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Research article

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A taxonomic review of the endemic Mexican genus *Ceratotrupes* Jekel, 1865 (Coleoptera: Geotrupidae: Ceratotrupini), with the description of an unexpected new species from the Sierra Madre del Sur

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Abstract. In this study, we revise the taxonomy of the endemic Mexican genus *Ceratotrupes* Jekel, 1865. It comprises three species, distributed in the Sierra Madre Occidental and Trans-Mexican Volcanic Belt (*Ceratotrupes fronticornis* (Erichson, 1847) and *Ceratotrupes bolivari* Halffter & Martínez, 1962), and the Sierra Madre del Sur (*Ceratotrupes sturmi* (Jekel, 1865)). We confirm *C. mniszewski* (Jekel, 1865) as a junior subjective synonym of *C. sturmi*. The examination of the holotype of *C. sturmi* and specimens recently collected in the Sierra Sur de Oaxaca (Oaxaca) and Omiltemi (Guerrero) allowed us to identify and describe a new species, *Ceratotrupes gonzaloi* sp. nov. from Omiltemi, Guerrero. We redescribe the morphology of *C. sturmi* and provide a diagnostic key to the four members of the genus *Ceratotrupes*. Photographs of the habitus and male genitalia of the four species, a distribution map, and observations on their ecology and biogeography are provided.

Keywords. Dor beetles, Mexico, Trans-Mexican Volcanic Belt, Sierra Madre Occidental, Sierra Sur.

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Introduction

The family Geotrupinae Latreille, 1802 is one of the most diverse and ancient groups of scarabaeoid beetles (Zunino 1984; Cambefort 1991; Gunter *et al.* 2016). It comprises large-sized species with a Holarctic distribution, which are primarily associated with excrement of medium and large-sized mammals, although some species may feed on mushrooms and other organic matter in various stages of decomposition (Howden 1955, 1964; Ruiz *et al.* 2019). The majority of geotrupine scarab beetles are dorsally dark coloured (except for some genera that include very colourful species, e.g., *Trypocopriss* Motschulsky, 1859, *Enoplotrupes* Lucas, 1869, *Phelotrupes* Jekel, 1865), with tegument dull to shining, while ventrally they normally exhibit metallic colouration, with bright, purple, blue to gold and green casts.

The systematics of geotrupid beetles is still far from being resolved (Howden 1982; Zunino 1984; Scholtz & Browne 1996; Verdú *et al.* 2004). Herein, we adopt the classification of Nikolajev (1970) and Bouchard *et al.* (2011), which considers the family Geotrupidae Latreille, 1802 to be subdivided into three subfamilies: Geotrupinae Latreille, 1802, Bolboceratinae Mulsant, 1842 and Taurocerastinae Germain, 1897. The 341 species today included in the subfamily Geotrupinae (Schoolmeesters 2021) are assigned to four tribes (Geotrupini Latreille, 1802, Ceratotruperini Zunino, 1984, Chromogeotrupini Zunino, 1984, and Cretogeotrupini Nikolajev, 1998), while the systematic position of two extinct species (i.e., *Geotrupoides* Handlirsch, 1906 spp.) is still uncertain. Zunino (1984) carried out an extensive systematic review of the subfamily Geotrupinae and established the two tribes Chromogeotrupini and Ceratotruperini. Only New World genera were assigned to Ceratotruperini (genotype: *Ceratotrupes* Jekel, 1865 by original designation), and among them the genus *Ceratotrupes* Jekel, 1865 (type species by original designation: *Geotrupes fronticornis* Erichson, 1847), which comprises three endemic species in Mexico: *C. fronticornis* (Erichson, 1847), *C. bolivari* Halffter & Martínez, 1962, and *C. sturmi* (Jekel, 1865). The three species occur in mixed woodland habitats of high elevations (2000–2800 m a.s.l.), mostly dominated by *Pinus* and *Quercus* trees, and situated in the Trans-Mexican Volcanic Belt (*C. bolivari* and *C. fronticornis*, which are partly sympatric), Sierra Madre Occidental and Sierra del Sur (*C. sturmi*).

Jekel (1865) described *Ceratotrupes* as a subgenus of *Geotrupes* Latreille, 1796, and described *C. sturmi* and *C. mniszechi* (Jekel, 1865) using two male specimens from Mexico, but no exact locality was provided. Boucomont (1902) treated *Ceratotrupes* as a subgenus of *Ceratophyus* Fischer, 1871, but later the same author reconsidered it to be a valid genus (Boucomont 1912). Afterwards, Halffter & Martínez (1962) revised *Ceratotrupes*, describing the new species *C. bolivari* from the municipality of Huitzilac, Morelos, and providing a detailed account on the behaviour, ecology and biogeography of all the members of the genus. In the same work, the authors provisionally suggested *C. mniszechi* (Jekel, 1865) was a junior synonym of *C. sturmi*, claiming, however, that the study of additional material, including the holotype of *C. mniszechi*, would have been critical to confirm this synonymy.

Howden (1964) studied and compared the type specimens of *C. sturmi* and *C. mniszechi*, and confirmed the synonymy proposed by Halffter & Martínez (1962). Later, Howden (1974) examined a series of *Ceratotrupes* (eight males and two females) from Omiltemi (Guerrero State) and Oaxaca (Oaxaca State:

Route 131, 20 mi S of Juchatengo, 6000 ft), and noticed the following characters: specimens from Juchatengo differed by the slender cephalic horn, different shape of the pronotal angles, and elytral interstriae without distinct secondary punctuation. Albeit some of these characters could match the original description of *C. mniszehi*, Howden eventually decided to consider it as simple morphological variation of *C. sturmi*.

During our intensive fieldwork activities in Omiltemi, Guerrero, and Sierra Sur of Oaxaca, we accumulated a consistent number of *Ceratotrupes* specimens, which were provisionally assigned to two distinct taxonomic units. We identified the specimens from Omiltemi as *C. sturmi*, while those collected in the Sierra Sur de Oaxaca were initially believed to belong either to *C. mniszehi* (junior subjective synonym of *C. sturmi*) or an undescribed species.

The goal of this research is threefold: (i) to describe the new species *C. gonzaloi* sp. nov. from Omiltemi, Guerrero; (ii) to redescribe the morphology of *C. sturmi* and provide clear diagnostic traits to separate it from its close relative *C. gonzaloi*; (iii) to provide an updated identification key to the four members of the genus (*C. bolivari*, *C. fronticornis*, *C. sturmi*, and *C. gonzaloi*), photographs of their habitus and male genitalia, and a distribution map showing the geographic range of each species. Additionally, new ecological and geographical observations on the four *Ceratotrupes* are given.

Material and methods

The material examined in this study is deposited in the following entomology collections:

- CEMT = Setor de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil (F.Z. Vaz-de-Mello)
- CMNC = Canadian Museum of Nature, Ottawa, Ontario, Canada (F. Génier)
- FMNH = Finnish Museum of Natural History, Helsinki, Finland (S. Tarasov, J. Mattila)
- IEXA = Instituto de Ecología, Xalapa, Veracruz, Mexico (V.V. Badillo)
- MNHN = Muséum national d'histoire naturelle, Paris, France (O. Montreuil, A. Mantilleri)
- NHML = The Natural History Museum, London, UK (M.V.L. Barclay)

In this study, we use the phylogenetic species concept (Wheeler & Platnick 2000). Anatomical terminology for the male genitalia follows Cristóvão & Vaz-De-Mello (2021), Zunino (1984), and Bovo & Zunino (1983). Verbatim label data are placed within quotes (“”), with data on separate labels separated by a forward slash (/). Specimens of *Ceratotrupes* were photographed with a Canon EOS 5D camera and a Canon MP-E 65mm, f/2.8, 1–5× macro lens, and a multifocus digital stereo microscope Leica Z16 APOA. Male genitalia were photographed under a Leica S9D stereo microscope, using a Canon EOS 500D attached. Pictures were subsequently enhanced and combined in plates in Adobe Photoshop and Illustrator CC 2015. The distribution map was generated in QGIS desktop ver. 3.22.0. The geographic range of each species of *Ceratotrupes* was inferred from recently collected material and distributional records retrieved from the literature (see taxonomic history of each species).

