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The first fossils of *Alloraphes* (Coleoptera: Staphylinidae: Scydmaeninae) described from Miocene Dominican amber

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Abstract

Alloraphes Franz, 1980 is a small Neotropical genus (14 species) of Scydmaeninae (Coleoptera: Staphylinidae) beetles. *Alloraphes* are typically discriminated from the morphologically similar *Stenichnaphes* Franz via their aedeagal characteristics. Consequently, female members of both genera are often difficult to correctly place. Here we describe the first fossil species of *Alloraphes* in amber, and document its presence on the island of Hispaniola during the Miocene. Two individuals of new species *Alloraphes cantusfurca* **sp. nov.** are morphologically described using CT-scan data and microscope imagery. As the first known fossil member of the genus, *A. cantusfurca* provides a vital calibration point for future phylogenetic analysis and extends the temporal and geographic range of the genus. The implications for the biogeography of related taxa are also discussed.

Key words: Stenichnini, paleoethology, ant-like stone beetles, Neotropical, Hispaniola

Introduction

Amber from the Dominican Republic (15–20 Ma) contains numerous and diverse invertebrate inclusions (Iturralde-Vinent & Macphee 2019; Penney 2010; Poinar & Poinar 1999). As of 2010, over 1,000 fossil species had been described from Dominican amber. Insect fossils comprise a significant proportion of this diversity, with over 426 named species in 21 orders (Penney 2010). Dominican amber was produced by trees in the tropical palaeo-rainforests that covered the island of Hispaniola in the Miocene (Penney 2010; Poinar & Poinar 1999). The Dominican amber faunal assemblage contains a high proportion of taxa endemic to Hispaniola, of which the majority are assignable to contemporary genera still known from Hispaniola or other West Indies islands (Peck & Perez-Gelabert 2012). Most fossil lineages in Dominican amber display remarkable genus-level evolutionary stasis, suggesting minimal faunal turnover in the region since the Miocene (Hörnschemeyer *et al.* 2010; Peck & Perez-Gelabert 2012).

Staphylinidae is the most diverse family in Coleoptera with over 66,459 valid species names as of writing; 464 being extinct (Irmler *et al.* 2018; Newton 2022). Within the subfamily Scydmaeninae, 70 fossil species have been described worldwide, representing all four supertribes but only half of all known tribes (Jałoszyński & Perkovsky 2016; Newton 2022). To date, only 2 species of Scydmaeninae, *Homoconnus conservatus* Franz, 1983 and *Neuraphes fossilis* Franz, 1983, have been described from Dominican amber, both in the tribe Stenichnini (= Glandulariini, Cyrtoscydmini). An additional three specimens in *Euconnus* (Franz 1983), *Microscydmus*, and *Mastigus* (Poinar & Poinar 1999) have been identified in Dominican amber, however these identifications are considered dubious, as no formal descriptions, verifiable specimen numbers nor repositories were provided (Chatzimanolis & Engel 2013; Franz 1983; Poinar & Poinar 1999). New Scydmaeninae fossils provide insight into the evolutionary history and ecology of this ubiquitous modern subfamily.

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Alloraphes Franz, 1980 (Scydmaeninae: Scydmaenitae: Stenichnini) is a relatively small Neotropical genus of Scydmaeninae, containing 14 nominal extant species restricted to Central and South America (Asenjo *et al.* 2019; Jałoszyński 2013, 2020; Newton 2022). *Alloraphes* is a part of the *Alloraphes-Parastenichnaphes-Stenichnaphes* generic complex; a grouping of genera which superficially resemble each other, largely being differentiated by their aedeagal characteristics (Jałoszyński 2013, 2015). Unidentifiable females of Stenichnini within Indonesia are observed with traits similar to *Alloraphes*, but without male conspecifics it is not possible to determine their taxonomic placement (Jałoszyński 2013, 2019). Both *Alloraphes* and *Parastenichnaphes* share a unique highly sclerotized basal pumping apparatus of the median aedeagus lobe, but with free parameres in *Alloraphes* and fused parameres in *Parastenichnaphes* (Jałoszyński 2013). The aedeagus of *Stenichnaphes* lacks the pumping apparatus, and more closely resembles the aedeagus of *Euconnus* (Jałoszyński 2013, 2015). *Alloraphes* can further be distinguished through the presence of an anterior metacoxal processes and setae present on the sides of the pronotum (Jałoszyński 2015). For a detailed description of the *Alloraphes-Parastenichnaphes-Stenichnaphes* generic complex see Jałoszyński (2015).

