

A new genus of hell ants from the Cretaceous (Hymenoptera: Formicidae: Haidomyrmecini) with a novel head structure

PHILLIP BARDEN^{1,2} , HOLLISTER W. HERHOLD² and DAVID A. GRIMALDI²

¹Department of Biological Sciences, New Jersey Institute of Technology, Newark, NJ, U.S.A. and ²Department of Invertebrate Zoology, American Museum of Natural History, New York, NY, U.S.A.

Abstract. An unusual Cretaceous trap jaw ant is described from Burmese amber dated to the Late Cretaceous. *Linguamyrmex vladi* **gen.n. sp.n.** is distinguished by an unusual suite of morphological characters indicating specialized predatory behaviour and an adaptive strategy no longer found among modern ant lineages. The clypeus, highly modified as in other closely related haidomyrmecine hell ants, is equipped with a paddle-like projection similar to *Ceratomyrmex*. X-ray imaging reveals that this clypeal paddle is reinforced, most probably with sequestered metals. Presumably this fortified clypeal structure was utilized in tandem with scythe-like mandibles to pin and potentially puncture soft-bodied prey. This unique taxon, which stresses the diversity of stem-group ants, is discussed in the context of modern and other Cretaceous trap jaw ant species.

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Introduction

The earliest definitive ants range in age from approximately 100 to 78 Ma and are described from six fossil deposits throughout Laurasia (Wilson *et al.*, 1967a; Dlussky, 1975, 1996; Wilson, 1985; Nel *et al.*, 2004) and a single locality in present-day Botswana (Dlussky *et al.*, 2004). Only two of the 45 named ant species from the Cretaceous are unambiguously assignable to extant lineages (belonging to crown-group Formicidae; Barden, 2017); the majority of early species are distinct from modern lineages – they are composites of modern features and plesiomorphic traits. All definitive Cretaceous ants possess a constricted waist segment, or petiole, and a distinct gland (the metapleural gland) visible as an opening on the metapleuron (LaPolla *et al.*, 2013). At the same time, many early ants exhibit shortened antennal scapes and often a very demarcate metanotal sclerite not found in modern species; these features are probably plesiomorphic. The phylogenetic position of noncrown group Cretaceous ants has been tested three times; however, only recently has there been an assessment of monophyly (Grimaldi

et al., 1997; Ward & Brady, 2003; Barden & Grimaldi, 2016). There is now evidence that nearly all described species from the Cretaceous are stem-group taxa – they are paraphyletic with respect to crown ants and so belong to lineages that arose prior to the common ancestor of all extant ants. Ultimately stem ants became extinct, sometime between the Late Cretaceous and Paleocene, and so the only window into these lineages, their morphology and behaviour, remains the study of fossil specimens (Barden & Grimaldi, 2016).

Some stem-group ants are now known to have exhibited a wide array of unusual adaptive features, primarily relating to mouthparts (Dlussky, 1996; Barden & Grimaldi, 2013, 2016; Perrichot, 2014). The haidomyrmecines, or ‘hell ants’ – defined by unique scythe-like mandibles that appear to have pivoted primarily in a vertical plane – are known from four genera and six species described in Burmese, Charentese (French), and Medicine Hat (Canadian) amber (Dlussky, 1996; Perrichot *et al.*, 2008, 2016; Barden & Grimaldi, 2012; McKellar *et al.*, 2013). Thus, haidomyrmecine ants are known from the oldest, as well as the youngest, Cretaceous ant-yielding deposits, spanning 22 Ma and what are now three continents. Hell ants are suspected to occupy a conspicuous position among the Formicidae, as sister to all other ants (Barden & Grimaldi,

Correspondence: Phillip Barden, Department of Biological Sciences, New Jersey Institute of Technology, Central King Building, Newark, NJ 07102, U.S.A. E-mail: pbarden@amnh.org

2016). This placement does not at all suggest that the common ancestor of all ants possessed such specialized mouthparts, but the enigmatic Cretaceous species offer a glimpse into lost adaptations and feeding strategies, particularly as no modern ants exhibit such features. Below is a chronological list of the descriptions of each species:

- *Haidomyrmex cerberus* Dlussky – the first hell ant was named 20 years ago by the prolific paleomyrmecologist Genady Dlussky (Dlussky, 1996). *Haidomyrmex cerberus* was described from a single partial worker specimen, providing the basis for what are now tribal synapomorphies for the Haidomyrmecini, established by Bolton (2003) and revised by Perrichot *et al.* (2016): unusual L-shaped mandibles and a bulging clypeus possessing a clypeal brush comprising dense, stout setae.

Locality: Burmese amber, ~98.8 Ma, Kachin State, Myanmar (Shi *et al.*, 2012)

- *Haidomyrmodes mammothus* Perrichot, *et al.* – described from both partial gyne and worker specimens, *H. mammothus* is the only alate specimen yet described (Perrichot *et al.*, 2008). In addition, the type material is the only reported conspecific worker and putative queen caste for any Cretaceous taxon and provides important information regarding sociality in early ants. The description of multiple specimens from an additional locality confirmed beyond any doubt that the highly unusual features observed in *H. cerberus* were not preservational. Largely similar to *H. cerberus*, *H. mammothus* possesses ocelli, which have long been presumed to be an ancestral ant trait (Wilson *et al.*, 1967b).

Locality: Charentese amber, ~100 Ma, Charentes, France (Perrichot *et al.*, 2010)

- *Haidomyrmex scimitarus*, *Haidomyrmex zigrasi* Barden & Grimaldi – reconstructions based on two entirely complete dealate (*H. scimitarus*) and worker (*H. zigrasi*) specimens suggested that the enigmatic L-shaped mandibles probably articulated, at least partially, in a vertical plane. In particular, the placement of trigger hairs on the clypeus as well as the hypognathous-like orientation of the head (all other non-haidomyrmecine ant heads are prognathous; Keller, 2011) suggested that hell ants were Cretaceous analogues to modern trap-jaw predators (Barden & Grimaldi, 2012). *H. scimitarus* is also the largest haidomyrmecine, measuring over twice the total length of most other species.

Locality: Burmese amber

- *Haidoterminus cippus* McKellar, *et al.* – the youngest known haidomyrmecine, *H. cippus* is described from a single worker specimen. This species extends the temporal and geographic range of hell ants considerably, indicating that the specialized mouthparts and probable trap-jaw behaviour were evidently successful for some time and over a wide area of Laurasia. *Haidoterminus cippus* is also unique among haidomyrmecines, possessing an elongate antennal scape somewhat similar to modern ant taxa.

