

RESEARCH PAPER

A predicted new *Geotrupes* from the mountains of Oaxaca, Mexico, and a description of the male of *Geotrupes lobatus* (Coleoptera: Geotrupidae)

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Abstract. *Geotrupes nuntiatius* Kohlmann & Arriaga-Jiménez, sp. nov., is described from the Mixteca shield, in the mountains of Oaxaca, Mexico. Its habitat, distribution, and ecology are discussed. The male of *Geotrupes lobatus* Howden, 1974 is described for the first time. An updated key of the genus for the state of Oaxaca is presented to facilitate identification. Photographs of the specimens, diagnostic features, and their aedeagi, as well as distribution maps, are also included.

Key words. Coleoptera, Geotrupidae, *Geotrupes*, identification key, new species, superspecies, vicariance, Last Glacial Maximum, paleoclimatic model, Mixteca shield, Mexico

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Introduction

HOWDEN (1974) made the last descriptions of Oaxacan *Geotrupes* Latreille, 1797 species forty-six years ago, describing two species from this state, *G. pecki* Howden, 1974 and *G. lobatus* Howden, 1974. Subsequently, HOWDEN (1980) described *G. reddelli* Howden, 1980 from a cave in Puebla, the last described species for Mexico. *Geotrupes pinalonensis* Howden, 1994, collected from the Sierra de las Minas, Guatemala, was the very last species of *Geotrupes* described for the American Continent.

The state of Oaxaca seems to be the area with the highest *Geotrupes* species richness in Mexico, with six recorded species, of which four are endemic. *Geotrupes truncaticornis* Howden, 1964 has been erroneously reported for Oaxaca by TROTTA-MOREU et al. (2008), based on misidentified material. This makes Oaxaca the state with the highest number of known endemic species and suggests a very active ongoing speciation process, where three endemic species apparently originated as recently as the Last Glacial Maximum (LGM), as discussed below.

After Oaxaca, the states of Puebla and Hidalgo are the most *Geotrupes*-rich areas, each with four species, with one endemic species present in each state (HOWDEN 2003).

RAHBEK et al. (2019) have indicated that mountains contribute disproportionately to terrestrial biodiversity, especially in the tropics, and call this phenomenon ‘Humboldt’s Enigma’. Mountain regions represent about 25 % of all land area; however, within them inhabit more than 85 % of the world’s species of amphibians, birds, and mammals (RAHBEK et al. 2019). RAHBEK et al. (2019) consider that the complex climatic characteristics of the rugged mountain terrain likely play a key role in generating and maintaining biological diversity. RAHBEK et al. (2019) base their studies on vertebrates, but insects have not been studied from this perspective. The state of Oaxaca could represent an ideal area for such type of studies, especially for beetles, a rather understudied group concerning tropical mountains.

Arriaga-Jiménez has been actively collecting beetles in the mountains of Oaxaca for the last three years and was able to trap one male of *G. lobatus* in the Sierra Sur (Sierra



de Miahuatlán). The original description of *G. lobatus* was based on three female specimens, and this recent collection allows us to describe the male of this extremely rare species.

This same collecting process has also led to the discovery of a new species of *Geotrupes* from the mountains of the Mixteca shield. The existence of a probable new species in the Mixteca was suggested based on a paleoclimatic model of the Last Glacial Maximum in Oaxaca (ARRIAGA-JIMÉNEZ et al. 2020). The new *Geotrupes* species described here elevates the known number of Mexican species to 17.

A key for all six known *Geotrupes* species from Oaxaca is also presented with photographs of the specimens, important characters, aedeagi, and distribution maps.

Materials and methods

Specimens collected by Alfonsina Arriaga-Jiménez (AAJ) and Asunción Martínez-Tomínez (AMT) during 2017 and 2018 in ‘El Cerro del Águila’ were studied. The holotype, allotype, and 138 paratypes (59 males and 79 females) of *Geotrupes nuntiatius* sp. nov. are deposited in the IEXA Colección Entomológica (Entomology Collection), Instituto de Ecología, Xalapa, Mexico. Further paratypes are deposited in the following institutes: 38 males and 39 females at the Colección Nacional de Insectos, Instituto de Biología (UNAM), Universidad Nacional Autónoma de México, Mexico; 30 males and 30 females at the Facultad de Estudios Superiores, Campus Tlaxcala (FEST), Tlaxcala, Mexico; 30 males and 30 females at the Coleoptera Collection of the Center of Biological Research of the Universidad Autónoma del Estado de Hidalgo (UAEH), Hidalgo, Mexico; 30 males and 30 females at the Centro de Estudios de Zoología de la Universidad de Guadalajara (CZUG), Zapopan, Mexico; 57 males and 65 females at the Canadian Museum of Nature (CMN) in Ottawa, Canada; 30 males and 30 females at the Coleção de Entomologia da Universidade Federal de Mato Grosso, Cuiabá (CEMT), Brazil; 42 males and 30 females at the Museum National d’Histoire Naturelle, Paris (MNHN), France; 34 males and 30 females at the Natural History Museum, London (NHMUK), England; 15 males and 15 females at the Entomological collection of the National Museum in Prague (NMPC), Czech Republic; and 6 male and 19 females in the personal collection of Julián Blackaller, La Paz, Baja California, Mexico (JBLPM). The male of *G. lobatus* is deposited in the IEXA Colección Entomológica (Entomology Collection), Instituto de Ecología, Xalapa, Mexico.

Body measurements were made to the nearest 0.1 mm using an ocular micrometer with a Zeiss Stemi DV4 stereoscope, Jena, Germany. Photographs were taken by: Susana Guzmán-Gómez (Instituto de Biología, Universidad Nacional Autónoma de México, IBUNAM, Mexico City, Mexico) using a Zeiss AXIO Zoom V16 microscope, a Zeiss AxioCam MRc5 camera, and the Zeiss efficient navigation multifocal technology program (Zeiss, Jena, Germany); BJCG using a multifocus digital microscope Leica Z16 APOA; Alfonso Aceves (INECOL) using a Canon T2i camera, extension tubes, a 100 mm macro, and an external Canon flash; and photographs of material from the

CMNC were taken by AAJ using a Leica Z16 system and LAS software for image stacking. The distribution maps were made using QGIS desktop 2.14.19.

Taxonomy

In his seminal paper on the genus *Geotrupes*, HOWDEN (1964) considered the existence of four subgenera for the Mexican fauna, each containing a varying number of species indicated here in parentheses: *Cnemotrupes* Jekel, 1866 (9), *Geotrupes* (1), *Onthotrupes* Howden, 1964 (1), and *Phelotrupes* Jekel, 1866 (1). Due to the lack of a male, HOWDEN (1980) wrote the following indication in his key for the Geotrupini of Mexico and Central America: *Geotrupes* (*Cnemotrupes*?) *lobatus*. Subsequently, the *Geotrupes* species considered in this study, which were placed in the subgenus *Cnemotrupes*, were transferred by ZUNINO (1984) into a separate genus *Onthotrupes*. To the sole original member of this group, *Onthotrupes onitidipes* (Bates, 1887), ZUNINO (1984) added: *O. guerreroensis* (Howden, 1964), *O. herbeus* (Jekel, 1866), *O. nebularum* (Howden, 1964), *O. pecki*, *O. sobrinus* (Jekel, 1866), and *O. viridiobscurus* (Jekel, 1866). This genus was placed with seven other genera by ZUNINO (1984) into a new solely American tribe, the Ceratotruperini. The genus *Onthotrupes* is distributed from the mountains of Durango in the Sierra Madre Occidental, Sierra Madre Oriental, Trans-Mexican Volcanic Belt, and Sierra Madre del Sur in Mexico, all the way to the mountain systems of Guatemala and El Salvador. HOWDEN (2003) revised this taxonomic action and considered *Onthotrupes* to be a subgenus of *Geotrupes* and added to the list of this group: *Geotrupes* (*O.*) *lobatus*, *G.* (*O.*) *sallei* Jekel, 1866, and *G.* (*O.*) *truncaticornis* Howden, 1964. The authors of this paper are following this last taxonomic usage.

Geotrupes (*Onthotrupes*) *nuntiatius* Kohlmann & Arriaga-Jiménez, sp. nov.

