthidium (*Canthidium*) *smithi* Bates 1889: 387 Mexico

COPRIS Geoffroy, 1762

= *Pilularius* Schrank 1798 = *Litocopris* Waterhouse, 1891 = *Pseudopedaria* Felsche, 1904 = *Paracopris* Balthasar, 1939 = *Palaeocopris* Pierce 1946 = *Insulicopris* Tsukamoto 1974
Synopsis. Zidek 2020

Copris boucardi Harold, 1869: 497 Mexico
Copris chimalapensis Mora-Aguilar and Delgado, 2015: 875 Mexico*
Copris halffteri Matthews, 1959: 133 Mexico
First State record from Oaxaca: Tejaltitlán, database from CONABIO.
Copris incertus Say, 1835: 175 Mexico
Copris juanmorai Mora-Aguilar and Delgado, 2015: 877 Mexico*
Copris klugi Harold, 1869: 498 Mexico

Copris laeviceps Harold, 1869: 496 Mexico Guatemala Belize Honduras Costa Rica
Copris lecontei isthmiensis Matthews, 1961: 102 Mexico
Copris lugubris Boheman, 1858: 42 Mexico Guatemala Belize El Salvador Honduras Costa Rica Panama
Copris matthewsi pacificus Delgado and Kohlmann, 2001: 348 Mexico Guatemala
Copris rebouchei Harold, 1869: 497 Mexico
Copris sallei Harold, 1869: 496 Mexico

DICHOTOMIUS Hope, 1838

= *Pinotus* Erichson, 1847 = *Brachycopris* Haldeman, 1848 = *Cephagonus* Luederwaldt, 1929
Synopsis. Kohlmann 2003

Dichotomius (*Selenocopris*) *amplicollis* (Harold, 1869: 501) Mexico Guatemala
Dichotomius (*Selenocopris*) *annae* Kohlmann and Solís, 1997: 350 Mexico Guatemala Honduras El Salvador Nicaragua Costa Rica Panama
Dichotomius (*Selenocopris*) *colonicus* (Say, 1835: 174) USA Mexico Guatemala
= *Pinotus bituberculatus* Harold, 1869
Dichotomius (*Dichotomius*) *satanas* (Harold, 1867: 98) Mexico Guatemala Belize Nicaragua Costa Rica Panama Colombia Ecuador Peru
Dichotomius (*Selenocopris*) *sagittarius* (Harold, 1869: 503) Mexico Belize

ONTHERUS Erichson, 1847

Synopsis. Génier 1996

Ontherus (*Ontherus*) *azteca* Harold, 1869: 503 Mexico Costa Rica Panama Colombia Ecuador Peru Paraguay Bolivia Brazil
Ontherus (*Caelontherus*) *mexicanus* Harold, 1868: 80 Mexico Guatemala

DELTOCHILINI Lacordaire, 1855

= Canthonini Lansberge, 1875

AGAMOPUS Bates, 1887

Synopsis. Costa-Silva *et al*. 2022

Agamopus lampros Bates, 1887**:** 42 Mexico El Salvador Guatemala Nicaragua Costa Rica Panama Colombia Venezuela

BOREOCANTHON Halffter, 1958

Synopsis. Edmonds 2022

Boreocanthon puncticollis Leconte, 1866: 381: USA, Mexico

CANTHON Hoffmannsegg, 1817

= *Coprobius* Latreille, 1829 = *Coeloscelis* Reiche, 1841 = *Paedohyboma* Kolbe, 1893
Synopsis. Halffter 2003

Canthon (*Glaphyrocanthon*) *championi* Bates, 1887: 31 Mexico Guatemala
Canthon (*Glaphyrocanthon*) *circulatus* Harold, 1868: 72 Mexico
Canthon (*Glaphyrocanthon*) *corporali* Balthasar, 1939: 199 Mexico
Canthon (*Canthon*) *cyanellus sensu lato* LeConte, 1859: 10 USA Mexico Guatemala Honduras Nicaragua Costa Rica Panama Colombia Venezuela Trinidad Ecuador Peru Brazil
Canthon (*Glaphyrocanthon*) *delgadoi* Rivera-Cervantes and Halffter, 1999: 119 Mexico
Canthon (*Glaphyrocanthon*) *euryscelis* Bates, 1887: 28 Mexico Guatemala Belize Honduras Costa Rica Panama
Canthon (*Glaphyrocanthon*) *femoralis* Chevrolat, 1834: 45 Mexico Guatemala Belize El Salvador Nicaragua
Canthon (*Canthon*) *humectus humectus* Say, 1832: 4 Mexico Guatemala
Canthon (*Canthon*) *humectus incisus* Robinson, 1948: 157 Mexico
Canthon (*Canthon*) *humectus sayi* Robinson, 1948: 156 Mexico

Canthon (*Canthon*) *indigaceus chevrolati* Harold, 1868: 119 USA Mexico Guatemala El Salvador Honduras Nicaragua Costa Rica Panama

Canthon (*Canthon*) *indigaceus indigaceus* LeConte, 1866: 380 USA Mexico

Canthon (*Glaphyrocanthon*) *leechi* (Martínez, Halffter and Halffter, 1964: 25) USA Mexico Guatemala Belize Honduras

Canthon (*Glaphyrocanthon*) *montanus* Rivera-Cervantes and Halffter, 1999: 131 Mexico Guatemala

Canthon (*Glaphyrocanthon*) *pacificus* Rivera-Cervantes and Halffter, 1999: 122 Mexico

Canthon (*Glaphyrocanthon*) *subhyalinus* Harold, 1867: 79 Mexico Costa Rica Panama Colombia Venezuela French Guiana Ecuador Peru Bolivia Brazil

Canthon (*Glaphyrocanthon*) *vazquezae* (Martínez, Halffter and Halffter, 1964: 25) Mexico Guatemala Nicaragua Costa Rica Panama