Locality: Medicine Hat amber, ~78.5 Ma, Alberta, Canada (McKellar *et al.*, 2013)

- *Ceratomyrmex ellenbergeri* Perrichot, *et al.* – an exceedingly unusual taxon described from four worker specimens of varying completeness. Retaining the same overall Cretaceous trap-jaw bauplan as other haidomyrmecines, *C. ellenbergeri* possesses a unique clypeal horn coated ventrally in elongate, tapered setae. The mandibles are correspondingly very long, apparently extended to pin prey between the mandibular points and lengthy clypeal projection. This configuration is a dramatic variant on the trap-jaw syndrome and would appear to confirm vertical mandibular articulation.

Locality: Burmese amber.

Of the six named haidomyrmecine species, four are from Burmese amber. As with other insect groups [Grimaldi *et al.*, 2009; e.g. camouflage in Neuroptera and Reduviidae (Wang *et al.*, 2016); social parasitism in staphylinid beetles (Yamamoto *et al.*, 2016); apomorphic symphytan wasps (Engel *et al.*, 2016); brood care in scale insects (Wang *et al.*, 2015)] and even vertebrate groups [tropical lizards (Daza *et al.*, 2016); non-avian theropods (Xing *et al.*, 2016)], this deposit has made a substantial contribution towards the reconstruction of the evolutionary history of ants. Here, we describe an additional unusual haidomyrmecine ant morphotype from Burmese amber, further expanding the complex history of stem-group ants.

Materials and methods

All studied material was mined from the Hukawng Valley in Kachin State, Republic of the Union of Myanmar. The amber or 'burmite' recovered from this deposit is dated to the Cenomanian (~98 Ma) based on radiometric uranium–lead dating (Shi *et al.*, 2012).

Light microscopy equipment included a Leitz Wetzlar stereoscope with 48–144× magnifications and a Nikon SMZ1500 stereoscope with Nikon NIS software (Melville, NY, U.S.A.) allowing for measurements and digital photography with z-stacking. X-ray micro-computed tomography (micro-CT) scanning of specimens BuPH-01 and BuPH-02 was performed at the American Museum of Natural History Microscopy and Imaging Facility. Scans were taken with a GE Phoenix vltomelx s240 (Germany), equipped with either a 240 or 180 kV X-ray source. Specimen BuPH-01 was scanned at 60 kV and 250 μ A with a voxel size of approximately 3 μ m. A total of 1800 images were taken with an exposure time of 1000 ms each. Specimen BuPH-02 was scanned at 80 kV and 200 μ A with a voxel size of approximately 8 μ m. In total, 1800 images were taken with an exposure time of 750 ms each. Specimen BuPH-02 is infiltrated with a large calcite inclusion, which obscured most of the clypeal horn. Volume reconstruction of raw X-ray images was achieved using GE PHOENIX DATOSIX v2.3.2 with automatic geometry correction and default settings. Volumes were postprocessed and rendered using VOLUME GRAPHICS VG STUDIO MAX v3.0 and 3D SLICER 4.7 nightly builds (Fedorov *et al.*, 2012). To explore the relative grey values of amber matrix, void space and fossil inclusion tissues for holotype specimen BuPH-01, histogram values (grey values and relative

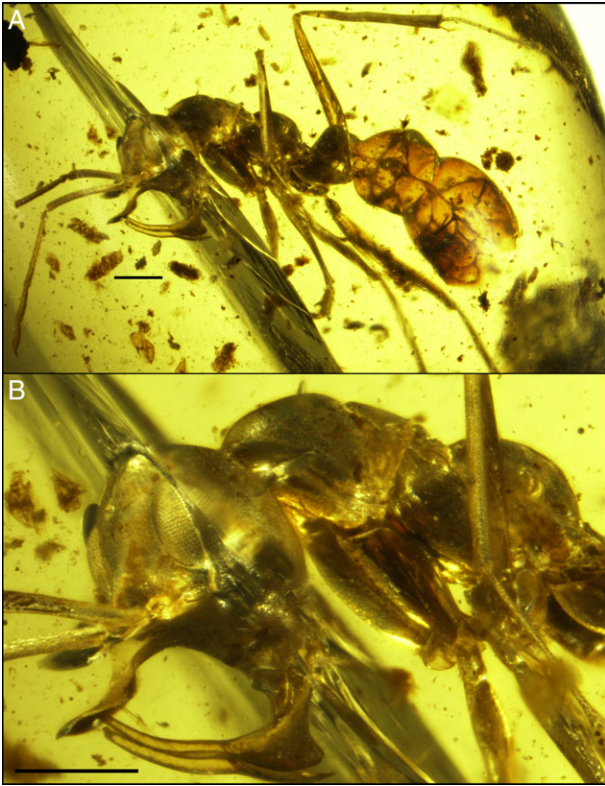


Fig. 1. Photomicrographs of *Linguamyrmex vladi*. (A) Lateral habitus view of holotype specimen BuPH-01. (B) View of head capsule and mesosoma. Scale bars, 0.5 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

frequency of grey value pixel occupancy) were exported and plotted in R v3.3.2 with GGPlot2 v2.1. While it is not possible to definitively infer density values or the elemental composition of materials present in the scan, grey values do provide relative information relating to the degree of X-ray attenuation for each material.

Results

Description

Order Hymenoptera Linnaeus, 1758
 Family Formicidae Latreille, 1809
 Tribe Haidomyrmecini Bolton, 2003

Genus *Linguamyrmex* Barden & Grimaldi, new genus

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Figs 1–5, 7, Video S1.

Diagnosis, worker. As in other haidomyrmecines (*Haidomyrmex*, *Haidoterminus*, *Haidomyrmodes*, *Ceratomyrmex*), head hypognathous-like with mandibles projecting primarily downward; mandible scythe-like, with flattened basal

margin leading to a curved apical tooth that is expanded perpendicular to axial plane of head. Cephalic clypeal ‘horn’ present but abbreviated, differs from *Ceratomyrmex* by horn stalk of *Linguamyrmex* being glabrous, that of *Ceratomyrmex* with fine, stiff setae of various lengths; clypeal horn much shorter in *Linguamyrmex*, less than head length/depth, stalk short, with the expanded, flat, paddle-shaped setose pad comprising >50% total horn length; clypeal pad slightly trough-shaped ventrally, covered with very short, dense velcro-like vestiture; trigger hairs originate not at base of stalk as in *Ceratomyrmex* but near basal margin of setose pad; ocelli present. In addition, *Linguamyrmex* with first and second gastral segments with deep constriction between them (a gastral constriction is figured in description of *Haidomyrmodes mammothus* but is less developed).

Type species. *L. vladi* sp.n.