(Figs 1, 3, 5, 10, 11)

Type material. HOLOTYPE: ♂ (deposited in IEXA; Figs 1a, 2b), ‘México, Mixteca (Cerro del Águila) Oaxaca / 27-VIII-18 / Coprotrampa / x-97.663923° W y- 17.130330° N / Bosque, 3210 m / Arriaga J.A. Col.’ [printed]. ALLOTYPE: ♀ (Fig. 1b), ‘México, Mixteca (Cerro del Águila) / Oaxaca / 20-VII-18 / Coprotrampa / x-97.685581° W y- 17.114517° N / Bosque, 3012 m / Arriaga J.A. Col.’ [printed]. PARATYPES (768 specimens): **MEXICO: OAXACA:** 17-VI-18 Mixteca (Cerro del águila) Oaxaca C.D. perro. 17.119718° -97.684495° 3065m Bosque AAJ col (2 ♂♂ CZUG, 2 ♀♀ CMN, 2 ♂♂ NMPC). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca C.D. perro 17°7’35.5” -97°39’55.65” 3135m Matorral AAJ col (10 ♂♂ IEXA, MNHN, 2 ♀♀ IEXA, NHMUK). 21-VII-18 Mixteca (Cerro del águila) Oaxaca C.D. vaca 17.12301° -97.67303° 2967m Bosque AAJ col (1 ♂). 19-VII-18 Mixteca (Cerro del águila) Oaxaca C.D. 17.126010° -97.681780° 2820m Matorral AAJ col (5 ♂♂ CMN, 4 ♀♀ MNHN, NHMUK). 17-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.119661° -97.684522° 3066m Bosque AAJ col (3 ♂♂ CZUG, IEXA). 13-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.130087° -97.708348° 2861 m Bosque AAJ col (1 ♀). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.13123° -97.70777° 2807 m Bosque AAJ col (1 ♂ UAEH, 2 ♀♀ CZUG). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.13232° -97.70776° 2791 m Bosque AAJ col (3 ♀♀ IEXA). 01-IX-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.183022° -97.727770° 2234m Bosque AAJ col (1 ♂ MNHN, 1 ♀ NMPC). 30-VIII-18 Mixteca (Cerro del

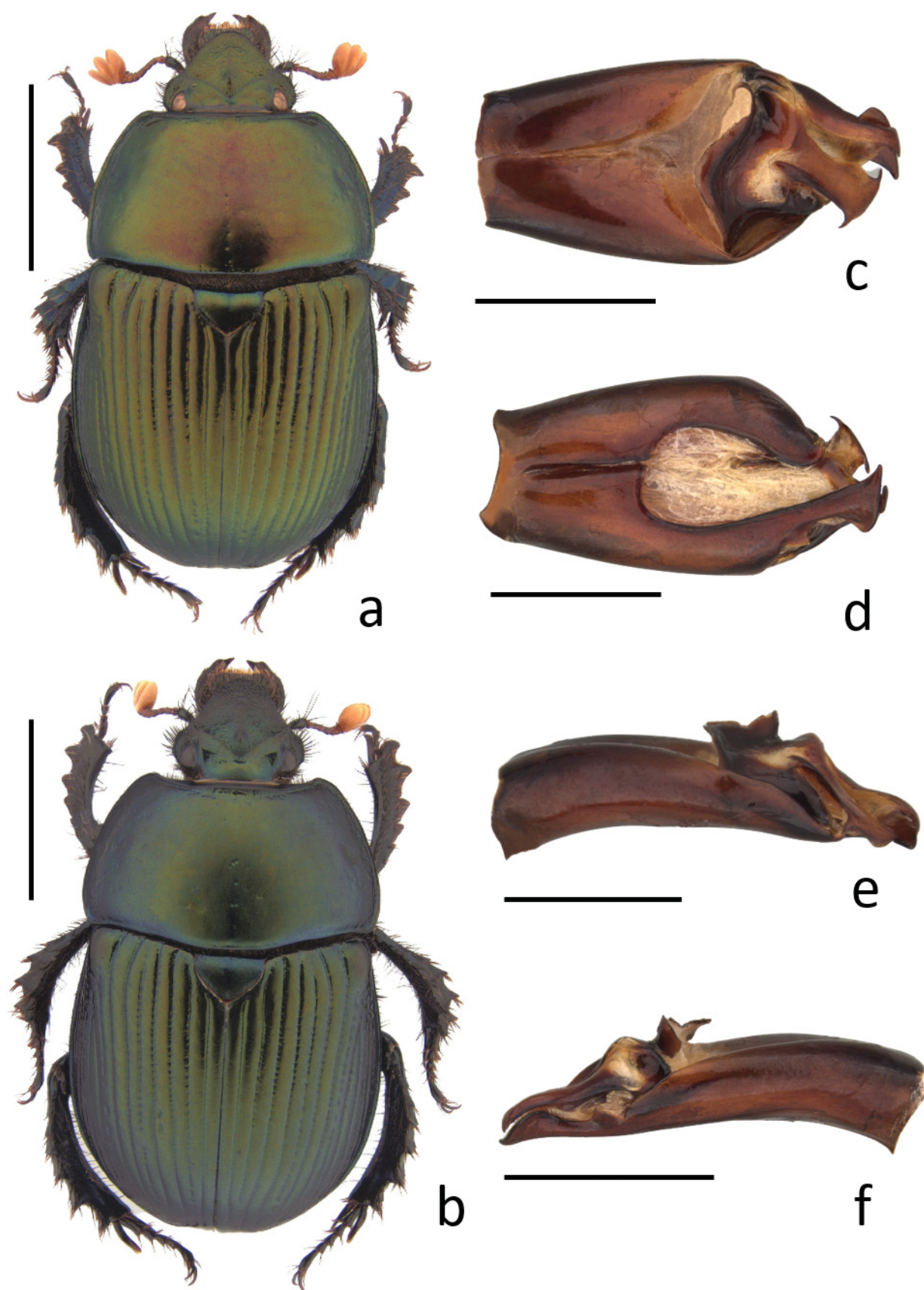


Fig. 1. *Geotrupes nuntiatius* Kohlmann & Arriaga-Jiménez, sp. nov.: a – male dorsal view (17.13087°N, -97.66402°W); b – female dorsal view (17.129932°N, -97.663673°W); c–f – male genitalia: c – in dorsal view, d – in ventral view; e–f – lateral views. Scale bars = 5 mm (a–b), 2 mm (c–f).

águila) Oaxaca Coprotrampa 17.152799° -97.713897° 2642m Bosque AAJ col (1 ♂ CMN). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.132831° -97.707548° 2839m Bosque AAJ col (1 ♂ CMN). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.133220° -97.707226° 2844 m Bosque AAJ col (1 ♂ FEST). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.133220° -97.707226° 2844 m Bosque AAJ col (4 ♂♂ CMN, 4 ♀♀ CZUG, IEXA,

2 ♀♀ NMPC). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.133487° -97.70781° 2804m Bosque AAJ col (1 ♂). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.133487° -97.706736° 2858m Bosque AAJ col (1 ♂, 1 ♀ IEXA). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.133381° -97.706166° 2849m Bosque AAJ col (4 ♂♂ CMN, 1 ♀ CMN). 22-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.123113° -97.673899° 3136 m Bosque AAJ col

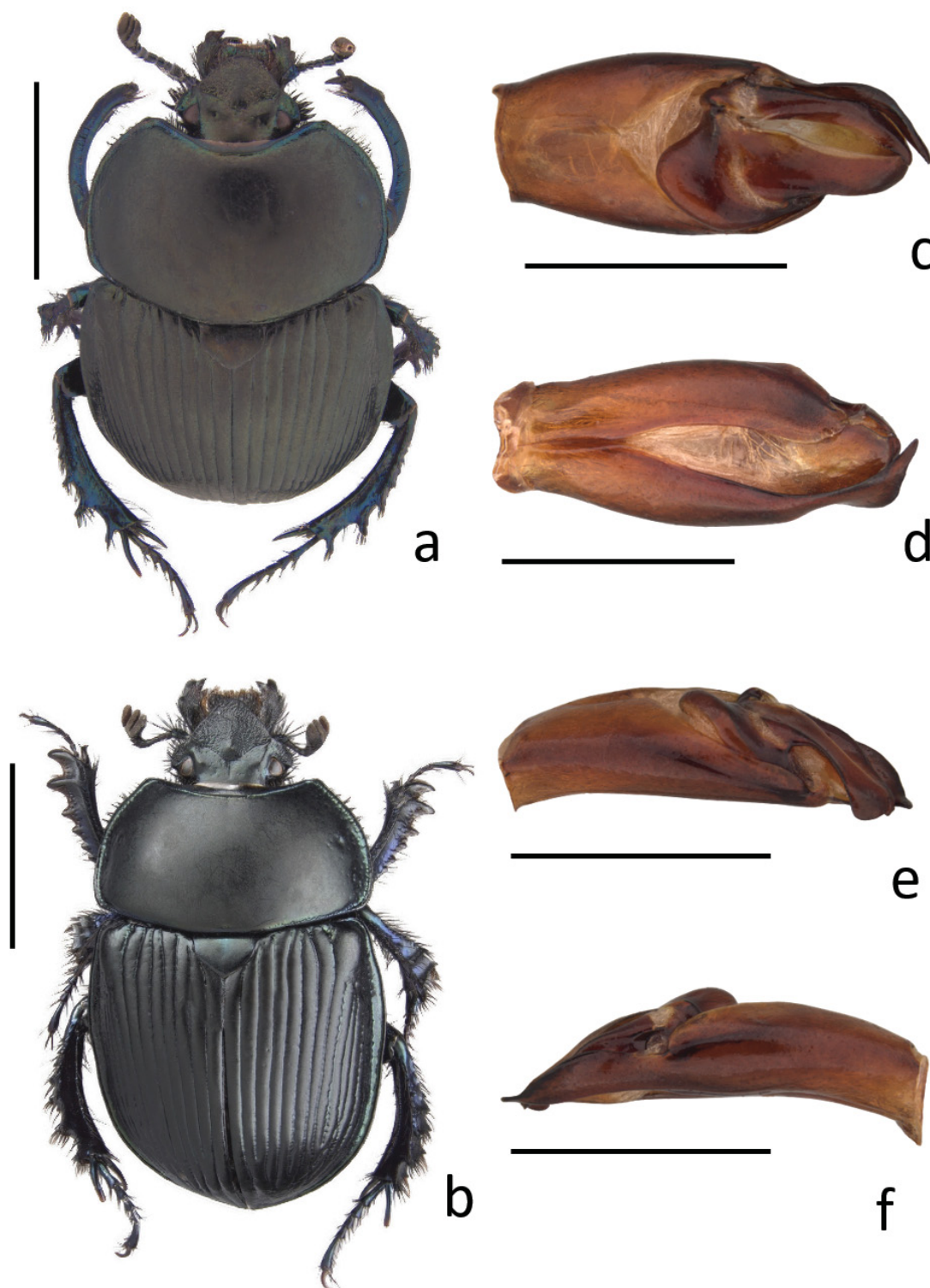


Fig. 2. *Geotrupes lobatus* Howden, 1974: a – male dorsal view (16.16096°N, -96.24452°W); b – female dorsal view (16.16096°N, -96.24452°W); c–f – male genitalia: c – in dorsal view, d – in ventral view; e–f – lateral views. Scale bars = 5 mm (a–b), 2 mm (c–f).