CRYPTOCANTHON Balthasar, 1942

Synopsis. Halffter 2003

Cryptocanthon chimalapensis Mora-Aguilar and Delgado, 2018: 794 Mexico*, ***

Cryptocanthon lobatus Howden, 1973: 41 Mexico***

First state record from Oaxaca: Ayautla, Uluapan, ex sifted leaf litter, Longino *et al.* cols (EMAC)

DELTOCHILUM Eschscholtz, 1822

= *Anamnesis* Vigors, 1826 = *Hyboma* LePeletier and Serville, 1828 = *Annamesis* Harold, 1869 = *Meghyboma* Kolbe, 1893 = *Telhyboma* Kolbe, 1893 = *Eudactylides* Paulian, 1939

Synopsis. Halffter 2003

Deltochilum (*Hybomidium*) *carrilloi* González-Alvarado and Vaz-de-Mello, 2015: 442 Mexico Guatemala Belize Nicaragua

Deltochilum (*Hybomidium*) *lobipes* Bates, 1887: 37 Mexico Guatemala Belize Honduras El Salvador Nicaragua

Deltochilum (Calhyboma) mexicanum Burmeister, 1848: 135 Mexico Guatemala Belize Honduras El Salvador Nicaragua

Deltochilum (*Deltohyboma*) *pseudoparile* Paulian, 1938: 283 Mexico Guatemala Honduras Nicaragua Costa Rica Panama

Deltochilum (*Deltochilum*) *scabriusculum* Bates, 1887: 38 Mexico Guatemala Nicaragua Costa Rica

Deltochilum (*Deltochilum*) *tumidum* Howden, 1966: 738 Mexico

MALAGONIELLA Martínez, 1961

Synopsis. Halffter 2003

Malagoniella (*Malagoniella*) *astyanax yucateca* (Harold, 1863a: 173) USA Mexico Costa Rica.

First record for Oaxaca State: Chacahua, 1m alt, 17-XII-1978, cebo hum., selva baja subc., B. Kohlmann col. (CNIN)

PSEUDOCANTHON Bates, 1887

= *Opiocanthon* Paulian, 1947

Synopsis. Halffter 2003

Pseudocanthon chlorizans (Bates, 1887: 34) Mexico Grenada Grenadine Curaçao

Pseudocanthon perplexus LeConte, 1847: 85 USA Mexico Guatemala Belize Nicaragua Costa Rica Grand Bahama Colombia Venezuela Brazil

ONITICELLINI Kolbe, 1905

EURYSTERNINA Vulcano, Martínez and Pereira, 1961

EURYSTERNUS Dalman, 1824

= *Aeschrotes* LePeletier and Serville, 1828 = *Eurysternodes* Martínez, 1988 = *Pareurysternus* Martínez, 1988 = *Amartinezuz* Özdikmen, 2009
Synopsis. Génier 2009

Eurysternus angustulus Harold, 1869: 506 Mexico Belize Guatemala

Eurysternus caribaeus (Herbst, 1789: 300) Mexico Belize Guatemala Honduras Nicaragua Costa Rica Panama Colombia Venezuela Trinidad and Tobago Guyana Suriname French Guiana Ecuador Peru Brazil Bolivia Paraguay Argentina

Eurysternus magnus Laporte, 1840: 93 Mexico Belize Guatemala El Salvador Honduras Nicaragua Costa Rica Panama

Eurysternus maya Génier, 2009: 2010 Mexico Guatemala Belize

Eurysternus mexicanus Harold, 1869: 505 Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica Panama Colombia Venezuela Trinidad and Tobago Guyana

Eurysternus foedus Guérin-Méneville, 1844: pl. 21, fig. 5, 5.a Mexico Guatemala Belize Nicaragua Costa Rica Panama Colombia Venezuela French Guyana Peru Ecuador Bolivia Brazil

Eurysternus obliteratus Génier, 2009: 129 Mexico Guatemala Belize

ONITICELLINA Kolbe, 1905

EUONITICELLUS Janssens, 1953

Euoniticellus intermedius (Reiche et al. 1849: 337) USA Hawaii Mexico Guatemala El Salvador Honduras Nicaragua Panama Colombia Mauretania Senegal Angola Ethiopia Republic of Guinea Ghana Ivory Coast Mozambique Somalia South Africa Southern Italy Arabian Peninsula Australia New Caledonia **

LIATONGUS Reitter, 1893

Liatongus rhinocerulus Bates, 1889: 391 Mexico

ONTHOPHAGINI Burmeister, 1846

Catalogue. Pulido Herrera and Zunino 2007 (New World)

DIGITONTHOPHAGUS Balthasar, 1959

= *Onthophagus* (*Digitonthophagus*) Balthasar 1959

Digitonthophagus gazella (Fabricius, 1787: 377) USA Hawai Mexico Guatemala El Salvador Honduras Nicaragua Colombia Venezuela Cuba La Española Jamaica Puerto Rico Ecuador Bolivia Paraguay Chile Brazil Easter Island Southern Africa Arabian Peninsula Madagascar India Philipines Japan Australia Papua New Guinea New Caledonia Vanuatu**

ONTHOPHAGUS Latreille, 1802

= *Chalcoderus* Erichson, 1848 = *Monapus* Erichson, 1848 = *Psilax* Erichson, 1848 = *Gonocyphus* Lansberge, 1885 = *Tauronthophagus* Shipp, 1895 = *Macropocopris* Arrow, 1920
Catalogue. Moctezuma et al. 2021 (Mexico)

Onthophagus acuminatus Harold, 1880: 30 Mexico Nicaragua Costa Rica Panama, Colombia Ecuador