Etymology. From Latin ‘lingua’, meaning tongue – in reference to the tongue-like clypeal projection – and the Greek ‘myrmex’, meaning ant.

Linguamyrmex vladi Barden & Grimaldi sp.n.

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Figs 1, 2A, 3F–I, 5.

Diagnosis. As for genus.

Description. Head: measuring 0.90 mm postero-anteriorly along dorsal margin, 0.96 mm in length/depth from vertex of head to anterior margin of clypeus. Occipital foramen positioned highly dorsad, just under vertex of head. Postgena broadly depressed; postgenal suture visible, deeply furrowed. Vertex broadly rounded and glabrous with gena gradually tapered ventrally towards mandibular socket and oral opening with fine, sparse setae. Ocelli faintly visible on vertex, positioned dorsally. Eye situated high on head capsule and bulging in frontal view, ovoid, measuring 0.38 mm in length and 0.25 mm in width when viewed laterally. Three antennal segments fully preserved (scape 0.94 mm in length; pedicel 0.12 mm; flagellomere I 0.55 mm). Antennal socket approximately in line with ventral margin of eye; socket exposed and immediately flanking a medial frontal triangle (*sensu* Perrichot *et al.*, 2016). Frontal triangle extends the vertex, contrasted with antennal sockets, which are present within cuticular depressions. Clypeal horn originating at both frontal triangle and clypeal stalk, both structures heavily sclerotized with cleared, membrane-like cuticle connecting from frontal triangle to stalk. Horn paddle-shaped, total length 0.64 mm, diameter 0.49 at greatest; narrow (0.04 mm) glabrous stalk 0.22 mm in length leading to setose pad; setose pad (0.42 in length) with long trigger hairs originating at pad base; dorsal margin of setose pad glabrous, underside coated in a large number of stout setae in centre and longer, more tapered setae along edges. Anterior margin of clypeus medially triangulate; distinct medial ridge extending to clypeal horn; lateral margins, beginning just above mandibular insertion, extending diagonally

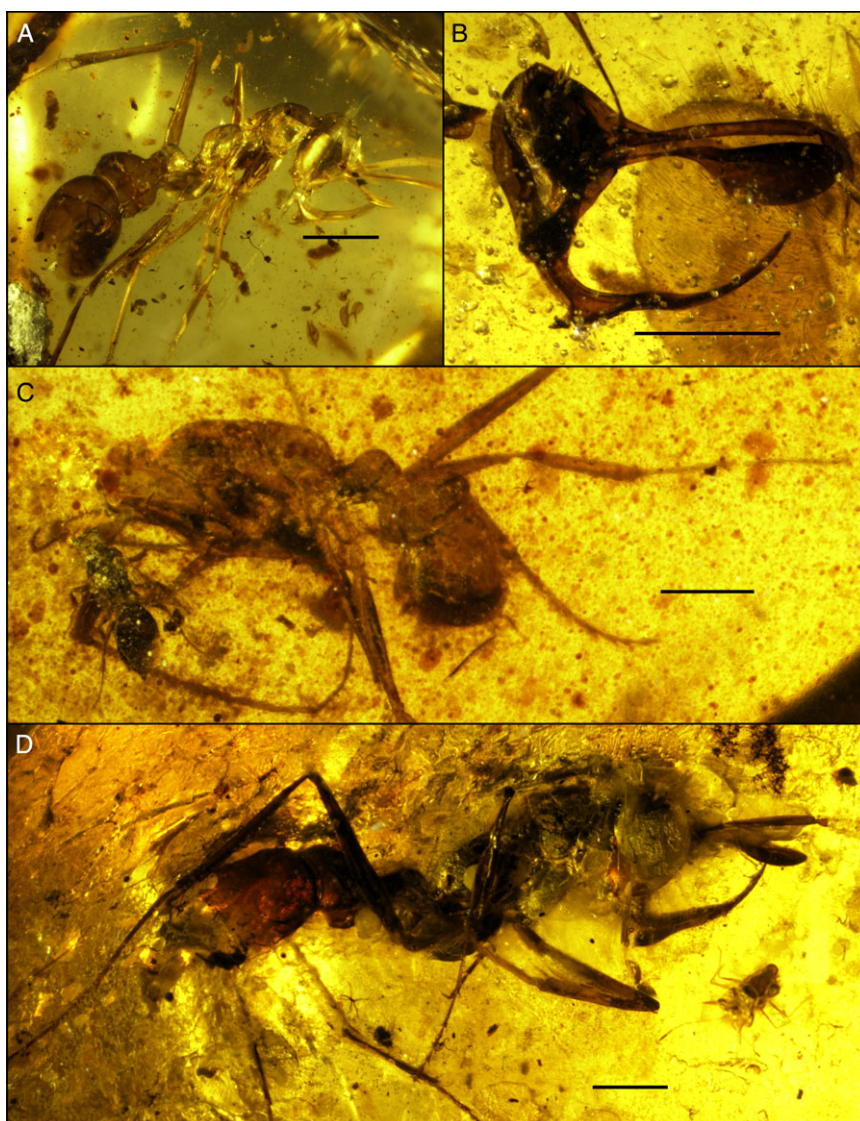


Fig. 2. Photomicrographs of *Linguamyrmex vladi* and *Linguamyrmex* sp. (A) Alternate lateral view of *L. vladi* holotype specimen BuPH-01. (B) Lateral head view of specimen BuPH-03, *Linguamyrmex* sp.; note that the specimen is heavily desiccated (alternate view in Fig. 4). (C) Posterolateral view of *Linguamyrmex* sp. specimen BuPH-04. (D) *Linguamyrmex* sp. specimen BuPH-02; much of the specimen is rendered invisible due to a large fissure and calcite infiltration (also rendered in Video S1). Scale bars, 1 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

toward clypeal horn. Cheek-like lobes projecting anteroventrally above mandible insertion. Mandible scythe-like, comprise a linear basal margin (0.55 mm in length) and curved apical tooth (0.92 mm measured as a straight line from base to tip, ignoring curvature) meeting nearly at right angle; preserved with apical teeth in parallel, nearly touching. Basal portion of mandible with anterior flange-like expansion, concave inner margin coated with pointed setae; leading edge of anterior flange expansion smooth; apical tooth rounded broadly with slight point. Maxillary and labial palps not visible.