(1 ♂ MNHN, 1 ♀ NMHUK). 20-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.152902° -97.715444° 2624 m Bosque AAJ col (4 ♂ MNHN, NMHUK, 2 ♂ NMPC). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.105464° -97.705154° 2810 m Bosque AAJ col (1 ♀ FEST). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.110796° -97.687456° 3010 m Bosque AAJ col (1 ♂, 2 ♀♀ CMN). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.111180° -97.687293° 3004 m Bosque AAJ col (1 ♀ FEST). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.111180° -97.687293° 3004 m Bosque AAJ col (1 ♂ CZUG). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.111627° -97.686797° 3015 m Bosque AAJ col (1 ♂ CMN). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.111627° -97.686797° 3015 m Bosque AAJ col (1 ♂ CMN, 1 ♀ CMN). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.113481° -97.685020° 3002 m Bosque AAJ col (2 ♂ UAEH, 1 ♀ CZUG). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.113481° -97.685020° 3002 m Bosque AAJ col (1 ♂ FEST). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.113481° -97.685002° 3002 m Bosque AAJ col (2 ♂ UAEH). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.114517° -97.685581° 3012 m Bosque AAJ col (1 ♂ FEST, 2 ♀♀ JBLPM). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.114517° -97.685581° 3012 m Bosque AAJ col (4 ♂ CZUG, IEXA, 7 ♀♀ CZUG, JBLPM, IEXA). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.114517° -97.685581° 3012 m Bosque AAJ col (2 ♂ CMN). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.114061° -97.685462° 3023 m Bosque AAJ col (2 ♀♀ FEST). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.125511° -97.681109° 3158 m Bosque AAJ col (4 ♂ FEST, IEXA, 2 ♀♀ FEST, JBLPM). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.125511° -97.681109° 3158 m Bosque AAJ col (1 ♀ UAEH). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.125511° -97.681109° 3158 m Bosque AAJ col (3 ♂ UAEH, 6 ♀♀ CZUG, UAEH). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.125921° -97.681559° 3168 m Bosque AAJ col (7 ♂ IEXA, JBLPM, NMHUK, UNAM, 5 ♀♀ CMN, FEST, JBLPM). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.125921° -97.681559° 3168 m Bosque AAJ col (5 ♂ JBLPM, 1 ♀ FEST, JBLPM). 23-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.125921° -97.681559° 3168 m Bosque AAJ col (9 ♂ CZUG, FEST, UAEH, 7 ♀♀ FEST, UAEH, 1 ♀ NMPC). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.125921° -97.681559° 3168 m Bosque AAJ col (4 ♂ UNAM, 5 ♀♀ FEST, JBLPM, UNAM). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.130874° -97.664017° 3234 m Bosque AAJ col (1 ♂ CZUG, 3 ♀♀ UAEH). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.130874° -97.664017° 3234 m Bosque AAJ col (2 ♂ FEST, 2 ♀♀ CMN, FEST). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.130874° -97.664017° 3234 m Bosque AAJ col (1 ♂, 8 ♀♀). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.130874° -97.664017° 3234 m Bosque AAJ col (3 ♂ CMN, 6 ♀♀ CMN, MNHN, UNAM). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.130330° -97.663923° 3219 m Bosque AAJ col (3 ♂ FEST, 1 ♀ FEST). 22-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.130330° -97.663923° 3219 m Bosque AAJ col (8 ♂ CZUG, UAEH, 7 ♀♀ CZUG). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.130330° -97.663923° 3219 m Bosque AAJ col (13 ♂ CMN, IEXA, UNAM, 8 ♀♀ IEXA, UAEH, UNAM, 3 ♀♀ NMPC). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.130330° -97.663923° 3219 m Bosque AAJ col (7 ♂ CZUG, IEXA, 8 ♀♀ CZUG, IEXA, UNAM, 1 ♂ NMPC). 20-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129932° -97.663673° 3222 m Bosque AAJ col (1 ♀). 13-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129932° -97.663673° 3222 m Bosque AAJ col (1 ♂ UAEH, 3 ♀♀ UAEH). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129932° -97.663673° 3222 m Bosque AAJ col (6 ♂ CMN, 2 ♀♀ CMN). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129433° -97.663794° 3220 m Bosque AAJ col (1 ♀). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129433° -97.663794° 3220 m Bosque AAJ col (1 ♀). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129433° -97.663794° 3220 m Bosque AAJ col (1 ♂, 8 ♀♀). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129433° -97.663794° 3220 m Bosque AAJ col (5 ♂, 6 ♀♀).

29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129433° -97.663794° 3220 m Bosque AAJ col (9 ♂, 11 ♀♀, 1 ♂ NMPC). 20-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128973° -97.663948° 3217 m Bosque AAJ col (9 ♂, 13 ♀♀). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128973° -97.663948° 3217 m Bosque AAJ col (10 ♂, 13 ♀♀). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128973° -97.663948° 3217 m Bosque AAJ col (10 ♂, 12 ♀♀). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128176° -97.661997° 3232 m Matorral AAJ col (1 ♀ CMN). 31-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128176° -97.661997° 3232 m Matorral AAJ col (6 ♂ CMN, IEXA, UNAM). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128176° -97.661997° 3232 m Matorral AAJ col (2 ♂, 10 ♀♀). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128176° -97.661997° 3232 m Matorral AAJ col (4 ♂ CMN, IEXA, UNAM, 5 ♀♀ CMN). 27-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128176° -97.661997° 3232 m Matorral AAJ col (1 ♂). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128176° -97.661997° 3232 m Matorral AAJ col (16 ♂, IEXA, UNAM, 6 ♀♀). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.127822° -97.662464° 3229 m Matorral AAJ col (8 ♂, 10 ♀♀ CMN, IEXA). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.127822° -97.662464° 3229 m Matorral AAJ col (2 ♂ CMN, 5 ♀♀ CMN, UNAM). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.127822° -97.662464° 3229 m Matorral AAJ col (14 ♂ CEMT, FEST, IEXA, UNAM, 11 ♀♀ CMN, FEST, JBLPM). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.127822° -97.662464° 3229 m Matorral AAJ col (2 ♂ MNHN, 4 ♀♀ MNHN, 2 ♀♀ NMPC). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.127822° -97.662464° 3229 m Matorral AAJ col (2 ♂, 1 ♀ NMPC). 20-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128058° -97.662982° 3241 m Bosque AAJ col (6 ♂ MNHN, NMHUK, 4 ♀♀ MNHN, NMHUK). 25-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128058° -97.662982° 3241 m Bosque AAJ col (7 ♂ CMN, MNHN, 18 ♀♀ CMN, MNHN, UNAM). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128058° -97.662982° 3241 m Bosque AAJ col (2 ♂). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128058° -97.662982° 3241 m Bosque AAJ col (2 ♂ CMN, 3 ♀♀ CMN). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128267° -97.663421° 3242 m Bosque AAJ col (6 ♂ MNHN, NMHUK, 7 ♀♀ NMHUK, UNAM). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128267° -97.663421° 3242 m Bosque AAJ col (5 ♂ CMN, 11 ♀♀ CMN, IEXA). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128860° -97.663403° 3236 m Bosque AAJ col (2 ♂ MNHN, UAEH, 2 ♀♀ NMHUK, 2 ♂ NMPC). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128860° -97.663403° 3236 m Bosque AAJ col (3 ♂ FEST). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128860° -97.663403° 3236 m Bosque AAJ col (4 ♂ UAEH, 13 ♀♀ CZUG, IEXA, 1 ♀ NMPC). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.129932° -97.663673° 3222 m Bosque AAJ col (3 ♂ UAEH, 3 ♀♀ CZUG). 19-VI-18 Mixteca (Cerro del águila) Oaxaca C.D. 17.13232° -097.70776° 2791 m Bosque AAJ col (12 ♂ CMN, MNHN, UNAM, 11 ♀♀ JBLPM, MNHN, NMHUK, UNAM, 1 ♂ NMPC). 1-IX-18 Mixteca (Cerro del águila) Oaxaca C.D. 17.13232° -097.70776° 2791 m Bosque AAJ col (3 ♂ CZUG, 1 ♀). 28-VI-17 Mixteca (Cerro del águila) Oaxaca Coprotampa 17°05'33.9" -97°39'18.1" 2744 m Bosque de pino-encino AMT col (1 ♀ UNAM, 1 ♂ NMPC). 13-VII-17 Mixteca (Cerro del águila) Oaxaca Micetotrampa 17°03'57.1" -97°38'13.5" 2629 m Bosque de pino-encino AMT col (1 ♀ UNAM). 13-VII-17 Mixteca (Cerro del águila) Oaxaca Coprotampa 17°05'16.9" -97°39'42.2" 2535 m Bosque de pino-encino AMT col (2 ♀♀ UNAM, 1 ♂ NMPC). 28-IX-17 Mixteca (Cerro del águila) Oaxaca Micetotrampa 17°05'18.5" -97°39'47.0" 2543 m Bosque de pino-encino AMT col (2 ♂ UNAM, 1 ♀ UNAM). 13-VII-17 Mixteca (Cerro del águila) Oaxaca Coprotampa 17°05'18.5" -97°39'47.0" 2543 m Bosque de pino-encino AMT col (2 ♀♀ JBLPM). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.125511° -97.681109° 3158 m Bosque AAJ col (2 ♂). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128267° -97.663421° 3242 m Bosque AAJ col (11 ♂, 12 ♀♀). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotampa 17.128973° -97.663948° 3217 m Bosque AAJ col (8 ♂, 6 ♀♀).