Here, we describe the first fossil species of *Alloraphes*, *A. cantusfurca* **sp. nov.**, from two individuals within Dominican amber (Fig 1). This new record extends the temporal range of this Neotropical genus to at minimum the Miocene (15–20 Ma). Thus far, only two extant species have been recorded from the West Indies, *A. jamaicae* from Jamaica (Jałoszyński 2013) and *A. iyonolanus* from Saint Lucia (Jałoszyński 2020). This study represents the first described member of the genus *Alloraphes* from the island of Hispaniola; however, it is likely the genus is still present on the island awaiting rediscovery.

Material and Methods

The Dominican amber sample examined (RSKM_P3301.54) is a part of the Royal Saskatchewan Museum collection (Regina, SK, Canada). In addition to the *Alloraphes* specimens, the amber piece contains two syninclusions: a complete Platygastroidea (Hymenoptera) specimen and an unidentified Diptera leg fragment. Following ICZN recommendations, the new taxon proposed in this work has been registered in ZooBank under the LSID urn:lsid:zoobank.org:act:20A59358-EF77-4192-8FEC-AF584C8DFE00.

Synchrotron X-ray micro-CT scans of sample RSKM_P3301.54 were recorded with the BioMedical and Imaging Therapy (BMIT) Bending Magnet (BM) beamline of the Canadian Light Source (CLS) and Synchrotron facility (Wysokinski *et al.* 2007). Sample RSKM_ P3301.54 was temporarily attached to an adjustable sample holder with reusable adhesive putty that is nearly X-ray translucent and leaves no residue on the samples. A monochromatic, quasi-parallel beam of X-rays was used for tomographic imaging. The photon energy was set to 20 keV. The detector was comprised of an optical system (Optique Peter, France) which relayed luminescent images from the scintillator plate to the camera with demagnification of 5×. A 40-micrometer thick gadolinium oxysulfide scintillator (Photonic Science, UK) and a PCO Edge 5.5 camera were used. The effective pixel size was 1.47 µm, and sample to detector distance was 5 cm. The sample was rotated through 180 degrees, and 1500 tomographic slices were generated (0.12-degree steps) with 100 ms exposure times. The resultant data sets were preprocessed, reconstructed, and stitched using the *Tofu* image processing and tomography reconstruction toolkit (Faragó *et al.* 2022) and Python scripts created at CLS. Phase retrieval (Paganin *et al.* 2002) has been applied to boost the image contrast.

Dragonfly 2022.1 software was used for 3D rendering of individual specimens, as well as the segmentation of specific anatomy. Binning produced a voxel size of 2.94 µm in the dataset. Thresholding tools were used in Dragonfly to differentiate between regions containing specimens, air pockets and amber based on their X-ray contrast. Artefacts were removed utilising paintbrush and editing tools in Dragonfly. To generate the shaded renderings presented in the paper, Meshmixer and Mesh Lab were used to process the mesh files utilising ambient occlusion, Laplacian smoothing, and quadratic edge collapse decimation. 3D Builder was used to remove non-manifold surfaces and fill gaps in the cuticle caused by CT imaging or deleting non-manifold surfaces. Finally, Z-Brush was used to take high quality screenshots of renders under high contrast lighting.

***Abbreviations and terminology*—**body measurement abbreviations and general morphological terminology used here are consistent with those used by Jałoszyński (2013). Terminology used to describe the male genitalia of beetles has varied over the years; the terms used here are consistent with those used by Lawrence & Ślipiński (2013). Institutional abbreviations include: RSKM—Royal Saskatchewan Museum, Regina, Canada.

