First member of the New World genus *Diceroderes* from early Miocene Mexican amber (Coleoptera: Tenebrionidae: Tenebrioninae: Toxicini)

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ABSTRACT

A new fossil species belonging to the extant Central American genus *Diceroderes* Solier, 1841 (Tenebrionidae: Tenebrioninae: Toxicini) is described based on an exquisitely preserved male specimen from early Miocene Mexican (Chiapas) amber (~23–16 Ma). High-resolution X-ray microtomography was used to document fine anatomical detail of soft tissues, including well-preserved male genitalia. *Diceroderes jiangkuni* sp. nov. can be most readily differentiated from congenerics by the clypeus with a transverse row of tubercles, apices of pronotal horns strongly angled upwards in the male, elytra rounded in lateral view, and all male tibiae lacking apical spines. This represents the first fossil record of Toxicini from Mexican amber and indicates that the genus persisted in the region since the early Miocene.

1. Introduction

Darkling beetles of the tribe Toxicini are a relatively small group of xylophagous and mycetophagous taxa belonging to the diverse darkling beetle subfamily Tenebrioninae (Bouchard et al., 2005). It is assumed that the larvae and adults feed primarily on decaying fungal fruiting bodies, but the beetles also occur under bark, in decaying wood, and some are apparently associated with lichens (Kompantseva, 1999; Nabozhenko and Ivanov, 2018). The cosmopolitan tribe is divided into three subtribes, Dysantina Gebien, 1922 (nine current genera), Nycteropina Lacordaire, 1859 (two genera), and Toxicina Oken, 1843 (four genera) (Bouchard et al., 2005; Bousquet et al., 2018; Nabozhenko and Ivanov, 2018); in total some 190 species have been described to date. The precise systematic position of Toxicini within Tenebrioninae remains unresolved, and a number of possible placements have been proposed based on adult and larval morphology as well as molecular data. Watt (1974) regarded toxicines as closely allied with the tribe Cossyphini based on the shared presence of a short flattened antennal club, abdominal sternites without exposed intersegmental membranes, and an uninverted aedeagus. In a cladistic analysis of adult and larval characters, Doyen and Tschinkel (1982) recovered Toxicini in a

polytomy together with their 'diaperine lineage' and 'tenebrionine lineage'. In the most comprehensive molecular study of Tenebrioninae conducted to date based on fragments of eight genes and a wide sampling of taxa, Toxicini was the sister group to Titaenini in maximum likelihood analyses (Kergoat et al., 2014). Two seven gene datasets consistently recovered Toxicini as sister to a monophyletic Bolitophagini (Gunter et al., 2014; Kanda, 2017). Members of these two tribes share a similar structure of eversible defensive glands (Tschinkel and Doyen, 1980) and many also have a similar rugose appearance with toothed pronotal and elytral margins and cephalic and pronotal horns.

The fossil record of Toxicini is sparse and includes only a single described species from Dominican amber, *Wattius reflexus* Doyen and Poinar (1994). Further undescribed *Wattius* Kaszab, 1982 specimens from the same deposit were mentioned by Smith and Sanchez (2015). Here we report the first fossil representative of the extant Central American genus *Diceroderes* Solier, 1841. The specimen described here originates from early Miocene amber mined in the Chiapas State in Mexico and provides evidence of the antiquity of the genus within Central America.