Fig. 3. Morphological detail of male protibiae: a – *Geotrupes nuntiatius* Kohlmann & Arriaga-Jiménez, sp. nov.; b – *G. lobatus* Howden, 1974; arrow pointing at the apical tooth on the profemur. Scale bar = 2 mm.



Fig. 4. Comparison of male genitalia: a – *Ceratotrupes bolivari* Halffter & Martínez, 1962; and b – *Geotrupes lobatus* Howden, 1974. Scale bar = 2 mm.

3 ♀♀). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.128267° -97.663421° 3242m Bosque AAJ col (2 ♂♂, 1 ♀). 23-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.128267° -97.663421° 3242m Bosque AAJ col (3 ♂♂, 4 ♀♀). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.125921° -97.681559° 3168m Bosque AAJ col (2 ♂♂ CEMT, NHMUK, 2 ♀♀ CEMT). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.114517° -97.685581° 3012m Bosque AAJ col (3 ♂♂ NHMUK, 4 ♀♀ CEMT). 23-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.132831° -97.707548° 2839m Bosque AAJ col (4 ♂♂ NHMUK, 3 ♀♀ CEMT). 23-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.130874° -97.664017° 3234 m Bosque AAJ col (4 ♂♂ NHMUK, 3 ♀♀ CEMT). 23-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.125511° -97.681109° 3158 m Bosque AAJ col (3 ♂♂ NHMUK, 1 ♀ CEMT). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.111627° -97.686797° 3015 m Bosque AAJ col (2 ♂♂ NHMUK, 3 ♀♀ CEMT). 21-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.114517° -97.685581°

3012m Bosque AAJ col (1 ♀ NHMUK). 24-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.152430° -97.714620° 2661m Bosque AAJ col (1 ♂ NHMUK). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.111180° -97.687293° 3004 m Bosque AAJ col (2 ♂♂ CEMT, 2 ♀♀ CEMT). 20-VI-18 Mixteca (Cerro del águila) Oaxaca C.D. exc. perro 17.159213° -97.721293° 2520m Bosque AAJ col (4 ♂♂ CEMT, 2 ♀♀ UNAM). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.110796° -97.687456° 3010 m Bosque AAJ col (3 ♂♂ CEMT, 5 ♀♀ UNAM). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.130330° -97.663923° 3219 m Bosque AAJ col (1 ♂ CEMT). 23-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.112194° -97.685904° 3024 m Bosque AAJ col (1 ♂ CEMT, 1 ♀ CEMT). 01-IX-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.152430° -97.714620° 2661m Bosque AAJ col (1 ♂ CEMT). 27-VI-17 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17°06'11.1" -97°39'23.2" 2732m Bosque de pino-encino AMT col (4 ♂♂ CEMT, IEXA, UNAM, 1 ♀ UNAM). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.111180° -97.687293° 3004 m Bosque AAJ col (1 ♀ CEMT). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.111627° -97.686797° 3015 m Bosque AAJ col (2 ♀♀ CEMT). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.114061° -97.685462° 3023 m Bosque AAJ col (1 ♀ CEMT, 2 ♂♂ 1 ♀ NMPC). 27-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.114061° -97.685462° 3023 m Bosque AAJ col (1 ♀ NMPC). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.111627° -97.686797° 3015 m Bosque AAJ col (1 ♀). 20-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.13072° -97.70813° 2825 m Bosque AAJ col (2 ♀♀ CEMT). 19-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.113481° -97.685020° 3002m Bosque AAJ col (1 ♀ UNAM). 24-VI-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.151172° -97.714956° 2633 m Bosque AAJ col (1 ♀ UNAM). 24-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.153153° -97.713830° 2632 m Bosque AAJ col (1 ♀ UNAM). 17-VI-18 Mixteca (Cerro del águila) Oaxaca C.D. exc. vaca 17.123698° -97.674714° 3154 m Bosque AAJ col (1 ♀ UNAM). 29-VIII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.13011° -097.10835° 2836 m Bosque AAJ col (1 ♀ UNAM, 2 ♀♀ NMPC). 23-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.129433° -97.662464° 3220m Bosque AAJ col (3 ♂♂, 8 ♀♀). 13-VII-18 Mixteca (Cerro del águila) Oaxaca Coprotrampa 17.13011° -097.10835° 2836 m Bosque AAJ col (1 ♂ UAEH, 5 ♀♀ CMN, UAEH). 27-VI-18 Mixteca (Cerro del águila) Oaxaca C.D. perro. 17.119718° -97.684495° 3065m Bosque AAJ col (1 ♂ MNHN). 20-VI-18 Mixteca (Cerro del águila) Oaxaca C.D. perro 17.152568° -97.713997° 2629m Bosque AAJ col (1 ♂ MNHN). 22-VII-18 Mixteca (Cerro del águila) Oaxaca C.D. exc. Borrego 17.123113° -97.673899° 3136 m Bosque AAJ col (1 ♀). (Localities with no indication represent specimens deposited at IEXA).

Diagnosis. Dorsally shining (Figs 1a–b); antennal club yellowish (Figs 1a–b); mandibles lacking a very pronounced rounded lobe (Figs 1a–b); legs black; male protibiae short and straight with apical teeth flattened (Fig. 3a); male profemora without a transverse ridge at its base and not having profemora ventrally excavated near coxae; pronotum, scutellum and elytral intervals shining, green, golden or blue with coppery reflections (Fig. 1a); posterior pronotal margin distinct in front of scutellum (Fig. 1a); elytral intervals convex (Fig. 1a); male procoxa forming a slender saddle-like structure at point of junction with trochanter; male mesoventrite with a distinct, projected keel in front of mesocoxae; aedeagus like Figs 1c–f.

Description of holotype. Male (Figs 1a, 3a), length 18.4 mm, greatest width 9.4 mm. Color dorsally golden-green with strong reddish-coppery pronotal reflections. Antennal club reddish-brown, unmodified; external face of terminal antennomere with a faint U-shaped furrow. Clypeus abruptly arcuate anteriorly; disc rugose and with small, conical tubercle posteriorly. Edge of ocular canthus obtusely angulate anteriorly. Pronotum with small, non-punctate depression by midline just behind anterior margin; posterior margin vaguely indicated in front of scutellum, otherwise absent; disc coarsely punctate anteriorly and laterally. Scutellum impunctate, midline impressed, sides arcuate on anterior third. Elytra distinctly striate, first stria terminated by scutellum, extending basally no more than one-third length of scutellum; striae shallowly, finely punctate, crenate. Protibia with apical tooth bent inwardly (Fig. 3a), apex shallowly emarginate; additional five teeth on outer margin unmodified; flattened ventral or inner surface with two distinct conical teeth, apical tooth slightly smaller; a third-minute tooth often evident on basal side of larger proximal tooth; mesotibia with three complete, transverse carinae on outer surface; metatibia with four complete, transverse carinae on outer surface; metafemur with tooth near trochanter lacking. Mesoventrite with small, distinct keel in front of mesocoxae. Aedeagus as in Figs 1c–f.

Description of allotype. Female (Fig. 1b), length 19.1 mm, greatest width 9.7 mm. Similar to male except in the following respects: protibia with seven unmodified teeth on outer edge, apical tooth simple (Fig. 1b); ventral surface of protibia lacking two large conical teeth; apical spur longer, thicker and bent inward (Fig. 1b); scutellum border strigose; coxa not forming a ridge at juncture with trochanter.

Variation. Body length 11.6–19.2 mm. Maximum width 6.9–10.1 mm. Coloration ranges from bright metallic light green to a bright metallic light blue, to a bright metallic green-gold to gold with reddish-coppery reflections. Middle of thorax can go from almost a smooth surface to a faint middle-line, to a faint middle-line with punctures.