Onthophagus alluvius Howden and Cartwright, 1963: 65 USA Mexico

Onthophagus anewtoni Howden and Génier, 2004: 55 Mexico

Onthophagus anthracinus Harold, 1873: 104 Mexico Guatemala Honduras Costa Rica Panama

Onthophagus aureofuscus Bates, 1887: 81 Mexico

Onthophagus batesi Howden and Cartwright, 1963: 21 USA Hawaii Mexico Belize Nicaragua Panama Colombia Lesser Antilles

Onthophagus belorhinus Bates, 1887: 69 Mexico Guatemala El Salvador Nicaragua Colombia Ecuador

Onthophagus carpophilus Pereira and Halffter, 1961: 59 Mexico
Onthophagus championi Bates, 1887: 74 Mexico Nicaragua Costa Rica
Onthophagus chiapanecus Zunino and Halffter, 1988a: 126 Mexico
First record for Oaxaca State: San Miguel Chimalapa, Torre antiincendios, 27-VI-2017, E. Mora-A. and L. Delgado cols. (EMAC)
Onthophagus chimalapensis Delgado and Mora-Aguilar, 2019: 586 Mexico*
Onthophagus chinantecus Moctezuma and Halffter, 2019: 2 Mexico*
Onthophagus chryses Bates, 1887: 76 Mexico Guatemala Costa Rica Panama
Onthophagus corrosus Bates, 1887: 78 Mexico
Onthophagus crinitus Harold, 1869: 510 Mexico Guatemala Belize El Salvador Nicaragua Costa Rica Panama Colombia
Onthophagus cuboidalis Bates, 1887: 79 Mexico
Onthophagus cyanellus Bates, 1887: 81 Mexico Guatemala Honduras Nicaragua Costa Rica Panama
= *O. mesoamericanus* Zunino and Halffter, 1988 (See Solís and Kohlmann 2023)
Onthophagus cyclographus Bates, 1887: 79 Mexico Guatemala
Onthophagus durangoensis Balthasar, 1939: 45 Mexico
= *O. knulli* Howden and Cartwright, 1963
Onthophagus etlaensis Kohlmann, Escobar and Arriaga-Jiménez, 2020: 2 Mexico* (described in Arriaga-Jiménez et al. 2020b)
Onthophagus gibsoni Howden and Génier, 2004: 66 Mexico
Onthophagus guatemalensis Bates, 1887: 73 Mexico Guatemala Belize
Onthophagus hoepfneri Harold, 1869: 512 USA Mexico El Salvador Nicaragua Costa Rica
= *Onthophagus texanus* Schaeffer, 1914
Onthophagus howdeni Zunino and Halffter, 1988a: 151 Mexico*
Onthophagus howdenorum Zunino and Halffter, 1988a: 142 Mexico*
Onthophagus igualensis Bates, 1887: 77 Mexico
First state record from Oaxaca: "Santa María Tonameca, 1987", database from Federico Escobar.
Onthophagus incensus Say, 1835: 173 USA Mexico Guatemala Honduras El Salvador Nicaragua Costa Rica Panama
Onthophagus istmenus Moctezuma, Sánchez-Huerta and Halffter, 2020: 281 Mexico*
Onthophagus ixtepecorum Moctezuma and Halffter, 2020b: 251 Mexico*
Onthophagus ixtlanensis Moctezuma and Halffter, 2020b: 252 Mexico*
Onthophagus lecontei Harold, 1871: 115 USA Mexico
Onthophagus marginicollis Harold, 1880: 31 Mexico Guatemala Cuba El Salvador Nicaragua Costa Rica Panamá Colombia Venezuela Guyana Ecuador Perú Brasil Bolivia
Onthophagus mateui Moctezuma and Halffter, 2020b: 253 Mexico*
Onthophagus maya Zunino, 1981: 78 Mexico Guatemala Belize
Onthophagus mexicanus Bates, 1887: 72 Mexico
Onthophagus neomirabilis Howden, 1973: 334 Mexico*
Onthophagus nitidor Bates, 1887: 67 Mexico
Onthophagus oaxacanus Zunino and Halffter, 1988a: 139 Mexico*
Onthophagus pedester Howden and Génier, 2004: 58 Mexico*, ***
Onthophagus petenensis Howden and Gill, 1993: 1096 Mexico Guatemala Belize Honduras
Onthophagus retusus Harold, 1869: 108 Mexico
Onthophagus rhinolophus Harold, 1869: 510 Mexico Guatemala Belize Honduras Panama Colombia Venezuela Ecuador
Onthophagus rufescens Bates, 1887: 78 Mexico
= *Onthophagus jalapensis* Balthasar, 1939
Onthophagus sanpabloetlorum Moctezuma and Halffter, 2020b: 255 Mexico*
Onthophagus santamariensis Moctezuma, Sánchez-Huerta and Halffter, 2020: 258 Mexico*
Onthophagus semiopacus Harold, 1869: 509 Mexico*

Onthophagus subcancer Howden, 1973: 335 Mexico
Onthophagus villanuevai Delgado and Deloya, 1990: 212 Mexico
Onthophagus zapotecus Zunino and Halffter, 1988b: 137 Mexico*, ***

PHANAEINI Hope, 1838

PHANAEINA Hope, 1838

COPROPHANAEUS Olsoufieff, 1924

Phanaeus (*Coprophanaeus*) Olsoufieff 1924
Synopsis. Edmonds and Zídek 2010

Coprophanaeus (*Coprophanaeus*) *corythus* (Harold, 1863a: 163) Mexico Guatemala Nicaragua Costa Rica Panama
Coprophanaeus (*Coprophanaeus*) *gilli* Arnaud, 1997: 4 Mexico Guatemala Honduras Costa Rica
Coprophanaeus (*Coprophanaeus*) *pluto* (Harold, 1863a: 164) Mexico Guatemala

