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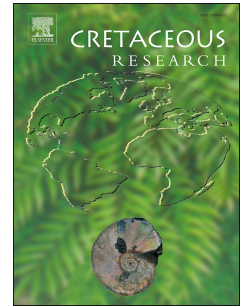
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New remarkable hell ants (Formicidae: Haidomyrmecinae stat. nov.) from mid-Cretaceous amber of northern Myanmar

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Abstract

Haidomyrmecines (hell ants) are a group of putatively predatory ants defined by mandibles that are dorsoventrally expanded, and highly modified heads with a variety of cranial appendages. These ants are known exclusively from three Cretaceous amber deposits in France, Myanmar, and Canada. Here we describe four new genera and five new species from specimens preserved in mid-Cretaceous (uppermost Albian–lowermost Cenomanian, ca. 99 Ma) amber from the Kachin State of northern Myanmar: *Dhagnathos autokrator* gen. et sp. nov., *Chonidris insolita* gen. et sp. nov., *Aquilomyrmex huangi* gen. et sp. nov., *Protoceratomyrmex revelatus* gen. et sp. nov., and *Linguamyrmex brevicornis* sp. nov. We propose a new subfamilial rank for hell ants, i.e., Haidomyrmecinae stat. nov., based on recent phylogenetic analyses. A diagnosis and a key to the genera and species of

Haidomyrmecinae are provided. The mouthparts and cranial features of these remarkable taxa display a series of morphological syndromes that likely relate to specialized prey capture. The diversity of these and other described hell ants underscores the extensive radiation of adaptive forms that were present early in ant evolution.

Keywords: Hymenoptera; stem-group ants; Haidomyrmecinae; Kachin amber; Myanmar

1. Introduction

The fossil history of ants and numerous other arthropod lineages have been redrafted in recent years due to significant discoveries in so-called Burmese amber, or burmite, from Kachin State, Myanmar. The paleobiota of this mid-Cretaceous (ca. 99 Ma) deposit is highly diverse and preserved with life-like fidelity (Grimaldi and Ross, 2017; Ross, 2019). Based on an array of Burmese amber specimens, we report remarkable new genera and species that dramatically extend our understanding of the ant family and its range of phenotypes; their mouthparts and cranial features display a series of morphological syndromes not seen in any modern lineages.

The first haidomyrmecine “hell ant” was unearthed in Northern Myanmar at least one hundred years ago. This early discovery is evidenced by the acquisition tag that accompanies the type specimen of *Haidomyrmex cerberus* Dlussky, 1996, the first described hell ant taxon. The tag (see AntWeb, 2019) indicates that R.C.J. Swinhoe sent T.D.A. Cockerell the specimen in 1920, as part of a series of amber collections that were sent to the Natural History Museum, London in the early 20th century (Cockerell, 1922). It would be another 76 years before the specimen was examined by Dlussky (1996), who described the enigmatic ant

with muted astonishment, stating that *Haidomyrmex* differed “from all known Formicidae, both recent and fossil, by the very peculiar structure of the cranio-mandibular system.” Dlussky was referencing the unique scythe-like mandibles and elongated head capsule that characterize the many species of hell ants known today. The sole specimen worked by Dlussky was reexamined by Engel and Grimaldi (2005), who refigured *H. cerberus* and stressed the enigmatic nature of its morphology (see also Perrichot et al., 2016 and Cao et al., 2020 for additional figures and a redescription). Additional haidomyrmecine material was subsequently described as *Haidomyrmodes mammuthus* Perrichot et al., 2008, in Albian-Cenomanian age French amber, which confirmed that the unique cranial morphology of hell ants was present in more than one species (Perrichot et al., 2008a). Incidentally, because the inclusions present in French amber spanned both workers and alates, these haidomyrmecines also represent the earliest direct evidence of reproductive division of labor in ants (Perrichot et al., 2008b). Aside from *H. mammuthus*, the majority of hell ants are recovered from Burmese amber, however, *Haidotermis cippus* McKellar, Glasier & Engel, 2013 from Campanian-age Canadian amber in Alberta, extends the temporal range of haidomyrmecines at least 20 million years (McKellar et al., 2013a). A total of nine genera and 14 species are now described. All but two genera and three species have been discovered in the last ten years, and four genera and five species are described here for the first time.

2. Material and methods

Material and repositories. A total of 17 specimens were examined, all originating from amber mines located near Noiye Bum Village, Tanai Town, Myitkina District of Kachin State, northern Myanmar (see locality in Kania et al., 2015: fig. 1; or Grimaldi and Ross, 2017: fig. 2). A radiometric dating of zircons from the amber-bearing bed gave a maximum

age of 98.79 ± 0.62 Ma (Shi et al. 2012), thus corresponding to the latest Albian–earliest Cenomanian (mid-Cretaceous), which may not be very different from the age of the amber itself (Smith and Ross, 2018; Yu et al., 2019).

The specimens are deposited in the following publicly accessible repositories: IGR, Geology Department and Museum of the University Rennes 1, France (one holotype); NIGPAS, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, China (six type specimens); HA, Huangyiren Amber Museum, Taiwan (three additional specimens); LA, Mineral & Gem Research Center, Hong Kong (one additional specimen); RM, Ruipoxuan Museum, Jinan, China (four additional specimens); XA, Lingpoge Amber Museum, Shanghai, China (one additional specimen). An additional specimen is from the private collection of Tyler Janowitz (TJ), Massachusetts, USA, figured here as it shows more clearly the head structures.

Condition of studied material. Details on the respective condition of the specimens are as follows:

IGR.BU-003. Alate gyne. Preserved without distortion, but missing right antennomeres XI–XII, left antennomeres IV–XII, apical portion of fore wings, portion of all right legs beyond femur, portion of left fore leg beyond tarsomere II and left hind leg beyond trochanter, and apico-dorsal portions of gaster beyond AIV. The amber piece is crossed by an internal fracture running obliquely to the head through the left compound eye, scapes, medioapical portion of the horn, and lower portion of the right gena. The piece broke at the level of this fracture during polishing, so the two fragments were immediately glued together. Originally preserved with a thrips (Thysanoptera), now in a separate fragment measuring $14.4 \times 10 \times 6$ mm.

NIGP171998. Alate gyne. A nicely preserved specimen exposed in right profile and dorsal views, without distortion, but with left side largely obscured by numerous air bubbles, and missing right antennomeres II–XII, tarsomeres II–V and IV–V of right and left hind legs, respectively. In a rounded piece of yellow amber measuring $13 \times 8 \times 5$ mm, with two spiders, two nematocerans (Diptera), and a beetle larva (Coleoptera).

NIGP171999. Alate gyne. A heavily distorted specimen exposed in dorsolateral views, displaying dorsoventral and lateral compression, and missing right antennomeres V–XII, left antennomeres II–XII, and the right hind leg beyond tibia. In a rounded piece of clear yellow amber measuring 16×3 mm.

NIGP172000. Alate gyne. An almost complete specimen exposed in dorsal and ventral views, without distortion, with apical sclerite of gaster damaged and sting apparatus detached from the body. In a rounded piece of clear yellow amber measuring $15 \times 13 \times 3$ mm, with few cockroach remains and numerous frass pellets and plant debris (wood fibers).

NIGP172001. Worker. Preserved without apparent distortion, with cuticle cleared on head, pronotum and legs, and missing apical portions of all legs and apical gastral segments. In an oval piece of clear yellow amber measuring $13 \times 9 \times 3$ mm, with two springtails and dipteran wings.

NIGP172002. Worker. A specimen exposed in profile views, without apparent distortion, missing apices of left antenna and left mid- and hind tarsomeres. In a piece of amber measuring $9 \times 8 \times 4$ mm, with a mite.

NIGP172003. Alate gyne. A specimen exposed in right anterolateral view, without apparent distortion, missing gaster and apices of wings. In a rounded piece of amber

123 measuring $31 \times 24 \times 6$ mm, with a Psocoptera contacting its right hind leg, a tiny parasitic
 124 wasp (Hymenoptera) and a beetle (Coleoptera).

125 HA03. Alate gyne. An almost complete specimen exposed in profile views, with slight
 126 lateral compression, partly covered with bubbles on its right side, missing right antennomeres
 127 V–XII, left antennomeres III and V–XII, the right fore leg and left mid leg beyond femur. In
 128 a round piece of clear yellow amber measuring 15×5 mm.

129 HA04. Alate gyne. A specimen exposed in profile and full facial views, with head and
 130 mesosoma distinctly compressed dorsoventrally, right side largely obscured by air bubbles,
 131 and missing tarsomeres II–V of right hind leg and apical gastral segments. In a rounded piece
 132 of clear yellow amber measuring $21 \times 15 \times 8$ mm.

133 HA06. Alate gyne. A complete specimen exposed in profile views, with distinct distortion
 134 of the dorsum of head and promesonotum, with numerous bubbles or debris covering parts of
 135 head, wings and petiole. In a quadrangular piece of clear yellow amber measuring $11 \times 5 \times 4$
 136 mm, with a beetle (Coleoptera) and a midge (Diptera).

137 LA01. Alate gyne. An exquisitely preserved specimen, without distortion, but missing
 138 right antennomeres VII–XII and tarsomeres of left mid leg and hind legs. Exposed in dorsal,
 139 profile and full facial views, in a quadrangular piece of clear yellow amber measuring 10×8
 140 $\times 6$ mm, with a staphylinid beetle (Coleoptera) and several domichnia (borings) from
 141 pholadid bivalves.

142 RM1. Alate gyne. A complete specimen exposed mostly in right lateroventral view,
 143 apparently weakly distorted but largely obscured by small bubbles contacting the body,
 144 organic debris floating in amber matrix, and internal fractures crossing the amber piece. In a

rounded piece of clear yellow amber measuring $39 \times 26 \times 8$ mm, with a psychodid fly (Diptera) and numerous domichnia (borings) from pholadid bivalves (Smith and Ross, 2018).

RM2. Alate gyne. A specimen exposed in left profile view, with dorsoventral distortion gradually increasing from head to gastral apex, and missing left antennomeres IV–XII. In a rounded piece of amber measuring $26 \times 14 \times 5$ mm, with a myriapod, a true bug, two mites, and numerous debris.

RM3. Alate gyne. A specimen exposed in profile views, with distinct longitudinal elongation, and missing left midleg, apical tarsomeres of left hind leg and gaster beyond third segment. In a round piece of amber measuring 15×4 mm, with a beetle, a fungus gnat and numerous insect and plant debris.

RM4. Worker. A complete, nicely preserved specimen, without distortion. Exposed in profile views in an amber piece measuring 21×4 mm, with plant debris.

TJ41-020. Alate gyne. A nearly complete specimen exposed in profile views, with numerous bubbles contacting the body, and with partial wings detached and floating in the amber matrix close to the specimen. In a rounded piece of amber slightly obscured by a suspension of microscopic particles ('dust').

XA01. Alate gyne. A specimen exposed in profile views, with distinct distortion affecting the head capsule and mesosoma, missing right antennomeres V–XII, left antennomeres IV–XII, most of legs beyond coxae, and apical portions of wings and gaster. Petiole and preserved anterior portion of gaster entirely concealed by wings. In a rounded piece of clear yellow amber measuring 20×7 mm, with a midge (Diptera).

