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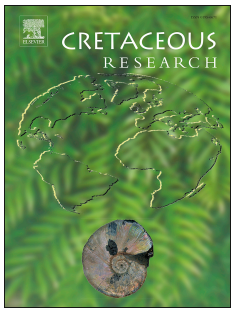

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A revision of *Haidomyrmex cerberus* Dlussky (Hymenoptera: Formicidae: Sphecomyrminae) from mid-Cretaceous Burmese amber

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ABSTRACT

The type species of the genus *Haidomyrmex* Dlussky, 1996 is revised. *Haidomyrmex cerberus* was originally described based on a partial worker specimen only, which was later re-figured with some erroneous characters. Two worker specimens

assignable to this species were recently discovered in the collection of Burmese amber from the Capital Normal University of Beijing. A revised description and comparison with the two other known species of *Haidomyrmex* are provided, and the diagnoses of the genus and species are emended.

Key words:
Haidomyrmecini
stem-group ants
Myanmar
trap-jaw ants
hell-ants.

1. Introduction

Fossils are unique records of the past diversity of life, providing the only evidence on stem groups or extinct lineages that vanished millions of years ago. Some fossils that are exquisitely preserved can provide a myriad of morphological and ecological data on an extinct taxon. But there are a lot of species known and described from a single fossil individual that is incompletely preserved, thus remaining only partially informative. In 1996, Dlussky described *Haidomyrmex cerberus*, the first ant species ever found in Burmese amber and a highly intriguing ant with a bizarre cranio-mandibular morphology. Unfortunately, the type and unique specimen was only partially preserved, missing parts of the antennae, legs and gaster. Some characters, especially those of the head, were also obscured due to the turbidity of the amber piece and the position in which the specimen was exposed. Still, Dlussky provided a rather detailed description including some hardly visible features, and he suggested this ant to be analogous to the modern trap-jaw ants, but placed the genus in the extinct Sphecomyrminae (Dlussky, 1996). This placement was followed by Bolton (2003) who erected a new tribe Haidomyrmecini for this genus. Engel and Grimaldi (2005: figs. 7–8), however, proposed a re-interpretation of the holotype and modified the generic diagnosis. In contrast to the features described by Dlussky (1996), Engel and Grimaldi (2005) could not see the inner tooth on the mandibles, the long trigger setae on the clypeus, the stiff seta on the third antennomere, the remnant ocelli, and the subpetiolar process. They also suggested that the mandibles were not preserved in their natural position but significantly distorted, and erroneously noted similarities with the genus *Brownimecia* Grimaldi, Agosti & Carpenter, 1997, from New Jersey amber. But the discovery of *Haidomyrmodes* Perrichot et al., 2008, a genus closely

similar to *Haidomyrmex*, later revealed that Dlussky (1996) had correctly interpreted the mandibles (Perrichot et al., 2008). The haidomyrmecines' bauplan was further confirmed by the subsequent discoveries of the genera *Haidoterminus* McKellar, Glasier & Engel, 2013, *Ceratomyrmex* Perrichot, Wang & Engel, 2016, and *Linguamyrmex* Barden & Grimaldi, 2017 (McKellar et al., 2013; Perrichot et al., 2016; Barden et al., 2017). But some confusion remains on the strict definition of *Haidomyrmex* and the Haidomyrmecini, since two additional species of *Haidomyrmex* were described with 12 antennal segments while depicted with only 11 segments (Barden and Grimaldi, 2012: fig. 4), and the presence of the trigger setae, reduced ocelli and inner mandibular tooth was confirmed on the holotype of *H. cerberus* (Perrichot et al., 2016: supplemental information).