Mesosoma. Pronotum broad, coated in fine setae; propleuron reduced, not visible in lateral view except where abutting head

capsule anteriorly. Pronotal length 0.72 mm, measured along dorsal margin. Mesonotum 0.34 mm; metanotum 0.24 mm; propodeum 0.49 mm. Weber's length 1.77 mm, mesosomal height 0.56 mm measured perpendicular to Weber's length line at pronotum. Procoxal length 0.72 mm, max width 0.22; mesocoxal length 0.31, max width 0.21; metacoxal length 0.49, max width 0.26; protrochantal length 0.14, max width 0.11; mesotrochantal length 0.19, max width 0.11; metatrochantal length 0.19, max width 0.12; profemoral length 1.01, max width 0.13; mesofemoral length 1.09, max width 0.12; metafemoral length 1.48, max width 0.18; protibial length 1.09, max width 0.11; mesotibial length 1.30, max width 0.08; metatibial length 1.59, max width 0.08. Trochantellus present, length included in

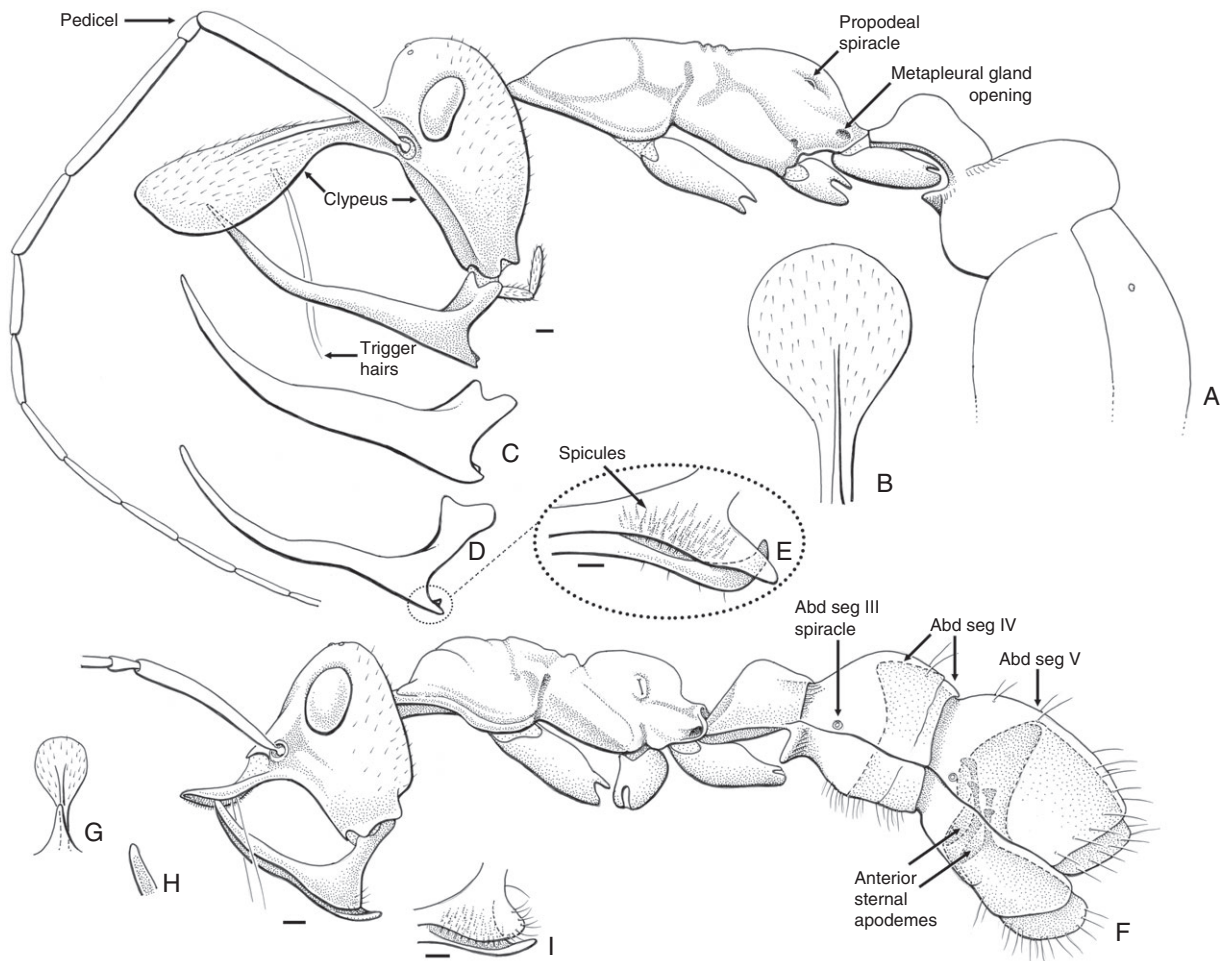


Fig. 3. Illustration of *Linguamyrmex vladii* and *Linguamyrmex* sp. (A) BuPH-04 lateral habitus. (B) Dorsal view of setose clypeal paddle, specimen BuPH-04. (C) Lateral view of specimen BuPH-02 mandible. (D) Lateral view of specimen BuPH-03 mandible (E) Enlarged view of BuPH-03 mandible (F) *Linguamyrmex vladii* holotype BuPH-01 lateral habitus. (G) Dorsal view of frontal triangle and clypeal paddle of specimen BuPH-01. (H) Apex of apical tooth of specimen BuPH-01. (I) Basal margin of mandibles, which corresponds with origin of apical tooth. Scale bars, 0.1 mm.

femur measurements. Three protibial spurs present, the largest approximately 2× length of other two; mesotibia with two spurs, the larger 2× the length of the smaller; two conspicuous setae of equal length positioned along anterior margin of mesotibial apex; metatibia with two spurs, the largest pectinate and ~3× the size of the smaller. Pretarsal claw with subapical tooth positioned closer to apex than to claw origin. Dorsal margin of propodeum gradually rounded, posterior margin with sheer face. Propodeal spiracle a dorsoventrally elongate slit situated medially. Metapleural gland opening gaping, present within horizontal invagination of cuticle, opening visible posteroventrally following well-developed bulla.

Metasoma. Petiole 0.49 mm in length, 0.49 mm in height at greatest, pedunculate; not tergosternally fused, deep suture visible; anterior margin gradually sloping; with gradually rounded dorsal margin; broadly attached to gastral segment I (abd seg III) with striated helcium clearly visible. Lateral sulcus

visible running anteroposteriorly along petiole, signifying incomplete fusion; ventral to sulcus lies thin, membranous cuticular expansion with distinct anteriorly positioned keel. Sternite III with pointed projection on anterior margin exhibiting striations running laterally. Circumgastral constriction present between gastral segments I and II with dorsal, posteriorly extended notch. Gastral cuticle translucent, revealing heavily sclerotized and expanded apodemes of gastral sternites IV and V withdrawn into the gaster.

Type material. Holotype, AMNH BuPH-01, in the Department of Invertebrate Zoology, American Museum of Natural History.