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2. Geological setting

Mexican amber from Chiapas State is mined predominantly in the vicinity of the Simojovel de Allende town from the La Quinta Formation, Mazantic Shale, and Balumtum Sandstone (Hurd et al., 1962; Solórzano Kraemer, 2010). The lithological background of the Chiapas amber-bearing beds has been reviewed by Serrano-Sánchez et al. (2015). The amber is well-known for preserving a diversity of biological inclusions including arthropods, fungi, flowers, seeds, pollen, leaves, vertebrates and is regarded as one of the most important deposits preserving Cenozoic insects (Lazell, 1965; Solórzano Kraemer, 2007). The fossil resin was most likely secreted by *Hymenaea* Linnaeus, 1753 trees as indicated by plant inclusions and comparison of the infrared spectra of the amber with resin of the extant *H. courbaril* Linnaeus, 1753 (Calvillo-Canadell et al., 2010; Lambert et al., 1989; Langnheim, 1966; Poinar and Brown, 2002). The age of Chiapas amber is most likely early Miocene, as suggested by fossil nannoplankton, crustaceans, and molluscs (Perrilliat et al., 2010; Serrano-Sánchez et al., 2015). $^{87}Sr/^{86}Sr$ analyses of material from the La Quinta Formation yielded an age of 22.88 Ma + 0.82 Ma – 0.95 Ma (Serrano-Sánchez et al., 2015) but not all Mexican amber may be contemporaneous given its different stratigraphic positions. The Mexican amber biota has been correlated with Dominican amber, which is believed to be Burdigalian based on palaeontological evidence (Iturralde-Vinent and Macphee, 2019; Solórzano Kraemer, 2007). The Chiapas early Miocene palaeoenvironment was reconstructed as a lowland tropical dry rainforest standing near the coast and resembling modern mangroves (Becerra, 2005; Solórzano Kraemer, 2007).

3. Material and methods

The amber piece studied herein originates from a mine near Simojovel in Chiapas State, southern Mexico. The amber piece was polished with sandpapers of gradually finer grits and finally with diatomite powder. Photographs under normal reflected light were taken with a Canon EOS 5D Mark III digital camera, equipped with a Canon MP-E 65 mm macro lens (F2.8, 1–5X), and with an attached Canon MT-24EX twin flash. Photomicrographs with green epifluorescence were taken using Zeiss Imager Z2 compound microscope under the eGFP mode (Zeiss Filter Set 10; excitation/emission: 450–490/515–565 nm). High-resolution X-ray microtomography (Zeiss Xradia 520 versa) was performed in the micro-CT laboratory of Nanjing Institute of Geology and Palaeontology, CAS. Due to the comparatively large size of the fossil specimen, a CCD-based 0.4 × objective was used, providing isotropic voxel sizes of 10.17 μm with the help of geometric magnification. During the scanning, the acceleration voltage for the X-ray source was 60 kV, and a thin filter (LE3) was used to avoid beam-hardening artefacts. To improve signal-to-noise ratio, 2001 projections over 360° were collected, and the exposure time for each projection was 2 s. The tomographic data were analysed using AVIZO software v. 2019.01.

The studied specimen is permanently deposited in the amber collection of the Nanjing Institute of Geology and Palaeontology (NIGP), Nanjing, China under the accession number NIGP173170. The publication LSID is urn:lsid:zoobank.org:pub:6F8C9A82-F8C1-4020-BEEF-1FEA5AB38BF7.

4. Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Family Tenebrionidae Latreille, 1802 Subfamily Tenebrioninae Latreille, 1802 Tribe Toxicini Lacordaire, 1859
Subtribe Dysantina Gebien, 1922
Diceroderes jiangkuni sp. nov.
Figs. 1–5
Etymology. The new species is named after Mr. Kun Jiang, the donor of the amber piece.

Locality and horizon. Mexican (Chiapas) amber; amber mine near Simojovel, Chiapas State, southern Mexico. Burdigalian–Aquitanian, early Miocene.

Type material. Holotype, NIGP173170, male

Diagnosis. Clypeus not deeply punctate, with a transverse row of tubercles. Frons approximately four times the width of eyes, with small supraorbital costae. Male pronotal horns smoothly rounded throughout, with the apex at the same vertical position as the base, pointed upwards, and dorsally tuberculate. Elytra in lateral view rounded from front to back, with rows of coniform tubercles.