Results and discussion

From 2017–2019 AAJ and GH carried out a series of dung beetle surveys in different mountainous areas of Omiltemi (Guerrero) and Oaxaca (Miahuatlán, San Sebastián Río Hondo, and Santo Domingo Ozolotepec), and several specimens of *Ceratotrupes* were collected. At first sight, the morphological differences between specimens collected at the two localities were very clear. Thus, we investigated more closely whether such phenotypic dissimilarity was simple intraspecific variation or it could justify the separation of these specimens into two species. Firstly, the comparative examination of the type specimens of *C. sturmi* and *C. mniszehi* (currently a synonym of *C. sturmi*) allowed us to confirm the

synonymy, and to identify all the specimens from Oaxaca as *C. sturmi*. All the specimens collected in Omiltemi, Guerrero, and historically identified in natural history collections as *C. sturmi* turned out to belong to an unexpected new species, which is here named *C. gonzaloi* sp. nov. Given the aforementioned facts, the genus *Ceratotrupes* today includes four species, two of them distributed in the mountains of the Trans-Mexican Volcanic Belt and Sierra Madre Occidental (i.e., *C. fronticornis*, *C. bolivari*), and two species only known from the mountains surrounding Omiltemi and Oaxaca, in southwestern Mexico (i.e., *C. gonzaloi* and *C. sturmi*, respectively). Given that no taxonomic or morphological ambiguities exist between *C. fronticornis* and *C. bolivari*, no additional specimens were studied in this research (see Halffter & Martínez 1962).

Systematics

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Superfamily Scarabaeoidea Latreille, 1802
Family Geotrupidae Latreille, 1802
Subfamily Geotrupinae Latreille, 1802
Tribe Ceratotrupini Zunino, 1984

Genus *Ceratotrupes* Jekel, 1865

Geotrupes (*Ceratotrupes*) Jekel, 1865: 540.

Geotrupes – Gemminger & Harold 1869: 1081 (syn.). — Bates 1887: 112.

Ceratotrupes – Boucomont 1912: 20. — Blackwelder 1944: 220. — Howden 1955: 162; 1964: 45; 1974: 569; 2003: 100. — Halffter & Martínez 1962: 149. — Zunino 1984: 106. — Trotta-Moreu *et al.* 2008: 53. — Smith 2009: 4.

Ceratophyus (*Ceratotrupes*) – Boucomont 1902: 11.

Type species

Geotrupes fronticornis Erichson, 1847 by original designation.

Ceratotrupes fronticornis (Erichson, 1847)

Fig. 1

Geotrupes fronticornis Erichson, 1847: 727.

Geotrupes (*Ceratotrupes*) *fronticornis* – Jekel 1865: 541;

Geotrupes fronticornis – Gemminger & Harold 1869: 1082. — Bates 1887: 112.

Ceratophyus (*Ceratotrupes*) *fronticornis* – Boucomont 1902: 11.

Ceratotrupes fronticornis – Boucomont 1912: 20. — Blackwelder 1944: 20. — Halffter & Martínez 1962: 151. — Howden 1964: 45; 2003: 100. — Zunino 1984: 107–109. — Blackaller 1993: 22. — Navarrete-Heredia *et al.* 2001: 49. — Martínez & Trotta-Moreu 2010: 130. — Trevilla-Rebollar *et al.* 2010: 487. — Trotta-Moreu & Lobo 2010: 46. — García *et al.* 2011: 184. — Ramírez-Restrepo & Halffter 2016: 213–214.

Diagnosis

This species can be separated from other members of the genus by having lateral edges of pronotum curved, anterior angles truncate in males, cephalic horn of male strongly compressed laterally, posteriorly not sulcate.

Material examined

MEXICO – **Distrito Federal** • 1 ♂; “Contreras Jul. 2003 M.C. Halffter leg.”; CEMT • 1 ♀; same collection data as for preceding; CEMT. – **Jalisco** • 1 ♂; “Concepción B. Aires, Paso Hondo 12 Jun. 2003 Curoe, Nogueira leg.”; CEMT • 1 ♀; same collection data as for preceding; CEMT. – **México** • 1 ♂; “km 45 cam. a Temascaltepec 2360 m a.s.l. Sep. 1971 pine-oak forest Martínez leg.”; CMNC 00031019. – **Michoacán** • 1 ♂; “Huajúmbaro 2160 m a.s.l. 13 Aug. 1999 G. Nogueira leg.”; CEMT • 1 ♀; same collection data as for preceding; CEMT • 1 ♂; “Los Azufres 19°49’55” N, 100°39’41” W 2916 m a.s.l. 2 Jul. 2005 past. Pinus. cow dung. Cabrero and Trotta leg.”; CEMT • 1 ♀; same collection data as for preceding; CEMT • 1 ♀; “13 mi. W of Hidalgo 12 Jul. 1963. F.D. Parker and L.A. Stange leg.”; CMNC 00031006 • 1 ♂; “70 km E of Morelia, Mil Cumbres 9000’ a.s.l. 8–10 Sep. 1969. pine-oak forest. S. and J. Peck leg.”; CMNC 00031009. – **Morelos** • 1 ♂; “Cuernavaca, Colonia del Bosque Jul. 1987. excr. de caballo [horse droppings] J. Blackaller leg.”; CEMT • 1 ♂; “Cuernavaca, Colonia del Bosque Jul. 2008. S. Boucher leg.”; CEMT • 1 ♀; “Cuernavaca, km 55 carr. México 31 Aug. 1958. bajo estiércol de caballo [under horse manure] W.M.W. Gibson leg. / H. and A. Howden Collection ex. A. Martínez coll.”; CMNC 00031003” • 1 ♀; same collection data as for preceding; CMNC 00031052. – **Querétaro** • 1 ♀; “Amealco Aug. 1957 G. Halffter leg. / H. and A. Howden Collection”; CMNC 00031022 • 1 ♀; same collection data as for preceding; CMNC 00031023 • 1 ♂; same collection data as for preceding; CMNC 00031024 • 1 ♂; same collection data as for preceding; CMNC 00031025 • 1 ♂; same collection data as for preceding; CMNC 00031050.

Redescription of the male

COLOUR. Body black, sometimes with purplish to bluish tinges on elytra; dorsally, tegument feebly shining; antennal segments dark brown, antennal club blackish to dark brown.

HEAD. Clypeus obtusely triangular, longitudinally crossed by a medial, high and triangular horn, either projected forward or raised vertically; from posterior side, horn basally narrow and apically thicker, tip narrowly rounded; clypeal punctation dense and superficial; genae squared; frons smooth, unpunctured, with two oblique ridges along inner side of eyes.

THORAX. In lateral view, pronotum weakly convex; in dorsal view, posterior edge of pronotum completely margined, lateral edges almost straight and parallel from posterior angles to midline, convergent towards anterior angles; anterior angles squared, and transversally truncated; pronotal disc with isolated and simple punctures, scattered and slightly deeper punctation near lateral and anterior edges; in lateral view, anteromedial projection slightly curved upward apically; in dorsal view, projection with sides convergent apically, tip emarginated at middle. Elytral interstriae slightly convex, unpunctured. Ventral side of thoracic sclerites (i.e., pro-, meso- and metasternum) with long, yellowish setae.

LEGS. Protibiae robust, with seven external teeth, ventral side with a longitudinal, crenulated carina; apical spur long and slender; meso- and metatibiae respectively with 3 and 4 entire, transversal carinae on posterior side; femora unmodified, with long yellowish setae.

Sexual dimorphism

Female specimens have clypeal horn distinctly lower; from above, the clypeal horn is triangular-shaped; pronotal punctation simple and strong, scattered on disc, gradually denser near lateral and anterior edges; anteromedial pronotal protuberance callus-like and transverse, depressed on superior side and close to anterior pronotal edge; anterior angles simply curved.

Ecology and biogeography

This species inhabits mixed pine-oak forests and meadows located between 1850 and 3000 m a.s.l. It is known from a few localities distributed across the southern Trans-Mexican Volcanic Belt, and small populations scattered across the Balsas basin (e.g., some specimens were collected in Ario de Rosales, Michoacán, and Chalma, Mexico State). Finally, *C. fronticornis* extends its distribution westward in the northern part of the Sierra Madre Occidental (Los Altares Durango). Howden (2003) recorded this species from Canelas, Sinaloa, and Talpa de Allende, Jalisco. The eastern limit of its area of distribution seems to be located in the southern borders of Mexico City, between San Lorenzo Acopilco and Cumbres del Ajusco National Park, with the easternmost record in Chalco, Mexico State, close to the Iztaccíhuatl-Popocatepetl National Park. Recently, *C. fronticornis* was recorded from Mexico City (Ramírez-Restrepo & Halffter 2016).