Examination and imaging. All specimens were studied, imaged and measured under simultaneous incident and transmitted light, at the State Key Laboratory of Palaeobiology and Stratigraphy, NIGPAS, using Zeiss Axio Zoom.V16 stereomicroscope and AxioCam 512 digital camera with Zen software, allowing for measurements and digital photography. Details of the holotype NA12 were imaged with a Nikon SMZ25 stereomicroscope and DS-Ri2 camera with NIS Elements software at the New Jersey Institute of Technology (NIJT). All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using HeliconFocus and Nikon Elements softwares.

Measurements, indices and terminology. The morphological terminology used in this study follows Bolton (1994) for most body structures, Harris (1979) for sculpture, Brown and Nutting (1949) for wing venation, and Boudinot et al. (2013) for wing cells. The measurements generally follow established measurements as used recently for ant systematics (e.g., Hita-Garcia et al., 2017). However, given the uniqueness of the cranial morphology of haidomyrmecines, measurements on the head structures and indices used in this study are explained below and illustrated in Fig. 1.

EL Eye length: in profile, the maximum diameter of eye

FWL Fore wing length: maximum distance from base to apex of wing

Hh Head height: in profile or full-face view, from lowermost to higher points of head capsule, measured vertically and excluding ocelli and horn

HL Head length: in profile, from basal insertion of mandibles to posteriormost point of head; in *Aquilomyrmex*, measured in dorsal view from base of horn to posteriormost point of head

190	HoL	Horn length: in profile, from base of elbow between vertical and horizontal ventral
191		surfaces of horn to anteriormost point of horn; in <i>Aquilomyrmex</i> , measured in dorsal
192		view from anteriormost point of eye to anteriormost point of horn
193	HW	Head width: in dorsal or full-face view, maximum width of head excluding eyes
194	MDL	Mandibular length: in profile, a straight distance from basal insertion to tip of
195		mandibles
196	MDaL	Length of apical portion of mandible: in profile, from midpoint of elbow between
197		basal and apical portions to tip of mandible
198	MDbL	Length of basal portion of mandible: in profile, from basal insertion of mandibles to
199		midpoint of elbow between basal and apical portions of mandible
200	MDtL	Length of triangular inner blade of mandible: in full-face view, from midpoint of
201		elbow between basal and apical portions of mandible to apex of inner blade
202	PTH	Petiole height: in profile, maximum height of petiole excluding subpetiolar process
203	PTL	Petiole length: in profile or dorsal view, maximum length of petiole
204	PTW	Petiole width: in dorsal view, maximum width of petiole
205	SL	Scape length: maximum length of scape excluding condylar neck
206	WL	Weber's length: in profile, maximum diagonal length of mesosoma
207	MDI	Mandibular index: $MDL/HL \times 100$
208	SI	Scape Index: $SL/HL \times 100$ (HL preferred to HW which is often hard to measure on
209		fossils)
210	OI	Ocular Index: $EL/HL \times 100$
211	EPI	Eye Position Index: in full-face view, $l1/l2 \times 100$ (see l1 and l2 in Fig. 1A)
212	HoI	Horn Index: $HoL/SL \times 100$
213		
214		

3. Systematic paleontology

Order Hymenoptera Linné, 1758

Family Formicidae Latreille, 1809

Subfamily **Haidomyrmecinae** Bolton, 2003, stat. nov.

Haidomyrmecini Bolton, 2003: 74, 261.

Remark. The unique cranio-mandibular complex and mesosomal structure of hell ants clearly distinguish them from other ant subfamilies as currently defined. Earlier studies suggested that haidomyrmecines may not belong to the Sphecomyrminae (Grimaldi et al., 1997; Perrichot et al., 2008a; McKellar et al., 2013). But, at the time, there were few Cretaceous ant taxa for testing this hypothesis phylogenetically. Recently, the first phylogenetic analysis to include hell ants recovered all haidomyrmecine genera as a monophyletic group outside of modern and stem ant lineages, potentially sister to all other ants (Barden and Grimaldi, 2016). This result was supported by the highly aberrant morphology of hell ants, which is not seen in any other lineages, modern or extinct. Moreover, a recent phylogenetic analysis that included all hell ant genera, including new taxa described herein, recovered haidomyrmecines as each others' closest relatives and consistently monophyletic, to the exclusion of sphecomyrmine terminals (Barden et al., submitted). In the same paper, a comparison of extant and Cretaceous morphospace also recovered haidomyrmecines as distinct from other stem and crown ants, while cranial morphospace overlaps among other stem ants and living taxa (Barden et al., submitted). There are no indications that scythe-like mandibles have evolved more than once, and so the monophyly of haidomyrmecines is best supported by this highly specific synapomorphy. In our view, the characteristic morphology of haidomyrmecines and

strong evidence for their monophyly warrant the placement of hell ants in their own subfamily, particularly as future paleontological work will undoubtedly reveal more Cretaceous taxa. We provide a diagnosis of the subfamily below.

Diagnosis (females). Mandibles scythe- or sickle-shaped, with linear basal portion leading to an elongate and dorsally curved apical portion tapering, with inner margin usually developed in a triangular blade pointing medially and ventrally (exception in *Aquilomyrmex* where the inner margin is simple); mandibles uniquely articulating in a vertical plane oblique to longitudinal axis of body, in addition to a moderate lateral opening. Clypeus elongate, with anterior margin broadly concave, smooth, and lateral margins leading posteriorly to an elevated brushy lobe just ventral to antennal insertion, or to a horn expanded anteriorly between toruli. Antennae 12-segmented, filiform, usually with third antennomere longest of basal three flagellomeres (exceptions are in *Haidomyrmex* where fourth antennomere is longest, and in *Haidomyrmodes* where basal flagellomeres are of equal length). Petiole with a short anterior peduncle, nodiform. Gastral constriction between AIII and AIV generally present, faintly to deeply impressed. Pygidium simple, unarmed. Sting robust, dorsally curved. Legs with procoxa distinctly longer than meso- and metacoxae, with trochantellus present on mid- and hind legs; tibial spur formula 1-2-2, rarely 1-1-2, and tibiae additionally with 1–4 subapical, stout setae. In gynes, the fore wing with 8 closed cells, with cross-vein 1r-rs absent or incomplete (present as a short tubular or nebulous stub not reaching Sc+R); cross-vein 2rs-m present, tubular; and cross-vein cu-a arising from M+Cu or Cu. Hind wing with jugal lobe present, with costal, basal and subbasal cells enclosed by tubular veins.

Genera included. *Aquilomyrmex* gen. nov.; *Ceratomyrmex* Perrichot, Wang & Engel, 2016; *Chonidris* gen. nov.; *Dhagnathos* gen. nov.; *Haidomyrmex* Dlussky, 1996; *Haidomyrmodes* Perrichot et al., 2008; *Haidotermius* McKellar, Glasier & Engel, 2013; *Linguamyrmex* Barden & Grimaldi, 2017; *Protoceratomyrmex* gen. nov.

Distribution. Canada, France, Myanmar; Cretaceous, Uppermost Albian to Campanian (100-79 Ma).

Genus *Dhagnathos* gen. nov.

(urn:lsid:zoobank.org:act:48DA68FC-1DF6-4A90-86DA-4EF527D762F4).

Type species: *Dhagnathos autokrator* sp. nov.

Etymology. The generic name is a combination of *Dha*, a single-edged sword with long, gently curved blade common throughout mainland Asia, and often called ‘the national sword of Burma’, and *gnathos* (Greek, meaning ‘jaw’), in reference to the mandibles’ shape. The name is masculine.

Diagnosis (gyne). Large, robust ant, body length ca. 14 mm. Clypeus funnel-shaped resulting from extreme posterior expansion, extends well beyond antennal insertions, with lateral margins raised into carinae arising above mandible insertion and converging posteriorly to form a clypeal horn; horn bent forward at right angle from frons, its tip gently rounded, not spatulate, its underside deeply furrowed, forming a channel opening toward the labrum; clypeal carinae, including horn’s edges, rimmed by stout, short, tooth-like denticles.

Mandibles scythe-like, the elbow between basal and distal portions with a strong (isosceles) triangular blade pointing medially and ventrally, the apical portion long, curved upwards and backwards, acutely tapering to the tip and with inner margin furrowed and serrated; mandibles widely spaced, approximated only apically, with inner blade not overlapping (in frontal view, when closed, with distal portions aligned with frontal carinae so that the labrum and clypeal area below horn are exposed). Labrum coated laterally by a brush of stiff, spine-like setae and long fine setae, dorsal surface sparsely covered by long fine setae, anterior

margin glabrous. Antennae elongate, with flagellomeres thin and long. Ocelli and compound eyes large, the latter reniform.

Dhagnathos autokrator sp. nov.

urn:lsid:zoobank.org:act:EC8760A9-9C00-44A9-9311-2EC5DE24A4B1

Figs. 2A–C, 3, 8G

Etymology. The specific epithet refers to *autokrátor* (Greek, meaning ‘self-ruler’), an individual who exercises absolute power, unrestrained by superiors; in reference to the highly powerful aspect of this ant.

Holotype. IGR.BU-003, alate female (Figs. 2A–C, 3E–G).

Additional specimens. HA03, XA01 and RM1, three alate females (Figs. 3A–3D).

Horizon and locality. Upper Cretaceous, upper Albian–lower Cenomanian (ca. 99 Ma); in amber from the Hukawng Valley, Kachin State, Myanmar.

Diagnosis. As for the genus, by monotypy.

Description (gyne). Body length ca. 14 mm. Cuticle generally smooth, without distinct sculpturing, sparsely covered by thin, long, erect setae, the head additionally densely covered by short, adpressed setae on vertex and genae.

Head only slightly longer than high and wide. Vertex and posteroventral surface rounded, anterior surface relatively flat, and genae shorter than eyes and projecting anteroventrally above mandible insertion into a cheek-like lobe. Ocelli present near top of vertex, conspicuous, ocellar diameter slightly larger than width of first antennomere; interocellar distance about half of ocellar diameter. Compound eyes bulging, reniform, 2.4× as long as wide, situated posteriorly on head (EPI 440). Antennae inserted between compound eyes around their midlength, closely flanking lateral edges of clypeus; base of antenna with basal

314 bulb exposed, inserted within thick annular torulus. Antenna geniculate, filiform; scape short,
 315 0.5× head length, weakly arched and broadened apically; first funicular article (pedicel) very
 316 short, 0.22× scape length, less than twice as long as wide, broadened apically; flagellomeres
 317 unusually slender, funicular article II (antennomere III) about 22× as long as wide; following
 318 antennomeres gradually decreasing in length and width. Posterior clypeal margin apparently
 319 fused, while horn is the result of *de novo* medial margin/ridge; anterior clypeal margin
 320 broadly rounded. Clypeal horn directed upward for its basal quarter, then bent at a right angle
 321 and directed forward for remaining length; horn gently rounded apically, without expanded
 322 lobe; dorsal surface of horn convex; ventral surface emarginate, its lateral margins prominent
 323 and prolonged basally into raised frontal carinae diverging anteriorly to reach the anterior
 324 margin of head, just above insertion of mandibles. Setation of horn consisting, on ventral
 325 surface, of a dense brush of short, peg-like denticles at apex; similar peg-like denticles widely
 326 spaced and arranged in a single row on each lateral margin, and becoming progressively
 327 denser and arranged in 2–3 longitudinal rows along lateral clypeal carinae; dorsal and ventral
 328 surfaces of horn sparsely covered by thin, long, erect setae. Labrum well exposed, large,
 329 nearly trapezoid, with anterior margin convex, posterior margin slightly emarginate medially,
 330 sides unsutured to clypeus so that anterior part of labrum is apparently movable; dorsal
 331 surface of labrum rimmed laterally by a longitudinal brush of stiff, spine-like setae, also
 332 densely coated by thin, erect setae becoming progressively longer and stiffer along lateral and
 333 posterior margins. Mandibles long (MDI 97), scythe-shaped, widely spaced basally and
 334 converging apically, with tips curved and acute, nearly reaching the rounded portion of the
 335 horn as preserved; basal portion linear, short; apical portion 5× as long as basal portion,
 336 curved dorsally and posteriorly, with dorsal surface concave and rimmed on each margin by
 337 row of acute teeth and thin, erect setae directed backwards; medioventral blade between basal
 338 and apical portions forming a large, isosceles, blunt tooth perpendicular to apical portion.