Description. Body oblong-oval, dorsoventrally convex, subparallel-sided, widest at pronotum. Dorsal surfaces densely punctate and tuberculate, glabrous (Figs. 1 and 2). Body length from clypeus to abdominal apex 7.8 mm, 3.6 mm wide across pronotum in anterior third. Body colour uniformly dark brown to black.

Head hypognathous, subglobular, coarsely and densely punctate, 1.7 mm long. Mandibles concealed. Maxillary palpi four-segmented, apical palpomere securiform. Labrum large, approximately two thirds of clypeal length, sub-trapezoidal with anterior margin slightly concave. Clypeus deeply impressed, lacking prominent punctures, with a transverse row of tubercles. Frontoclypeal suture distinct, frons approximately four times the width of eyes (Fig. 3A). Frons with low supraorbital costae. Compound eyes large, oval, slightly emarginate, seemingly lacking interfacetal setae. Temples pronounced, as long as eyes. Antennae 11-segmented, separated by three times the length of the basal antennomere, reaching to the anterior third of the pronotum. Antennomere 1 subcylindrical, parallel-sided, 2.7 times longer than the following segment; antennomere 2 sub-globular, half the length of the following segment; antennomere 3 2.5 times longer than wide, widest apically; antennomeres 3–8 filiform, longer than wide, shortening apically except for antennomere 8, equally wide; antennomeres 9–11 widened and flattened, forming a distinct club, together 1.8 times wider than the preceding segment, forming a very compact club giving the impression of a single fused segment with boundaries between individual segments only visible as fine and indistinct lines, apical antennomere gradually tapering apically (Fig. 3B and C, 4C). Ratio of antennomere lengths (in mm): 0.38 : 0.13: 0.30 : 0.27: 0.20 : 0.18: 0.17 : 0.24: 0.16 : 0.11: 0.09. At least the distalmost antennomeres with simple setiform sensilla on apex. Vertex of head dome-shaped, with deeply impressed circular punctures.

Pronotum strongly transverse and arched, 2.9 mm long, 1.23 times wider than long. Dorsal surface rugose and coarsely punctate. Male with elongate pronotal horns placed on pronounced protuberances (Fig. 3A: pnp). Tusk-like horns twice the length of the head, curving symmetrically around the head so that the horn apex is at the same vertical position as the base, with four rows of tubercles dorsally (Fig. 4A), apparently glabrous, apex pointed and directed upwards. Pronotum widest in the anterior third, tapering posteriorly. Lateral pronotal margin crenulate, expanded and flattened. Posterior pronotal angles
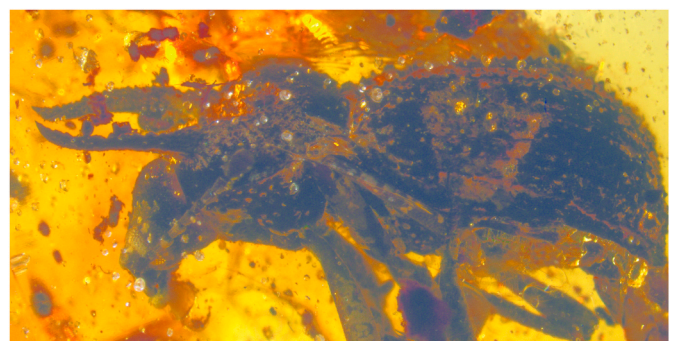