Ceratotrupes fronticornis and *C. bolivari* are sympatric in the area between Mexico City and the southern border of the State of Mexico, as well as in Tapalpa, Jalisco and Durango, Sierra Madre Occidental (Fig. 6).

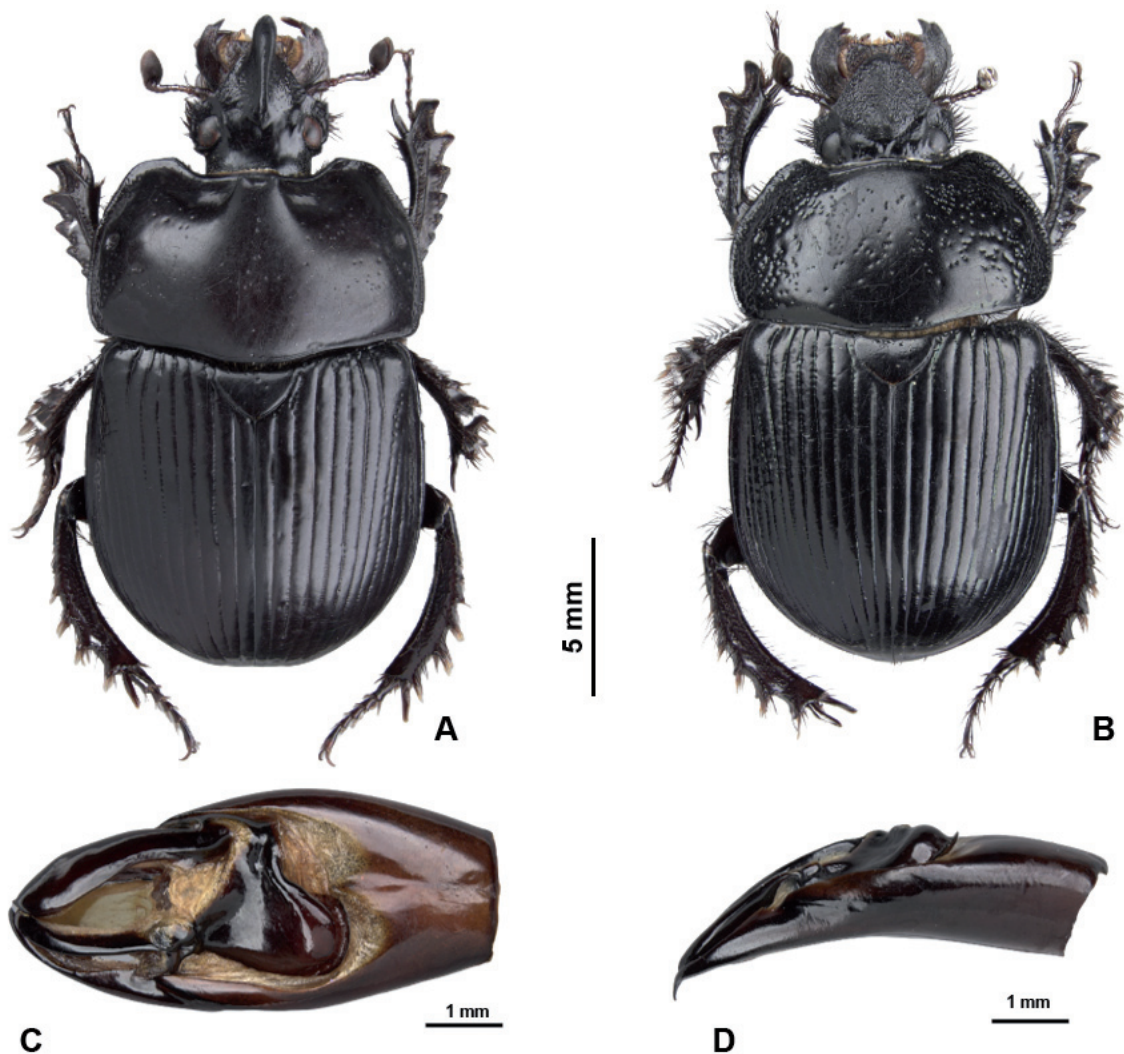


Fig. 1. *Ceratotrupes fronticornis* (Erichson, 1847) (CMNC). A–B. Dorsal habitus of male (A) and female (B). C–D. Aedeagus in dorsal (C) and lateral view (D).

Ceratotrupes bolivari Halffter & Martínez, 1962

Fig. 2

Ceratotrupes bolivari Halffter & Martínez 1962: 153.

Ceratotrupes bolivari – Howden 1964: 46; 1974: 569; 2003: 100. — Zunino 1984: 109. — Morón & Deloya 1991: 216. — Navarrete-Heredia *et al.* 2001: 49. — Delgado & Márquez 2006: 84. — Halffter *et al.* 2008: 284. — Smith 2009: 4. — Trotta-Moreu & Lobo 2010: 46. — García de Jesús *et al.* 2013: 151, 158–159, 164–167. — Pérez-Villamares *et al.* 2016: 446–448. — Arriaga-Jiménez *et al.* 2018: 8; 2020: 498. — Alvarado *et al.* 2020: 5.

Diagnosis

Males and females of *C. bolivari* have lateral edges of pronotum and anterior angles completely curved; apical antennal lamella with semi-elliptical groove (Fig. 2C); anteromedial pronotal projection of male very long, almost reaching tip of cephalic horn.

Type material examined

Paratypes

MEXICO – **Morelos** • 1 ♂; “Morelos Huizilac 2400 m a.s.l. / 20 Sep. 1953 S. Bolivar / Paratype / *Ceratotrupes bolivari* Halffter & Martínez”; CMNC 00030977 • 1 ♂; “La Venta 2500 m a.s.l. 18 Sep. 1953 / S. Bolivar, H. & A. Howden / Paratype / *Ceratotrupes bolivari* Halffter & Martínez Collection”; CMNC 00030981 • 1 ♂; “Valle Grande, Rio Frio 20 Nov. 1952 J. Hendrichs / Paratype / *Ceratotrupes bolivari* Halffter & Martínez det. 1960”; CMNC 00030982. – **Durango** • 1 ♂; “La Campana, 19 mi. W. of El Salto 22 Sep 1950 Ray F. Smith / Howden coll. ex. A. Martínez coll. / Paratype / *Ceratotrupes bolivari* sp.n (male) Halffter & Martínez”; CMNC 00030984 • 1 ♂; “Rio Frio 2950 m a.s.l. 19 Sep. 1953 S. Bolivar / Paratype / *Ceratotrupes bolivari* sp.n (male) Halffter & Martínez”; CMNC 00030985.

Additional material examined

MEXICO – **Durango** • 1 ♂; “Reserva ‘La Michilía’ 17 Jul.–9 Aug. 1987 bosque de pino-encino [pine-oak forest], trampa NTP 80 [NTP80 trap] / S. Anduaga”; CEMT • 1 ♀; “20 mi. E of El Salto. 8000’ a.s.l. 17–19 Jun. 1971 / H.F. Howden leg.”; CMNC 00030989. – **Sinaloa** • 1 ♀; “Loberas 1900 m a.s.l. 10 Jul. 1994 / G. Nogueira leg.”; CEMT • 1 ♀; “Loberas 1990 m a.s.l. 6 Aug. 1994 luz Hg [Hg light] D. Curoe leg.”; CEMT. – **Sonora** • 1 ♂; “3 km NW of Yécora, on hwy 16 1600 m a.s.l. 17–18 Jul. 1996. Oak, pine, juniper forest. human feces / W.D. Edmonds and P Reyes”; CEMT • 1 ♂; same collection data as for preceding; CEMT • 1 ♀; same collection data as for preceding; CEMT.