Additional material examined. Although not named, three specimens, BuPH-02 (Figs 2D, 3C, 7, Video S1), BuPH-03 (Figs 2B, 3A, B, 4) and BuPH-04 (2C), were studied and are

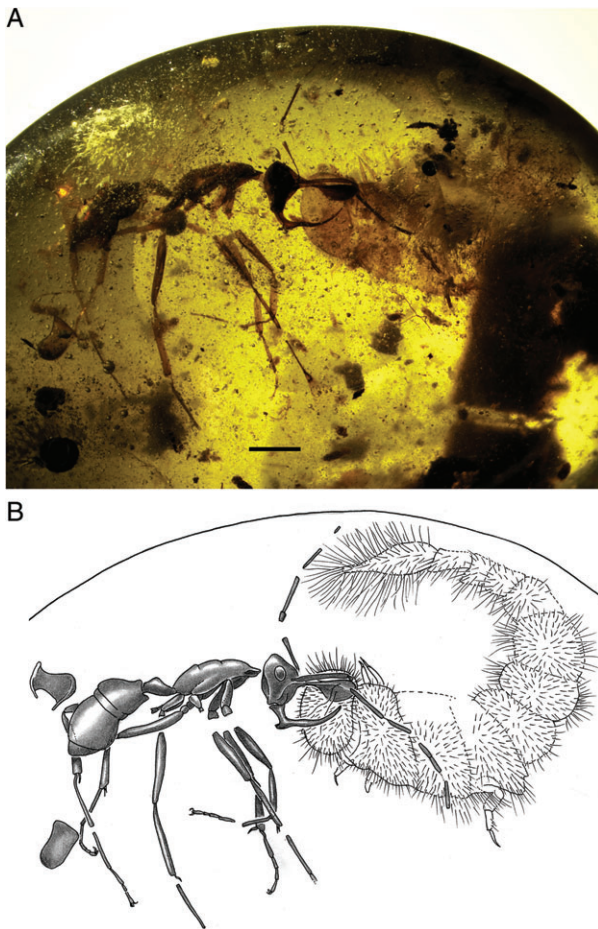


Fig. 4. Photomicrograph and illustration of *Linguamyrmex* sp. Specimen BuPH-03. (A) Photomicrograph in lateral view of *Linguamyrmex* sp. and beetle larvae. Scale bar, 1.0 mm. (B) Rendering of specimen BuPH-03. [Colour figure can be viewed at wileyonlinelibrary.com].

illustrated here. These three specimens probably represent additional species, particularly with respect to overall size and clypeal paddle composition. Moreover, these specimens possess mandibles that appear to interlock basally, joining the distal apical tooth portions of the mouthparts (Figs 3D, E, 7, Video S1). As the inner surface of each mandible is concave, their joining forms a channel that is open dorsally near the pointed mandibular apex (Fig. 7). However, there remains some ambiguity regarding the reliability of measurements and identification of other discrete features due to incomplete preservation. We therefore delay description until more complete material is obtained. Measurements are provided here (in mm): (BuPH-02) [BuPH-03] {BuPH-04} Head length measured postero-anteriorly along dorsal margin (1.14) [0.87] {0.69}, head depth (1.48) [1.22] {1.2}, scape length (1.56) [1.36] {1.28}, paddle length (1.5) [1.52] {1.26}, paddle diameter (–) [~0.57] {–}, eye length (–) [–] {0.29}, eye width (–) [–] {0.19}, basal margin of mandible (0.71) [0.53] {0.39}, apical tooth (1.97) [1.57] {1.48}, pronotal length (1.08) [0.97] {0.8}, mesosomal height (~0.81) [~0.75] {0.66}, Weber's length

(2.64) [2.49] {1.99}, petiole length (0.82) [0.76] {0.60}. Unfortunately, no specimen retained all antennal segments, preventing a reliable comparison of scape length relative to all other segments. In addition, all specimens, including the type, are missing terminal abdominal segments.

Etymology. In reference to Vlad III, or Vlad Dracula (c. 1429–1476), prince of a region of Romania then called Wallachia. His moniker, Vlad the Impaler, refers to his favoured and frequent method of execution, which inspired the vampirous character Count Dracula fictionalized by Bram Stoker in 1897. The patronym is in reference to the presumed impalement of prey by *Linguamyrmex* and its liquid diet (see later).

Systematic comments. Haidomyrmecines have been recovered as monophyletic (Barden & Grimaldi, 2016) and have traditionally been placed as tribe within Sphecomyrminae (Bolton, 2003). The subfamily is defined largely by plesiomorphic features and is now suspected to be paraphyletic (Barden & Grimaldi, 2016). We tentatively follow this subfamilial assignment here but note that, following additional phylogenetic analyses, haidomyrmecines may be best served by the erection of a separate subfamily.

Discussion

In crown-group ants, trap-jaw behaviour has evolved at least four times in three subfamilies: Formicinae, Myrmicinae and Ponerinae (Larabee & Suarez, 2014). Species employing trap jaws are capable of 'setting' their mandibles in the open position before rapidly striking them closed, usually in the service of prey capture but occasionally in a defensive effort (Patek *et al.*, 2006; Larabee & Suarez, 2015). While mechanisms for storing and releasing the potential energy required for swift prey capture vary, nearly all modern trap-jaw ants possess trigger hairs that initiate mandible closure. All described haidomyrmecines possess elongate, paired setae present on the clypeus. These setae have been interpreted as trigger hairs (Barden & Grimaldi, 2012; McKellar *et al.*, 2013; Perrichot *et al.*, 2016) and probably function as sensors for rapid mandible closure, as in modern trap-jaw ants. In all cases, these elongate clypeal setae rest directly in the most probable path of mandibular motion. Additionally, all hell ants exhibit an unusually modified clypeal sclerite, which stretches from the anteroventral margin of the head, near the oral opening, to the apex of the head – a syndrome unknown in other ants. The elongated nature of the clypeus may be a modification that would allow for the capture of prey positioned anteriorly – a strategy that would otherwise be untenable given the hypognathous head. The clypeal cuticle of 'hell ants' is characteristically raised along the upper margin, always with a clypeal brush composed of shortened, stout setae. Mandibular apices, in turn, are dorsally expanded to meet this clypeal process when fully closed, and would therefore be effective in prey capture. In some cases, raised clypeal cuticle may appear as a slight node whereas in the most extreme sense,