PHANAEUS MacLeay, 1819

= *Lonchophorus* Germar, 1824 = *Onthurgus* Gistel, 1857 = *Palaeocopris* Pierce, 1946
Synopsis. Edmonds and Zídek 2012

Phanaeus (*Phanaeus*) *amethystinus* Harold, 1863: 169 Mexico
Phanaeus (*Phanaeus*) *blackalleri* Delgado, 1991: 1 Mexico
Phanaeus (*Phanaeus*) *damocles* Harold, 1863a: 165 Mexico
Phanaeus (*Phanaeus*) *daphnis* Harold, 1863a: 166 Mexico
Phanaeus (*Phanaeus*) *demon* Laporte, 1840: 81 Mexico
Phanaeus (*Notiophanaeus*) *dionysius* Kohlmann, Arriaga-Jiménez and Rös, 2018a: 67 Mexico*
Phanaeus (*Notiophanaeus*) *edmondsi* Moctezuma, Deloya, and Halffter, 2019a: 251 Mexico*
Phanaeus (*Notiophanaeus*) *endymion* Harold, 1863a: 169 Mexico Belize Guatemala
Phanaeus (*Phanaeus*) *mexicanus* Harold, 1863a: 171 Mexico
Phanaeus (*Phanaeus*) *nimrod* Harold, 1863a: 167 Mexico*
Phanaeus (*Phanaeus*) *sallei* Harold, 1863a: 168 Mexico Belize Guatemala
Phanaeus (*Phanaeus*) *tridens* Laporte, 1840: 81 Mexico
Phanaeus (*Phanaeus*) *victoriae* Moctezuma et al. 2021: 466 Mexico*
Phanaeus (*Notiophanaeus*) *zapotecus* Edmonds, 2006: 31 Mexico*
Phanaeus (*Notiophanaeus*) *zoque* Moctezuma and Halffter, 2017: 47 Mexico*

SULCOPHANAEUS Olsoufieff, 1924

Phanaeus (*Sulcophanaeus*) Olsoufieff 1924
= *Eucopricus* Gistel, 1857
Synopsis. Edmonds 2000

Sulcophanaeus chryseicollis (Harold, 1863a: 164) Mexico Guatemala Honduras

SISYPHINI Mulsant, 1842

SISYPHUS Latreille, 1807

Synopsis. Morón 2003b

Sisyphus mexicanus Harold, 1863a: 172 Mexico Nicaragua Costa Rica
Sisyphus submonticolus Howden, 1965: 842 Mexico

Discussion

Flightless species

Seven flightless species and four genera are recorded for Oaxaca, six of them endemic to this state: *Canthidium howdeni*, *Cryptocanthon chimalapensis*, *C. lobatus*, *Nanotermitodius peckorum, N. andersoni* (Fig. 2), *O. pedester*, and *O. zapotecus*. They are mountain species distributed in the Sierra Norte and Sierra Sur. In this sense, Oaxaca records 32% of the flightless species of Mexico, considered some of the most vulnerable species by its reduced capacity to move, low vagility, and microendemic distribution.

Figure 2. Habitus of endemic species from Oaxaca. **Upper left:** *Geotrupes lobatus.* **Upper right:** *Nanotermitodius andersoni*. **Lower left:** *Phanaeus dionysus* holotype. **Lower right:** *Phanaeus dionysus* allotype.

A similar area with a high density and diversity of flightless species are the mountains of Costa Rica, with seven species distributed in four genera: *Ateuchus* (1), *Canthidium* (1), *Cryptocanthon* (2), and *Onthophagus* (3) (Kohlmann et al. 2019). Another high flightless species density area is the Colombian Andes (Martínez-Revelo et al. 2020). Martínez-Revelo et al. (2020) report ten flightless species in this area, six for the Cordillera Oriental and four for the Cordillera Occidental, all *Cryptocanthon*. Interestingly, all five Colombian fully winged *Cryptocanthon* species are distributed in the lowlands. The trend for flightlessness in Mesoamerica seems confined to genera consisting of small-sized species (Kohlmann et al. 2019). Kohlmann et al. (2019) explain that the mountain areas where these flightless species are distributed represent old geological emergences with long-term habitat stability. All these species live in steep, deeply incised mountains that acted as refugia during glacial events (Kohlmann et al. 2019; Solís et al. *in press*) where species distributions could be adjusted altitudinally rather than areally.

Endemic species

Forty-five percent of the 252 taxa cited in this work are endemic to Mexico, and 18% are endemic to Oaxaca. However, Oaxaca shares many unique species with the state of Guerrero, especially those that inhabit the Sierra Madre del Sur. A similar pattern is followed with species inhabiting the Sierra Norte of Oaxaca, that are also distributed within the states of Veracruz and Puebla, with some shared species between the Chimalapas area with Chiapas and Veracruz (Kohlmann 2022). The 46 known species endemic to Oaxaca belong to the genera *Agrilinellus* (1), *Cephalocyclus* (2), *Gonaphodioides* (2), *Oxyomus* (1), *Pseudocoelotrachelus* (1), *Ataenius* (1), *Nanotermitodius* (2), *Rhyparus* (1), *Ceratotrupes* (1), *Geotrupes* (4), *Ateuchus* (1), *Canthidium* (5), *Cryptocanthon* (1), *Copris* (2), *Onthophagus* (15), *and Phanaeus* (6). The vast majority of these endemisms are distributed in the montane forests, mainly in cloud forests, and oak and pine-oak forests (Fig. 1).