Differential diagnosis. For the differential diagnosis, see the key below.

Etymology. From the Latin word *nuntiat* (part. masc. nom. sing.), meaning the announced one. The name derives from the fact that a species distribution model for the Last Glacial Maximum in Oaxaca predicted this species existence (ARRIAGA-JIMÉNEZ et al. 2020).

Collection circumstances. The species has been collected in traps baited with human dung and mushrooms (Agaricales and Boletales), as well as directly under sheep, cow, and dog dung. The collections were made from June to September in the “Cerro del Águila” (Fig. 5) in the Sierra de Tlaxiaco and communities around it in the Mixteca shield of Oaxaca, Mexico. It is part of the Sierra Madre del Sur, with a mountain range from 2.200 to 3.250 m a.s.l. This area is characterized by pine, oak and pine-oak forests, with some areas with shrublands near the communities. This mountain has a sub-humid climate with heavy rains in the summer, with mean annual temperatures ranging from 10° to 16°C and medium precipitations oscillating from 800 to 1.500 mm per year (INEGI 2008).

Taxonomic notes. The new species, *G. nuntiat* sp. nov., is veritably halfway between *G. pecki* and *G. viridiobscurus*. The aedeagus (Figs 1c–f) is more similar to *G. pecki* (Figs 8c–f) than to *G. viridiobscurus* (Figs 9c–f). However, the beetle’s external appearance (Figs 1a–b) is indistinguishable from *G. viridiobscurus* (Figs 9a–b), except for the coloration, where the specimens of *G. nuntiat* sp. nov. are very bright, ranging from green, to blue or golden-black with a reddish-coppery tint *versus* the specimens of *G. viridiobscurus* being a dull bluish or greenish-black.

Color as a character has been much maligned in taxonomy. However, HILL (2017) has now proposed that the mitonuclear species compatibility concept is the best current method for diagnosing species. This mitonuclear compatibility leads, among other things, to the evolution of species-typical coloration as part of speciation reinforcement processes. Thus, species-typical coloration evolves as a signal of coadapted mitochondrial-genotype genes. HILL (2017) presents as a case study the nearly perfect agreement between bird species boundaries according to mtDNA types and those drawn according to species-typical songs or coloration. Therefore, coloration might be a valid taxonomic character, which should be used judiciously and concomitantly with other concordant characters.

Geotrupes (Onthotrupes) lobatus Howden, 1974

(Figs 2, 3, 4, 5)

Geotrupes lobatus Howden, 1974: 573 (original description).

Geotrupes lobatus: HOWDEN (1980): 1960 (key); HOWDEN (2003): 97, 99 (atlas); TROTTA-MOREU et al. (2008): 42, 47, 50, 51 (distribution model); KOHLMANN et al. (2018): 21 (key).

Material examined. MEXICO: OAXACA: Sierra Sur. 26-VI.18 CD. 96.244523° W. 16.16096° N. Bosque. 3059 m. Arriaga J.A. Col. (1 ♂, IEXA Entomology Collection, Xalapa, Mexico).

Description. Male (Fig. 2a). Body length 13.7 mm. Maximum width 8.3 mm. Color black with distinct greenish-blue cast along margins of head, labium, mandibles, antennal base, pronotum, humeral angles, base of elytral striae, and legs. Antennal club unmodified, grayish-black. Mandible with a large rounded lobe on outer margin just basal to a sharp apical tooth (Figs 2a and 3b). Clypeus intermediate between U- and V-shaped, disc closely, contiguously punctate; posterior tubercle low. Vertex largely impunctate, a median sulcus present in anterior half. Ocular canthus broadly arcuate and with a strong greenish-blue cast.

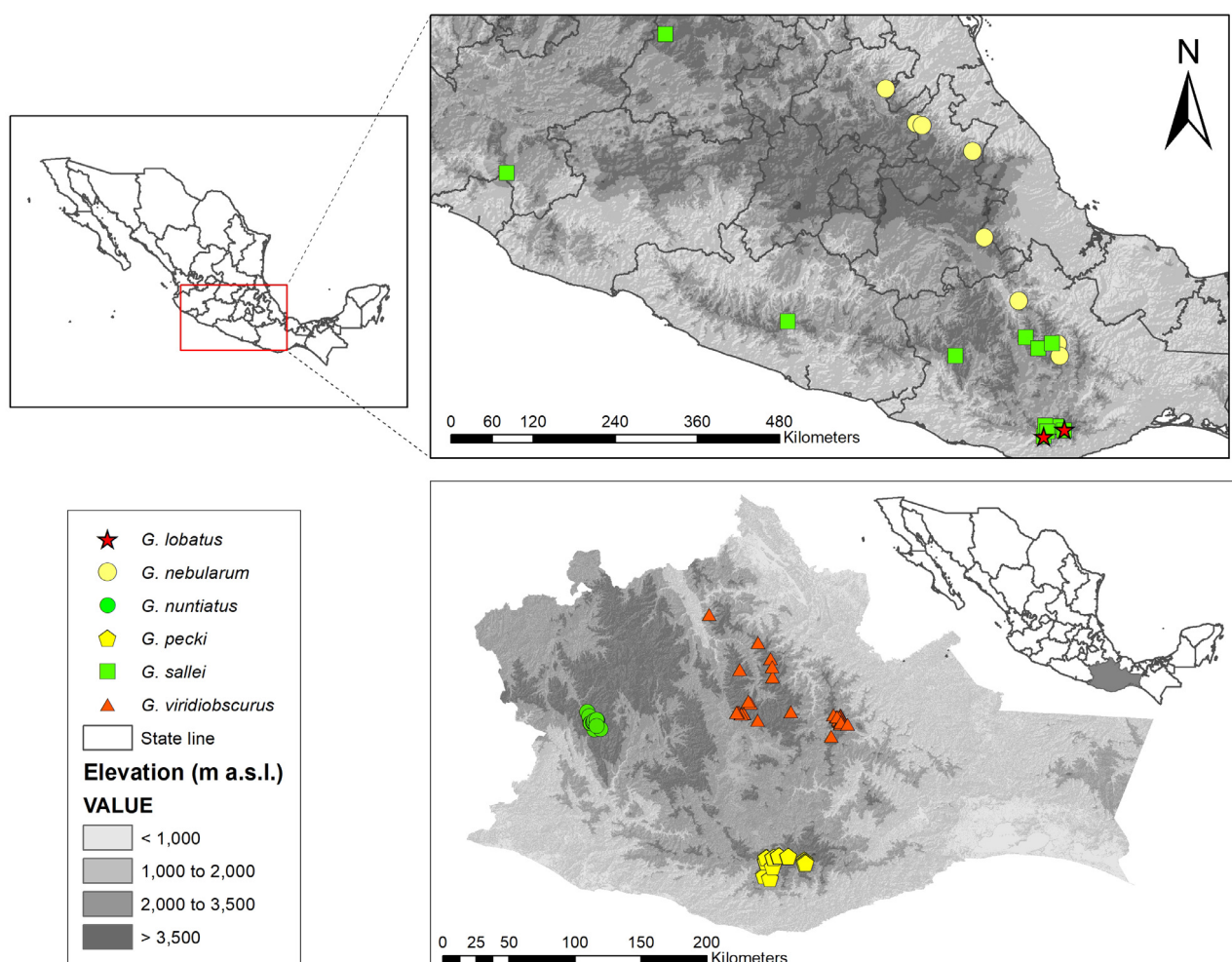


Fig. 5. Map showing the known distribution of *Geotrupes lobatus* Howden, 1974, *G. sallei* Jekel, 1866, and *G. nebulare* Howden, 1974 (upper map) and the known distribution of *G. nuntiatus* Kohlmann & Arriaga-Jiménez, sp. nov., *G. viridiobscurus* Jekel, 1866, and *G. pecki* Howden, 1974 (lower map).

Pronotum lacking anterior concavity; posterior marginal line almost absent; disc smooth and impunctate except along anterior and lateral margins, punctures with strong greenish-blue cast. Scutellum impunctate, pentagonal in shape, slightly indented along midline. Elytral striae distinct, first stria terminated by scutellum; striae not crenate or punctate except for outer ten striae which are vaguely punctate. Protibia with seven teeth along outer margin and a row of five small teeth on ventral surface; apical tooth long, slender and spiniform, inwardly curved (Fig. 2a); apical spur short, curved, and spiniform; tibiae long and slender forming an arch (Figs 2a and 3b). Profemur forming a strong transverse ridge or tooth at its base (Fig. 3b). Meso- and metatibia each with three complete transverse carinae on outer surface. Metafemur with a small ventral tooth basally at posterior border. Prosternum with a rounded projection. Mesoventrite excavated and carinate on either side in front of mesocoxae. Aedeagus like Figs 2c–f. **Taxonomic notes.** HOWDEN (1980) indicates in his couplet 8: ‘fore tibiae not distinctly longer than in females’. This is a mistake as the male has distinctly longer and curved protibiae (Figs 2a and 3b). It is strange to read this assertion because HOWDEN (1980) did not have any male of *G. lobatus* for study, only females. Elongate protibiae seem to

be more adapted to sexual coupling, as is common in many other scarab beetles, than to digging a nest. The only other Mexican species of *Geotrupes* that has elongate protibiae is *G. onitidipes*. Both species share other characteristics such as being black with metallic reflections, having a grayish black antennal club, and pronotum punctate only near margins.