Systematic Palaeontology

Order Coleoptera Linnaeus, 1758

Family Staphylinidae Latreille, 1802

Subfamily Scydmaeninae Leach, 1815

Tribe Stenichnini Fauvel, 1885

Genus *Alloraphes* Franz, 1980

Alloraphes cantusfurca sp. nov.

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(Figs. 1–3)

Type Material: Holotype specimen RSKM_P3301.54a ♂, Paratype specimen RSKM_P3301.54b ♂, Dominican amber, Yanigua Formation, Miocene 20–15 Ma (Iturralde-Vinent & Macphee 2019) (Commercial specimen, Dominican Republic, El Valle).

Diagnosis. The main feature which separates *A. cantusfurca* from other taxa is its structure of aedeagus; long slender median lobe, parameres slender with rounded apices possessing singular long setae. Other characteristics informative in combination include; frons and vertex confluent without impression, pronotum with arcuate antebasal transverse groove without median pit, elytra modified with impressed apical region and pointed apices, aedeagus in ventral view (Fig. 2G) with slight asymmetry in apex of median lobe; apical projections not visible.

Description—BL = 0.83 mm, BW = 0.34 mm. Body (Fig. 2A, C) is ovate, convex and pubescent, weakly constricted between head and pronotum, and distinctly constricted between pronotum and elytra.

Head (Fig. 2C) prognathous, sub-triangular, slightly wider than long (HL = 0.13 mm, HW = 0.16). Vertex weakly convex, shallow concave depression between eyes (Fig. 3H). Frons flat, gradually declining anteriorly, posteriorly confluent with vertex. Frons constricted between antennal insertions, projecting anteriorly, subtriangular in shape. Strongly convex and moderately coarsely faceted compound eyes cover temporal region, forming widest portion of head. Occipital constriction slightly narrower than vertex. Antennal insertion visible dorsally (Figs. 2A,C; 3D,E), separated by >1.5 times diameter of antennal socket.

Labrum (Fig. 3E), anterior margin straight, lateral margins rounded.

Mandibles (Fig. 3I) slightly asymmetrical compared to one another. Median tooth difficult to discern in CT-scan rendering.

Maxillary palps strongly elongate; palpomere I small, approximately as long as it is broad; palpomere II strongly elongate, pedunculate and gradually thickening distally; palpomere III strongly elongate and slightly longer than II, nearly cylindrical in distal half with widest point near distal end; palpomere IV approximately half as long as III, subconical with pointed apex delimited by a sulcus.

Labial palps (Fig. 3F) narrowly separated at base; composed of 3 palpomeres: palpomere I and III similar length and width; palpomere II is longer than I and III combined, thin and pointed.

Antennae long relative to body length (0.26 times total body length; AnL = 0.30 mm), clavate, covered in setae; composed of 9 flagellomeres which gradually increase in size, scape and pedicle each larger than flagellomere I. Antennomeres IX–XI form indistinctly delimited club.

Pronotum (Fig. 2C) 1.21 times as long as wide, broadest at middle (PL = 0.23 mm, PW = 0.19). In dorsal view, pronotum convex, bell-shaped; anterior and lateral margins rounded. Pronotum anterior angles not distinctive, poorly developed; with short, dense, and sub-erect setae present on sides of pronotum; antebasal groove distinct, lacking median pit.

Prosternum (Fig. 2D) small, rectangular, wider than long. Intercoxal process acute.

Mesonotum with scutellum visible, sub-triangular in shape with rounded apex.