Fig. 1. General habitus of *Diceroderes jiangkuni* sp. nov. (holotype, NIGP173170) in lateral view under normal reflected light. Scale bar: 1 mm.
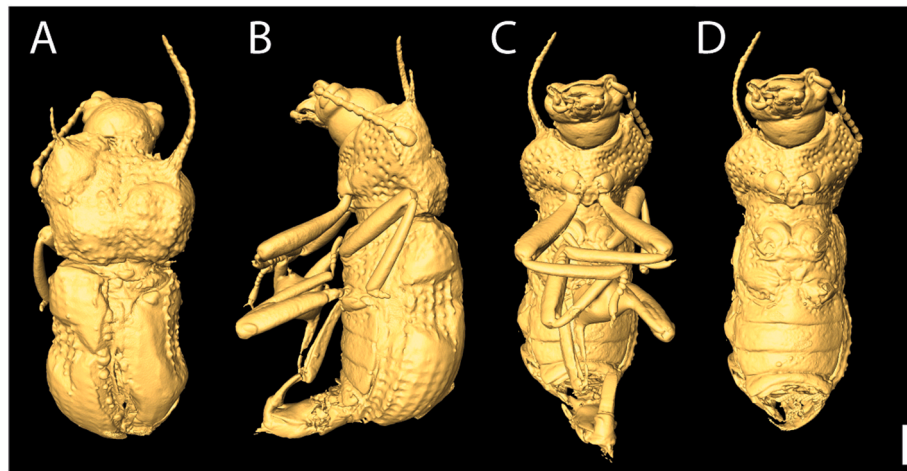
Fig. 2. Micro-CT reconstruction of the general habitus of *Diceroderes jiangkuni* sp. nov. (holotype, NIGP173170). A, dorsal view; B, lateral view; C, ventral view; D, ventral view with the aedeagus and legs omitted for clarity. Scale bar: 1 mm.
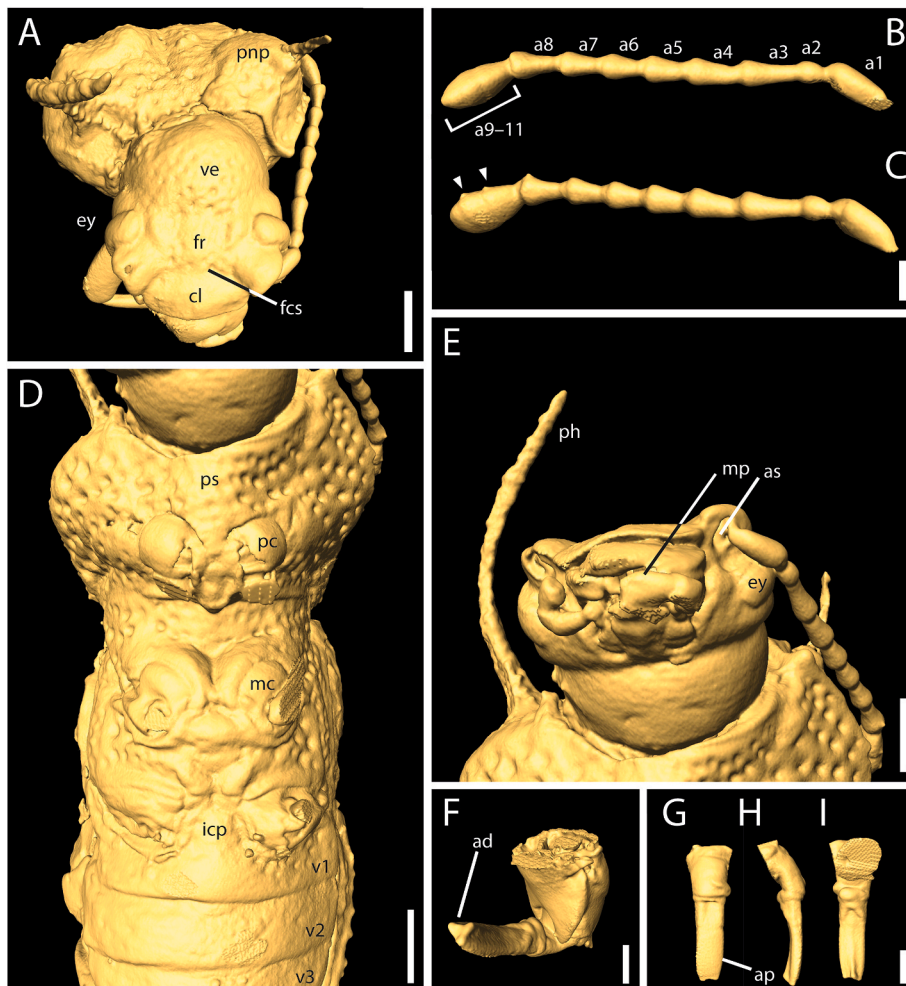