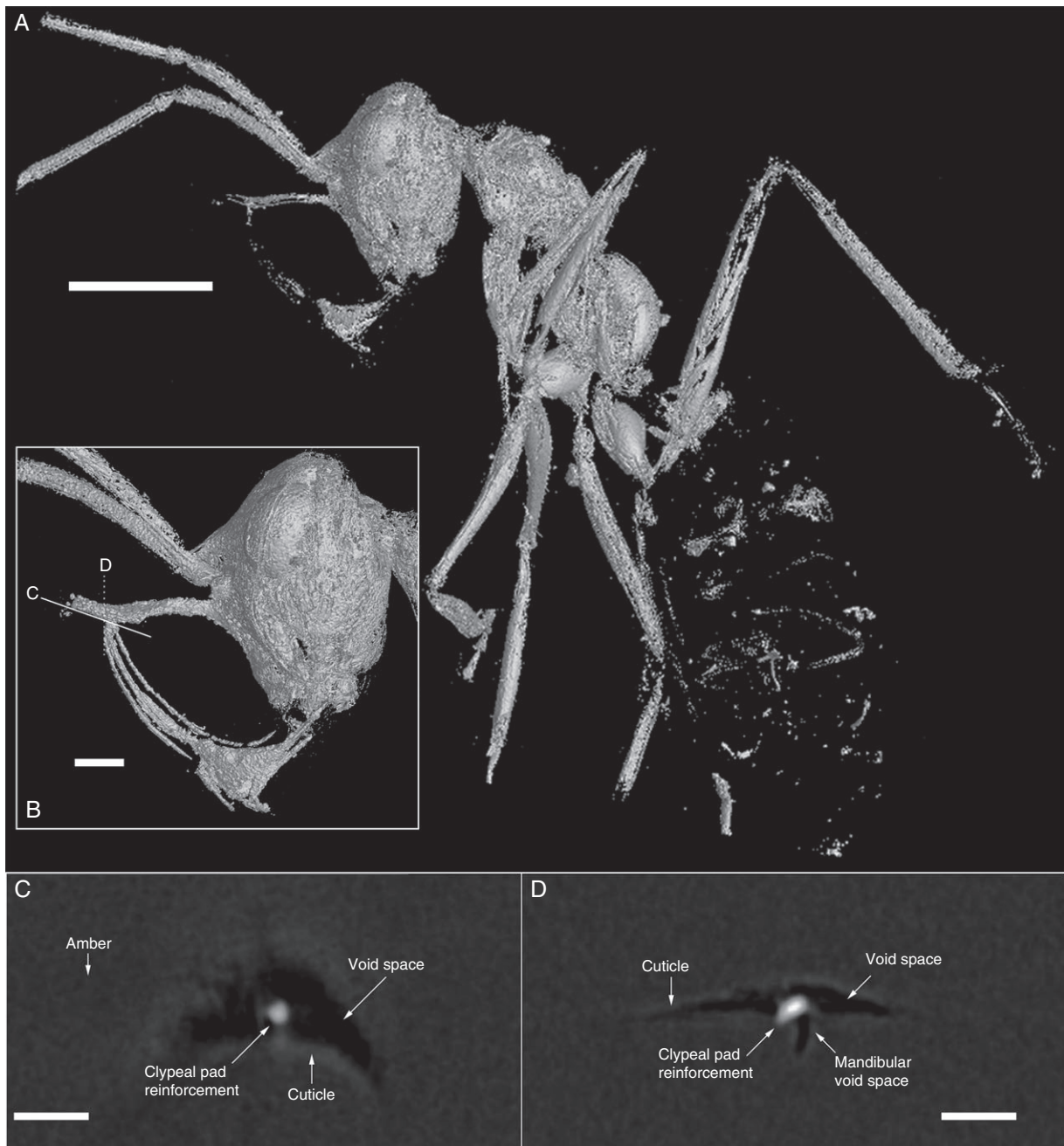


Fig. 5. Three-dimensional reconstruction and two-dimensional X-ray 'slices' of *Linguamyrmex vladi*. (A) Three-dimensional reconstruction of specimen BuPH-01 in lateral view. Some elements are irrecoverable in X-ray imaging due to the similar attenuation properties of both amber and thin cuticle. Scale bar, 0.75 mm. (B) Lateral view of head capsule, mandibles and clypeal paddle. Planes C and D correspond with panels C and D, respectively. Scale bar, 0.2 mm. (C) Cross-section of clypeal paddle from oblique dorsal view. Labels demonstrate approximate pixel 'grey values' for each fossil material, which in turn represent relative X-ray attenuation levels. (D) Cross-section of clypeal paddle from frontal view. Scale bar, 0.08 mm in each cross-section.

as in *Ceratomyrmex* and, to a lesser extent, *Linguamyrmex*, the clypeus is distended into a conspicuous cephalic horn. Here, the function of the clypeal process acting as a pinning or stopping point is underscored. Almost certainly, the modifications of the mandibles and clypeus occur in a complementary fashion.

Remarkably, during the course of X-ray imaging, we observed significant heterogeneity in the X-ray penetration of the clypeal paddle (Figs 5B–D, 6). Density and elemental composition are rendered solely into 'grey values' that indicate the degree of X-ray attenuation, a solid black pixel with a grey value

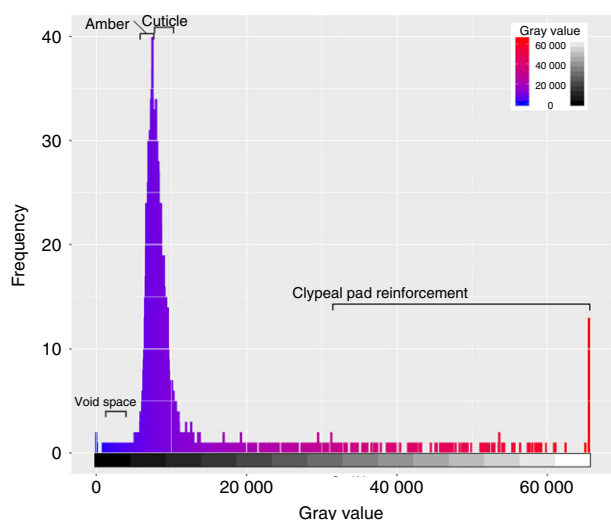


Fig. 6. Histogram of grey values present in Fig. 5B–D. The *x*-axis corresponds to grey values for all pixels used in the reconstruction of Fig. 5B (head and associated mouthparts). The *y*-axis indicates the relative frequency of each grey value. The grey value ranges for all fossil materials are labeled. [Colour figure can be viewed at wileyonlinelibrary.com].