Another similarity between both species is the shape of the aedeagus. In turn, both aedeagi look very similar to the aedeagi of *Ceratotrupes*, in particular of *C. bolivari* Halffter & Martínez, 1962 (Fig. 4a), probably suggesting some kind of taxonomic relationship or even an evolutionary bridge between both genera.

Distribution and ecology. HOWDEN (1974) described *Geotrupes lobatus* based on three female specimens that he had collected in the Sierra Sur (Sierra de Miahuatlán) under human feces at 2,450 m. One of us (AAJ) collected the additional specimen during June at a pine forest at 3,050 m a.s.l. (Fig. 5) in the same area, directly under dog dung. However, considering AAJ’s sampling effort in this area (10 pitfall traps every 200 meters in a range from 2,200 to 3,200 m a.s.l.), with a high number of collections for other Geotrupinae species, we presume this is not a strict coprophagous species, possibly a mycetophagous one.

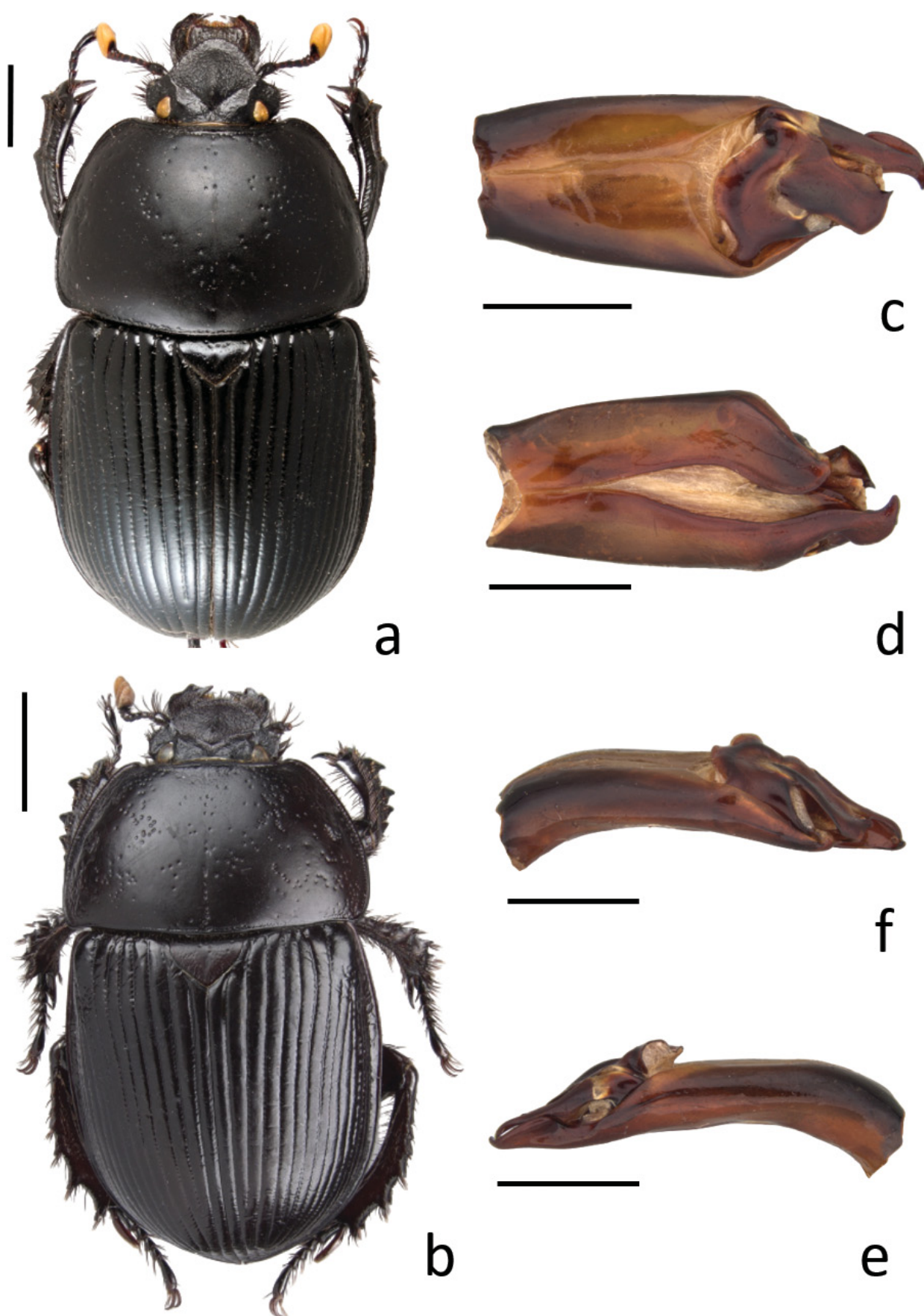


Fig. 6. *Geotrupes sallei* Jekel, 1866: a – male dorsal view (16.19231°N, -96.45711°W); b – female dorsal view (holotype Howden CMN); c–f – male genitalia: c – in dorsal view, d – in ventral view; e–f – lateral views. Scale bars = 5 mm (a–b), 2 mm (c–f).

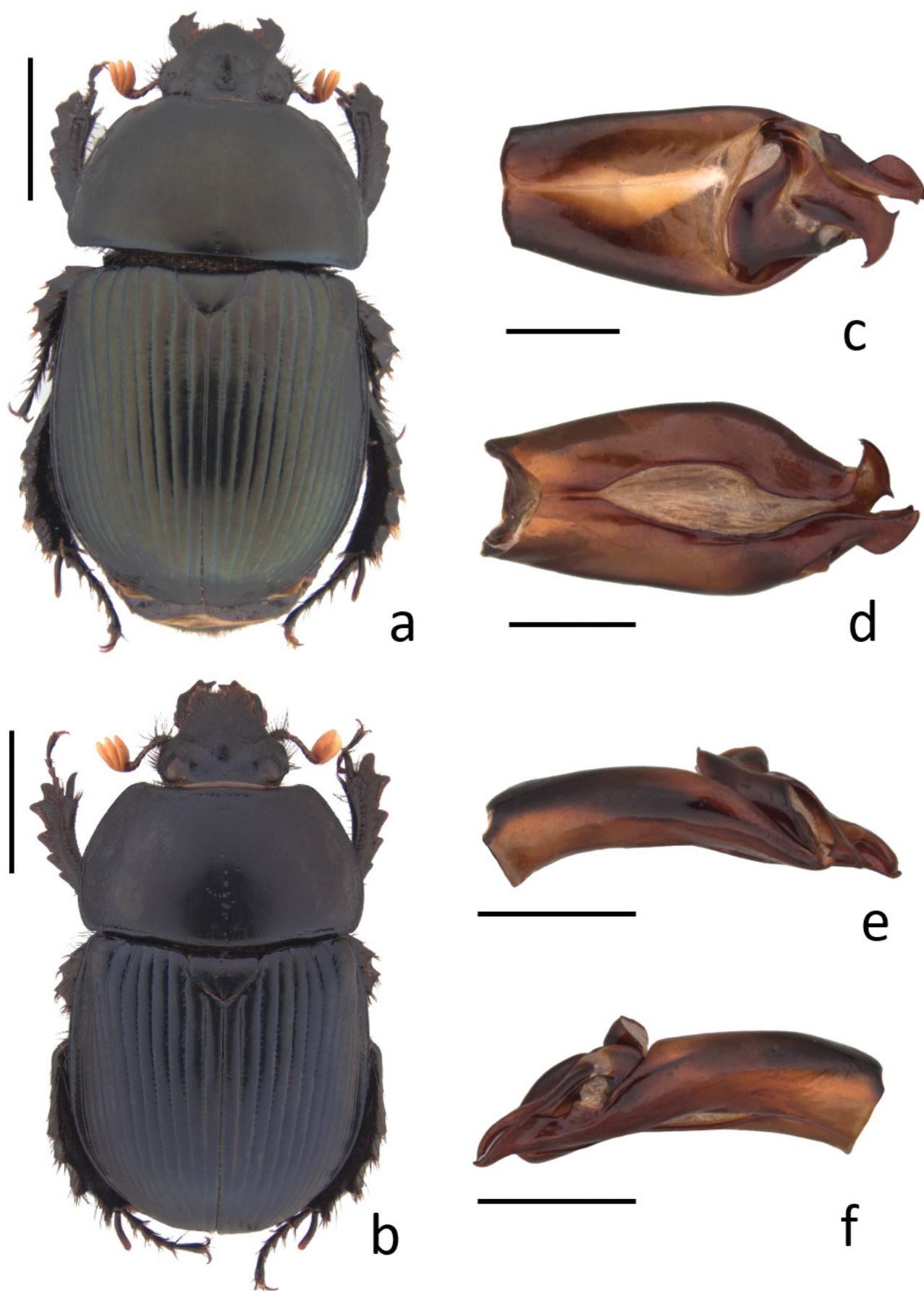


Fig. 7. *Geotrupes nebularum* Howden, 1974: a – male dorsal view (19.03638°N, -97.17138°W); b – female dorsal view (19.2533°N, -97.98433°W); c–f – male genitalia: c – in dorsal view, d – in ventral view; e–f – lateral views. Scale bars = 5 mm (a–b), 2 mm (c–f).