Fig. 3. Micro-CT reconstruction of morphological details *Diceroderes jiangkuni* sp. nov. (holotype, NIGP173170). A, head and pronotum in anterior view; B–C, antennae in lateral (B) and dorsal (C) views, triangles delineate the sutures between the three apical antennomeres; D, thorax and abdominal base in ventral view, with legs omitted for clarity; E, head in ventral view; F, abdominal apex with aedeagus; G–I, aedeagus. Abbreviations: a1–11, antennomeres 1–11; ad, aedeagus; ap, apex of aedeagus; as, antennal socket; cl, clypeus; ey, eye; fcs, frontoclypeal suture; fr, frons; icp, intercoxal process of the first ventrite; mc, mesocoxa; mp, maxillary palpomere; pc, procoxa; ph, pronotal horn; pnp, pronotal protuberance; ps, prosternum; v1–3, ventrites 1–3; ve, vertex. Scale bars: 500 μm (A, F–I), 200 μm (B–C), 1 mm (D–E).

approximately right-angled. Posterior margin slightly sinuate, such that pronotum is shortest medially. Scutellum difficult to observe, apparently shield-shaped and wider than long.

Prosternum short before procoxae, as long as the greatest width of procoxal cavities, deeply punctate with rounded pits separated by no more than twice the pit diameter. Prosternal process as long as the anteroposterior diameter of the procoxae, reaching beyond the procoxal cavities, apically rounded and declined. Procoxal cavities transverse, narrowly separated by less than half of their width. Mesoventrite before mesocoxae as long as maximum mesocoxal width. Mesocoxal cavities open, approximately round, separated by their maximum width (Fig. 3D: mc). Metacoxal cavities large and transverse, separated by a
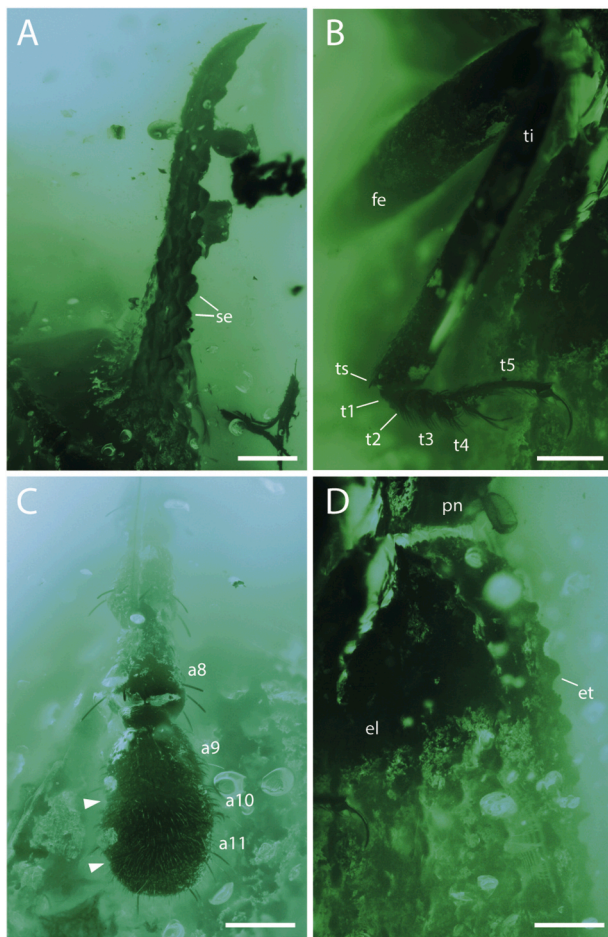
Fig. 4. Morphological details of *Diceroderes jiangkuni* sp. nov. (holotype, NIGP173170) under green epifluorescence. A, pronotal horn; B, mesothoracic leg; C, antennal apex, triangles delineate the sutures between the three distal-most segments; D, elytral base. Abbreviations: a8–11, antennomeres 8–11; el, elytron; et, elytral tubercle; fe, mesofemur; pn, pronotum; se, serrations of the pronotal horn; t1–5, mesotarsomeres 1–5; ti, mesotibia; ts, mesotibial spur. Scale bars: 400 μm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 5. Morphological details of *Diceroderes jiangkuni* sp. nov. (holotype, NIGP173170) aedeagus under normal reflected light. Note that the apical portion of the aedeagus could not be scanned and so does not appear in the reconstructions in Fig. 3F–I. Scale bar: 200 μm.