339 Palps long (visible on specimen HA03), coated dorsally in fine, tapered setae, maxillary palp
 340 with 6 segments, as long as head capsule when combined; labial palp with 5 segments.
 341 Mesosoma. Pronotal collar pronounced, concealing propleuron in dorsal view, separated
 342 from remaining pronotal dorsum by a distinct transverse ridge; pronotal dorsum strongly
 343 concave immediately anterior to ridge, nearly flat posterior to ridge; promesonotal suture
 344 deeply impressed. Mesoscutum as long as pronotum (excluding neck) in dorsal view, about
 345 as broad as long; mesoscutal dorsal outline feebly convex, with long parapsidal furrows
 346 almost reaching anterior mesonotal margin, converging posteriorly but not touching.
 347 Mesoscutellum posteriorly expanded, in dorsal view concealing median portion of
 348 metanotum; dorsal and posterior mesoscutellar surfaces concave, their junction forming a
 349 sharp angle; dorsal mesoscutellar surface with a deep, broad, transverse groove immediately
 350 posterior to scuto-scutellar suture. Metanotum medially as high as long, with posterior
 351 surface forming distinct angle with pronotal dorsum. Propodeum 1.25× as high as long,
 352 dorsal and declivitous surfaces meet at pronounced right angle, forming conspicuous ridge;
 353 dorsal surface nearly flat, declivitous surface faintly concave; propodeal spiracle slit-like,
 354 opening posteriad, at junction of propodeal dorsum and sides; metapleural gland orifice
 355 opening laterally, protected by guard setae. Legs long and robust (mostly visible on specimen
 356 HA03); mesocoxa distinctly shorter than pro- and metacoxae; small trochantellus present on
 357 mid- and hind legs; all femora distinctly swollen in their basal half, tibiae swollen in their
 358 apical half; ventral margin of protibia apically with large calcar gently curved, protibia
 359 possessing small subapical point, and two straight, stout setae less than half as long as calcar;
 360 mesotibia apically with two long, straight, pectinate spurs, and two short, stout setae;
 361 metatibia apically with one long, pectinate spur and one long, simple spur; tarsomeres I–IV
 362 of all legs with pairs of stout setae along entire ventral surface (8–10 pairs on tI, 4–5 pairs on
 363 tII, 3 pairs on tIII, 2 pairs on tIV), and apically with 2 pairs of stout setae each flanking a

spatulate spine; additionally the ventral surface of tarsomeres I–IV covered by dense brush of thin, erect setae; pretarsal claws strong, with a distinct subapical tooth.

Fore wing with $Rs \cdot f_2$, basal portion of $Rs \cdot f_3$, $M \cdot f_4$, and Cu_1 nebulous, all other veins tubular; pterostigma elongate, ca. $6\times$ as long as broad; a short stub of cross-vein $1r-rs$ present, nebulous; $Rs \cdot f_1$ half as long as $M \cdot f_1$, both distinctly arched; $Rs \cdot f_2$ and $Rs \cdot f_3$ nearly at right angle, $Rs \cdot f_2$ half as long as $M \cdot f_2$; $2rs-m$ present, situated beyond apex of pterostigma; discal and subdiscal cells pentagonal; $cu-a$ arising from $M+Cu$ and proximal to $M \cdot f_1$ ($Cu \cdot f_1$ short); vein Cu with both Cu_1 and Cu_2 present. Hind wing with jugal lobe present; anterior margin with 5 median and 22 distal hamuli; vein C present; vein R present, reaching distal wing margin; $Rs \cdot f_1$ more than twice as long as $1rs-m$; $cu-a$ arising from $M+Cu$, proximal to fork of $M \cdot f_1$ and Cu ($Cu \cdot f_1$ short); $Rs \cdot f_2$, $M \cdot f_2$, Cu , and $A \cdot f_2$ present, not reaching wing margin.

Metasoma with petiole short-pedunculate, almost $0.6\times$ as high as long; petiolar tergite a broadly convex node, with anterior surface approximately twice as long as posterior face; subpetiolar process present, in profile forming a high, transverse, lamella pointing ventrally, with anterior face concave, posterior face vertical; not fused tergosternally, suture visible; attaching broadly to gaster. Gaster elongate. First gastral tergite with helcium pronounced, forming a post-petiolar peduncle, with anterior surface behind helcium high, oblique, and dorsal surface strongly convex, short; anteriormost part of first gastral sternite with a distinct mesal process (keel) pointing anteroventrally below helcium. Second gastral segment distinctly longer than first, with presclerite largely exposed to form a deep, broad constriction between first and second gastral segments (abdominal segments III and IV). Gastral segments unfused with deep lateral suture. Following segments poorly preserved, pygidium apparently broadly acute towards sting shaft.

Measurements (holotype IGR.BU-003; in mm). HL 2.50; HoL ca. 1.70; EL 1.20; ocelli diameter 0.20; MDbL 0.40, MDtL 0.55, MDaL 2.00; length/width of antennomeres: I (scape)

1.15/0.16, II (pedicel) 0.26/0.14, III 2.16/0.10, IV 1.50/0.07, V 1.34/0.07; WL 3.85; FWL (as preserved) 6.35 (7.90 on specimen DHA4); PL 1.84, PH 1.00, PW 0.67.

Genus *Chonidris* gen. nov.

urn:lsid:zoobank.org:act:664B304C-41C9-4F39-9561-2B055E815C3B

Type species: *Chonidris insolita* gen. et sp. nov.

Etymology. The generic name is a combination of *choní* (Greek, meaning ‘funnel’) and *idris* (Greek, meaning ‘ant’), in reference to the shape of the clypeus. The name is feminine.

Diagnosis (gyne). Highly similar to *Dhagnathos*, but smaller (body length ca. 9 mm), with clypeus triangulate and expanded posteriorly into rounded horn, lateral margins of clypeus raised into serrated carina; propodeum with posterodorsal ridge; ventral margin of petiole with pointed spicule-like process and lamella; gastral segments I and II (abdominal segments III and IV) with conspicuous constriction. Separable from *Dhagnathos* with clypeal horn, apical portion of mandibles, and flagellomeres distinctly more compact; with inner margin of mandible projecting medioventrally into a large triangular blade that is gradually tapering to the tip of mandible; this blade with ventral corner rounded and dorsomedial margin serrate; in frontal view, when mandibles closed, ventral corners of blades slightly overlapping and medial margins almost parallel, nearly touching, so that labrum and clypeal area ventral to horn are entirely concealed, and mandibles are encased in clypeal triangle.

Chonidris insolita sp. nov.

(urn:lsid:zoobank.org:act:3A8ED551-78C9-4B0F-8E10-6C94641F5A08).

Figs. 2D–F, 4, 8F

414 *Holotype*. NIGP171998, alate female (Figs. 2D, 4H).

415 *Paratype*. NIGP172003, alate female (Figs. 2E, 4F–G).

416 *Additional specimens*. HA04 and RM2, two alate females (Figs. 2F, 4A–E).

417 *Horizon and locality*. Upper Cretaceous, upper Albian–lower Cenomanian (ca. 99 Ma); in
418 amber from the Hukawng Valley, Kachin State, Myanmar.

419 *Etymology*. The specific epithet derives from *insolitus* (Latin, meaning ‘strange’), and refers
420 to the unusual accommodation of the mandibles within the clypeus.

421 *Diagnosis*. As for the genus, by monotypy.

422 *Description* (gyne). Body length around 10 mm. Cuticle smooth, densely covered by short
423 adpressed setae; additionally with long, thin, erect setae sparsely covering head capsule,
424 mesosoma, legs, and apical portions of gastral segments I–III, setae more densely covering
425 pygidium.

426 Head about as long as broad, longer than high, circular in frontal view. Vertex and
427 posteroventral surface strongly rounded, anterior surface flat, with short genae (ca. 0.2× eye
428 length) projecting into cheek-like lobe anteroventrally above mandible insertion. Ocelli
429 distinct, positioned on small, raised, triangular prominence; ocellar diameter as broad as base
430 of first antennomere, interocellar distance about one ocellar diameter. Compound eyes
431 bulging, oval, 0.6× as broad as long, removed from lateral margins of head capsule. Antennae
432 inserted between compound eyes below their midlength, closely flanking lateral edges of
433 clypeus at base of horn’s stalk; base of antenna with basal bulb exposed, inserted within thick
434 annular torulus opening obliquely dorsad; antenna elongate; scape ca. 0.8× head length,
435 weakly arched, cylindrical; pedicel very short, 0.2× scape length, about as long as wide,
436 slightly broadened apically; first flagellomere longest antennomere, about 8× as long as wide
437 (assessed from paratype, where antennae are flattened and elongate but respective ratios are
438 kept); following antennomeres gradually decreasing in length. Posterior and lateral margins

of clypeus (epistomal sutures) visible, indicating the horn is the result of an elevated anterior margin. Clypeal horn short (HoI 28–30), expanded at right angle from frons, strongly arched with dorsal surface convex and ventral surface furrowed; lateral margins prolonged basally on frons into raised carinae diverging toward anterior angles of head, just above insertion of mandibles; ventral surface and lateral carinae rimmed by row of short, peg-like denticles, and long, fine, erect setae. Labrum exposed between clypeal carinae, with anterior margin broadly convex and slightly notched medially, posterior margin obscured; dorsal surface coated by long, thin, erect setae. Dorsal margin of mandibles curved dorsally immediately from base, in profile view without distinct elbow, their tips reaching nearby horn's apex, dorsal mandibular margin armed apically as series of sharp, curved teeth; largest apical tooth preceded by two medial teeth of equal length following slight gap; basal portion of mandible (from base to base of medioventral blade) short, simple; distal portion projected medially and ventrally in a large, triangular blade tapering to the tip; the blade with dorsal surface concave, ventral corner rounded, and apical half serrate; tip of mandible with a preapical tooth immediately following the blade and projected posteriorly, and one apical acute tooth curved posteriorly; when mandibles closed, their medial margins parallel and closely approximated, slightly overlapping at ventral corner of blade; accommodated in the triangular clypeal cavity (i.e., concealing the anterior clypeal margin, labrum and ventral surface of horn); maxillary palp with 5 visible segments, labial palp with 3 visible segments.