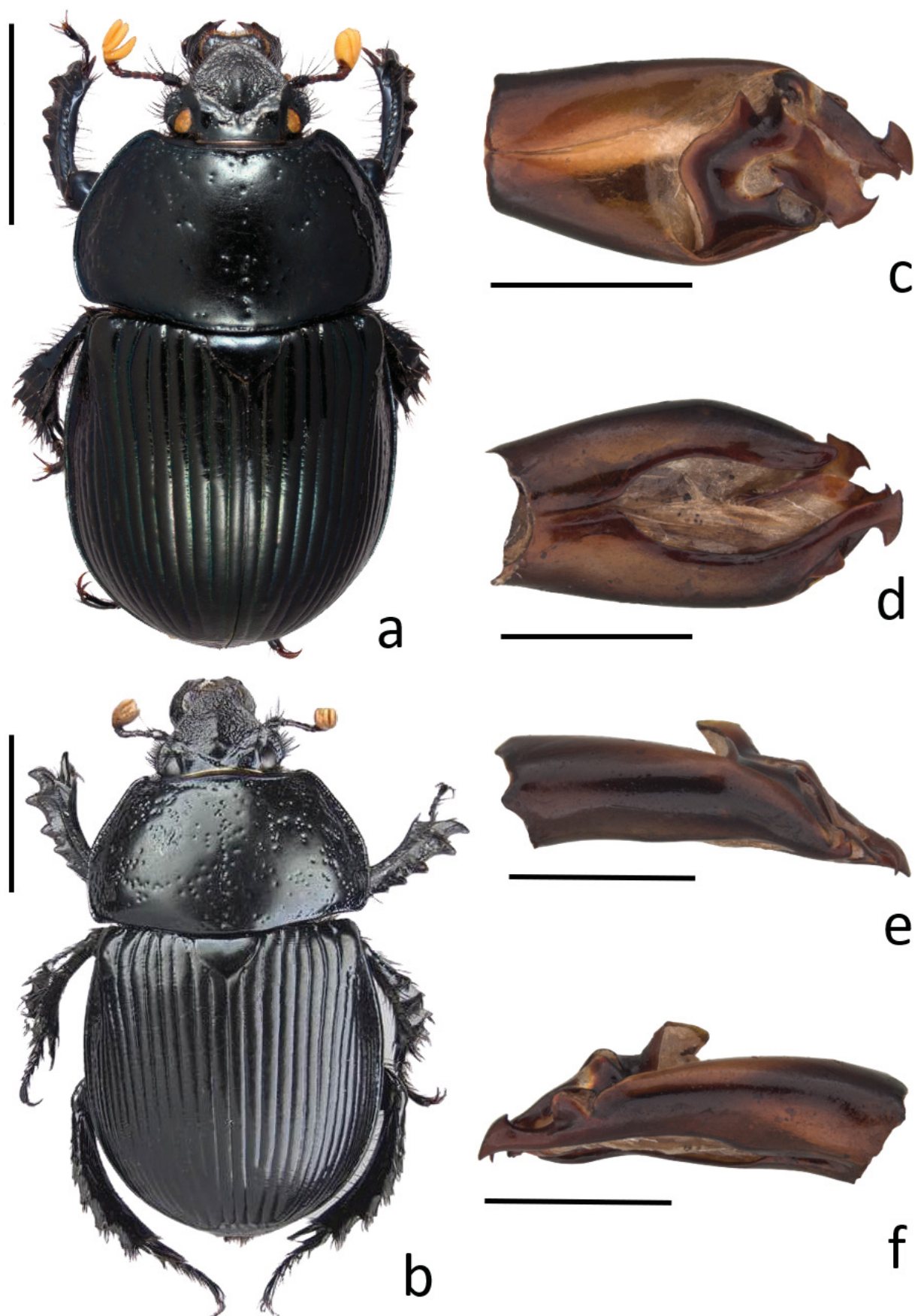


Fig. 8. *Geotrupes pecki* Howden, 1974: a – male dorsal view (16.17325°N, -96.24708°W); b – female dorsal view (16.12138°N, -96.45222°W); c–f – male genitalia: c – in dorsal view, d – in ventral view; e–f – lateral views. Scale bars = 5 mm (a–b), 2 mm (c–f).

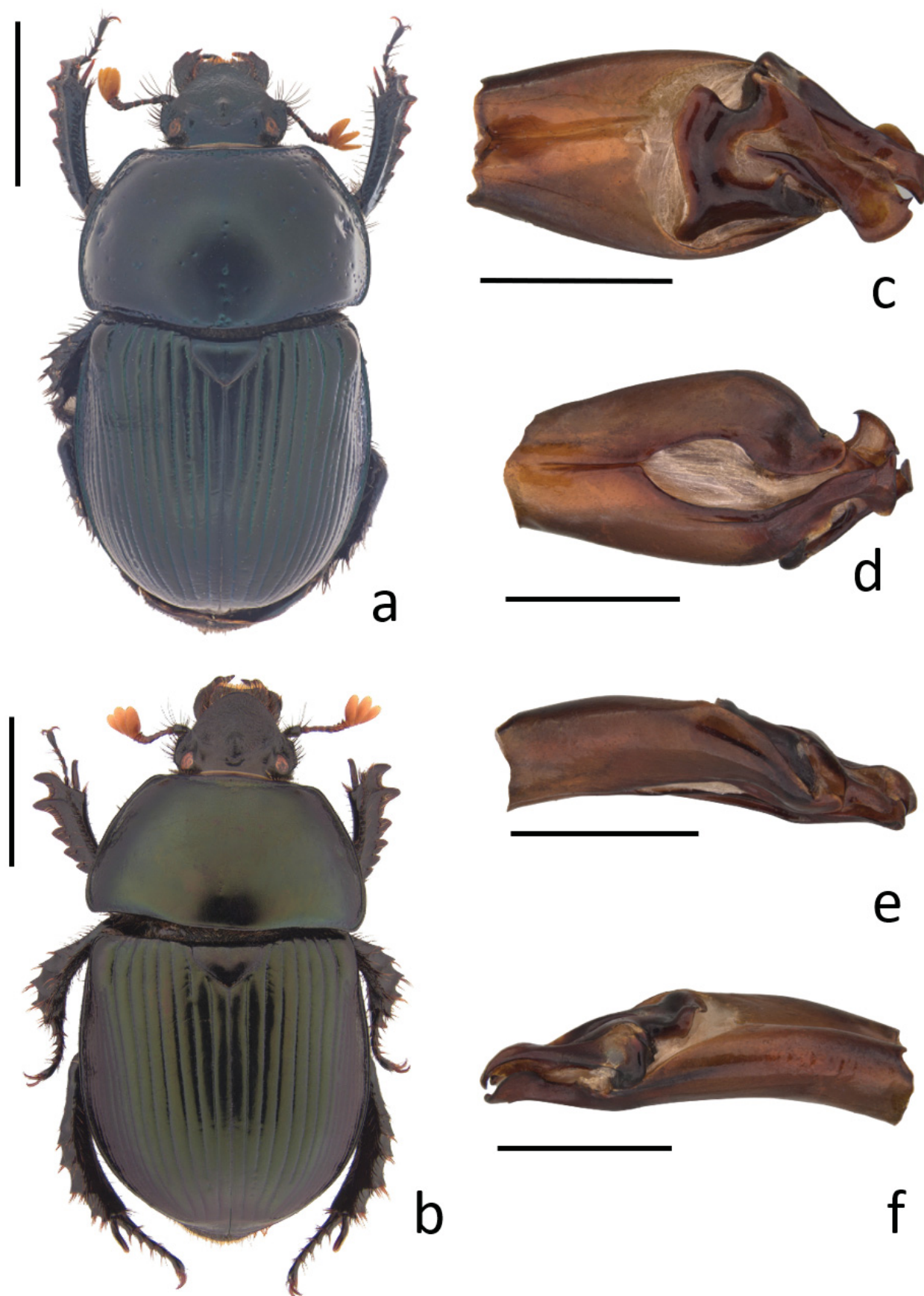


Fig. 9. *Geotrupes viridiobscurus* Jekel, 1866: a – male dorsal view (17.44361°N, -96.50361°W); b – female dorsal view (16.160961°N, -96.244523°W); c–f – male genitalia: c – in dorsal view, d – in ventral view; e–f – lateral views. Scale bars = 5 mm (a–b), 2 mm (c–f).