It is interesting to note the high endemicity registered for the Geotrupinae (71%), followed by the Scarabaeinae genera *Canthidium* (41%), *Phanaeus* (40%), and *Onthophagus* (34%). *Nanotermitodius* (Fig. 2) is the only genus endemic to Oaxaca. Nearctic (*Ceratotrupes*, *Geotrupes*, *Onthophagus*) and Neotropical (*Nanotermitodius, Canthidium*, *Phanaeus*) elements have high speciation and endemicity rates in the mountains of Oaxaca. A similar phenomenon occurs in the Costa Rica mountains (Kohlmann et al. 2019), where the greatest dung beetle diversity and endemicity are concentrated in the cloud forests of the tropical mountains (Kohlmann et al. 2007). This pattern is repeated in the Atherton Tablelands and in tropical rainforests of Australia (see Aristophanous 2014; Bell et al. 2007), where wet tropical mountains harbor distinct, small-bodied, species-rich dung beetle assemblages with sub-regionally endemic flightless species. Endemism seems to be higher in the tropical mountains than in the tropical lowlands of Oaxaca (Table 1 and Fig. 1). Most of the reported Oaxaca Geotrupidae and Scarabaeidae endemics are montane, with four exceptions, permitting short linear displacements that still maintain the same ecological characteristics, while allowing a cenocron to concentrate in a small area (Kohlmann et al. 2019). In contrast, lowland species must travel greater linear distances, presenting a much more extended distribution than endemic species, in Oaxaca this kind of species probably be found in adjacent states in future studies. As mentioned above, species that inhabit the lowlands may be present in similar habitats in adjacent states even though they have not yet been recorded. For example, *O. ixtepecorum* is likely to extend its distribution into the Pacific lowlands. While species such as *O. santamariensis*, *O chinantecus* and *O. istmenius*, may also be distributed in lowland areas of the Zoque forest in Chiapas and/or in the Uxpanapa in Veracruz.

The high mountain biodiversity and endemicity phenomenon seem to follow the recently proposed concept of "Humboldt's Enigma". Rahbek et al. (2019) have proposed that tropical mountains contribute disproportionately to the biodiversity of the Earth, presenting hotspots of extraordinary and puzzling richness. They also suggest that the complex climatic characteristics of rugged mountains play a crucial role in generating and maintaining biodiversity. A highly fractured topography gives rise to complicated microclimatic mosaics where suitable habitats can be isolated despite their proximity (Rahbek et al. 2019). The complex topography not only results in higher species richness (speciation driver) but also in more range-restricted species and, consequently, a higher proportion of endemism.

Introduced species

Two introduced species from Africa are recorded: *Digitonthophagus gazella* and *Euoniticellus intermedius*. Both species were introduced in the USA during the 1970s for dung control and had been spreading southward since. *Digitonthophagus gazella* was reported for the first time in Oaxaca in 1989 in Puerto Angel (Kohlmann 1994). In collections, the only record found so far for *E. intermedius* is from 2009 in San Sebastián de las Grutas, its possible invasion must have occurred before 1999 when it was recorded for the first time in Chiapas (Morales Morales et al., 2004). *Euonitecillus intermedius* has already reached Panama, whereas the movement of *D. gazella* seems to have become stalled around Managua, Nicaragua, and not expanded farther south (Solís and Kohlmann 2012).

Doubtful, misidentified, and possible unconfirmed species

Some publications and insect collection material have cited species from the state of Oaxaca, which are, without a doubt, misidentified. We found seven species erroneously mentioned as distributed in Oaxaca state, as follows: 1) *Ceratotrupes bolivari* Halffter and Martínez is distributed in the Trans-Mexican Volcanic Belt (TMVB) in central Mexico, extending to the north in the Sierra Madre Occidental. Specimens attributed to Oaxaca may refer to *C. sturmi*. 2) *Geotrupes truncaticornis* Howden is an endemic species from Guerrero not from Oaxaca. Both misidentifications reported by Trotta-Moreu et al. (2008) for Oaxaca. 3) *Termitodius chaki* Reyes-Castillo and Martínez (1979) was cited from Oaxaca by Galante et al. (2003) but these specimens correspond to a new species of the genus *Nanotermitodius* (Skelley et al. 2022). 4) *Copris armatus* Harold, 5) *Onthophagus chevrolati* Harold, and 6) *Phanaeus quadridens* (Say) are also distributed in the TMVB and are not distributed in Oaxaca. Specimens of *C. armatus* cited by Ramírez-Ponce et al. (2009) were identified as *C. klugi* as later confirmed by Morón (pers. comm.). *O. chevrolati* and *P. quadridens* reported by Barrera (1969*)* are referable to *O. aureofuscus* and *P. damocles*, respectively. 7) *Canthon speciosus* is cited from Oaxaca by Moctezuma (2021) based on molecular data reported by Nolasco-Soto et al. (2020). We prefer to act conservatively and consider it as *C. cyanellus*, till the proper nomenclatural change has been published. 8) Ramírez-Ponce et al. (2019) cite *Copris halffteri* Matthews from the agricultural environs of Zaachila. This cite needs confirmation, as in 2017 one of us (B.K.) collected in this same area but could only find *C. lugubris* and *C. lecontei*. *Copris halffteri* seems to be so far a species distributed in the upper reaches of the Balsas Depression. This paper reports many unidentified taxa and determinations must be considered with care. We found two species that may later prove to be residents of Oaxaca, although their presence there needs confirmation. *Deltochilum sublaeve* Bates inhabits the slopes of the Gulf of Mexico in tropical lowland localities in Chiapas, Tamaulipas, and Veracruz (González-Alvarado and Vaz-de-Mello, 2015) in the Veracruzan province (Morrone 2014). We did not find specimens from Sierra Norte localities attributable to *D. sublaeve*, but it may occur in Oaxaca. *Phanaeus melampus* Harold is a rare species with only four precise localities known in rainforest and cloud forest in Veracruz and Chiapas (Edmonds 1994; Navarrete-Gutiérrez and Edmonds 2006) its presence at these localities suggests it may also occur in Oaxaca; especially on the western slope of the Sierra Norte from Tuxtepec to Ixtlán de Juárez.