Finally, despite the discovery of several hundreds of additional specimens of *Haidomyrmex* in Burmese amber during the last decade, it is striking that none could be assigned to *H. cerberus* again (Perrichot, pers. data from various institutional and private collections). Instead, they largely belong to *H. scimitarus* Barden & Grimaldi, 2012, more rarely to *H. zigrasi* Barden & Grimaldi, 2012, the two other species described more recently (Barden and Grimaldi, 2012). A reason for this could be that the type specimen of *H. cerberus*, although described in 1996, originated from an early collection of Burmese amber that was sent to Cockerell by Swinhoe in 1920 (Ross and York, 2000; Zherikhin and Ross, 2000). Thus, the holotype might have been collected from a locality and/or geological stratum that was potentially distinct from the current localities from where Burmese amber were mined for the last decade. However, in a study of 250 ants from the Burmese amber collection that was recently established at the Capital Normal University of Beijing, two out of nine *Haidomyrmex* are assignable to *H. cerberus*. This discovery allows for a complemental description

of the species and emendations for the generic and specific diagnoses.

2. Material and methods

Depository, horizon, and specimen handling

This study is based on new amber material from Hukawng Valley in Kachin State of northern Myanmar located at the north end of Noije Bum, at 26°15′N, 96°34′E, some 18 km south-west of the town of Tanai. This deposit is dated to 98.79 ± 0.62 Mya based on radiometric uranium-lead dating (Shi et al., 2012), and the recent finding of an ammonite embedded in amber and assignable to *Puzosia* (*Bhimaites*) supports a Late Albian–Early Cenomanian age of the amber (Yu et al., 2019). The amber is housed in the Key Lab of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, China. (CNUB; Dong Ren, Curator)

Specimen No. CNU-HYM-MA2019051 is complete, without apparent distortion, and preserved in a piece of yellow amber containing a suspension of bubbles and organic fragments. Specimen No. CNU-HYM-MA2019052 is almost complete, missing only the left antenna beyond scape and left foreleg beyond femur, and is only weakly distorted. It is preserved in a piece of clear yellow amber with stellate hairs, fragments of a spider web and organic debris, and has tiny bubbles or dust covering the cuticle in places. Both amber pieces were ground and polished to form small cabochons prior to acquisition, but a further polishing in the CNU Lab was made using silicon carbide papers for us to inspect the specimens in optimal views.

The specimen CNU-HYM-MA2019051 was examined and photographed using a Nikon SMZ 25 microscope equipped with a Nikon DS-Ri 2 digital camera system.

The specimen CNU-HYM-MA2019052 was examined and photographed using a Leica MZ8 stereomicroscope equipped with a Canon 5D Mark II digital camera, and stacks of photographs taken at different focal planes were merged using Helicon Focus software. The line drawing and figures were produced using Adobe CC (Illustrator and Photoshop). Measurements were obtained using the measurement tool of Nikon software.

The type specimen NHM-In.20182 was examined and photographed at the Sackler Lab of the Natural History Museum of London in 2013. The photographs are available on AntWeb (at www.antweb.org).

3. Systematic palaeontology

Family Formicidae Latreille, 1809

Subfamily Sphecomyrminae Wilson & Brown, 1967

Tribe Haidomyrmecini Bolton, 2003

Genus *Haidomyrmex* Dlussky, 1996

Type species. Haidomyrmex cerberus Dlussky, 1996: 451, fig. 1. See also: Engel and Grimaldi, 2005: 11, figs. 7–8; Perrichot et al., 2016: fig. S3D.

Diagnosis (emended from Barden and Grimaldi, 2012). Gracile ants of varied body lengths (3.5 – 8.0 mm), lacking extensive cuticular microsculpture; ocelli present as pit-like traces or absent (not visible on part of specimens); eyes bulging; antennae long, pedicel very short, ca. 0.20 – 0.12x length of scape, 1st flagellomere (F1) bearing a stiff, erect seta on ventral surface; F2 (rarely F3) longest of basal three

flagellomeres; clypeus posteriorly developed into an elevated setose lobe just below antennal insertions, the lobe coated by a brush of stiff spines and bearing a pair of fine, long trigger setae around anterolateral corners; frontal triangle prominent, positioned just behind clypeal lobe, anteriorly with tuft of stiff setae; face and gena distended; mandible scythe or L-shaped, with short, straight basal portion and long apical portion curved upward; inner surface of mandibles shallowly concave, the ventral corner between basal and apical portions with a triangular blade pointing inward; mandibles apparently moving vertically and laterally; when closed, mandibles parallel and vertically aligned, with inner blades overlapping and tips of apical portion meeting clypeal brush; pronotum with narrow neck; thoracic sutures oblique; legs long and slender; pretarsal claw with small subapical tooth; propleuron very well-developed; propodeum with shallow or steep declivity; petiole nodiform, with short anterior peduncle, subpetiolar process present; gaster without constriction between first and second segments; sting large and entirely retractable.