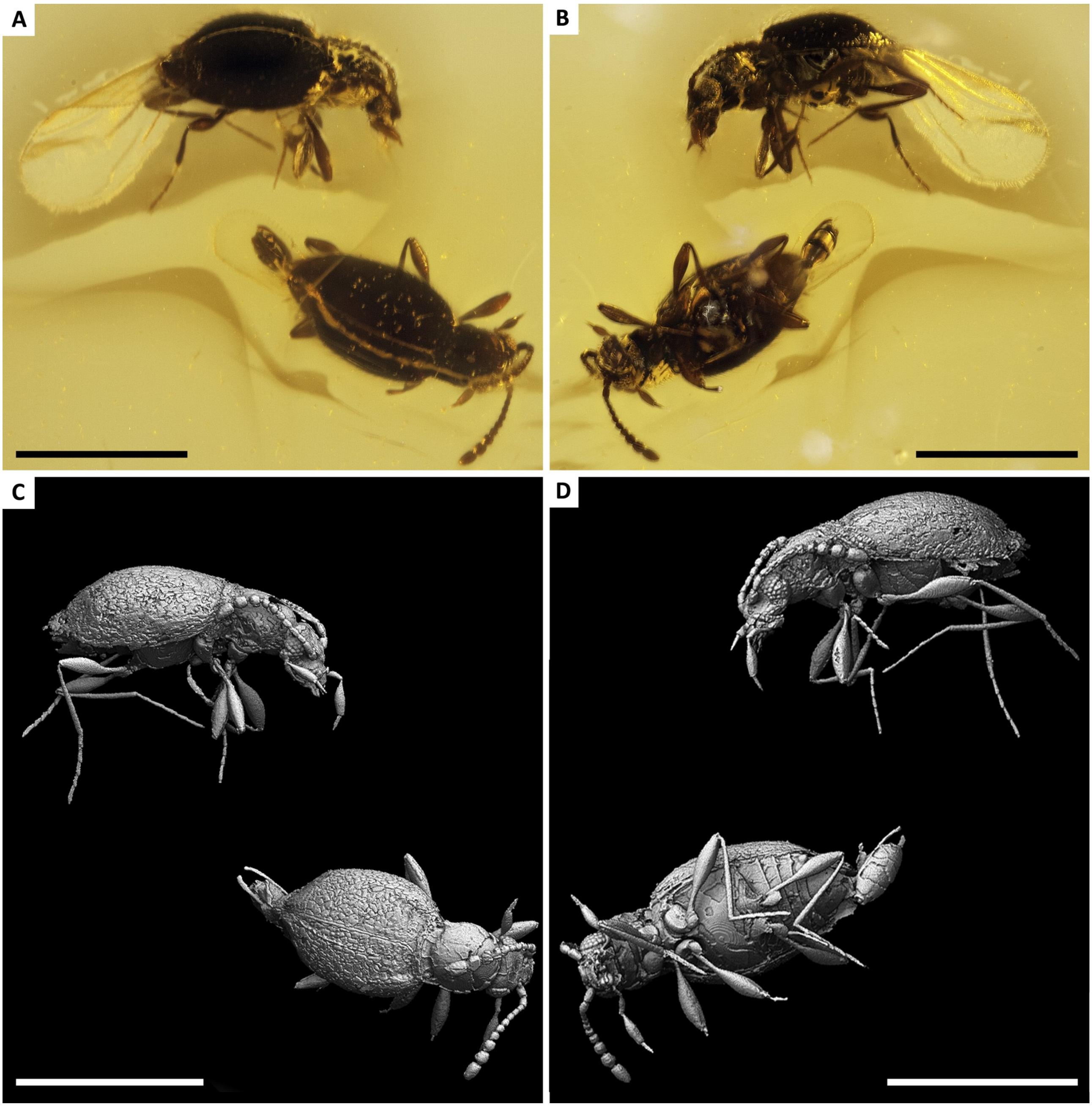

FIGURE 1. *Alloraphes cantusfurca*, RSKM_P3301.54 habitus and synchrotron X-ray μ-CT renderings of male (holotype) and male (paratype). **1A**, top down view; **1B**, underside view preserved in amber. Corresponding CT renders of male (holotype) and male (paratype) **1C,** top down view; **1D,** underside view. Scale bars = 0.5 mm (1A–D).

Mesoventral intercoxal process acute and projecting ventrally, connecting anteriorly with anterior ridge. Metaventrite laterally ridged; posterior transversely ridged. Metacoxal process acute and triangular, unclear if metacoxal process is notched in middle, due to artefacts in 3D renderings and limited visibility in amber.