Mesosoma about twice as long as high. Pronotal collar short, separated from remaining pronotal dorsum by a distinct transverse ridge; pronotum nearly vertical immediately anterior to ridge, feebly convex posterior to ridge (dorsum); posterior pronotal margin with distinct thickening dorsally. Promesonotal suture complete, appears flexible. Mesoscutum shorter than pronotum, mesoscutal dorsal outline faintly convex, with long parapsidal furrows converging posteriorly to reach anterior mesonotal margin. Mesoscutellum prominent; dorsal

mesoscutellar surface convex, posterior surface slightly concave, their junction forming a sharp angle. Metanotum medially as high as long, with posterior surface forming distinct angle with propodeal dorsum. Propodeum 1.5× as high as long, dorsal and declivitous surfaces flat, separated by thin ridge, forming sharp angle; propodeal spiracle slit-like atop rounded nodule, situated around junction of propodeal dorsum and sides. Metapleural gland orifice a small circular concavity. Mesopleuron and metapleuron coated in thin, tapered setae. Legs robust, mesocoxa distinctly shorter than pro- and metacoxae, small trochantellus present on mid- and hind legs; all femora moderately swollen in their basal half; ventral margin of protibia apically with large calcar and two straight, stout setae less than half as long as calcar; mesotibia apically with two long, straight, spurs, one pectinate and one simple; additionally with three short stout setae; metatibia apically with one long, pectinate spur, one long, simple spur, and one short, stout seta; tarsomeres I–IV of all legs with pairs of short, stout setae along entire ventral surface (6 pairs on tI, 3 pairs on tII, 3 pairs on tIII, 2 pairs on tIV), and apically with 2 pairs of simple, stout setae each flanking a spatulate seta (= plantar lobe); pretarsal claws strong, with a distinct subapical tooth and pulvillus.

Wing venation as in *Dhagnathos* except, in fore wing, the pterostigma 3× as long as broad, cross-vein $Rs \cdot f1$ not arched, short stub of $1r-rs$ tubular, $M \cdot f2$ extremely short ($1m-cu$ almost arising at level of $Rs \cdot f2$). Hind wing with 11 distal hamuli present, jugal lobe not visible, but lobe may be lost due to damage.

Metasoma. Petiole short-pedunculate, massive, 0.84× as high as long; in profile, with posterior margin oblique and broadly attached to first gastral tergite (AIII); tergite and sternite of petiole and AIII unfused (suture distinct); petiolar tergite a strongly convex node, with anterior surface approximately twice as long as posterior surface which is nearly vertical in its anterior half, oblique in its posterior half; petiolar sternite with subpetiolar process and lamella (in profile) with a high, transverse tooth pointing ventrally, with anterior face flat,

posterior face concave; process followed by a smaller but distinct triangular tooth. First gastral segment bell-shaped; tergite with helcium faintly pronounced, with anterior surface behind helcium high, oblique, and dorsal surface strongly convex, short; anteriormost part of first gastral sternite with a distinct mesal process (keel) projecting anteroventrally below helcium. Second gastral segment (AIV) distinctly longer than first, with presclerite largely exposed to form a deep, broad constriction between AIII and AIV. Following segments more or less telescoped, pygidium convex, sting well exerted, distinctly arched dorsally.

Measurements (in mm) (holotype NIGP171998), [paratype NIGP172003], {specimen RM2}. HL [1.42] {1.68}; HoL [0.86] {0.658}; EL [0.72]; MDL [1.44] {1.10}; length of antennomeres: I (scape) [1.00] {0.96}, II (pedicel) [0.17] {0.21}, III [1.42] {0.92}; WL (3.66) {3.30}; FWL (5.2) {5.50}; PL (1.33), PH (excluding process) (1.12).

Genus *Aquilomyrmex* sp. nov.

urn:lsid:zoobank.org:act:5AFEF07E-2228-4A9D-AEC1-8D2680267734

Type species: *Aquilomyrmex huangi* gen. et sp. nov.

Etymology. The generic name is a combination of *aquilex* (Latin, meaning ‘dowser’), and *myrmex* (Greek, meaning ‘ant’), and refers to the dowsing stick-like clypeal and labral processes. The name is masculine.

Diagnosis (gyne). Head dorsoventrally flattened, with large compound eyes situated dorsolaterally at anterior margin of head; with prominent, anteriorly protruding frontal shelf, clypeal horn and labrum. Antennae inserted laterally on frontal shelf, well in front of compound eyes and above base of clypeal horn; antennal scape long. Apex of clypeal horn bifurcated widely, with each bifurcation subsequently terminating in a bilobed pad; lateral margins of horn connecting obliquely with anteroventral angles of head, just above

mandibular insertion, connected by a cleared vertical cuticle, rimmed by short thin erect setae and occasional serrations. Labrum situated ventrally of horn, with size and shape similar to horn except for apex, which is only bifid; ventral margin coated by peg-like denticles on its basal half. Mandibles sickle-shaped, inserted ventrally very close to compound eyes, with all margins smooth (triangular blade absent) and acute tips converging between labral apex. Legs very long, with femora distinctly swollen basally, and apically with two flange-like cuticular lobes flanking the base of tibia. Petiole node-shaped, with small subpetiolar process. A deep, girdling constriction between first and second gastral segments.

Aquilomyrmex huangi sp. nov.

urn:lsid:zoobank.org:act:9C026315-9D66-406B-BF2E-401F12305A2D

Figs. 2G–H, 5, 8C

Holotype. NIGP172000, alate female (Figs. 2G, 5G–H).

Paratype. NIGP171999, alate female (Figs. 5–F).

Additional specimens. HA06 and RM3, two alate females (Figs. 5A–D).

Horizon and locality. Upper Cretaceous, Lower Cenomanian (ca. 99 Ma); in amber from the Hukawng Valley, Kachin State, Myanmar.

Etymology. The specific epithet is a patronym honoring Mr. Huang Yiren who provided four specimens for this study.

Diagnosis. As for the genus, by monotypy.

Description (gyne). Estimated body length around 9 mm. Cuticle smooth, densely covered by minute, adpressed setae, the pygidium additionally with dense, fine, erect setae.

Head prognathous, dorsoventrally flattened; in dorsal view, with lateral margins slightly converging posteriorly, occipital corners broadly rounded, posterior margin straight. Vertex

539 elongate, nearly flat. Ocelli forming a small, weakly prominent triangle situated on vertex far
540 posteriorly to posterior eye margins. Compound eyes large, oval, with outer margin only
541 feebly extending beyond side of head laterally, situated dorsolaterally near anterior margin of
542 head. Genae much reduced. Antennae inserted anteriorly to anterior margin of compound
543 eyes, dorsally to base of clypeal horn, and immediately flanking lateral edges of a prominent
544 frontal shelf; frontal shelf is distributed into a three-pronged projection comprising a median
545 membranous support stalk, flanked by strong, turreted toruli partially concealing antennal
546 bases in dorsal view; membranous stalk is flattened laterally, appearing as a slender line in
547 dorsal view; in lateral view, stalk appears broad with conspicuous medial hole (potentially
548 arising from desiccation; however, present in holotype and paratype), lower portion of stalk
549 with ventral margin fused to the dorsal margin of the clypeal horn. Base of antenna with basal
550 bulb exposed. Antenna geniculate, 12-segmented; scape long (SI 140), weakly arched in its
551 basal half; pedicel short, $0.10\times$ scape length, less than twice as long as wide, broadened
552 apically; antennomere III and XII longest flagellomeres, AIII cylindrical, about $3.6\times$ as long
553 as wide, following flagellomeres gradually (weakly) increasing in width, apical flagellomere
554 with rounded apex. Clypeal horn dorsoventrally flattened, protruding anteriorly (HoI 50),
555 gently curved dorsally toward apex; with dorsal surface convex in profile view, ventral
556 surface apparently concave; terminus of membranous horn bifurcated widely, with each
557 bifurcation terminating in a subsequent bilobed pad; each pad with a small, medial, rounded
558 lobe and a larger, lateral, rounded lobe, with tapered setae present along these lobes; lateral
559 margins of horn connecting obliquely with anteroventral angles of head, just above
560 mandibular insertion, by a cleared vertical cuticle, rimmed by short, thin, erect setae and
561 occasional serrations. Labrum situated ventrally to horn, with to horn in size and shape
562 except for apex only bifid (not each bifurcation bilobed; i.e., with the form of a snake
563 tongue); ventral surface coated by short, darkened, thick, peg-like denticles on its basal half,

564 additionally with sparse, long, fine, erect setae throughout. Mandibles sickle-shaped, inserted
565 very close to compound eyes, lateral to hypostoma in ventral view; weakly spaced basally
566 and converging apically, with tips acute and reaching to horn's apex between anterior median
567 notch of labrum and clypeal horn; basal portion linear, directed ventrally; apical portion
568 about 3× as long as basal portion, curved dorsally approximately at 45° from basal portion,
569 with dorsal surface apparently concave and smooth. Palps short, not reaching to occipital
570 margin; maxillary palp with 5 visible segments, labial palp with 3 visible segments.

571 Mesosoma elongate, distinctly longer than high and wide. Pronotal neck pronounced,
572 about as long as wide, 0.4× as wide as maximal width of pronotal dorsum; pronotal dorsum
573 distinctly lower than remaining mesosomal dorsum, with posterior margin strongly concave.
574 Promesonotal suture present, complete. Mesoscutum in dorsal view shorter than pronotum
575 (excluding neck), shorter than broad, with a distinct oblique anterior face forming a sharp
576 angle with pronotal dorsum. Mesoscutal dorsal outline strongly convex, with faint parapsidal
577 furrows converging posteriorly, almost reaching posterior mesoscutal margin. Mesoscutellum
578 anteriorly flat, posteriorly strongly convex; anterior half bordered on each side by sharp
579 carina converging posteriorly toward posterior convexity. Metanotum medially exposed in
580 dorsal view, about half as long as mesoscutum. Propodeum convex, about as high as long,
581 dorsal and declivitous surfaces forming a continuous curve; propodeal spiracle slit-like,
582 situated high on sides, opening posteriad. Metapleural gland orifice a circular concavity at
583 posteroventral margin of propodeum. Legs very long, slender. Mesocoxa only slightly shorter
584 than procoxa, half as long as metacoxa. Small trochantellus present on mid- and hind legs.
585 All femora distinctly swollen in their basal half, more than twice as broad as apical portion;
586 ventral margin of each femur apically with two flange-like cuticular lobes flanking the base
587 of tibia, these lobes increasingly larger from fore- to hind legs. Tibiae gradually increasing in
588 width apicad. Dorsal surface of mid- and hind tibiae with a longitudinal row of 18–20 short,

589 erect, stiff setae, and a paired row of long, erect, fine setae. Ventral margin of protibia
 590 apically with large calcar gently curved and one stout seta less than half as long as calcar;
 591 additionally the dorsal margin with three small, stiff setae. Mesotibia apically with two small,
 592 simple spurs; dorsal margin with 4 short, stiff setae. Metatibia apically with one long,
 593 pectinate spur and one short, simple spur; dorsal margin with 2 stiff setae. Tarsomere I of all
 594 legs elongate, longer than combined length of following tarsomeres II–V; tarsomere I of fore
 595 leg coated with longitudinal row of stiff setae on dorsal margin, and dense, short, fine, erect
 596 setae throughout; tarsomere I of hind leg very long, 0.8× as long as tibia. Pretarsal claws with
 597 a distinct subapical tooth.

598 Fore wing with veins M·f4 and Cu1 nebulous, not reaching wing margin; remaining veins
 599 tubular; cross-vein 1r-rs absent; Rs·f1 faintly arched; M·f1 distinctly arched, twice as long as
 600 Rs·f1; Rs·f2 nearly at right angle with Rs+M, half as long as M·f2; Rs+M and M·f2 not
 601 aligned, so that discal cell pentagonal, with vein 1m-cu distinctly longer than M·f1; second
 602 submarginal cell long, cross-vein 2rs-m situated far beyond apex of pterostigma; cross-vein
 603 cu-a arising from Cu, shortly distal to M·f1. Hind wing with 14 distal hamuli, jugal lobe not
 604 visible, base of hind wing lost.