Haidomyrmex cerberus Dlussky, 1996

Figs. 1–3

New material examined. CNU-HYM-MA2019051 and CNU-HYM-MA2019052, both workers, deposited in insect fossil collection of Capital Normal University, Beijing (CNUB); holotype NHM.In.20182, in Natural History Museum, London, U.K.

Emended diagnosis (from Dlussky, 1996). Worker. Body length 4.5 to 5 mm. Antenna with scape about as long as combined length of three following segments, F1 1.3 –

1.4 times of pedicel length, F2 longest of basal three flagellar articles, ca. 2.2 times of pedicel length; clypeal lobe coated by stiff setae evenly arranged in rows, those on ventral margin longer and thicker; mandibles scythe shaped, elbowed at right angle, with anterior margin of inner blade bearing a longitudinal row of 7–8 spine-like setae, apical portion with acute tip but without serration; mesonotum with scutellum distinctly convex; propodeum gradually sloped; subpetiolar process keel-like, with anterior surface nearly vertical.

Description of new material. Based on CNU-HYM-MA2019051, with differential characters from CNU-HYM-MA2019052 in brackets. All measurements are in millimeters (mm). Total body length ca. 4.50 [4.90]. Head, mesosoma and petiole sparsely covered by thin erect setae; legs (except coxae and trochanters) and outer surface of mandibles more densely covered by thin setae; pygidium and hypopygium setulose [antenna and outer surface of mandibles densely covered by fine decumbent setae; remaining body sparsely covered by thin, short erect setae]. Height of head capsule (from anterior clypeal margin to highest point of vertex) 0.80; length (from anterior surface of clypeal lobe to occipital margin) 0.52. Ocelli absent [reduced to pit-like traces]. Length/width of compound eyes 0.30/0.20. Antenna inserted between compound eyes and flanking prominent frontal triangle; total length of antenna 2.55; scape ca. 4 times as long as pedicel, F1 ca. 1.4 times length of pedicel [1.3x]; FII ca. 2.2 times length of pedicel; lengths of antennomeres: scape 0.53, pedicel 0.12; flagellomeres F1–F10: 0.16, 0.23, 0.22, 0.20, 0.20, 0.22, 0.18, 0.17, 0.16, 0.21; apex of scape slightly broadened, its ventral margin bearing short erect setae; FI with stiff, erect seta on ventral surface (Fig. 2B). Clypeal process a small hemispheric lobe (maximal diameter 0.12) moderately elevated, dorsal surface coated by brush of stiff

spine-like setae gradually longer and thicker toward ventral margin of lobe, ventral surface with one visible pair of trigger setae [two pairs visible] flanking tips of mandibles; trigger seta length 0.31. Anterior clypeal margin concave, bearing 4 erect stiff setae (Fig. 2C). Mandibles (Fig. 2C) parallel and close to each other, basal portion 0.51 in length (ignoring slight curvature), curved apical portion 0.67 in length; curved portion gradually tapered to an acute point, apex nearly reaching to tip of clypeal process, ventral margin of curved portion coated in dense setae from base to terminal quarter; inner surface of mandibles concave, particularly from inner triangular blade to apical two thirds of curved portion; anterior margin of triangular blade with a row of 7–8 spine-like setae directed inward (Fig. 2C); triangular blades overlapping posteriorly, apparently symmetrical and each with a single minute tooth. Maxillary palps (Fig. 2D) long, exposed length 0.53, with 5 visible articles (basal article mostly concealed between mandibles). Labial palps (Fig. 2D) short, exposed length 0.08, with only 2 apical articles visible (but palp formula should be 5:3 according to undescribed specimens of *Haidomyrmex* with palpomeres fully exposed; Perrichot, pers. data from various institutional and private collections).