Redescription of the male

COLOUR. Body black, sometimes with purplish to bluish tinges near pronotal edges, and on elytral striation; dorsally, shining, pronotal tegument sometimes silky; antennal segments brown, antennal club brownish.

HEAD. Clypeus obtusely triangular, longitudinally crossed by a medial, high and triangular horn, projected forward, with apex curved upward; from posterior side, horn with medial, shallow depression; horn slightly narrow basally and thicker near apex, tip narrowly rounded; clypeal punctation dense and superficial; genae squared; frons smooth, unpunctured, with two oblique ridges along inner side of eyes. Apical antennal lamella with semi-elliptical groove (Fig. 2C).

THORAX. In lateral view, pronotum weakly convex; in dorsal view, posterior edge of pronotum completely margined, lateral edges evenly curved from posterior to anterior angles; fine punctures concentrated on midline of pronotal projection, isolated punctures close to lateral and anterior edges; in lateral view,

anteromedial projection dorsally slightly depressed; in dorsal view, basal region of projection with sides convergent, apical region with parallel or slightly divergent sides; apex of projection widely emarginated at middle. Elytral interstriae slightly convex, unpunctured. Ventral side of thoracic sclerites (i.e., pro-, meso- and metasternum) with long, yellowish setae.

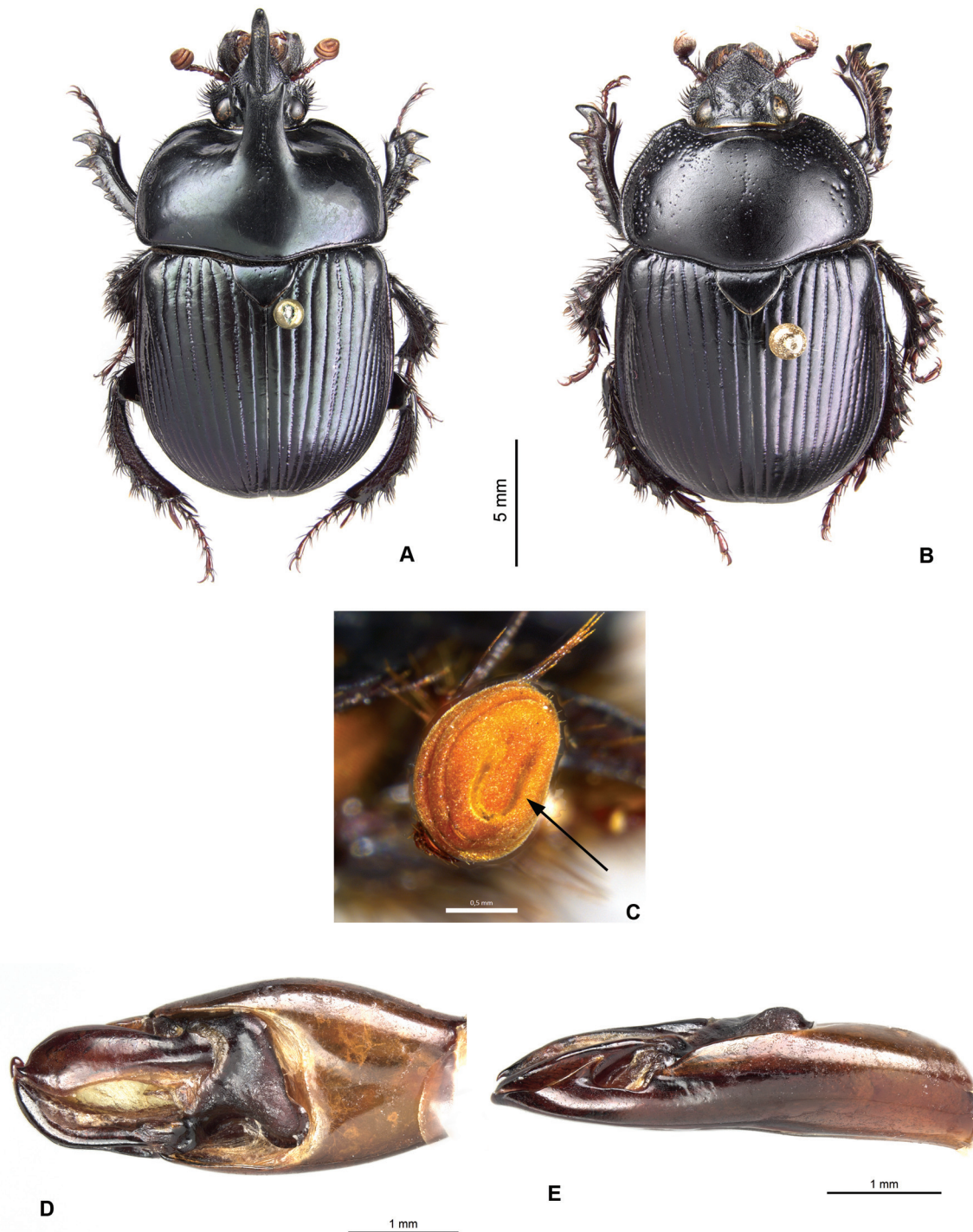


Fig. 2. *Ceratotrupes bolivari* Halffter & Martínez, 1962 (CMNC). **A–B.** Dorsal habitus of male (A) and female (B). **C.** Detail of the elliptical groove of the last antennal lamella. **D–E.** Aedeagus in dorsal (D) and lateral view (E).

LEGS. Protibiae robust, with six external teeth, ventral side with a longitudinal, crenulated carina; apical spur long and slender; meso- and metatibiae respectively with 3 and 4 entire, transversal carinae on posterior side; femora unmodified, with long yellowish setae.

Sexual dimorphism

Female specimens have clypeal horn distinctly lower; from above, clypeal horn triangular-shaped; pronotal punctation simple, shallower and sparse on disc, stronger and denser near lateral and anterior edges; anteromedial pronotal protuberance callus-like and transverse, depressed on superior side and close to anterior pronotal edge; anterior angles simply curved.

Ecology and biogeography

Among the members of the genus, *C. bolivari* is the species with the widest distribution (Fig. 6). It inhabits pine, oak, or mixed pine-oak forests, and open areas with alpine pastures between 900 and 3000 m a.s.l. (Halffter & Martínez 1962).

The geographic range of this species encompasses the Sierra Madre Occidental. Its northernmost limit of distribution is located in the Mesa de Huracán with records from Yepachic, Chihuahua (unpublished data, material collected by P. Reyes-Castillo and W.D. Edmonds in 1996 and deposited in MNHN and IEXA), while the southernmost records come from the Sierra de Tapalpa, Jalisco. To the east, the distribution of *C. bolivari* is limited by the Trans-Mexican Volcanic Belt, and specifically by the Cofre de Perote. To date, the easternmost records are a series of specimens collected in Omitlán de Juárez (Sierra de Pachuca, Hidalgo) (Halffter *et al.* 2008).

Ceratotrupes sturmi (Jekel, 1865)

Figs 3, 5A–B

Geotrupes (Ceratotrupes) sturmi Jekel, 1865: 543.

Geotrupes (Ceratotrupes) mniszehi Jekel, 1865: 544 (Fig. 5C–D).

Geotrupes sturmi – Gemminger & Harold 1869: 1085. — Bates 1887: 112.

Geotrupes mniszehi – Gemminger & Harold 1869: 1083. — Bates 1887: 113.

Ceratophyus (Ceratotrupes) sturmi – Boucomont 1902: 11.

Ceratophyus (Ceratotrupes) mniszehi – Boucomont 1902: 11.

Ceratotrupes sturmi – Boucomont 1912: 20. — Blackwelder 1944: 220. — Halffter & Martínez 1962: 155. — Howden 1964: 47; 1974: 569; 2003: 100. — Zunino 1984: 109. — Trotta-Moreu *et al.* 2008: 42–43, 48, 54. — Trotta-Moreu & Lobo 2010: 46.

Ceratotrupes mniszehi – Boucomont 1912: 20. — Blackwelder 1944: 220. — Halffter & Martínez 1962: 153, 155, 157. — Howden 1964: 47; 1974: 569. — Zunino 1984: 109.