605 Metasoma. Petiole short-pedunculate, twice as long as broad; petiolar tergite a broadly
 606 convex node, with anterior and posterior surfaces subequal in length; posterior surface
 607 oblique in its basal half, horizontal in its distal half; broadly attached to base of first gastral
 608 tergite; subpetiolar process reduced to a small, laterally flattened rectangle present ventrally
 609 to petiole node ascent. First gastral segment bell-shaped; first tergite with helcium
 610 pronounced, forming a post-petiolar peduncle, with anterior surface posterior to helcium
 611 high, oblique, and dorsal surface strongly convex, short. Deep, girdling constriction between
 612 first and second gastral segments (abdominal segments III and IV). Second gastral segment
 613 distinctly longer than first, with deep lateral sulcus. Dorsum and lateral margins of pygidium

coated in dense, tapered setae, hypopygium with long, sparse setae at terminus. Third valvula present. Sting present, strong.

Measurements (in mm) (holotype NIGP172000), [specimen RM3]. HL (1.40) [1.33], HW (1.05), Hh (0.50); HoL (0.86); EL (0.56 in dorsal view); MDL (ca. 1.00); length of antennomeres: I (scape) (1.47) [1.80], II (pedicel) (0.16) [0.18], III-XII (0.25, 0.18, 0.16, 0.13, 0.13, 0.16, 0.13, 0.13, 0.13, 0.25); WL [3.50]; PL (0.61).

Genus *Protoceratomyrmex* gen. nov.

urn:lsid:zoobank.org:act:D219838A-DEFE-4E2C-9599-2FFDE59970C4

Type species: *Protoceratomyrmex revelatus* gen. et sp. nov.

Etymology. The generic name is a combination of *proto-* (Greek, meaning ‘first’), and the most similar genus *Ceratomyrmex*, in reference to the very slight clypeal horn resembling an initial stage of the dramatically developed horn of other horned hell ants. The name is masculine.

Diagnosis (worker). Head configuration similar to *Haidomyrmex*, *Haidomyrmodes*, *Haidotermis*, *Ceratomyrmex*, and *Linguamyrmex*; head capsule tear-drop shaped, broadened posteriorly, gradually tapering anteriorly; head distinctly broad, approximately as wide as long. Mandibles scythe-like with abbreviated dorsal development and widened mandibular “elbow” relative to other haidomyrmecine taxa; clypeus with well-defined lateral and posterior sulci, a slight triangulate cuticular elevation present near posterior clypeal margin, flanked by elongate trigger hairs; posterolateral clypeal margins broadly rounded; frontal triangle present as a laterally flattened rectangular elevation between antennal sockets approximately equal in height to clypeal horn; eyes reduced, ocelli absent; pronotum broadened laterally; mesosoma with distinct metanotal sclerite; propodeal spiracle circular,

gaping; petiole pedunculate with broadly rounded node; ventral margin of petiole unarmed;
 constriction present between abdominal segments III and IV with medial v-shaped projection
 on first gastral tergite visible dorsally.

***Protoceratomyrmex revelatus* sp. nov.**

urn:lsid:zoobank.org:act:02E35429-75CB-45F0-8446-AE4598E48E21

Figs. 6A–B, 8B

Holotype. NIGP172002, worker (Figs. 6A–B).

Horizon and locality. Upper Cretaceous, upper Albian–lower Cenomanian (ca. 99 Ma); in
 amber from the Hukawng Valley, Kachin State, Myanmar.

Etymology. The specific epithet derives from *revelatus* (Latin, meaning ‘reveal’ or ‘show’),
 and refers to the clypeal margins, horn, and frontal triangle, which informed interpretations of
 morphological development in hell ants.

Diagnosis. As for the genus by monotypy.

Description (worker). Total length 4.30 mm. Cuticle generally glabrous throughout.

Head. Vertex broad, gradually rounded posterolaterally, medially flattened; head capsule
 tapered gradually toward anterior margin with maximum width at vertex approximately 2×
 that at mandibular insertion; head flattened anteriorly, with steep elevational incline present
 dorsally to oral opening; ventral surface of head severely depressed around occipital foramen.
 Ocelli absent, oval-shaped eyes reduced, positioned near midlength of head in lateral view,
 with dorsal margin abutting vertex of head. Mandibles scythe-like, laterally flattened,
 dorsoventrally expanded, appearing broad in lateral view; medial margin of mandibles
 slightly bowed anteriorly, producing cup-like curvature; dorsally developed apical tooth
 arising gradually, producing curved dorsal mandibular margin from basal arm of mandible,

triangulate blade present anteroventrally at “elbow” junction of basal mandibular margin and apical tooth, fine setae present on the lateral margin of this expansion; dorsal margin of mandible unarmed; length of apical tooth and basal margin of mandibles approximately equal. Maxillary palps elongate, ca $0.75\times$ length of head capsule, comprising six equally sized palpomeres; labial palps stout, roughly equal in length to two maxillary palps, comprising four equally sized palpomeres. Clypeus elongate and steeply elevated, sclerite is well defined by sulci, posterior and lateral margins meet broadly as gradually rounded suture; small, triangulate clypeal horn present, slight anterior widening visible from oblique view; long, fine seta present at base of clypeal horn, approximately $2\times$ length of horn itself, reaching beyond apex of mandibles as preserved (second, symmetrical hair flanking horn presumably lost). Antennal sockets present just dorsad posterior margin of clypeus; antenna with scape elongate, third antennomere more than twice as long as following one. Cuticle raised between antennal sockets into laterally flattened projection, likely homologous with “frontal triangle” of other haidomyrmecine taxa; projection with sharp anterior face, slightly declined dorsal face, and gradually sloping posterior face, 0.23 mm in length and 0.08 at greatest height.

Mesosoma. Pronotum and propleuron anteriorly extended into neck to meet and accommodate depression of head; propleuron reduced in lateral view, only faintly visible; pronotum broadly arched and dome-like; expanded ventrally in lateral view, with maximum height approximately equal to pronotal length in dorsal view; posterior margin of pronotum demarcated by well-defined mesonotum, resulting in a sharply circular posterior margin; in lateral view, posterior margin of pronotum nearly extending to posterior margin of mesonotum. Maximum height of pronotum, mesonotum, metanotum, and propodeum all approximately equal, with metanotum and propodeum slightly lower in elevation. Propodeum height and length approximately equal, broadly rounded dorsally; large propodeal spiracle

situated high, circular and gaping; metapleural gland opening slightly oval-shaped. Procoxa approximately twice as long as mid- and hind coxae; femur and tibia of each leg coated in fine setae; protibia with large calcar and two stiff setae approximately 0.33× length of calcar; mid- and hind legs with two tibial spurs of equal size; trochantellus present on mid- and hind legs; tarsomeres with fine, stiff setae on underside; conspicuous pretarsal claw present.

Metasoma. Petiole longer than high, node-shaped, coated in short, fine setae; peduncle short, comprising approximately 0.2× length of petiole itself; petiole node broadly rounded, with anterior surface gradually increasing in elevation, slightly flattened dorsally; posterior surface of petiole attaches to gastral segment I (abdominal segment III) broadly, following a slight decrease in elevation; ventral margin of petiole appears unarmed, without any process or tooth. Abdominal segment III with significant helcium, approximately equal in length to petiole peduncle; sternite possessing a slight ventral keel, triangulate and projecting just ventral to petiole as preserved. Darkened lateral sulci visible on each gastral segment, present along lower one-third of the gaster. Deep constriction present as circular banding between abdominal segments III and IV, this circular constriction interrupted by slight v-shaped posterior expansion of abdominal tergite III, visible from above. Pygidium with elongate, tapered setae; third valvula visible above sting; sting curved near apex.

Measurements (in mm) (holotype NIGP172002). HL 0.82; EL 0.20; HoL ca. 0.09; MDbL 0.36, MDtL 0.09, MDaL 0.41; length of antennomeres: I (scape) 0.42, II (pedicel) 0.08, III–XII 0.27, 0.13, 0.14, 0.12, 0.08, 0.10, 0.10, 0.11, 0.10, 0.12; WL 1.21; PL 0.33, PH 0.25.

Genus *Linguamymex* Barden & Grimaldi, 2017

Type species: *Linguamymex vladi* Barden & Grimaldi, 2017: 839.

***Linguamymex brevicornis* sp. nov.**

urn:lsid:zoobank.org:act:D91488C6-3BEB-4A21-9F0E-3101BB9CCA85

Figs. 6C–E, 7

Etymology. The specific epithet is a combination of *brevi* (Latin, meaning ‘short’) and *cornus* (Latin, meaning ‘horn’), and refers to the smaller clypeal horn compared to the type species *L. vladi*.

Holotype. NIGP172001, worker (Figs. 6C, 7D).

Additional specimens. LA01, alate female (Figs. 6D, 7A–B), and RM4, worker (Figs. 6E, 7C).

Horizon and locality. Upper Cretaceous, upper Albian–lower Cenomanian (ca. 99 Ma); in amber from the Hukawng Valley, Kachin State, Myanmar.

Diagnosis (females). Closely similar to *L. vladi*, but differs from this species by having a shorter clypeal horn (horn index $HoI = 31\text{--}34$ in *L. brevicornis*, 56 in *L. vladi*), with stalk much reduced, slightly broader than long, with the setose pad more hexagonal and aligned with stalk (circular and with a distinct bend between stalk and clypeal pad in *L. vladi*), and with clypeal pad coated in stout setae. It is also differentiated by the mandibles with two teeth on ventral corner of medioventral blade (teeth absent in *L. vladi*) and, in workers, with the apical mandibular portion shorter than basal portion (apical portion longer in *L. vladi*). In addition to the difference in the proportion of the mandible, the female castes of *L. brevicornis* differ by their size (body length ca. 7 mm in gyne, 4 mm in worker), by the antennae with flagellomeres compact in worker, more elongate in gyne, and by subpetiolar process present in worker.

Description (gyne). Total length of body around 7 mm. Cuticle minutely shagreened, densely covered by adpressed, minute setae, the apical gastral segments additionally with sparse pilosity of long, fine, erect setae becoming gradually denser toward apex.

Head. As in *Linguamyrmex vladi*, but with compound eyes slightly reniform, emarginate in middle of posterior margin. Ocelli distinct, positioned on a prominent cuticular triangle, in dorsal view, with posterior margin of lateral ocelli aligned with posterior margin of eyes. Antenna filiform, with flagellomeres elongate, cylindrical except apical one, which has acute tip; third antennomere twice as long as following one. Antennal sockets immediately flanking a medial frontal triangle that is sharply expanded anteriorly above clypeal horn, and connecting ventrally with dorsal surface of horn by a cleared, laterally flattened cuticle; frontal triangle projection terminates anteriorly at approximately same length as clypeal horn with slight indentation just dorsad clypeal horn, giving the appearance of a second, small, broadly rounded horn. Clypeal horn originating at base of frontal triangle, short and straight, in profile view almost perpendicular to longest axis of head. Horn paddle-shaped, with short, compact stalk and hexagonal, setose pad; stalk apparently glabrous, 0.10 mm in length, 0.12 mm in width; setose pad 0.26 mm in length, 0.20 mm at greatest diameter, with anterior margin straight, transverse; dorsal surface of setose pad glabrous, ventral surface densely and uniformly coated with very short, velcro-like vestiture; trigger hairs not visible. Lateral clypeal margins extending from above mandibular insertions toward horn as gently curved lines. Anterior clypeal margin broadly concave. Labrum visible. Mandible scythe-shaped; basal portion linear, short, meeting apical curved portion nearly at right angle; medioventral triangular blade bearing one large apical tooth and one small preapical tooth, with concave dorsal surface coated with pointed setae; apical portion of mandible posterior to medioventral blade 1.6× as long as blade, with tip broadly rounded. Mandibles preserved in closed position (with tips of apical portion reaching nearby clypeal setose pad), almost entirely parallel and closely approximated, except ventral corners of blades overlapping and tips slightly diverging. Maxillary palps 5-segmented, labial palps 3-segmented.