Elytra (Fig. 2A,C) sub-ovoid in shape (EL = 0.47 mm, EW = 0.34 mm, EI = 1.40 mm) modified with pointed apices which are impressed. Surface structure and sculpture of elytra difficult to discern in amber microscopy and CT model. Distinct sub-humeral lines present, with lengths approximately one-third of elytral length. Elytra densely covered with long, sub-erect setae. Pygidium not exposed.

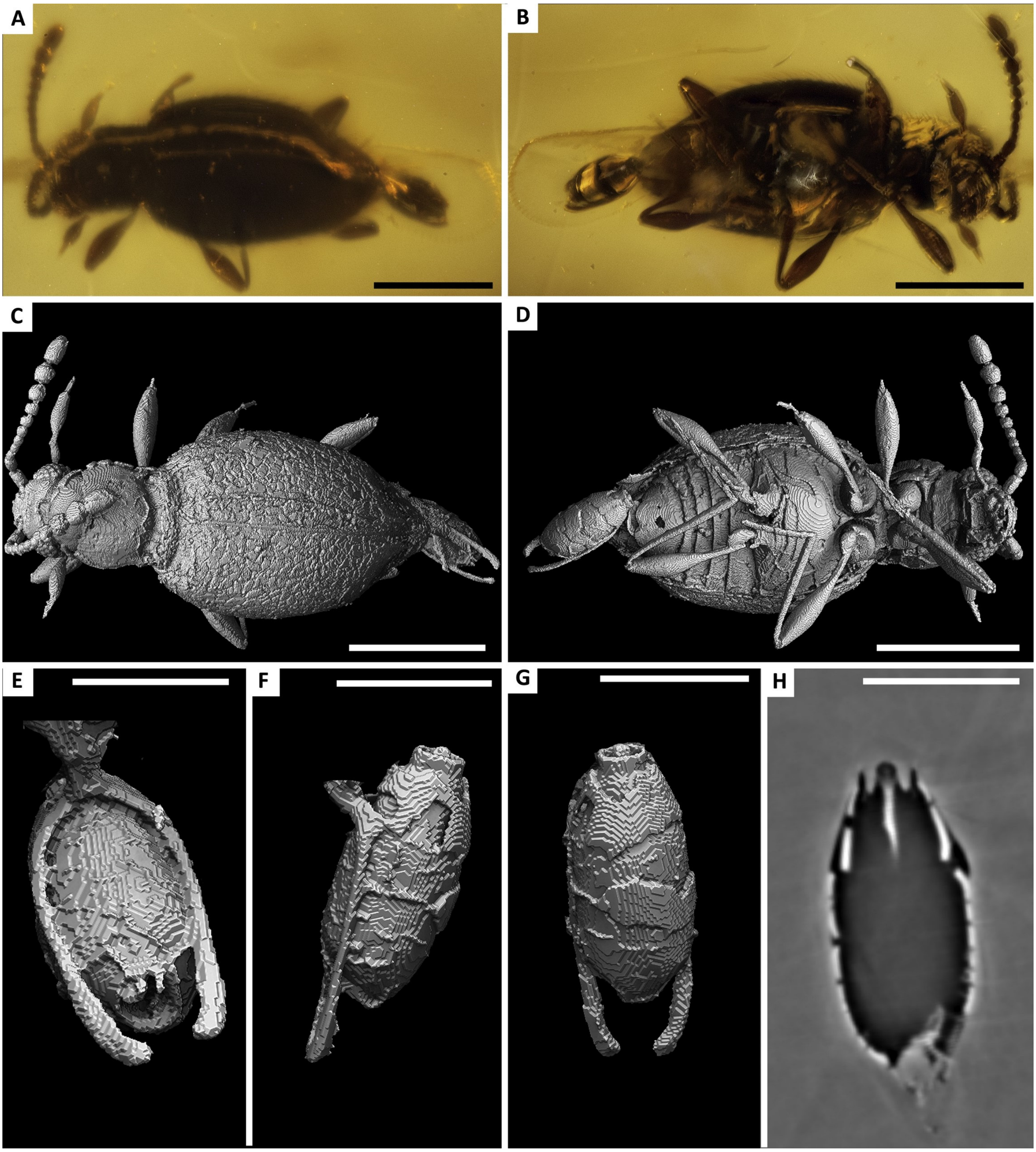

FIGURE 2. *Alloraphes cantusfurca,* RSKM_P3301.54a with focus on male (holotype) habitus and synchrotron X-ray µ-CT renderings. **2A,** dorsal view of male holotype in amber; **2C**, corresponding view of CT render. **2B,** ventral view of male holotype in amber; **2D,** corresponding view of CT render. Male (holotype) genitalia: **2E** dorsal view; **2F** left lateral view; **2G** ventral view; **2H** CT slice conditions. Scale bars = 0.25 mm (2A–D) and = 0.1 mm (2E–H).

Legs (Fig. 3E) moderately long and slender. Procoxae and mesocoxae sub-globular and weakly conical; metacoxae strongly transverse. Trochanters all short and lenticular. Femora clavate, tibiae long and slender, both covered in long setae. Tarsomeres long and slender; tarsomeres I–III similar in length, tarsomere IV slightly shorter and tarsomere V slightly longer. Tarsomeres covered in dense setae. Simple tarsal claws present.