Diagnosis

Within the genus, *C. sturmi* is here considered to be related to *C. gonzaloi* sp. nov., and it can be separated by the following diagnostic characters: posterior edge of pronotum with a thin, medial margin (Fig. 3A, C); clypeal horn slender, laterally narrower, tip obtuse (Fig. 3A, D); pronotal projection narrower, with convergent sides (Fig. 3A, D); elytral interstriae unpunctured. Furthermore, the male genitalia exhibit a series of clear morphological differences: distal tip of right ventral lobe of phallobase curved medially (Fig. 3J); shorter branch of the bifurcation of the right lobe of the phallobase longer than in *C. gonzaloi* (Fig. 3L); different shape of the parameres (Fig. 3F; arrows indicate the main differences); in lateral view, left paramere with a distinct lobe beneath the apical spur (Fig. 3G). It is noteworthy that *C. sturmi* and *C. gonzaloi* share with *C. bolivari* the presence of an apical, acute tooth on left paramere.

Type material examined

Holotype of *C. sturmi*

MEXICO • ♂; “Juquila [printed] / Mexico, Salle Coll. [printed] / 844 [green label, printed] / Sp. figured. [printed] / Ceratotrupes Sturmi Jekel, male symbol [handwritten] / Ceratotrupes sturmi Jekel, type apud Sallé [handwritten] / B.C.A. Col., II(2)., Geotrupes sturmi [printed] Jek / Holotype [white label with red border, printed]”; NHML.

Holotype of *C. mniszechi*

MEXICO • ♂; “Collection Mniszech [printed] / Ex-Musaeo VAN LANSBERGE [printed] / Geotr. (Ceratotrupes) Mniszechi Jekel [green label, handwritten] / Holo TYPUS Ceratotrupes mniszechi Jek [red label, handwritten except TYPUS, printed]”; MNHN.

Additional material examined

MEXICO – Oaxaca • 1 ♂; “20 mi S of Juchatengo, Rt. 131. 6000’ alt. 27–30 May 1971. H.F. Howden leg.”; CMNC 00031072 • 1 ♀; same collection data as for preceding; CMNC 00031071 • 1 ♂; “Oaxaca, km 164.5, carr. 131, Oax.–Pto. Escondido. 1800–2000 m a.s.l. 24–26 Jun. 1995. A. Perez and J. Blackaller leg. Bosque de Encino, en excremento [oak forest, in excrement]”; <http://id.luomus.fi/NC.04>; FMNH • 1 ♂, 1 ♀; “Cerro del Vidrio, 1800 m a.s.l. 26 May 2004. G. Nogueira leg. / Ceratotrupes sturmi Jekel, 1866, M.A. Morón det. Mayo 2007”; <http://id.luomus.fi/NC.05>, <http://id.luomus.fi/NC.06>; FMNH • 1 ♂; “Rm 164.5, carr. Oaxaca–Puerto Escondido. 1500–1650 m a.s.l. 17–20 Jun. 1993. coprotrampa [coprotrap]. L. Delgado leg.”; CEMT • 1 ♀; same collection data as for preceding; CEMT • 15 ♀♀; “Oaxaca, 4 km S of Lachao. 16°12.1’ N, 97°08.17’ W. 1710 m a.s.l. 1–24 Jun. 2006. D. Curoe leg.”; CEMT • 3 ♂♂; same collection data as for preceding; CEMT • 1 ♂; “km 164.5 carr. Oaxaca–Puerto Escondido. 17–20 Jun. 1993. 1550–1650 m a.s.l. coprotrampa [coprotrap]. L. Delgado leg. / Ceratotrupes sturmi (Jek.) / DET. H.F. HOWDEN”; CMNC 00031062 • 1 ♀; same collection data as for preceding”; CMNC 00031067.

Redescription of the male

COLOUR. Body black with purple iridescence, especially on both dorsal and ventral sides; dorsally, tegument shining, pronotal disc occasionally weakly silky; antennal segments brown, antennal club yellow.

HEAD. Clypeus obtusely triangular and elongated, with a medial, high and triangular horn; from posterior side, horn narrow and longitudinally sulcate, tip narrowly rounded; clypeal punctation dense, coarse and superficial; genae squared, with elevated and acuminate angle, genal punctation obsolete; frons smooth, unpunctured, with two oblique ridges along inner side of eyes.

THORAX. In lateral view, pronotum weakly convex; in dorsal view, posterior edge of pronotum finely margined at middle, lateral edges weakly curved from posterior angles to midline, straight and convergent from midline to anterior angles; anterior angles obtusely squared; pronotal disc unpunctured, sides with strong and coarse punctures sparsely distributed from posterior to anterior angles; in lateral view, anteromedial projection curved upward apically; in dorsal view, projection with sides convergent apically, tip narrowly emarginated at middle. Elytral interstriae slightly convex, unpunctured, apex of elytra with distinct but shallow punctation. Ventral side of thoracic sclerites (i.e., pro-, meso- and metasternum) with long, yellowish setae.

LEGS. Protibiae robust, with six external teeth, ventral side with a longitudinal, crenulated carina; apical spur long and slender; meso- and metatibiae respectively with 3 and 4 entire, transversal carinae on posterior side (among the examined material, only one specimen shows four entire carinae on both meso- and metatibiae); femora unmodified, with long yellowish setae.