Mesosoma. Long and slender; depth (greatest dorso-ventral distance) 0.45, length (including neck) 1.98. Neck narrow and long, pronounced in lateral view. Pronotum elongate; pronotal dorsal outline feebly convex in its anterior third, flat and sloped in its posterior two thirds (Fig. 1A, B; Fig. 2A). Mesosomal length 0.38; mesonotum convex (Fig. 1A, B), maximum width 0.12 and 0.08 in height. A distinct metanotal sclerite posteriorly to this bulging mesoscutellum. Propodeum longer than high, gradually sloping posteriorly; metapleural gland opening semicircular, facing posteroventrad; metapleural bulla developed, roughly hemispherical. Legs long and slender. Length of procoxa 0.65, mesocoxa 0.39, metacoxa 0.32. Length of meso- and

metatrochanters 0.20. Length of pro- and mesofemur ca.1.00, metafemur 1.84. Length of protibia 0.86, mesotibia 0.91, metatibia 1.67. Protibia apically with one long pectinate spur (calcar) and two short simple spurs. Mesotibia with two simple spurs, metatibia with one large pectinate spur and one short simple spur (Fig. 1D). Several short and stiff setae also present apically on hind tibia. Total length of pro-, meso-, and metatarsi 1.10, 1.37, 1.90, respectively. Basal tarsomere longest, remaining four tarsomeres shortening gradually, length of metatarsal segments I–V: 0.87, 0.46, 0.30, 0.18, 0.20. Surface of tarsomeres covered with fine setae. Pretarsal claws with distinct subapical tooth, arolium well-developed.

Metasoma. Petiole (Fig. 1C) with short anterior peduncle, dorsal margin broadly rounded, strongly narrowed posteriorly; petiole length 0.58, maximal height 0.32. Subpetiolar process (Fig. 1C) 0.06 at greatest height, in profile a small triangle with posterior margin distinctly longer than anterior margin. Lateral sulcus visible running anteroposteriorly along petiole. First gastral segment with helcium pronounced, forming a narrow post-petiolar peduncle. Gaster 1.45 in length (excluding sting), with gastral segment I 0.48, segment II 0.57; sutures between tergite and sternite of segments I and III distinct; distal part of gastral segment V (pygidium and hypopygium) setulose. Sting long, robust; externalized part enclosed by gonostyli/third valvulae.

Locality and horizon. Hukawng Valley, Kachin State, northern Myanmar; formed near the Aptian-Cenomanian boundary (Shi et al., 2012), ca. 99 Mya.

Remarks. Assignment of these two specimens to *H. cerberus* is based on the similarities in the body sizes (4.5 to 5 mm, *vs.* 8 mm for *H. scimitarus* and 3.5 mm for

H. zigrasi). The antennae are also similar, with the scape as long as the three following antennomeres combined (*vs.* scape distinctly longer in *H. scimitarus* and *H. zigrasi*), and with F1 ca. 1.2 times the length of pedicel, F2 ca. twice the length of pedicel (*vs.* F1 twice as long as pedicel, F2 4 times the length of pedicel in *H. scimitarus*; F1 slightly shorter than pedicel, F2 as long as pedicel in *H. zigrasi*). Finally, the body covered by dense patches of erect setae, combined with the dense pubescence of the basal antennomeres and outer surface of the mandibles, are characteristic of *H. cerberus*, but absent in the other two species.

4. Conclusion

The present discovery confirms that all species of *Haidomyrmex* possess similar mandibles with the inner surface armed with a triangular blade, and paired trigger setae ventrally on the clypeus. It is likely that they all have the inner surface of mandibles concave and with a ventral row of stiff setae, although these characters could not be assessed for *H. zigrasi* since the only know specimen has the mandibles tightly closed. The specimen CNU-HYM-MA2019052 is preserved with the mandibles entirely aligned and their triangular blades overlapping, suggesting that the inner concavities form a tube-like channel. Similar concave mandibles forming a channel were observed on *Linguamyrmex*, another genus of haidomyrmecine ants that might have used this system to feed on liquid (Barden et al., 2017). Some extant ants feed on honeydew or hemolymph (Hölldobler and Wilson 1990; Saux et al. 2004). It indicates that *Haidomyrmex* might have fed on liquid too, as maybe all members of the Haidomyrmecini, or so-called “hell ants”. This tribe currently contains seven species within five genera of potentially highly specialized predators, and