of 0 indicating a material that is entirely X-ray-transparent. Conversely, material with higher X-ray attenuation due to either high density or absorption coefficient (material-based value impacted by compositional factors including atomic number) will register as higher grey values (e.g. 1 μm of carbon will appear as a lower grey value than 1 μm of iron in the same scan). Scan results indicate that the underside of the clypeal paddle appears to be reinforced, either by greater cuticular density or, more likely (based on the great contrast in X-ray attenuation shown in Fig. 6), through the incorporation of metals into cuticle. This reinforcement occurs primarily along the centre of the paddle and, as the specimen is preserved with the mandibles largely ‘closed’ and positioned near this spot, suggests that the reinforcement is intended to accommodate mandibular impact. Insects are known to sequester metals – in particular, calcium, manganese, zinc, and iron – in ovipositors and mandibles, to increase strength and reduce wear [ants (Edwards *et al.*, 1993); Orthoptera and Coleoptera (Vincent & Wegst, 2004); Isoptera (Cribb *et al.*, 2008); Hymenoptera (Quicke *et al.*, 1998)]. By bracing the contact region of the clypeal paddle, *Linguamyrmex* may have been able to withstand repeated misfires (i.e. missing prey) or perhaps complete penetration of soft-bodied prey such as larvae. While possible, it is unlikely that the reinforcement area is the result of mineral infilling or partial contamination, due to its distance from amber fractures elsewhere in the specimen and its significantly higher density (Video S2). With respect to density, the grey values corresponding to the paddle centre are approximately 30% greater than the next closest found within the head capsule.

The mandibles and paddle of *Linguamyrmex* may have functioned to puncture soft-bodied prey and feed on the haemolymph. Although this would be a novel strategy, this

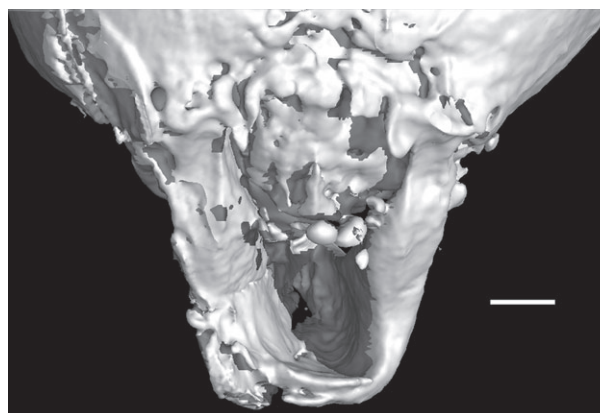


Fig. 7. Ventral view of *Linguamyrmex* sp. Computed tomography scan rendering. Mandibles of specimen BuPH-02 viewed from below, demonstrating the channel-like structure produced when mandibles are placed together in parallel.

morphological arrangement is itself entirely novel and it is not at all apparent how these ants could otherwise masticate food items. Although it is obtained from their own larvae, some living ant species do utilize haemolymph as a food source (Masuko, 1989; Ward & Fisher, 2016). As with other haidomyrmecines, *Linguamyrmex* foragers probably hunted with their mandibles cocked wide open and gaping, quickly snapping shut vertically when the tips of the trigger hairs touched prey, evidently with sufficient force that, were the clypeal paddle not reinforced, it might have been damaged. Teeth at the base of the mandibles overlap each other, apparently locking the two mandibles together to move in unison. With prey pinned against the furrowed paddle, the mandibles would be embedded into soft cuticle, while haemolymph from the prey could be channelled into the gutter between the mandibular tusks (Fig. 7, Video S1); a large droplet would then accumulate in the elbowed section, held in place by the surface tension from the minute, dense spicules. The haemolymph droplet could then be guided through the opening at the base of the mandibles by the spicules (which point backwards) and by the negative pressure created by absorption/suction from the adjacent glossa. Specimen PH-03 is preserved adjacent to a large beetle larva. Its mandibles are not embedded into the larva, but the proximity is consistent with this being prey. The presence of the tube-like channel located between the mandibles along with the distinct mesal teeth indicates that these animals probably did not masticate, but rather fed on liquid. Nevertheless, these features do not preclude the possibility that they also functioned to grasp prey items while being immobilized by the sting.

There are multiple examples of predatory specialization in ants, particularly within the subfamily Ponerinae (Hölldobler & Wilson, 1990) and the cryptic lineages that diversified early within crown-group Formicidae (Rabeling *et al.*, 2008; Brandão *et al.*, 2010). In perhaps the most dramatic case, the unique mandibles of the Neotropical ponerine genus *Thaumatomyrmex* Mayr possess elongate mesal and apical teeth modified into sparsely arranged spikes (Kempf, 1975). Incredibly, these

mouthparts effectively function as shears utilized solely for the removal of defensive setae from polyxenid millipedes (Brandão *et al.*, 1991).

Although it may not be possible to definitively ascertain the behaviour of *Linguamyrmex*, this new taxon highlights the adaptive diversity of a highly specialized, extinct lineage of Cretaceous, stem-group ants. Just as the diversity and adaptive spectrum of carnivorous theropod dinosaurs could not have been predicted by the study of modern vertebrates alone, the bizarre adaptations of haidomyrmecines (indeed, their existence) would remain unknown if not for preservation in amber.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:

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Video S1. Computed tomography renderings of *Linguamyrmex vladi* holotype AMNH BuPh-1 and BuPh-2.

Video S2. Video representation of AMNH BuPh-1, highlighting clypeal paddle reinforcement. Included are two-dimensional ‘slice’ views at multiple angles, along with a three-dimensional reconstruction.