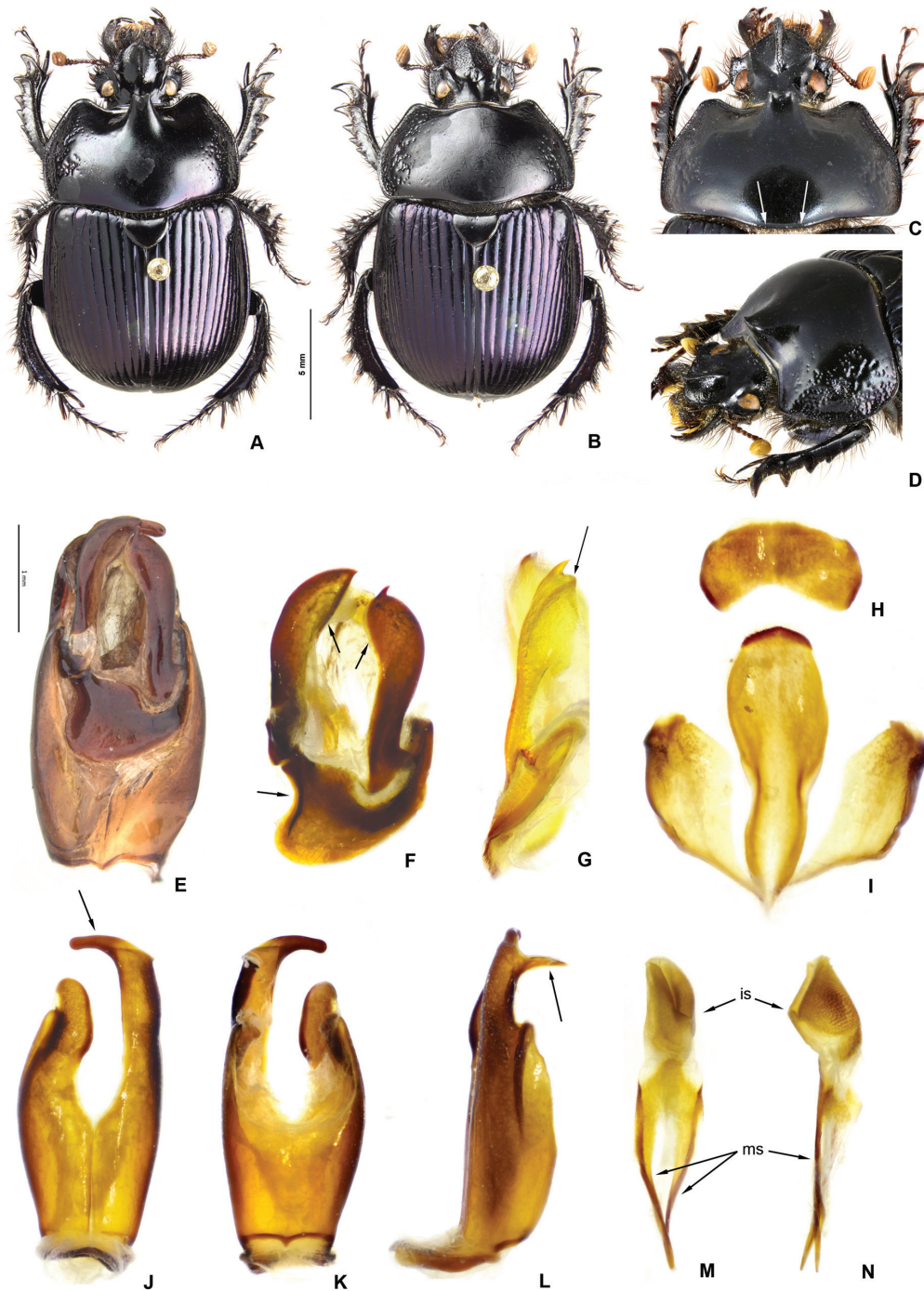


Fig. 3. *Ceratotrupes sturmi* (Jekel, 1865) (CMNC). **A–B.** Dorsal habitus of male (A) and female (B). **C.** Details of head and prothorax; arrows indicate posteromedial edge of pronotum margined. **D.** Details of cephalic horn and pronotal projection of male. **E.** Aedeagus in dorsal view. **F.** Parameres in dorsal view; arrows indicate main differences between *C. sturmi* and *C. gonzaloi* sp. nov. **G.** Right paramere in lateral view; arrow indicates lobe beneath apical spur. **H.** Tergite. **I.** Pleurotergites. **J.** Phallobase in ventral view; arrow indicates curved margin of ventral lobe. **K.** Phallobase in dorsal view. **L.** Phallobase in lateral view; arrow indicates long bifurcation. **M.** Internal sac (is) and median struts (ms) in dorsal view. **N.** Internal sac and median struts in lateral view.

Sexual dimorphism

Female specimens have the clypeal horn distinctly shorter and clearly depressed posteriorly; from above, the clypeal horn is triangular-shaped, apex almost reaching clypeal edge; anteromedial pronotal protuberance callus-like and transverse, depressed on superior side and close to anterior pronotal edge.

Remarks

This species was originally described using the specific epithet “*sturmi*”, which is probably the derived genitive form of the Latinization “Sturmius” (Jekel 1865). Nonetheless, later authors, from Gemminger & Harold (1869) to today’s publications, indicated the same species as “*sturmi*”. According to Art. 31.1 of the ICZN (1999), the original spelling of the species-group name must be preserved. However, Art. 33.3.1 suggests that an “incorrect subsequent spelling” must be maintained if in prevailing use in the literature, which is the case for *Ceratotrupes sturmi*.

Jekel (1865) described *C. sturmi* and *C. mniszechi* on two specimens from the Sallé and Mniszech collections and today deposited in the NHML and MNHN, respectively. In addition, the author mentioned the generic “Mexico” as type locality of the two species. The holotype of *C. mniszechi* does not have any label saying “Mexico”. However, Jekel’s handwritten label (“Collection Mniszech”) and the match between the morphology of the specimen and its original description remove any doubt to its identity (Fig. 5C–D).

At the same time, the holotype of *C. sturmi* has a label indicating “Mexico. Salle Coll.” and a second saying “Juquila”, a locality near Oaxaca (Fig. 5A–B). Probably the latter was added subsequently to the description of the species. At the moment, there is no evidence that indicates who might have attached this label to the holotype. Nonetheless, the morphology of the holotype matches perfectly with specimens recently collected in the mountains around Oaxaca (cephalic horn slender; pronotal projection clearly narrower distally; pronotal posterior edge with margin).

Ceratotrupes gonzaloi sp. nov.

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Fig. 4

Diagnosis

The following characters separate *C. gonzaloi* sp. nov. from its close relative, *C. sturmi*: posterior edge of pronotum without margin at middle (Fig. 4C); clypeal horn of male stronger, laterally wider (Fig. 4A, D), tip depressed at middle; pronotal projection larger, with parallel sides (Fig. 4A, D); elytral interstriae very finely and densely punctate. Male genitalia differ as follows: distal tip of right ventral lobe of phallobase straight and directed obliquely upward (Fig. 4J); shorter branch of the bifurcation of right lobe of phallobase distinctly shorter than in *C. sturmi* (Fig. 4L); parameres differently shaped (Fig. 4F; arrows indicate the main differences); in lateral view, left paramere simple, without distinct lobe beneath apical spur (Fig. 4G).

Etymology

This species is dedicated to Gonzalo Halffter (1932–2022), a renowned academic, researcher and entomologist, who passed away during the preparation of the current paper. Founder of INECOL and Biosphere Reserves, UNESCO, his research in the biogeography and ecology of beetles is a corner stone for research in Mexico and worldwide. But above all, Gonzalo, Dr Halffter, our “Maestro”, was our mentor, teacher, colleague, and our endearing and lovely friend.

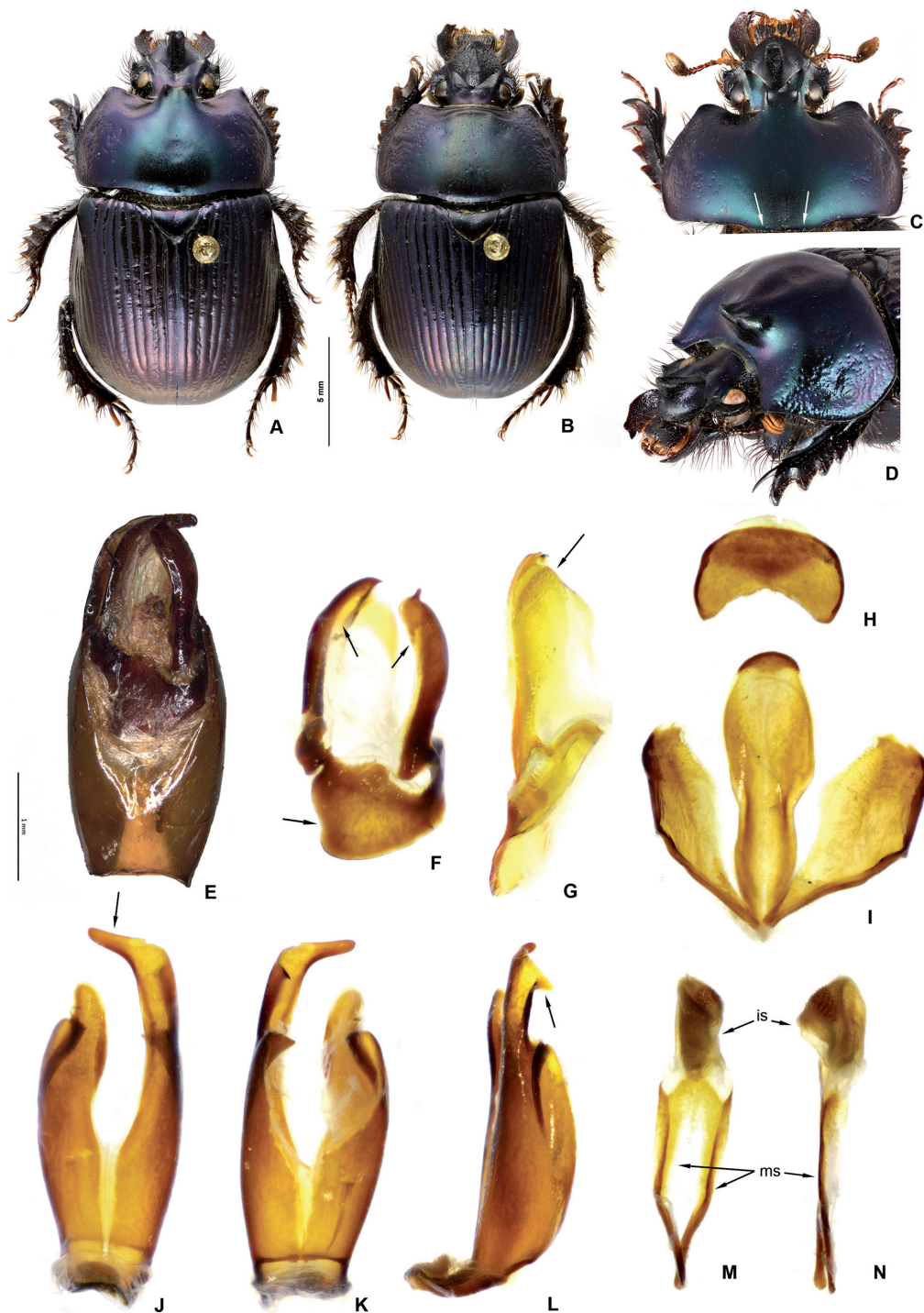


Fig. 4. *Ceratotrupes gonzaloi* sp. nov. (CMNC). **A–B.** Dorsal habitus of male (A) and female (B). **C.** Details of head and prothorax; arrows indicate posteromedial edge of pronotum without margin. **D.** Details of cephalic horn and pronotal projection of male. **E.** Aedeagus in dorsal view. **F.** Parameres in dorsal view; arrows indicate main differences between *C. gonzaloi* sp. nov. and *C. sturmi*. **G.** Right paramere in lateral view; arrow indicates absence of lobe beneath apical spur. **H.** Tergite. **I.** Pleurotergites. **J.** Phallobase in ventral view; arrow indicates straight margin of ventral lobe. **K.** Phallobase in dorsal view. **L.** Phallobase in lateral view; arrow indicates the short bifurcation. **M.** Internal sac (is) and median struts (ms) in dorsal view. **N.** Internal sac and median struts in lateral view.