State richness comparisons

The richest Mexican states in dung beetles are Chiapas, Oaxaca, and Veracruz (Morón 2003a). The most recent data summarize 193 species in Chiapas, with 129 Scarabaeinae, 57 Aphodiinae, and 7 Geotrupidae species (Gómez-Gómez 2013; Escobar-Hernández et al. 2019; Sánchez-Hernández et al. 2019; Moctezuma and Halffter 2020a, 2021b; Chamé-Vázquez and Sánchez-Hernández 2022; Skelley and Keller 2022). Veracruz is home to 182 species, 96 of Scarabaeinae, 75 Aphodiinae and 11 Geotrupidae species (Cartwright and Woodruff 1969; Gordon and Cartwright 1980; Raković 1986; Verdú et al. 2006; Skelley et al. 2007; Deloya 2011; Minor 2017; Joaqui et al. 2019; Moctezuma and Halffter 2021a). The geographic location of Oaxaca includes six biogeographic provinces (Morrone 2014), including the Chiapas Highlands province represented by the Chimalapas region. The Isthmus of Tehuantepec is a strong biogeographic barrier separating species on either side (Halffter and Morrone 2017), while the intricate topography with high mountains makes Oaxaca the most diverse state in Mexico for dung beetles and probably other groups.

Morón (2003a) reported 100 species for the three groups treated here; since then, increased attention to Oaxacan fauna has resulted in at least 30 papers in ecology and taxonomy including descriptions of more than 50 new species.

Aphodiinae. Oaxaca is home to more than 38 species of Aphodiini and 30 species of Eupariini (Table 2), making it the most species-rich Mexican state for Aphodiini. The fauna includes 22 species of *Ataenius*, representing 7.6% of all 290 described *Ataenius* species. The latest previous species count for Oaxaca was done by Minor (2017), who reported 34 species of Aphodiini and 21 of Eupariini. Minor reports 140 species of Aphodiini and 69 for Eupariini for Mexico. Aphodiini are usually found in the Nearctic region above 2000 m, whereas Eupariini dominates in the Neotropical region (Minor 2017). As shown in Table 2 the Aphodiini tend to be more numerous in North America, their numbers diminishing as we progress further South, whereas the contrary holds for Eupariini. However, considering the species density per unit area, Oaxaca is an extraordinarily biodiverse area for both tribes. Oaxaca comes in first place regarding Aphodiini before the state of Durango (0.0308 species/100 km2) and in second place regarding Eupariini after the state of Veracruz (0.0418 species/100 km^2) (Cabrero et al. 2010; Minor 2017).

The genus *Nanotermitodius* (Rhypariini) is the only known dung beetle genus endemic to Oaxaca (Fig. 2). The natural history of this genus is not entirely known, although is presumed to have a close association with termites (Howden 2003a). Its status as a flightless endemic makes the group a candidate for specific conservation measures (Baur et al. 2002).

The native vegetation of the state is under siege by deforestation and the transformation of the landscape for agricultural purposes (Velásquez et al. 2003). Presently, only about 22% of the total state surface remains covered by autochthonous vegetation, a present threat especially to species with very restricted distributions.

Table 2. The number of species and species density of Aphodiini and Eupariini in Oaxaca, Mexico, USA, Panama, Colombia, and the Guianas (Ratcliffe 2002; Riley and Wolfe 2003; Gordon and Skelley 2007; Minor 2017; Hielkema and Hielkema 2019; Pardo-Locarno and Schoolmeesters 2019**;** Clavijo-Bustos et al. 2021).

	Aphodiini species number	**Eupariini species number**	**Aphodiini density per 100 km^2**	**Eupariini density per 100 km^2**
USA and Canada	252	74	0.0013	0.0004
Texas	52	44	0.0075	0.0063
Mexico	140	69	0.0071	0.0035
Oaxaca	38	30	0.0404	0.0319
Panama	9	22	0.0119	0.0291
Colombia	10	44	0.0009	0.0038
The Guianas	9	61	0.0019	0.0132

Table 3. The number of species and species density of *Neoathyreus* and *Geotrupes* in Texas, Oaxaca, Puebla, and Panama (Ratcliffe 2002; Riley and Wolfe 2003; Arriaga et al. 2020a).

	***Neoathyreus* species number**	***Geotrupes* species number**	***Neoathyreus* density per 100 km^2**	***Geotrupes* density per 100 km^2**
Texas	0	3	0.0000	0.0004
Oaxaca	5	6	0.0053	0.0064
Veracruz	6	4	0.0083	0.0056
Puebla	1	4	0.0029	0.0117
Panama	7	0	0.0093	0.0000

Cabrero-Sañudo et al. (2007), in their study of state distributions of Aphodiinae, reported 28 Aphodiini species for Oaxaca. Using the ACE and Chao2 parametric estimators, their modelling predicted values of 30 and 29 species for Oaxaca, respectively (Cabrera-Sañudo et al. 2007). Using these estimators, values of 92.59% and 96.15% of known species richness were obtained, respectively. If we compare these predictions with the presently reported number of 38 species, it is evident that the previously mentioned estimators do not seem to be very efficient as predictors, at least at a state-level, where a pronounced orography and environmental history affects biodiversity numbers. These estimators should make better predictions if used for smaller or more environmentally homogeneous study areas.

Geotrupidae. Oaxaca harbors the highest state number of *Geotrupes* species in Mexico, with six species (four of them endemics) in the state (Arriaga-Jiménez et al. 2020a). Hidalgo and Puebla (Table 3) tie for the second richest states with four species each, each state with only one endemic species (Howden 2003b). Chiapas and Veracruz are home to two species. Oaxaca is also home to *Ceratotrupes sturmi*, an endemic species with three congeners.