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References

- Barden, P. (2017) Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. *Myrmecological News*, **24**, 1–30.
- Barden, P. & Grimaldi, D. (2012) Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. *American Museum Novitates*, **3755**, 1–16.
- Barden, P. & Grimaldi, D. (2013) A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa*, **3681**, 405–412.
- Barden, P. & Grimaldi, D.A. (2016) Adaptive radiation in socially advanced stem-group ants from the Cretaceous. *Current Biology*, **26**, 515–521.
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, **71**, 1–370.
- Brandão, C.R.F., Diniz, J.L.M. & Tomotake, E.M. (1991) *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). *Insectes Sociaux*, **38**, 335–344.
- Brandão, C.R.F., Diniz, J.L.M. & Feitosa, R.M. (2010) The venom apparatus and other morphological characters of the ant *Martialis heureka* (Hymenoptera, Formicidae, Martialinae). *Papéis Avulsos de Zoologia (São Paulo)*, **50**, 413–423.
- Cribb, B.W., Stewart, A., Huang, H., Truss, R., Noller, B., Rasch, R. & Zalucki, M.P. (2008) Insect mandibles – comparative mechanical properties and links with metal incorporation. *Naturwissenschaften*, **95**, 17–23.
- Daza, J.D., Stanley, E.L., Wagner, P., Bauer, A.M. & Grimaldi, D.A. (2016) Mid-Cretaceous amber fossils illuminate the past diversity of tropical lizards. *Science Advances*, **2**, e1501080.
- Dlussky, G.M. (1975) Superfamily Formicoidea Latreille, 1802. Family Formicidae Latreille, 1802. *Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR*, **147**, 114–122.
- Dlussky, G.M. (1996) Ants (Hymenoptera: Formicidae) from Burmese amber. *Paleontologicheskii Zhurnal*, **30**, 449–454.
- Dlussky, G.M., Brothers, D.J. & Rasnitsyn, A.P. (2004) The first Late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. *Insect Systematics and Evolution*, **35**, 1–13.
- Edwards, A.J., Fawke, J., McClements, J.G., Smith, S.A. & Wyeth, P. (1993) Correlation of zinc distribution and enhanced hardness in the mandibular cuticle of the leaf-cutting ant *Atta sexdens rubropilosa*. *Cell Biology International*, **17**, 697–698.
- Engel, M.S., Huang, D., Alqarni, A.S. & Cai, C. (2016) An unusual new lineage of sawflies (Hymenoptera) in Upper Cretaceous amber from northern Myanmar. *Cretaceous Research*, **60**, 281–286.
- Fedorov, A., Beichel, R., Kalpathy-Cramer, J. *et al.* (2012) 3D slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging*, **30**, 1323–1341.
- Grimaldi, D., Agosti, D. & Carpenter, J.M. (1997) New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. *American Museum of Natural History*, **3208**, 1–43.
- Grimaldi, D.A., Engel, M.S. & Nascimbene, P.C. (2009) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, **3371**, 1–71.
- Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Belknap Press, Cambridge, Massachusetts.
- Keller, R.A. (2011) A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. *Bulletin of the American Museum of Natural History*, **355**, 1–90.
- Kempf, W.W. (1975) A revision of the Neotropical ponerine ant genus *Thaumatomyrmex* Mayr (Hymenoptera: Formicidae). *Studia Entomologica*, **18**, 95–126.
- LaPolla, J.S., Dlussky, G.M. & Perrichot, V. (2013) Ants and the fossil record. *Annual Review of Entomology*, **58**, 609–630.
- Larabee, F.J. & Suarez, A.V. (2014) The evolution and functional morphology of trap-jaw ants (Hymenoptera: Formicidae). *Myrmecological News*, **20**, 25–36.
- Larabee, F.J. & Suarez, A.V. (2015) Mandible-powered escape jumps in trap-jaw ants increase survival rates during predator-prey encounters. *PLoS ONE*, **10**, e0124871.
- Masuko, K. (1989) Larval hemolymph feeding in the ant *Leptanilla japonica* by use of a specialized duct organ, the ‘larval hemolymph tap’ (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, **24**, 127–132.
- McKellar, R.C., Glasier, J.R. & Engel, M.S. (2013) A new trap-jawed ant (Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous amber. *The Canadian Entomologist*, **145**, 454–465.
- Nel, A., Perrault, G., Perrichot, V. & Néradeau, D. (2004) The oldest ant in the lower Cretaceous amber of Charente-maritime

- (SW France)(Insecta: Hymenoptera: Formicidae). *Geologica Acta*, **2**, 23–30.
- Patek, S.N., Baio, J.E., Fisher, B.L. & Suarez, A.V. (2006) Multifunctionality and mechanical origins: ballistic jaw propulsion in trap-jaw ants. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 12787–12792.
- Perrichot, V. (2014) A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae). *Myrmecological News*, **19**, 165–169.
- Perrichot, V., Nel, A., Néraudeau, D., Lacau, S. & Guyot, T. (2008) New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften*, **95**, 91–97.
- Perrichot, V., Néraudeau, D. & Tafforeau, P. (2010) Charentese amber. *Biodiversity of Fossils in Amber from the Major World Deposits* (ed. by D. Penney), pp. 192–207. Siri Scientific Press, Manchester.
- Perrichot, V., Wang, B. & Engel, M.S. (2016) Extreme morphogenesis and ecological specialization among Cretaceous basal ants. *Current Biology*, **26**, 1468–1472.
- Quicke, D.L., Wyeth, P., Fawke, J.D., Basibuyuk, H.H. & Vincent, J.F. (1998) Manganese and zinc in the ovipositors and mandibles of hymenopterous insects. *Zoological Journal of the Linnean Society*, **124**, 387–396.
- Rabeling, C., Brown, J.M. & Verhaagh, M. (2008) Newly discovered sister lineage sheds light on early ant evolution. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 14913–14917.
- Shi, G., Grimaldi, D.A., Harlow, G.E. *et al.* (2012) Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research*, **37**, 155–163.
- Vincent, J.F. & Wegst, U.G. (2004) Design and mechanical properties of insect cuticle. *Arthropod Structure & Development*, **33**, 187–199.
- Wang, B., Xia, F., Wappler, T., Simon, E., Zhang, H., Jarzembowski, E.A. & Szwedo, J. (2015) Brood care in a 100-million-year-old scale insect. *eLife*, **4**, e05447.
- Wang, B., Xia, F., Engel, M.S. *et al.* (2016) Debris-carrying camouflage among diverse lineages of Cretaceous insects. *Science Advances*, **2**, e1501918.
- Ward, P.S. & Brady, S.G. (2003) Phylogeny and biogeography of the ant subfamily Myrmeciinae (Hymenoptera : Formicidae). *Invertebrate Systematics*, **17**, 361–386.
- Ward, P.S. & Fisher, B.L. (2016) Tales of dracula ants: the evolutionary history of the ant subfamily Amblyoponinae (Hymenoptera: Formicidae). *Systematic Entomology*, **41**, 683–693.
- Wilson, E.O. (1985) Ants from the Cretaceous and Eocene amber of North America. *Psyche*, **92**, 205–216.
- Wilson, E.O., Carpenter, F.M. & Brown, W.L. (1967a) The first Mesozoic ants. *Science*, **157**, 1038–1040.
- Wilson, E.O., Carpenter, F.M. & Brown, W.L. (1967b) The first Mesozoic ants, with the description of a new subfamily. *Psyche*, **74**, 1–19.
- Xing, L., McKellar, R.C., Xu, X. *et al.* (2016) A feathered dinosaur tail with primitive plumage trapped in mid-Cretaceous amber. *Current Biology*, **26**, 1–9.
- Yamamoto, S., Maruyama, M. & Parker, J. (2016) Evidence for social parasitism of early insect societies by Cretaceous rove beetles. *Nature Communications*, **7**, 13658.

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