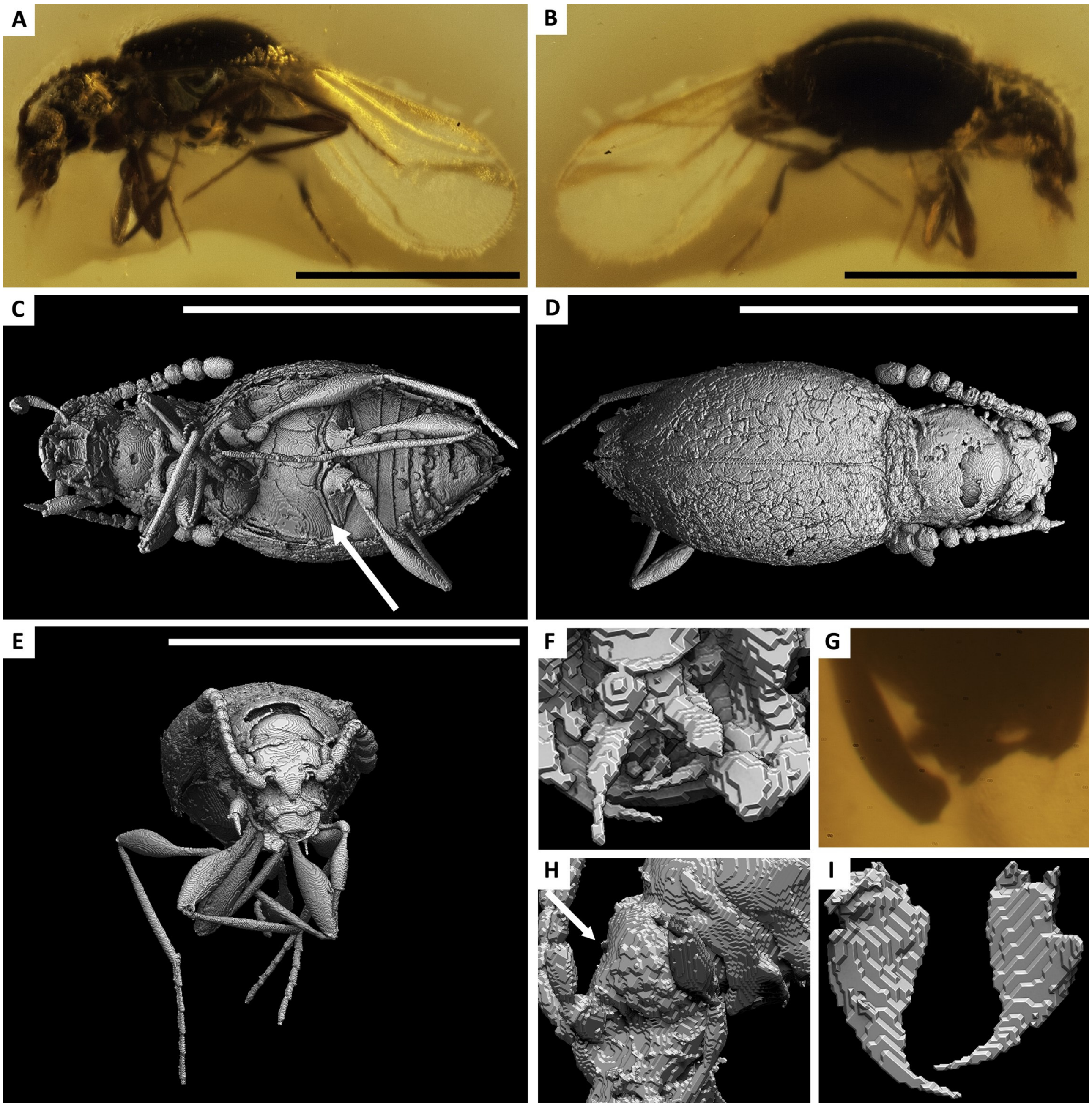

FIGURE 3. *Alloraphes cantusfurca,* RSKM_P3301.54b with focus on male (paratype) habitus and X-ray µ-CT renderings. **3A,** dorsal view in amber; **3C,** dorsal view of CT render arrow pointing toward transverse ridge. **3B,** ventral view of in amber; **3D** corresponding view of CT render. **3E,** anterior view of CT render. **3F,** dorsal view of paratype CT render with focus on labial palps, **3G,** compound microscope zoomed in image of holotype's aedeagus with focus on setae on the apex of parameres **3H,** zoomed in left lateral view of holotype's head, arrow points to depression between eyes **3I,** zoomed in ventral view of mandibles separated from CT render. Scale bars = 0.5 mm (3A–F).

Abdomen (Fig. 2D) with unmodified sternites. Sternites of similar sizes, with sternite I and V being slightly larger than II–IV. Sternites I–V unmodified, whilst VI connate; suture between sternite V and VI shallow.

Aedeagus (Fig. 2E–G) weakly asymmetrical in apical region (AeL = 0.17 mm). Parameres free and weakly expanding distally and long, extending past median lobe by approximately one-third of their total length. Parameres apices rounded, with singular long setae (Fig. 3G). Internal structure somewhat preserved (Fig. 2H), with basal pumping apparatus bearing medial sclerotized projection extending internally and evidence of muscle fibre attachments.

Paratype measurements (in mm): BL = 0.72, HL = 0.11, HW = 0.13, AnL = 0.30, PL = 0.18, PW = 0.17, EL = 0.43, EW = 0.30, EI = 1.45.