encompassing most of the Late Cretaceous: *Haidomyrmex* (3 sp.), *Ceratomyrmex* (1 sp.) and *Linguamyrmex* (1 sp.), from Burmese amber; *Haidomyrmodes* (1 sp.) from Albian-Cenomanian French amber; and *Haidoterminus* (1 sp.) from Campanian Canadian amber (Perrichot et al., 2008, 2016; Barden and Grimaldi, 2012; McKellar et al., 2013; Barden et al., 2017; Barden, 2017: table. 1). Indeed, all female haidomyrmecines share long sickle to L-shaped mandibles that uniquely moved in a vertical plane aligned with the longitudinal axis of the body, and a clypeus elongate and posteriorly with a prominent setose pad (*vs*. short mandibles transversely aligned and moving laterally, and clypeus transverse and anteriorly setose in the remaining Sphecomyrminae).

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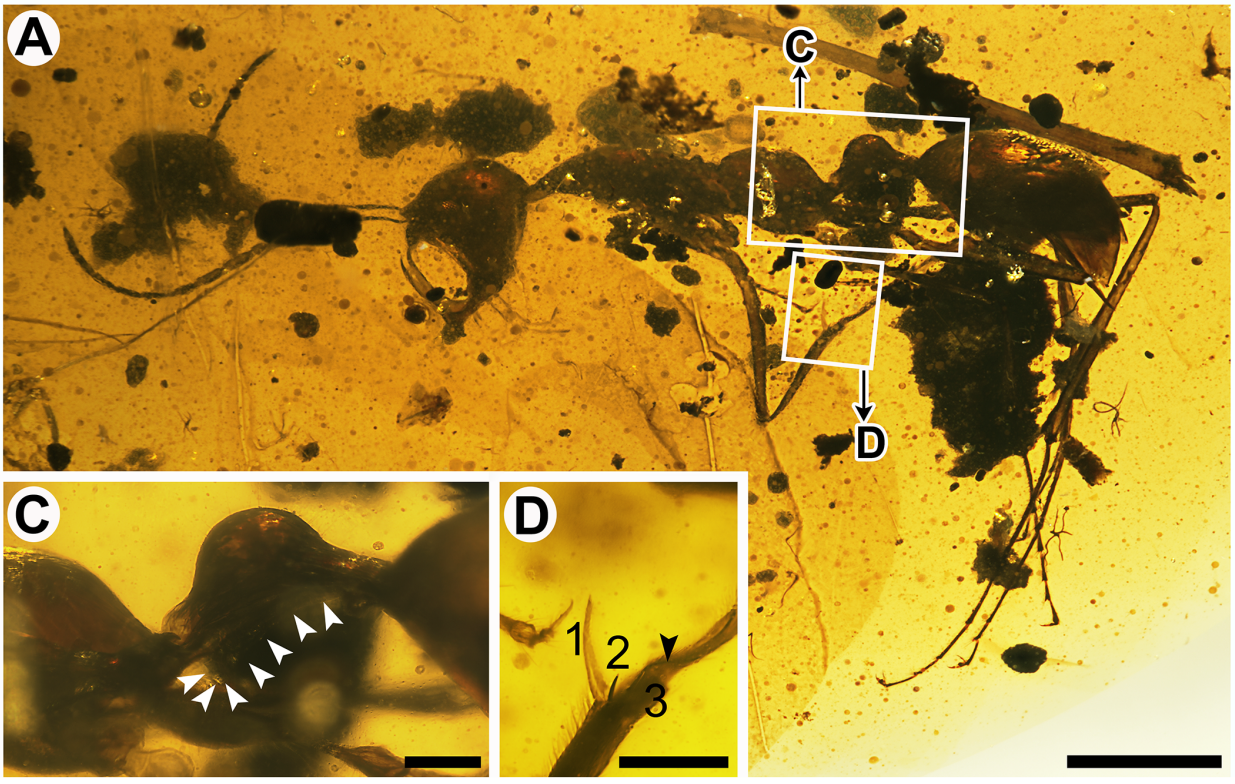
Figure Captions

Fig. 1. *Haidomyrmex cerberus*, new material CNU-HYM-MA2019051 from Myanmar amber. A, Left lateral general habitus. B, Line drawing of general habitus. C, Photograph of petiole in lateral view. D, Right protibial spurs. (Scale bars for A, 1 mm, B, 1 mm, C, 0.2 mm, D, 0.2 mm.)