Type material examined

Holotype

MEXICO • 1 ♂; “Guerrero, Omiltemi / 25 Aug. 1965 / G.V.V. Halffter leg. / Cebo, exterior bosque, 1° Estación día, bosque nebuloso, pino (modificado) / Halffter 73-18 / HOLOTYPE *Ceratotrupes gonzaloi* Arriaga-Jiménez et al., 2022 / Canadian Museum of Nature, Musée canadien de la NATURE”; CMNC 00031076.

Paratypes

MEXICO – **Guerrero** • 1 ♂; “Guerrero, Omiltemi; 7300’ alt. / Aug. 14-15 1966 / Ball-Whitehead leg. / Specimen photographié par François Génier / *Ceratotrupes sturmi* (Jekel), Det. H.F. Howden 69 / Canadian Museum of Musée canadien de la NATURE”; CMNC 00031074 • 1 ♂; “Guerrero, Omiltemi / Aug. 1965 / P. Reyes C. leg. / Halffter 73-29 / Canadian Museum of Musée canadien de la NATURE”; CMNC 00031075 • 1 ♂; “Guerrero, Omiltemi / 99°41’27.9”W, 17°33’37.9”N / 2244 m a.s.l. / 09 Aug. 2018 / Arriaga J.A. leg. / bosque de galería, coprotrampa / <http://id.luomus.fi/NC.07>; FMNH • 1 ♂; Guerrero, Omiltemi / 25 Jul. 1965 / G. y V. Halffter leg. / camino bosque nebuloso, pino (modificado), 1° estación, cebo excremento, excremento humano, noche-día, Bosque nebuloso / *Ceratotrupes sturmi* (Jekel, 1866), H.F. Howden, 1973”; <http://id.luomus.fi/NC.08>; FMNH • 1 ♂; “Guerrero, Omiltemi / 25 Jul. 1965 / G. y V. Halffter leg. / camino bosque nebuloso, pino (modificado), 1° estación, cebo excremento, excremento humano, noche-día, Bosque nebuloso / *Ceratotrupes sturmi* (Jekel, 1866), H.F. Howden, 1973, Howden 73-26”; <http://id.luomus.fi/NC.09>; FMNH • 1 ♀; “Guerrero, Tetipac / 2 Aug. 1990 / excremento burro / Fco. E. Figueroa”; CEMT. – **Jalisco** • 1 ♂; “Jalisco, Estación Científica Las Joyas / 1900 m a.s.l. / Aug 1997 / Sancampús Reg. Pino, necrotrampa 8F / M. Lopez”; CEMT • 1 ♀; “Jalisco, Estación Científica Las Joyas / 1900 m a.s.l. / Aug 1997 / Sancampús Reg. Pino, necrotrampa 7D / M. Lopez”; CEMT.

Description of the male

COLOUR. Body black with strong purple to greenish iridescence on pronotum and elytra; dorsally, tegument shining, head and pronotal disc silky; antennal segments brown, antennal club brownish.

HEAD. Clypeus obtusely triangular and elongated, with a medial, high triangular horn; from posterior side, horn wide and longitudinally sulcate, tip slightly to distinctly depressed at middle; head punctation very obsolete and superficial; genae squared, with elevated and acuminate angle; frons smooth, unpunctured, with two weak and oblique ridges along inner side of eyes.

THORAX. In lateral view, pronotum weakly convex; in dorsal view, posterior edge of pronotum without margin at middle, lateral edges weakly curved from posterior angles to midline, straight and convergent from midline to anterior angles; anterior angles obtuse; pronotal disc either unpunctured or with a few, shallow punctures across midline, sides with strong and coarse punctures sparsely distributed from posterior to anterior angles; in lateral view, anteromedial projection curved upward apically; in dorsal view, projection with sides parallel, tip widely emarginated at middle. Elytral interstriae slightly convex, very finely and densely punctate. Ventral side of thoracic sclerites (i.e., pro-, meso- and metasternum) with long, yellowish to brownish setae.

LEGS. Protibiae robust, with six external teeth, ventral side with a longitudinal, crenulated carina; apical spur long and slender; meso- and metatibiae each with four entire, transversal carinae on posterior side; femora unmodified, with long yellowish setae.

Sexual dimorphism

Female specimens have the clypeal horn distinctly shorter and slightly depressed posteriorly; from above, the clypeal horn is triangular-shaped, apex almost reaching clypeal edge; anteromedial pronotal

protuberance callus-like and transverse, depressed on superior side and close to anterior pronotal edge. Female specimens of *C. gonzaloi* sp. nov. are very similar to those of *C. sturmi*, but they can be distinguished by the posterior edge of the pronotum not having a margin at the middle, and the presence of very fine and dense punctation on the elytral interstriae.