5. Discussion and conclusion

Placement in the extant genus *Diceroderes* is indicated by the pronotum with two anteriorly projecting horns, antenna with a compact three-segmented club with segments fused and only sutures visible, clypeus depressed and projecting past genal margin, and membranes between ventrites concealed. The genus *Diceroderes* is known from five recent species endemic to Mexico, Guatemala and Honduras that were recently revised by Smith and Cifuentes-Ruiz (2015); a sixth putatively new undescribed species was also mentioned from Guatemala by the same authors. These rather rare beetles have been collected from leaf litter, rotting wood, or from under bark in oak and pine forests. Curiously, there are no recorded associations with polypore fungi (Smith and Cifuentes-Ruiz, 2015). Extant representatives of the genus are flightless. Although we were not able to confirm the absence of wings in *D. jiangkuni* sp. nov., the elytral humera are obtuse, as in modern *Diceroderes* species, likely indicating the lack of functional flight wings. The tuberculate clypeus, low supraorbital costae, and rounded elytron in lateral view of *D. jiangkuni* sp. nov. closely resembles the Mexican species *D. subtriplehorni* Smith and Cifuentes-Ruiz (2015) and *D. ocozocoautlaensis* Smith, 2015. The lack of a transverse anterior ridge on the pronotum of *D. jiangkuni* sp. nov. resembles *D. ocozocoautlaensis*, while this structure is present in *D. subtriplehorni*. *D. jiangkuni* sp. nov. may be sister to *D. ocozocoautlaensis* and *D. subtriplehorni* (species with rounded elytra), as the shape of its aedeagus (Fig. 3F–I and 5) is more similar to species with non-rounded elytra, namely *D. mexicanus* Solier, 1841, *D. cusucoensis* Smith, 2015, and *D. skelleyi* Smith, 2015. *D. jiangkuni* sp. nov. differs from both most notably in the structure of the male pronotal horns and lack of an apical tibial spine on all legs.

An interesting and hitherto unexplained morphological structure present in extant *Diceroderes* species and in *D. jiangkuni* sp. nov. are the pronounced anteriorly projecting pronotal horns. Pronotal horns are present in both males and females, although they tend to be shorter, thicker and bluntly pointed in the latter (Smith and Cifuentes-Ruiz, 2015). Among Tenebrioninae, the function of sexually dimorphic horns was best studied in the North American species *Bolitotherus cornutus* Panzer, 1794 belonging to the tribe Bolitophagini, where male's pronotal and clypeal horns are used to dislodge or push rivals during courtship rituals and female guarding (Benowitz et al., 2012; Conner, 1988). Sexual selection in *B. cornutus* has been shown to favour males with larger horns and larger body sizes (Conner, 1989; Formica et al., 2011). Even in bolitophagine genera where males do not possess this form of weaponry, such as in the genus *Eledona* Latreille, 1796, aggressive encounters between males on fungi still occur but are restricted to charging against opponents and head butting (E. Tihelka, pers. observ.). In Toxicini, members of *Toxicum* have been documented to engage in combat, but horns are present only in males (Yamazaki,

subtriangular process of the basal ventrite (Fig. 3D: icp).