763 Mesosoma. Pronotal collar pronounced but not concealing entire propleuron in dorsal view;
 764 pronotal dorsum weakly convex. Promesonotal suture present, complete. In dorsal view,
 765 mesoscutum as long as pronotum (excluding neck), about as broad as long, with lateral and
 766 posterior margins carinate; posterior mesoscutal margin broadly concave; dorsal mesoscutal
 767 surface with long parapsidal furrows almost reaching anterior mesonotal margin, converging
 768 posteriorly but not touching. In profile view, pronotal dorsal outline feebly convex,
 769 mesoscutal dorsal outline nearly flat. Mesoscutellum prominent posteriorly; posterior
 770 mesoscutellar surfaces concave, their junction forming a sharp angle; dorsal mesoscutellar
 771 surface with a deep, broad, transverse groove immediately posterior to scuto-scutellar suture.
 772 Metanotum medially as high as long, with posterior surface forming distinct angle with
 773 pronotal dorsum. Propodeum 1.3× as high as long; in profile view, propodeal dorsum
 774 distinctly lower than pronotal dorsum; propodeal dorsum nearly flat, declivitous surface
 775 feebly convex, their junction broadly rounded. Propodeal spiracle slit-like, oriented posteriad.
 776 Metapleural gland opening circular, gaping. Legs long and robust, mesocoxa distinctly
 777 shorter than pro- and metacoxae; small trochantellus present on mid- and hind legs; all
 778 femora distinctly swollen in their basal half, tibiae swollen in their apical half; ventral margin
 779 of protibia apically with large calcar and two simple, stout setae less than half as long as
 780 calcar; mesotibia apically with two long, straight, pectinate spurs, and two short, straight,
 781 stout setae; metatibia apically with one long, pectinate spur and one long, simple spur.
 782 Tarsomeres I–IV of all legs with pairs of stout setae along entire ventral surface (8–10 pairs
 783 on tarsomere I, 4–5 pairs on tarsomere II, 3 pairs on tarsomere III, 2 pairs on tarsomere IV),
 784 and apically with 2 pairs of stout setae each flanking a spatulate spine; additionally the
 785 ventral surface of tarsomeres I–IV covered by dense brush of fine, erect setae; pretarsal claws
 786 thick, with a distinct subapical tooth.

Fore wing with veins M·f4 and Cu1 nebulous, not reaching wing margin; remaining veins tubular; cross-vein 1r-rs absent; Rs·f1 faintly arched; M·f1 distinctly arched, twice as long as Rs·f1; Rs·f2 nearly at right angle with Rs+M, half as long as M·f2; Rs+M and M·f2 not aligned, so that discal cell pentagonal, with vein 1m-cu distinctly longer than M·f1; second submarginal cell long, cross-vein 2rs-m situated far beyond apex of pterostigma; cross-vein cu-a arising from Cu, shortly distal to M·f1. Hind wing with jugal lobe present.

Metasoma. Petiole short-pedunculate; petiolar tergite forming a broadly convex node, with anterior surface approximately twice as long as posterior surface; subpetiolar process present, in profile a high, transverse, tooth pointing ventrally, with anterior surface concave, posterior surface vertical; transverse sulcus visible across petiole near basal margin. First gastral segment with helcium pronounced, forming a post-petiolar peduncle, with anterior surface posterior to helcium high, oblique, and dorsal surface strongly convex, short; anteriormost part of first gastral sternite with a distinct mesal process pointing anteroventrally below helcium. Second gastral segment distinctly longer than first, with presclerite largely exposed to form a deep, broad constriction between first and second gastral segments (abdominal segments III and IV). Posterior margin of gastral segments II onward with sparse, elongate setae. Pygidium nearly glabrous while hypopygium with sparse setae; pygidium apparently broadly acute towards sting shaft.

Wingless female (worker). Smaller than gyne (total length of body around 4 mm), and with the following differences: compound eyes oval, ocelli faintly visible, not positioned on a prominent cuticular triangle. Antenna more compact, with flagellomeres II–IX gradually broadened apically, apical flagellomere with rounded apex. Clypeal setose pad more quadrangular, the ventral surface with a pair of trigger hairs originating at pad base. Mandible

with medioventral triangular blade larger and apical portion (posterior to blade) reduced, 0.6× as long as blade.

Mesosoma and metasoma as in *L. vladi* except propodeum higher than long, petiole with subpetiolar process present, and girdling constriction deeper between abdominal segments III and IV (AIII with an oblique posterior surface). Protibia with one large apical spur (calcar) and two short stout setae; mesotibia with two simple spurs and three conspicuous setae positioned along anterior margin of tibial apex; metatibia with one pectinate and one simple spur, additionally with a brush of 8–10 setae flanking the pectinate spur. Sparse, erect setae positioned on dorsum of pronotum, propodeum, petiolar tergite, and first and second gastral tergites and sternites. Pygidium not preserved.

Measurements (in mm) (worker holotype NIGP172001) [worker specimen RM4] {gyne specimen LA01}. HL [0.82] {0.82}; EL [0.21] {0.42}; HoL [0.17] {0.36}; MDL [0.59] {0.80}; length of antennomeres: I (scape) (0.57) [0.67] {1.04}, II (pedicel) (0.09) [0.12] {0.14}, III–XII (0.35, 0.17, 0.16, 0.15, 0.15, 0.13, 0.13, 0.12, 0.13, 0.17) {0.80, 0.40, 0.34, 0.32, 0.31, 0.30, 0.30, 0.32, 0.32, 0.35}; WL [1.29] {2.29}; PL {0.70}.

Key to genera and species of Haidomyrmecinae:

1. Clypeus posteriorly with a slightly elevated setose lobe positioned just ventrad or between antennal insertion 2
- ▶ Clypeus posteriorly projecting forward into a cephalic horn arising ventrad, between, or dorsad antennal insertion 5
2. Antenna compact, with flagellomeres short (<2× as long as broad); first flagellomere as long as or longer than second one

- 836 3
- 837 ▶ Antenna elongate, with flagellomeres long ($>2\times$ as long as broad); first flagellomere
- 838 shorter than second one *Haidomyrmex*
- 839 species: 4
- 840 3. All flagellomeres nearly of same length; clypeal setose pad positioned anterior to
- 841 antennal insertion; ocelli present; two metatibial spurs
- 842
- 843 *Haidomyrmodes mammothus* Perrichot et al., 2008
- 844 ▶ Flagellomere I longest of basal four flagellar articles; clypeal setose pad positioned
- 845 slightly posterior to antennal insertion; ocelli absent; one metatibial spur
- 846
- 847 *Haidotermius cippus* McKellar, Glasier & Engel, 2013
- 848 4. Flagellomere II longest of basal three flagellar articles; frontal triangle moderately
- 849 elevated; vertex, ventral margin of mandibles, and antennomeres densely setose;
- 850 mandibles with medioventral blade bearing at least one large apical tooth, with tip of
- 851 apical portion tapered to acute point, smooth; ocelli reduced to pit-like traces; subpetiolar
- 852 process present *Haidomyrmex*
- 853 *cerberus* Dlussky, 1996
- 854 ▶ Flagellomere II longest; frontal triangle strongly elevated; vertex, ventral margin of
- 855 mandibles, and antennomeres mostly glabrous; mandibles with medioventral blades
- 856 asymmetrical, left one bearing three small teeth, right one bearing two larger teeth; tip of
- 857 apical portion tapered to sharp point, smooth; ocelli and subpetiolar process absent ...
- 858 *Haidomyrmex scimitarus* Barden & Grimaldi, 2012
- 859 ▶ Apical flagellomere longest; frontal triangle feebly elevated; vertex, ventral margin of
- 860 mandibles, and antennomeres mostly glabrous; mandibles with medioventral blade

- 861 bearing a single apical tooth, with tip of apical portion tapered to blunt point and minutely
 862 serrate; ocelli absent; subpetiolar process a minute tooth
 863
 864 *Haidomyrmex zigrasi* Barden & Grimaldi, 2012
- 865 5. Posterior clypeal projection not furrowed ventrally (= without lateral ridges), forming a
 866 pointed or paddle-shaped horn; long, paired trigger setae present, arising from base of
 867 clypeal process or ventral surface of apical setose pad; peg-like denticles absent or
 868 present only on ventral setose pad; labrum not obviously exposed
 869 6
- 870 ▶ Posterior clypeal projection distinctly furrowed ventrally, with lateral ridges originating
 871 above mandible insertions, and converging posteriorly to form the lateral margins of a
 872 horn; paired trigger setae absent; peg-like denticles present along lateral clypeal ridges, or
 873 on labrum, or both; labrum exposed ventrally of horn
 874 9
- 875 6. Clypeal horn a small triangulate cuticular elevation; one pair of trigger setae positioned at
 876 base of horn; compound eyes small (OI 24); ocelli absent; flagellomeres II–X compact,
 877 barely longer than wide *Protoceratomyrmex revelatus* gen. et. sp.
 878 nov.
- 879 ▶ Clypeal horn paddle-shaped, comprising basal stalk and apical setose pad; compound
 880 eyes small to large (OI 26–39); ocelli present; flagellomeres II–X elongate, distinctly
 881 longer than wide
 882 7
- 883 7. Clypeal horn and curved apical portion of mandibles extremely long, reaching high above
 884 vertex (HoI 140; MDI 130); peg-like denticles present on ventral setose pad; 2 pairs of
 885 trigger setae positioned at base of horn's stalk; frontal triangle fused with horn, not

- 886 distinguishable; gastral constriction between AIII and AIV at most faintly impressed
 887 *Ceratomyrmex ellenbergeri* Perrichot, Wang & Engel, 2016
- 888 ▶ Clypeal horn and curved apical portion of mandibles distinctly shorter, not reaching
 889 above vertex (MDI 70); peg-like denticles absent; 1 pair of trigger setae positioned on
 890 ventral surface of apical setose pad; frontal triangle connecting with horn by cleared
 891 cuticular membrane; gastral constriction between AIII and AIV deeply impressed
 892 *Linguamyrmex*
 893 species: 8
- 894 8. Clypeal horn reduced (HoI 25–35), with stalk almost indistinct and apical setose pad
 895 hexagonal, as broad as (worker) or smaller than (gyne) compound eye's length (EL);
 896 mandibles with medioventral blade bearing two teeth and, in worker, surpassing
 897 midlength of apical curved portion; compound eyes small in worker (OI 25); propodeum
 898 higher than long *Linguamyrmex brevicornis* gen.
 899 et. sp. nov.
- 900 ▶ Clypeal horn conspicuous (HoI 56), with stalk short, not surpassing frontal triangle in
 901 dorsal view, and apical setose pad circular, broader than EL in worker; mandibles with
 902 medioventral blade smooth and not reaching to midlength of apical curved portion;
 903 compound eyes large in worker (OI 39); propodeum longer than high
 904 *Linguamyrmex vladi* Barden & Grimaldi, 2017
- 905 ▶ Clypeal horn enormous (HoI 95–105), with apical setose pad circular, nearly as broad as
 906 head in dorsal view, and stalk about as long as pad; mandibles with medioventral blade
 907 smooth and, in worker, not reaching to midlength of apical curved portion; compound
 908 eyes large in worker (OI 44); propodeum longer than high
 909
 910 *Linguamyrmex rhinocerus* Miao & Wang,

2019

9. Body and legs robust; mandibles scythe-shaped, with medioventral triangular blade present; in frontal view, the outline of apical portion of mandibles aligned with clypeal lateral ridges; clypeal horn gradually tapering to rounded tip; genae elongate, the mandibles inserted far from compound eyes 10

- Body and legs gracile; mandibles sickle-shaped, with medioventral triangular blade absent; clypeal horn and labrum protruding horizontally, their tip with a deep median notch; apical lateral margins of horn bilobed; genae strongly reduced, the mandibles inserted close to compound eyes *Aquilomyrmex huangi* gen. et. sp. nov.