Etymology. The species epithet *cantusfurca* refers to the species' aedeagal characteristics, with the parameres resembling the shape of a tuning fork. The epithet combines the Latin terms *cantus* for "song" and *furca* for "fork".

Remarks—*Alloraphes cantusfurca* **sp. nov.** is placed in the genus *Alloraphes* according to the following set of characteristics from the revised genus diagnosis by Jałoszyński (2013): head subtriangular, vertex not expanded dorso-caudad; occipital constriction only slightly narrower than vertex; thick and long bristles absent on head but present on sides of prothorax; posterior margins of eyes adjacent to occipital constriction; submentum demarcated latterly from hypostomae by sutures; maxillary palpomere III strongly elongate, palpomere IV nearly four times long as broad at base; antennae with indistinctly delimited club composed of antennomeres IX–XI; base of pronotum with transverse groove connected at each end to shallow lateral impression or pit, without sub-lateral carinae; prothoracic hypomeral ridges complete; basisternal part of prosternum much shorter than procoxal cavites. In males, the aedeagus in ventral view (Fig. 2G) has slight asymmetry in the apical region with a basal pumping apparatus bearing a medial sclerotized projection extending internally with evidence of muscle fibre attachments; parameres free. Syninclusion is identified as *A.cantusfurca* due to it sharing diagnostic characters and morphological traits with holotype (Fig. 1).