Fig. 2. *Haidomyrmex cerberus*, new material CNU-HYM-MA2019051. A, Photograph of right lateral general habitus. B, Photograph of first flagellomere in lateral view. C, Photograph of mandibles in lateral view. D, Photograph of palps in lateral view. (Scale bars for A, 0.5 mm, B, 0.2 mm, C, 0.2 mm, D, 0.2 mm.)

Fig. 3. *Haidomyrmex cerberus*. Photographs of new material CNU-HYM-MA2019052. A, Habitus in right lateral view. B, Habitus in ventral view. C, Head in ventral view. (Scale bars: A, B, 1 mm; C, 0.5 mm)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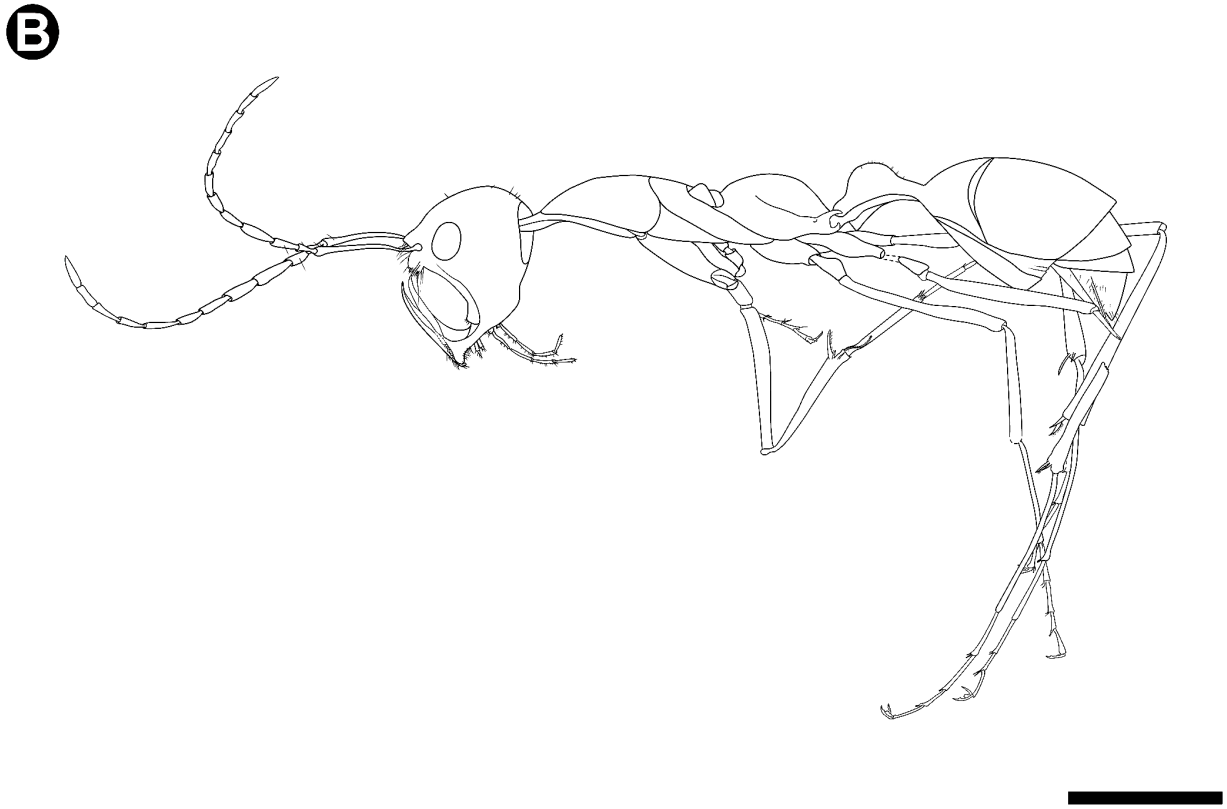
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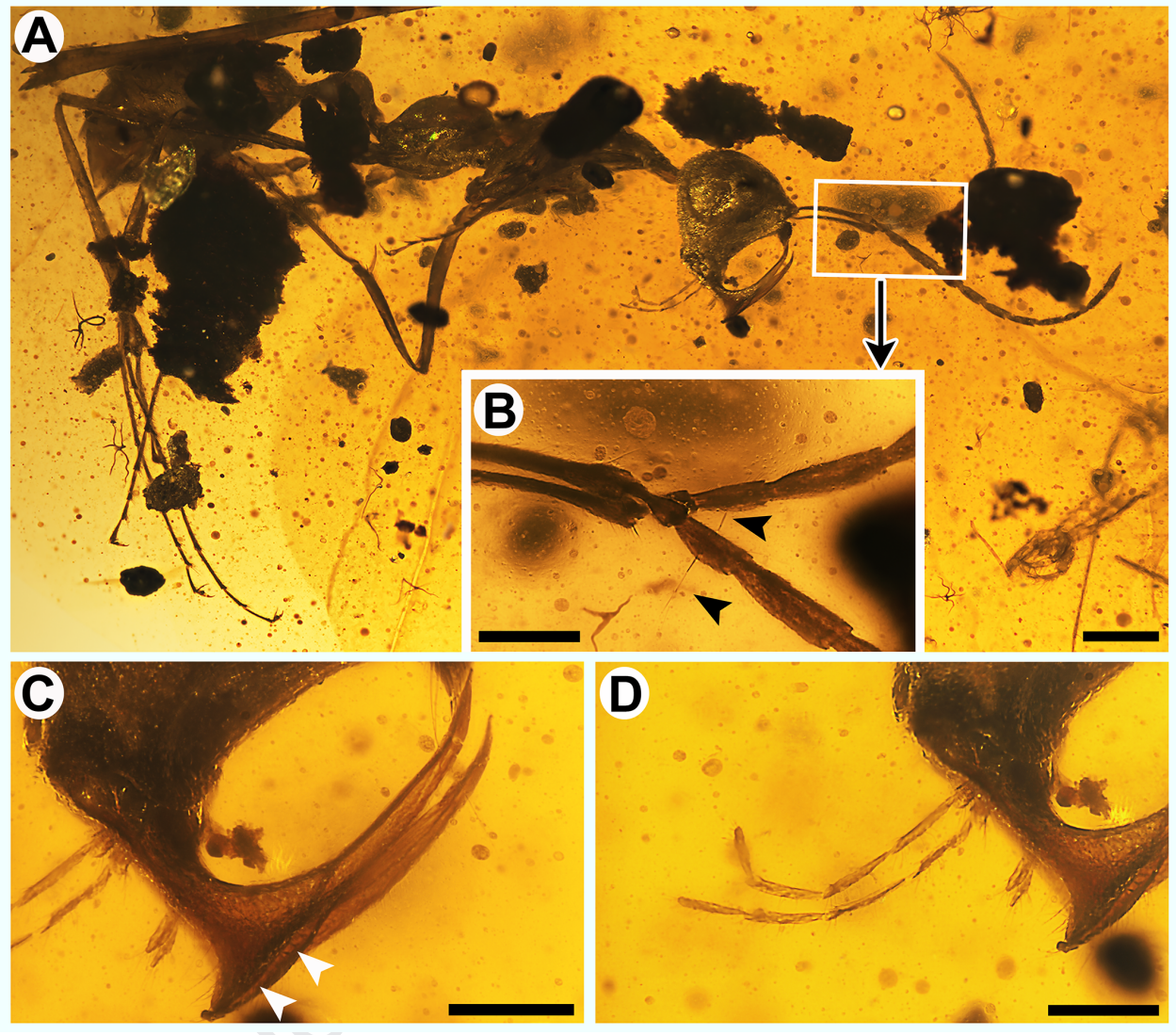
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