10. Mandibles with apical curved portion much longer than basal portion and entirely serrate along dorsal margin; with medioventral blade an isosceles tooth not projecting beyond mandibular elbow (labrum and clypeal surface below horn entirely exposed when mandibles closed); ocelli large, antennomeres and compound eyes distinctly elongate *Dhagnathos autokrator* gen. et. sp. nov.

- Mandibles with apical curved portion not distinctly longer than basal portion; with medioventral blade a large triangle gradually tapering to tip of apical portion (labrum and clypeal surface below horn entirely concealed when mandibles closed); dorsal margin of mandibles serrate along distal half of medioventral projection, bidentate apically; ocelli, antennomeres, and compound eyes more reduced *Chonidris insolita* gen. et. sp. nov.

4. Discussion

Even as Dlussky remarked on the unique cranio-mandibular system of hell ants, his bewilderment was related to a single taxon. Discoveries over the last decade and the taxa described here expand the boundaries of the group's morphology. Most striking is the extent to which the clypeus and mandibles are exaggerated. While all previously known hell ants possess cranial nodes or horns (Dlussky, 1996; Perrichot et al., 2008a, 2016; Barden and Grimaldi, 2012; McKellar et al., 2013a; Barden et al., 2017; Miao and Wang, 2019), these appendages are the product of elevations that originate in the posterior region of the clypeus in *Haidomyrmex*, *Haidomyrmodes*, *Haidotermis*, *Ceratomyrmex*, and *Linguamyrmex*. The clypeus itself is drawn out dorsoventrally, matching the elongation present in the head capsule. This scheme is echoed in *Protoceratomyrmex*. However, the cranial horns present in *Aquilomyrmex*, *Chonidris*, and *Dhagnathos* are the product of an anterior clypeal margin that is extended dorsally as well as posteriad, resulting in a furrowed clypeal sclerite with a medial depression and ventrally concave horn (Figs. 1, 8; see also Barden et al., submitted). The visible epistomal sutures of *Chonidris* and *Protoceratomyrmex* highlight the two distinct cuticular origins of horns in haidomyrmecines (Figs. 5, 6). In *Aquilomyrmex*, the ventrally concave clypeus comprises the entire anterior expansion of the head capsule, and this expanded clypeus is matched by an equally extended labrum that is coated in thick denticles. The parallel modifications of the clypeus and mandibles in all haidomyrmecine taxa strongly suggest that these two features interacted during mouthpart movement, most likely to aid in prey capture.

5. Concluding remarks

Hell ant cranial morphology is unlike any modern group, a reflection of ancient diversification ultimately bound for extinction. Phylogenetic analyses have recovered

haidomyrmecines as a stem-group lineage that diverged from modern ants prior to the most common recent ancestor of all living ants (Barden and Grimaldi, 2016; Barden et al., submitted). This phylogenetic placement, molecular divergence estimates (Moreau and Bell 2013) and the presence of crown ants in Cretaceous amber (Grimaldi and Agosti, 2000; McKellar et al., 2013b; Zheng et al., 2018; Perrichot, 2019) indicate that hell ants and early members of extant lineages overlapped for tens of millions of years. The extinction of haidomyrmecines following their diversification remains an outstanding question in ant evolution, as is the function and evolutionary history responsible for this striking expansion into unparalleled phenotypic space.

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Figures legends

Fig. 1. Measurements of cranial structures shown on 3D models. A, head of *Dhagnathos* gen. nov. in full facial view. B, head of *Dhagnathos* gen. nov. in lateral view. C, head of *Aquilomyrmex* gen. nov. in dorsal view. D, head of *Aquilomyrmex* gen. nov. in lateral view. Scale bars: 1 mm.

Fig. 2. Representative alate females of *Dhagnathos autokrator* gen. et sp. nov. (A–C, holotype IGR.BU-003), *Chonidris insolita* gen. et sp. nov. (D–F), and *Aquilomyrmex huangi* gen. et sp. nov. (G–H). Habitus (A), head in lateral (B) and frontal (C) views. Habitus of holotype NIGP171998 (D), head of paratype NIGP172003 (E) in anterolateral view, head of specimen HA04 (F) in frontal view. Habitus of holotype NIGP172000 (G), head of specimen TJ41-020 (H) in lateral view. Scale bars: 1 mm (A, D, G), 0.5 mm (B, C, H), 0.2 mm (E, F).

Fig. 3. Overview and details of alate females (gynes) of *Dhagnathos autokrator* gen. et sp. nov. Specimen HA03 (A), specimen XA01 (B), specimen RM1 (C–D), and holotype IGR.BU-003 (E–G). Habitus (A, B, C), fore wing (D), mandibles, clypeus and labrum in lateral views (E, F), wings, propodeum and petiole (G). Abbreviations: cc, lateral clypeal carina; cd, clypeal denticles; cp, clypeal process (horn); lss, labral spine-like setae; mib, mandibular inner blade; mp, mesal process of 1st gastral sternite; pdr, propodeal ridge; spp, sub-petiolar process. Scale bars: 2 mm (A–C), 1 mm (D, G), 0.5 mm (E, F).

Fig. 4. Overview and details of alate females (gynes) of *Chonidris insolita* gen. et sp. nov. Specimen HA04 (A–B), specimen RM2 (C–E), paratype NIGP172003 (F–G), and holotype

1103 NIGP171998 (H). Habitus (A, C, F), heads (B, D, H), wings in lateral view. Scale bars: 1 mm
 1104 (A, C, E, F), 0.25 mm (B, D, G, H).

1105

1106 **Fig. 5.** Overview and details of alate females (gynes) of *Aquilomyrmex huangi* gen. et sp.
 1107 nov. Specimen RM3 (A–C), specimen HA06 (D), paratype NIGP171999 (E–F), and holotype
 1108 NIGP172000 (G–H). Habitus (A, E), heads (B, D), hind leg and first metasomal segments (C)
 1109 in lateral view. Head in dorsolateral view (F), head in dorsal view (G), head in ventral view
 1110 (H). Scale bars: 1 mm (A, E), 0.25 mm (B–D, F–H).

1111

1112 **Fig. 6.** Representative females of *Protoceratomyrmex revelatus* gen. et sp. nov. (A–B) and
 1113 *Linguamyrmex brevicornis* gen. et sp. nov. (C–E). Habitus (A) and head (B) of worker
 1114 holotype NIGP172002. Habitus of worker holotype NIGP172001 (C), head of gyne specimen
 1115 LA01 in dorsal view (D), head of worker specimen RM4 (E) in lateral view. Abbreviations:
 1116 cp, clypeal process; ft, frontal triangle; ts, trigger setae. Scale bars: 1 mm (A, C), 0.25 mm
 1117 (B, D, E).