As for species richness of the tribe Athyreini, Oaxaca (5) comes in second place, after Veracruz (6), as the state most species-rich in *Neoathyreus* (Howden 2003b). Oaxaca shows a balance between northern and southern elements (Table 3). As with the Aphodiini and Eupariini, *Geotrupes* is a Nearctic representative, whereas *Neoathyreus* is a Neotropical one. As for the genus *Bolbelasmus*, Oaxaca is the most species-rich state, with three species.

Scarabaeinae. A comparative analysis of two species-rich genera, *Onthophagus* and *Canthidium* is shown in Table 4. The first genus is of Nearctic (Oriental invasion) origin, and the second of Neotropical origin, Harold (1867) observed that they represent ecological equivalents. *Onthophagus* becomes less species-rich as it enters the South American continent, whereas the biodiversity of *Canthidium* diminishes as it enters North America. However, the highest species density for these two genera is recorded in Costa Rica, the country labeled as the most biodiverse in the world per unit area (Obando 2002; Ávalos 2019). The very high biodiversity levels of Costa Rica are attributable to intricately complex orography (Obando 2002; Ávalos 2019), and this is perhaps also the case for Oaxaca.

Incorrect Latinization

Onthophagus sanpabloetlorum was described from Oaxaca (Moctezuma and Halffter 2020b). The name derives from the collecting locality, San Pablo Etla. According to Article 30.2.4 of the ICZN (1999): "if the name ends in a-, the gender is feminine".

Therefore, the stem *sanpabloetla* should be considered to have feminine gender. According to Article 31.1.2, the latinization of *sanpabloetla* in the feminine plural genitive should proceed as: "A species-group name, if a noun in the genitive case (see Article 11.9.1.3) formed directly from a modern personal name, is to be formed by adding to the stem of that name… -arum if of women; the stem of such a name is determined by the action of the

Table 4. The number of species and species density of *Canthidium* and *Onthophagus* in Texas, Oaxaca, Costa Rica, Panama, and the Guianas (Ratcliffe 2002; Riley and Wolfe 2003; Solís and Kohlmann 2012; Hielkema and Hielkema 2019; Kohlmann et al. 2019; Solís and Kohlmann 2023).

	Canthidium **species number**	***Onthophagus*** **species number**	***Canthidium*** **density per 100 km²**	***Onthophagus*** **density per 100 km²**
Texas	1	21	0.0001	0.0030
Oaxaca	12	49	0.0128	0.0522
Costa Rica	25	41	0.0488	0.0801
Panama	19	26	0.0252	0.0345
The Guianas	34	11	0.0073	0.0024

original author when forming the genitive." Therefore, to the stem *sanpabloetla,* the suffix *-arum* should be added to form the correct latinized species name of *sanpabloetlarum*.

However, according to Article 32.5.1, incorrect latinizations are not to be considered inadvertent errors and, as such, are not to be corrected: "Incorrect transliteration or latinization, or use of an inappropriate connecting vowel, are not to be considered inadvertent errors.", and therefore the species-name remains as initially published, *sanpabloetlorum*.

Revalidation of *Phanaeus* (*Notiophanaeus*) *dionysius*

Phanaeus (*Notiophanaeus*) *dionysius* Kohlmann et al. 2018a: 67.

Phanaeus (*Notiophanaeus*) *zapotecus* Kohlmann, Arriaga-Jiménez and Rös, 2018 (new synonymy by Moctezuma and Halffter 2021b).

Phanaeus (*Notiophanaeus*) *dionysius* Kohlmann, Arriaga-Jiménez and Rös, 2018 (restoration of species status).

In 2018, Kohlmann et al. (2018a) described *Phanaeus dionysius* from Oaxaca (Fig. 3). In 2021 Moctezuma and Halffter (2021b) synonymized this species with *Phanaeus zapotecus* Edmonds, 2006, based mainly on the variation of external morphology and the endophallite. These species belong to the *P. endymion* species group. The holotype of *P. zapotecus* could not be found in the INECOL insect collection, where it should have been kept. We here restore *Phanaeus dionysius* to species status for the following reasons:

1) A previously innominate character is the pronotal process of the female. In the case of *P. dionysius* the central tubercle is more anteriorly projected than the lateral tubercles (Fig. 3a, c, g, e), whereas, in the case of *P. zapotecus*, the tubercles are almost aligned (Fig. 3b, d, f, h, i), the central tubercle not projecting anteriorly.

2) The morphology of the aedeagus, which is different between both species as indicated in the original description (fig. 3b, 3c, 3d, 3e; Kohlmann et al. 2018a), is dismissed offhand by Moctezuma and Halffter (2021b) because it "is not taxonomically informative to separate species", despite Moctezuma and Halffter's (2021b) comment that it had been considered an important character by previous authors (Edmonds 1994; Price 2005; Arnaud 2002; Moctezuma and Halffter 2017; Moctezuma et al. 2017, 2019a). In another paper, Moctezuma et al. (2021) indicate that the genital structures of males (aedeagus, endophallites) were found to be homogeneous in the *P. amethystinus* (except *P. genieri*), *P. tridens*, *P. quadridens*, and *P. vindex* species groups; however, not so in the *P. endymion* species group. In harmony with all the previously mentioned studies, this paper considers that differences in the aedeagus are valid and determinant.