Key to the *Geotrupes* of Oaxaca

- 1 Antennal club grayish-black (Fig. 2b); each mandible with a considerably pronounced rounded lobe; legs metallic blue; male protibiae long and rounded with apical teeth spiniform; male profemora with a strong transverse tooth at its base (Fig. 3b); aedeagus as in Figs 2c–f; Sierra Sur (Sierra de Miahuatlán). *G. lobatus* Howden, 1974
- Antennal club yellowish (Figs 1a–b) or reddish-brown (Fig. 6a) to brown; mandibles lacking a pronounced rounded lobe (Fig. 1a); legs black; male protibiae short and straight with apical teeth flattened; male profemora without a transverse ridge at its base. 2
- 2 Dorsally shining; pronotum, scutellum and elytral intervals shining, often green, golden or blue with coppery reflections (Figs 1, 7a, 8, 9); elytral intervals convex (Figs 1, 7, 8); smaller species (13–22 mm); males not having profemora ventrally excavated near procoxae. 3
- Dorsally opaque; pronotum, scutellum, and frequently elytral intervals finely shagreened; elytral intervals flattened centrally (Fig. 6a); large species (22–26 mm); males having profemora ventrally excavated near procoxae; aedeagus as in Figs 6c–f; mountains in central Mexico (Guerrero, Guanajuato, Jalisco) and mountains of Oaxaca (Mixteca Shield, Sierra Norte, Sierra Sur). *G. sallei* Jekel, 1866
- 3 Posterior pronotal margin fine but distinct, except in front of scutellum (Fig. 7a); male mesoventrite with a distinct carina in front of mesocoxae; male procoxa forming a broad saddle-like structure at the point of junction with trochanter; aedeagus as in Figs 7c–f; Sierra Madre Oriental (Hidalgo, Puebla, Veracruz) and Sierra Norte. *G. nebularium* Howden, 1964
- Posterior pronotal margin distinct in front of scutellum (Figs 1, 8, 9); male mesoventrite with a distinct, projected keel in front of mesocoxae; male procoxa forming a slender saddle-like structure at the point of junction with trochanter. 4
- 4 Elytral striae finely punctate or crenulate except near suture (Figs 1, 8b); elytra bluish-black, greenish-black, or golden-black sometimes with reddish-coppery tint (Figs 1, 8b); pronotum punctate laterally (Figs 1, 8b); Sierra Norte or Mixteca. 5
- Elytral striae virtually impunctate, at most vaguely crenulate (Fig. 8a); elytra black with faint tinge of green or blue on elytron; pronotum generally heavily and grossly punctate (Fig. 8a); aedeagus like Figs 8c–f; Sierra Sur (Sierra de Miahuatlán). *G. pecki* Howden, 1974
- 5 Elytra dull bluish-black (Fig. 9b); aedeagus as in Figs 9c–f; Sierra Norte (Sierra de Ixtlán, Sierra de Juárez, Sierra Mazateca, and Nudo del Zempoaltépetl). *G. viridiobscurus* Jekel, 1866
- Elytra bright green, blue, or golden-black with reddish-coppery tint (Fig. 1a); aedeagus as in Figs 1c–f; Mixteca (Sierra de Tlaxiaco). *G. nuntiatus* sp. nov.

Discussion

Geotrupes nuntiatus sp. nov., *G. pecki*, and *G. viridiobscurus* form an *Artenkreis* (RENSCH 1928), a group of related species replacing each other geographically. This German word, later translated into English by MAYR (1931) as *superspecies*; according to MAYR's (1982) latest definition is 'A group of geographically vicariant populations (previously considered polytypic species) the members of which (also called allospecies) have been isolated sufficiently long to have reached species level'. It has also been defined as 'a group of closely related species' (LINCOLN et al. 1998). The three species are characterized by having a distinct posterior pronotal margin in front of the scutellum (Figs 1, 8, 9); the male mesoventrite with a distinct, projected keel in front of the mesocoxae; and male procoxae forming a slender saddle-like structure at the point of junction with the trochanter.

This last proposal is based on recent collecting and taxonomic studies of dung beetles of the genus *Geotrupes* in the mountains of Oaxaca (KOHLMANN et al. 2018, ARRIAGA-JIMÉNEZ et al. 2020), which have evidenced the existence of a vicariant speciation pattern, where one species occupies the northern mountain system (Sierra Norte, *G. viridiobscurus*) and the other one (*G. pecki*) the southern mountainous range (Sierra Sur) (Fig. 10). A study of this possible vicariant speciation mechanism was analyzed under the light of a paleobiogeographic/paleoclimatic mapping analysis of both *Geotrupes* species' distribution during Late Quaternary glaciation events (ARRIAGA-JIMÉNEZ et al. 2020). Based on these paleomaps a possible speciation mechanism was suggested, in which one common ancestor lived at the bottom of the Valle de Oaxaca (Oaxaca Valley) during the Last Local Glacial Maximum (LLGM, 21.000–17.500) and whose possible continuous distribution was broken into two (or more) separated areas on mountain tops as the climate became warmer toward the present. This model proposed that the fragmentation and isolation of habitats might have promoted genetic differentiation of populations resulting in vicariant speciation as suggested by a sky-island dynamic process.

Based on this model for the Last Local Glacial Maximum for the mountains of Oaxaca, the existence of a *Geotrupes* species was predicted for the area of the Mixteca (KOHLMANN et al. 2018, ARRIAGA-JIMÉNEZ et al. 2020). This area formed a climatically continuous area with the Sierra Norte and Sierra Sur during the LLGM. The area then started separating according to the following model sequence: (Sierra Norte+Mixteca+Sierra Sur) → (Sierra Norte+Mixteca, Sierra Sur) → (Sierra Norte, Mixteca, Sierra Sur) (Fig. 10). The estimated model dates for these three processes are 21.000 to 17.500; 12.000 to 10.000; 8.500 to 7.500, respectively (ARRIAGA-JIMÉNEZ et al. 2020). The Mixteca area was accordingly sampled by one of us (AAJ) and as predicted by the model a new species was found in the Cerro del Águila (Fig. 11), Sierra de Tlaxiaco. It is highly probable that other new and related species forming part of this *superspecies* might be found in the Mixteca, most probably at Cerro Negro, Sierra de

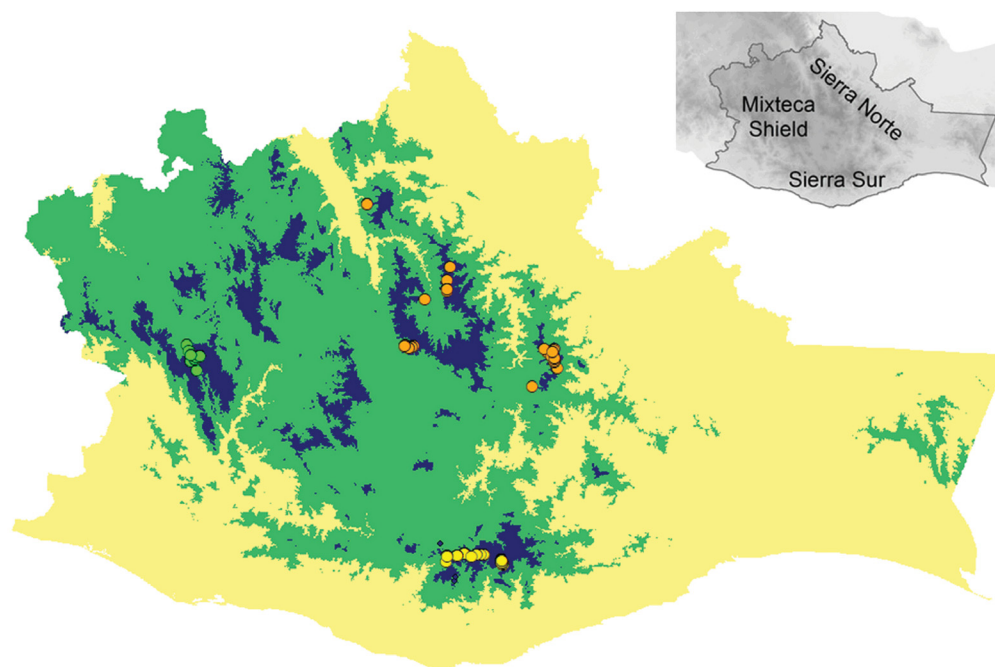


Fig. 10. Projection of potential distribution for *Geotrupes viridiobscurus* Jekel, 1866 and *G. pecki* Howden, 1974 in the state of Oaxaca, representing the estimated climatic range at the Hueyatlaco-I glaciation scenario (20–17.5 kyr ago), based on the actual distribution of both species. Areas in green (1,265–2,390 m a.s.l.) correspond to the modern temperature range of *G. viridiobscurus* (orange locality points, Sierra Norte) and *G. pecki* (yellow locality points, Sierra Sur). Areas in blue are too cold and areas in yellow are too warm. Areas in blue are very similar to the present-day projected climatic distribution (2,300–3,400 m a.s.l.). The green points represent the localities of *G. nuntiatu*s Kohlmann & Arriaga-Jiménez, sp. nov., the new species being described in this study and belonging to this species group. It falls within the modelled distribution area (modified from ARRIAGA-JIMÉNEZ et al. 2020).



Fig. 11. Native vegetation (pine forest and montane shrubland) at the top of Cerro del Águila, Mixteca, Oaxaca.

Tamazulapan, and at Cerro Verde, Sierra de Nochixtlán; all these mountains present altitudes around 3.000 m and are thus very likely places for finding specimens belonging to *Geotrupes*.

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