Discussion

As the first fossil representatives of *Alloraphes*, *A. cantusfurca* **sp. nov.** provides vital insight into the evolutionary history of the genus during the Middle Miocene (15–20 Ma) (Iturralde-Vinent & Macphee 2019). Correctly differentiating members of the morphologically similar *Alloraphes-Parastenichnaphes-Stenichnaphes* complex can be challenging in modern settings. *A. cantusfurca* externally resembles to *A. cayennensis*, although in *Alloraphes* external habitus is often not a diagnostic character. *A. cantusfurca and A. cayennensis* share similar aedeagus habitus with their paramares both being thin and long, although in *A. cayennensis* the apical region is pointed, while in *A. cantusfurca* it is rounded. Apical projections within *A.cantusfurca* are hard to visualise while in *A. cayennensis* the apical projection is prominent and hooked (Jałoszyński 2020). *A.cantusfurca* possesses a singular long seta on the apex of its paramere, a trait in which it shares with *A. myrmecophilus* (Jałoszyński 2013). The majority of described *Alloraphes* appear to possess multiple setae on their parameres, making the discovery of another single setae *Alloraphes* an exciting prospect (Jałoszyński 2013, 2020).

Amber is unique in preserving direct evidence of ecologically relevant behaviours, such as symbiotic relationships, predator-prey dynamics and oviposition (Arillo 2007; Poinar 2010; Grimaldi & Ross 2017). Here, the holotype's aedeagus is externally projected, likely due to pressure being applied to the abdomen as it became engulfed in viscous resin (Chen 2020). Within the amber record significant bias exists to preserve arthropods which live within or share close proximity to resinous trees (Solórzano Kraemer *et al.* 2018). Extant Stenichnini are associated with leaf litter, soils and decaying wood spending the majority of their life on the forest floor (Arnett & Thomas 2000; Jałoszyński & Perkovsky 2016). The entrapment of *A. cantusfurca* within resin likely occurred whilst in flight, being blown into a viscous stalagmite like resin flow (Jałoszyński & Perkovsky 2016; Solórzano Kraemer *et al.* 2015, 2018). *Hymenea* trees, the main resin producing plant for Dominican amber, are noted to produce resin flows close to the ground ideal for the entrapment of flying or active runner arthropods (Poinar 2010; Solórzano Kraemer *et al.* 2018). The amber piece is notably free of litter components such as insect frass, botanical material or dirt. The resin likely captured *A. cantusfurca* and solidified on the tree bark instead of falling and engulfing the beetles and surrounding forest floor impurities (Perrichot 2004).

Alloraphes cantusfurca is the first member of the genus to be formally described from the island of Hispaniola (fossil or extant). Scydmaeninae are observed on Hispaniola through extant taxa *Microsydmus* (*Neoscydmus) atomus* Reitter, 1883 and *Euconnus dominicae* Franz, 1991 (Peck 2006; Peck & Perez-Gelabert 2012). Extant *Alloraphes* have been recorded from Jamacia and Saint Lucia in the West Indies (Jałoszyński 2020). As these beetles are exceptionally small (0.83–0.72 mm) and the proclivity for Stenichnini to inhabit leaf litter, it is likely that there are extant members of the genus still living on Hispaniola awaiting discovery and description. Frank & Thomas (2019) estimated that approximately 75% of Staphylinidae species are left to be described from the tropics. Collections within the region are likely to hold numerous specimens waiting for taxonomic study highlighting the importance to collaborate with and improve local knowledge bases (Peck 2016; Engel *et al.* 2021).

Comparing *A. cantusfurca* to extant taxa highlights how *Alloraphes* has changed since the Miocene, or potentially indicate ancestral character combinations or states within the genus. It will be interesting to see if future work reveals extant species of *Alloraphes* present on Hispaniola or additional species represented as fossils. Their presence as well-preserved fossils may help inform phylogenetic analyses of the group and shed some light on whether there have been persistent populations on the island, or repetitive dispersal events that have shaped their modern distribution.

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We would like to thank Dr Rich Leschen for directing us to Dr Paweł Jałoszyński, who identified the specimens as *Alloraphes* and provided literature on the genus. Most notably Dr Jałoszyński highlighted an incorrect diagnosis of the RSKM_P3301.54b as female; we thank him for his level of professionalism and quality of constructive criticism during the writing process.

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