Elytra strongly convex and subparallel, rounded in lateral view, 3.2 mm long, 1.38 times longer than their combined width, narrower than maximum width of pronotum, apparently not distinctly depressed around the scutellum. Surface coarsely tuberculate, coniform granules organised into 9 or 10 longitudinal rows (Fig. 4D). Lateral margins subparallel sided. Elytral epipleura narrow, complete to apices, widest basally.

Legs long, robust. Femora exceeding the width of the pronotum and elytra, with a shallow groove ventrally for the reception of tibiae. Tibiae slender, with two apical spurs, lacking apical spine. Tarsal formula 5-5-4. Basal four tarsomeres globular and subequal, distalmost tarsomere longer than the preceding four segments combined. Tarsi densely setose ventrally, tarsal claws thin and long, lacking dentation, with at least two long setae (Fig. 4B).

Abdomen with five subequal glabrous and coarsely punctate ventrites, broadest basally and tapering apically. Anterior process of ventrite 1 subtriangular. Membranes between ventrites not visible. Aedeagus of uninverted tenebrionoid type, approximately triangular in cross-section, shape as in Fig. 3F–I and 5. Note that the apical portion of the aedeagus could not be scanned and so does not appear in the microtomographic reconstructions in Fig. 3F–I.
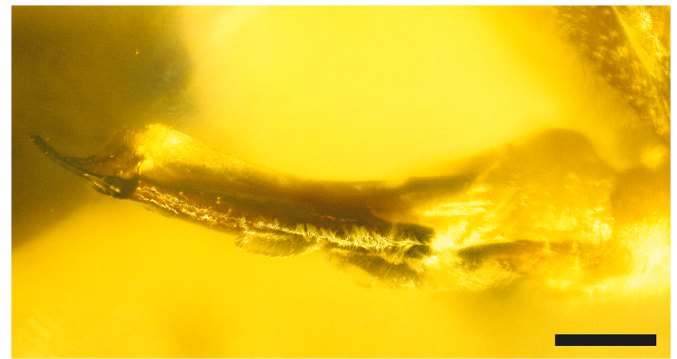
2009). The precise function of the pronotal horns in *Diceroderes* still remain a mystery, as the genus is scarcely encountered and no detailed behavioural observations are available to date. Smith and Cifuentes-Ruiz (2015) found no wear on the horns in all 88 of their examined specimens but noted that males had glandular openings on horns, implying that they may be used in semiochemical communication.

Being contemporaneous with fossil toxicines from Dominican amber (Doyen and Poinar, 1994; Smith and Sanchez, 2015), *D. jiangkuni* sp. nov. shares its place with *Wattius reflexus* and undescribed *Wattius* fossils as the earliest representative of Toxicini, demonstrating that the subtribe Dysantina diversified by the early Miocene. Today dysantines have a pantropical distribution, being absent in Nearctic, Palearctic and Antarctic realms. Dysantina is the only Toxicini subtribe that occurs in the New World. The high degree of morphological conservation in fossils belonging to *Diceroderes* and *Wattius* suggests that the subtribe Dysantina began to diversify and colonised the New World by the Miocene. The discovery of *D. jiangkuni* sp. nov. in Mexican amber falls within the extant distribution range of the genus, which is confined to Mexico and Central America. This indicates that *Diceroderes* persisted in the region with limited dispersal since the early Miocene. A similar pattern has been noted in some other Mexican amber arthropods as well, reflecting the relative ecological stability of rainforests in the region in the Cenozoic (Solórzano Kraemer, 2007).

Author statement

C.C. and E.T. conceived and designed the research. C.C. scanned the specimen. E.T. drafted the manuscript to which A.S., C.C., and D.H. contributed.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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