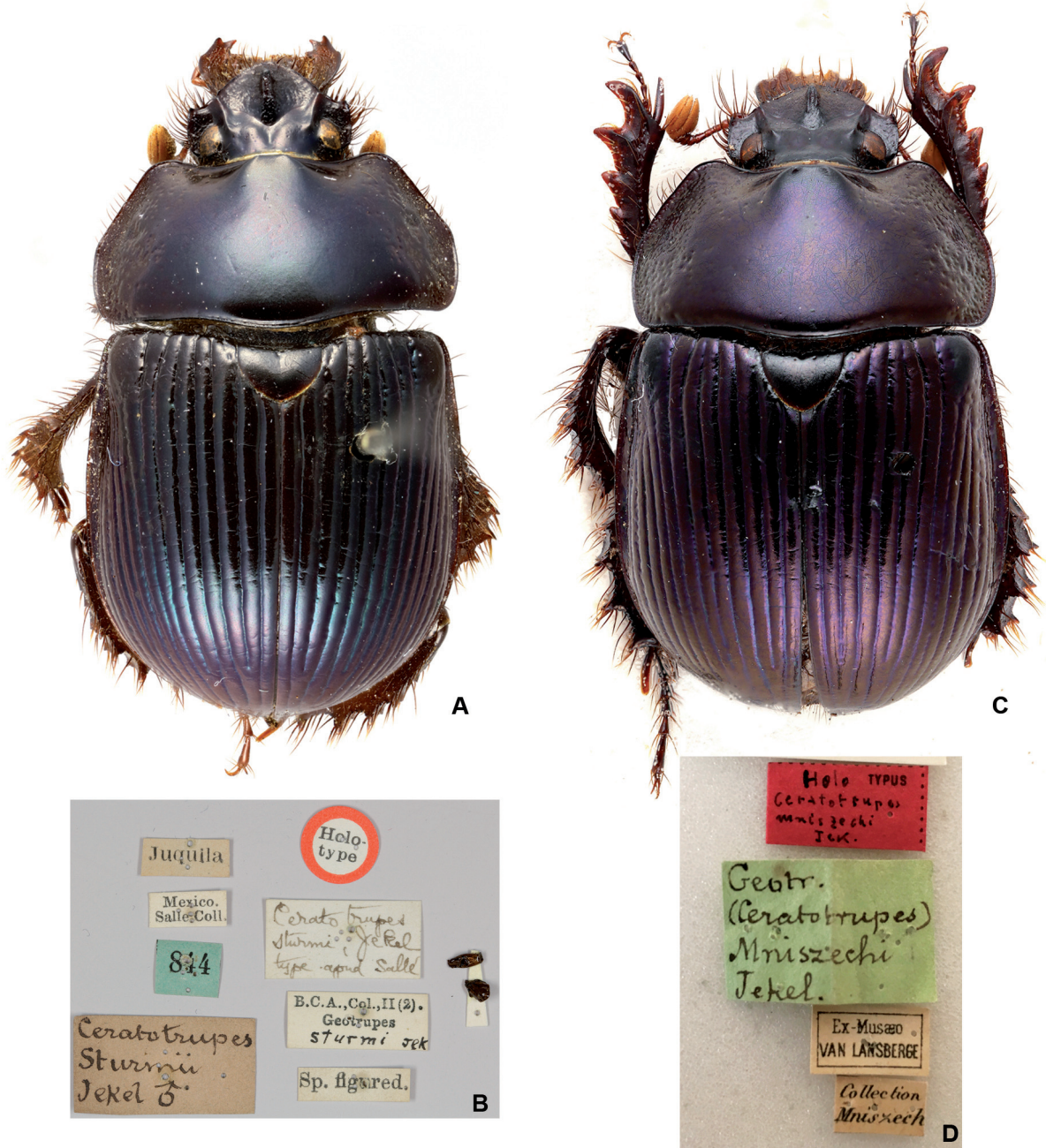


Fig. 5. Type specimens and original labels. **A–B.** *Ceratotrupes sturmi* (Jekel, 1865), holotype, ♂ (NHML). **A.** Dorsal habitus. **B.** Labels. **C–D.** *Ceratotrupes mniszeechi* (Jekel, 1865), holotype, ♂ (MNHN). **C.** Dorsal habitus. **D.** Labels.

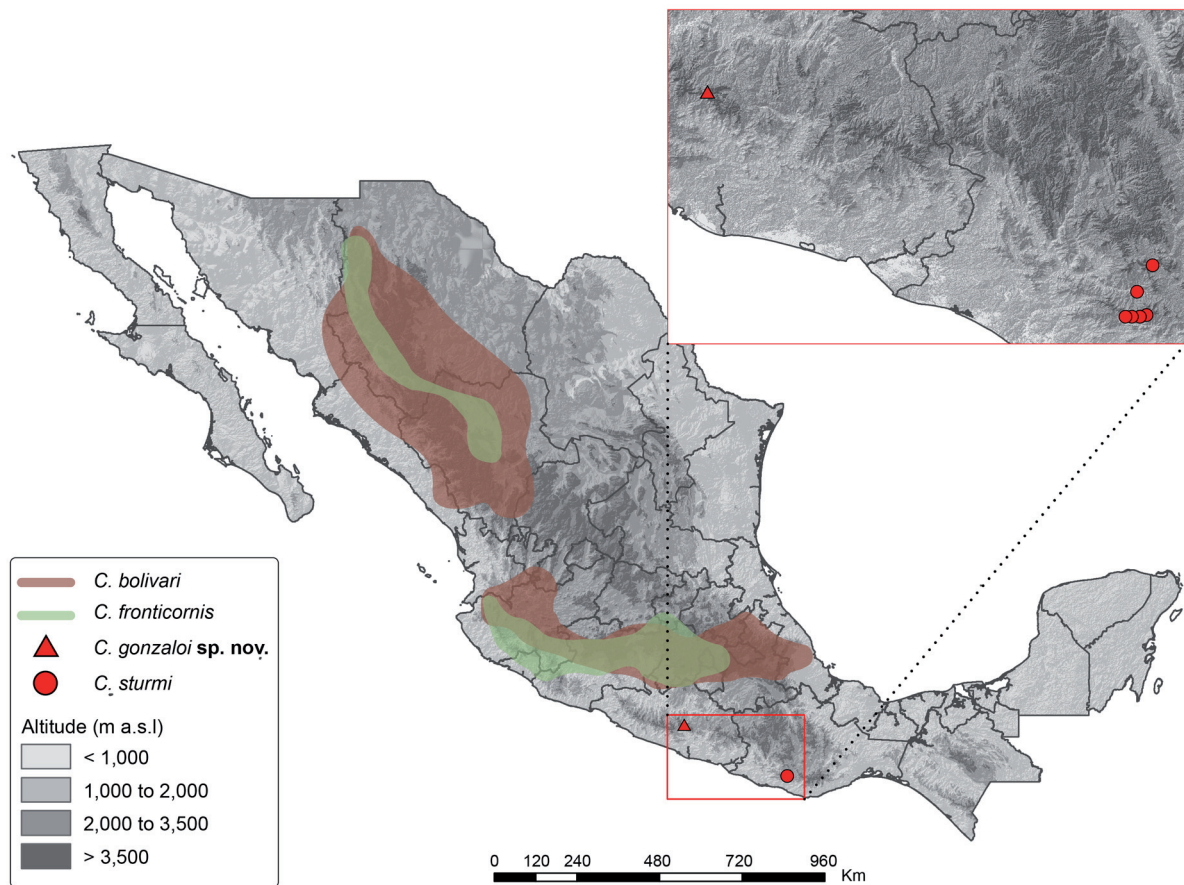


Fig. 6. Geographic distribution of the genus *Ceratotrupes* Jekel, 1865.

Ecology and biogeography

This species occurs in the Sierra Madre del Sur and it seems to be restricted to the surrounding mountains of Omiltemi, Guerrero, where it occurs exclusively in pine forest. Many of the specimens historically identified as *C. sturmi* in natural history collections instead belong to this new species. Howden (1974, 2003) noticed that specimens identified as *C. sturmi* showed some geographically restricted differences, such as shape of cephalic horn and genitalia in males, elytral punctation and posterior edge of pronotum with or without margin at middle. During this research we examined the specimens mentioned by Howden (Juquila and Juchatengo, Oaxaca, and Omiltemi, Guerrero; CMNC) and confirm that they belong to different species, namely *C. gonzaloi* sp. nov. (Omiltemi) and *C. sturmi* (Oaxaca).

Identification key to the species of the genus *Ceratotrupes* Jekel, 1865

1. Anterior half of lateral edges of pronotum curved 2
 - Anterior half of lateral edges of pronotum straight and convergent 3

2. Anterior angles of pronotum of male evenly curved; outer surface of the first antennomere of antennal club with a deep elliptical groove (Fig. 2C); middle and posterior trochanters densely and clearly punctate *C. bolivari* Halffter & Martínez, 1962
 - Anterior angles of pronotum of male obtusely squared; outer surface of the first antennomere of antennal club either without or with a feeble groove; middle and posterior trochanters with scattered punctures *C. fronticornis* (Erichson, 1847)

3. Posteromedial edge of pronotum without margin (Fig. 4C); clypeal horn strong, as large as one third the distance between inner margin of eyes, tip medially depressed (Fig. 4A, C); anteromedial pronotal projection with parallel sides (Fig. 4A, D), apically almost as large as half the distance between inner margin of eyes, apical edge widely depressed, with lateral protrusions distant; elytral interstriae very finely and densely punctate *C. gonzaloi* sp. nov.
- Posteromedial edge of pronotum margined (Fig. 3C); clypeal horn thin, as large as one fifth of the distance between inner margin of eyes, tip medially not depressed, narrow and blunt (Fig. 3A, C); anteromedial pronotal projection with convergent sides, apically almost as large as one third of the distance between inner margin of eyes, apical edge very narrowly depressed, with lateral protrusions very close; elytral interstriae unpunctured *C. sturmi* (Jekel 1865)

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The authors want to thank Maxwell Barclay (NHML), François Génier (CMNC) and Olivier Montreuil (MNHN) for the loan of type and non-type material of *C. sturmi* and *C. gonzaloi*, as well as for the access to the Coleoptera collections. The holotype of *C. mniszewski* (MNHN) was examined and photographed by AAJ and MR. In addition, we would like to thank Delfino Hernández, Roberto Arce, Cuauhtémoc Deloya and Viridiana Vega (IEXA) for having loaned us some of the *Ceratotrupes* specimens analysed in this study. This research was partly supported by the EU Synthesys programme (FR-TAF-1210).

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