3) Moctezuma and Halffter (2021b) do not mention the differences shown by both species regarding their biology, distribution, and ecology. *Phanaeus zapotecus* is distributed in the Sierra Madre del Sur, lives in evergreen pine-oak forests, and feeds solely on macromycetes, whereas *P. dionysius* is distributed in the Sierra Norte, lives in a deciduous oak-scrub forest, and feeds solely on dung. This suggestion that distribution and ecology are important species dividers is not new, and it appears in a paper by Moctezuma et al. (2021) on the *P. tridens* species group. They conclude that the species within this group have vicariant distributions mainly driven by environmental conditions steered by geography (mountains acting as geographic barriers) and ecology (dry forests, humid forests, temperate mountains). A recent work by Janzen et al. (2011) regarding Lepidoptera did show that cryptic skipper butterfly species can be separated by caterpillar coloration, food plant, and ecology and at the same time showed less than a 2% COI sequence divergence, which is the conventional threshold used to separate species using mtDNA. Janzen et al. (2011) study suggests the existence of a considerable number of cryptic species that differences in color, food source, and ecology can only separate.

The case of both *Phanaeus* species is similarly related to the situation presented by *Geotrupes nuntiatus, G. pecki,* and *G. viridiobscurus* distributed in the same mountain areas (Kohlmann et al. 2018a; Arriaga-Jiménez et al. 2020a). Both genera have been impacted by late glaciation mechanisms, forming closely related species, where the main morphological differences express themselves at the aedeagus level (Arriaga-Jiménez et al. 2020a). Speciation has been recent (see Arriaga-Jiménez et al. 2020c for a detailed model) in these two groups forming a veritable Artenkreis process.

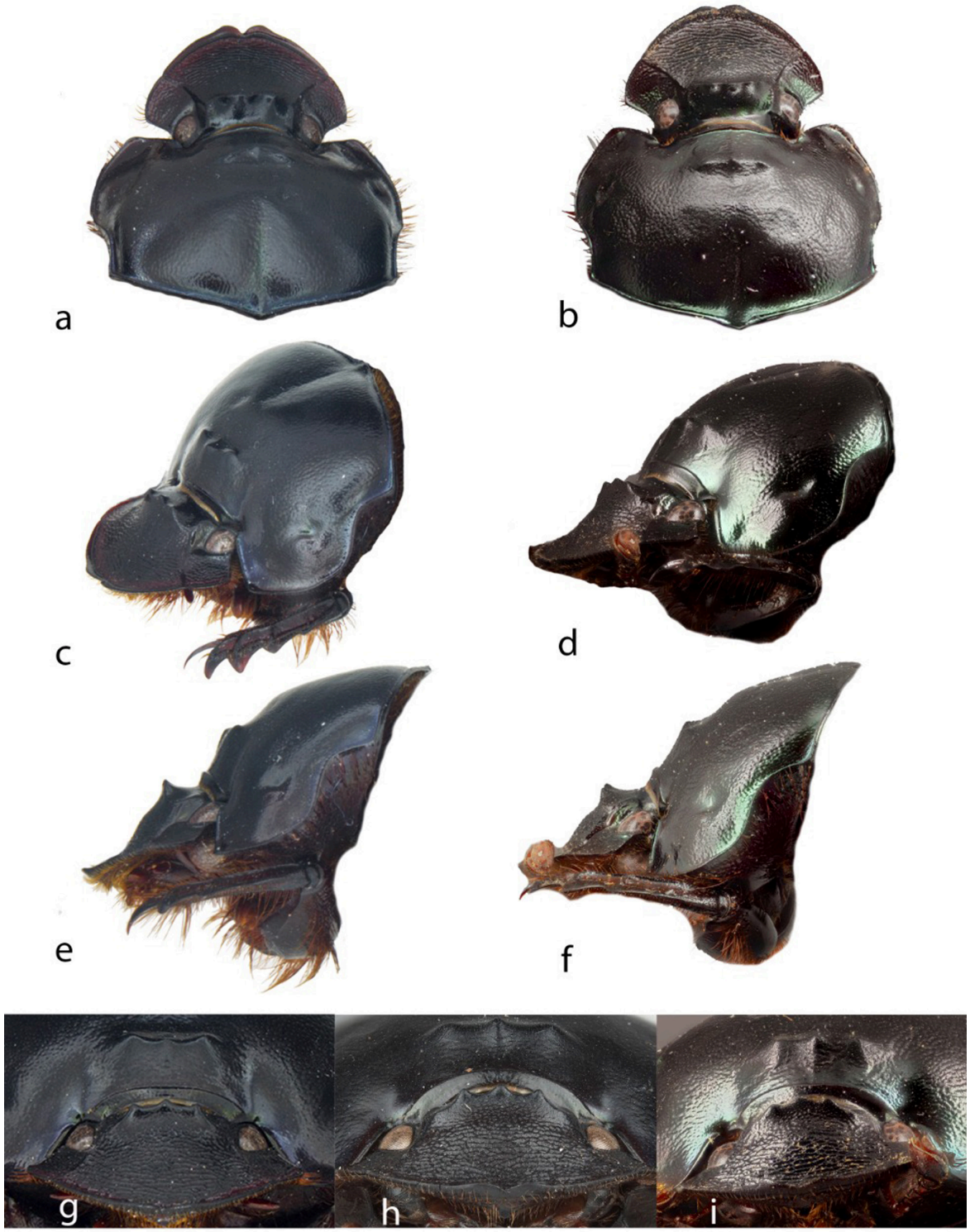

Figure 3. *Phanaeus dionysius* and *P. zapotecus* females' characters. **a)** Female dorsal view of allotype of *P. dyonysius* in IEXA. **b)** Female dorsal view of paratype of *P. zapotecus* in TAMUIC. **c)** Female three-quarter view of allotype of *P. dyonysius* in IEXA. **d)** Female three-quarter view of paratype of *P. zapotecus* in TAMUIC. **e)** Female lateral view of allotype of *P. dyonysius* in IEXA. **f)** Female lateral view of paratype of *P. zapotecus* in TAMUIC. **g)** Female frontal view of allotype of *P. dionysius* in IEXA. **h)** Female frontal view of paratype of *P. zapotecus* in TAMUIC. **i)** Female frontal view of paratype of *P. zapotecus* in CMN.

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