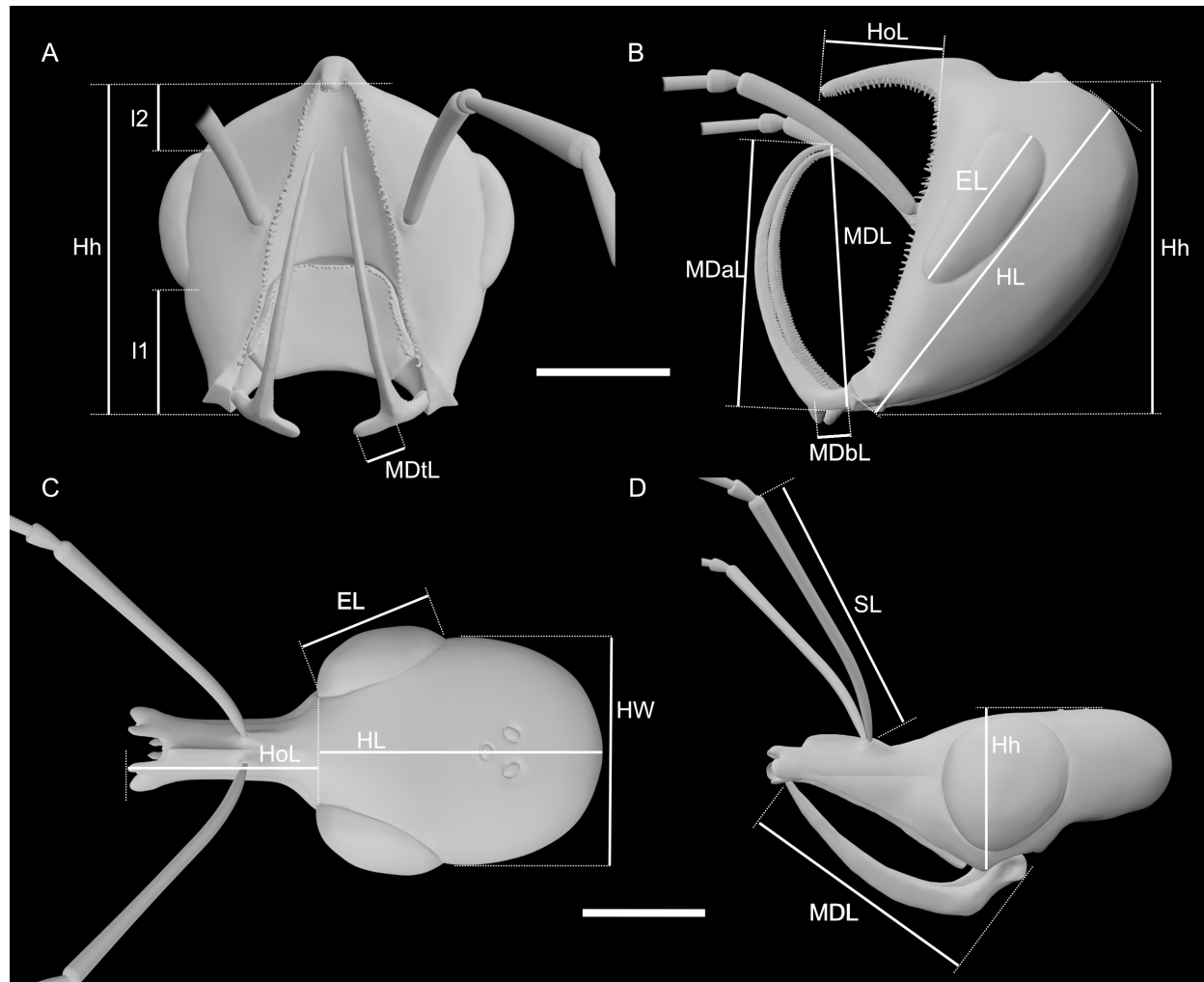
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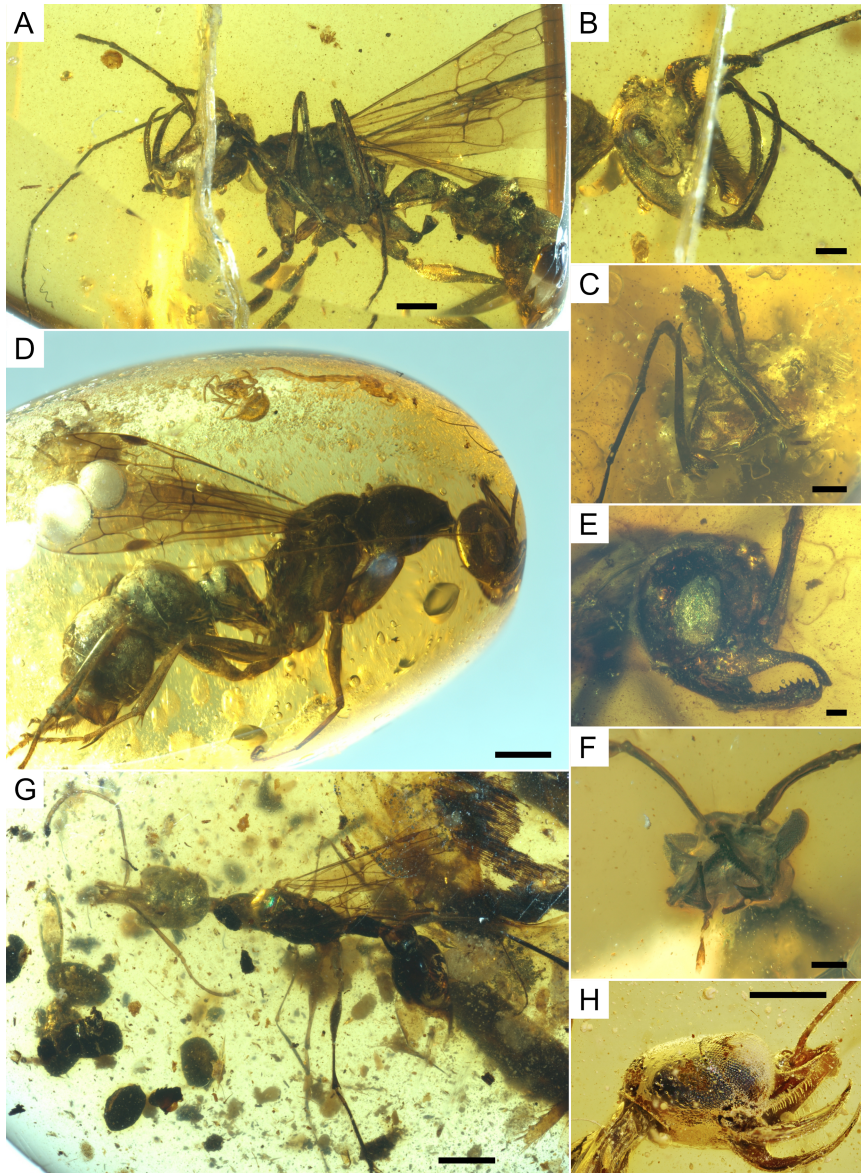
1119 **Fig. 7.** Overview and details of females of *Linguamyrmex brevicornis* gen. et sp. nov. Gyne
 1120 specimen LA01 (A–B), worker specimen RM4 (C), worker holotype NIGP172001 (D).
 1121 Habitus (A, C), head and mesosoma in dorsal view (B), head in ventrolateral view (D). Scale
 1122 bars: 0.5 mm.

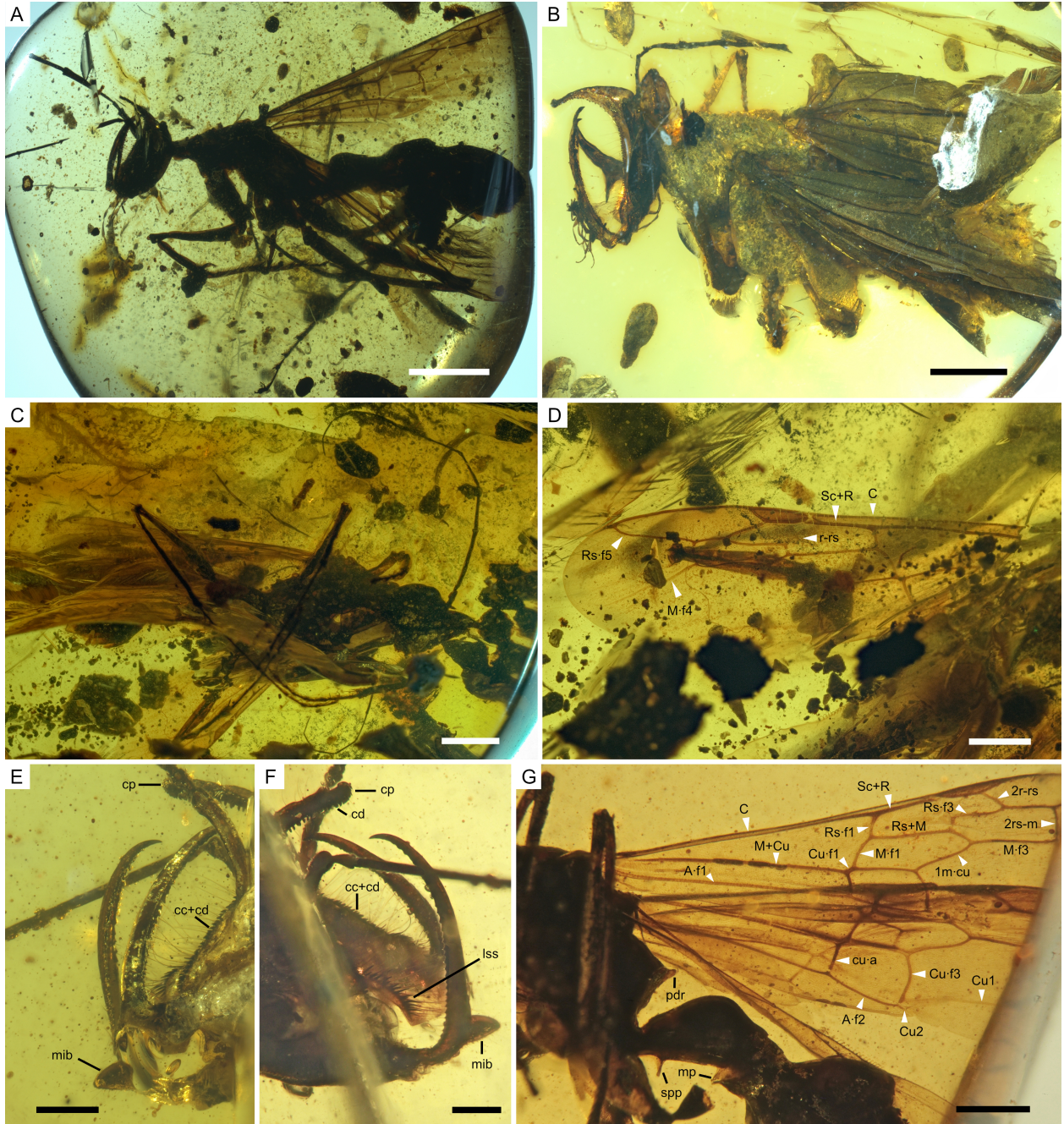
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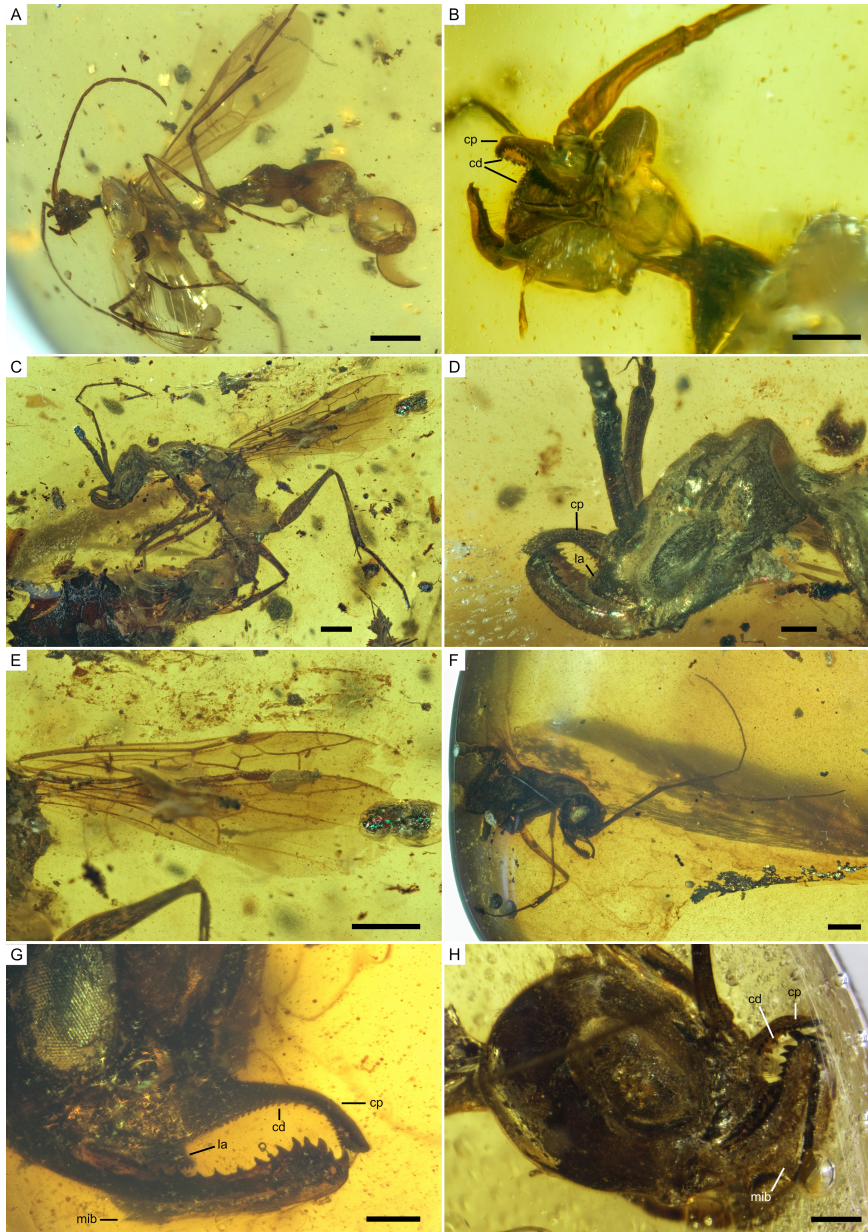
1124 **Fig. 8.** Artistic reconstructions of the heads of hell ants in lateral view, with mandibles
 1125 closed. A, *Haidomyrmex*. B, *Protoceratomyrmex* gen. nov. C, *Aquilomyrmex* gen. nov. D,
 1126 *Linguamyrmex*. E, *Ceratomyrmex*. F, *Chonidris* gen. nov. G, *Dhagnathos* gen. nov. Scale
 1127 bars: 0.5 mm.

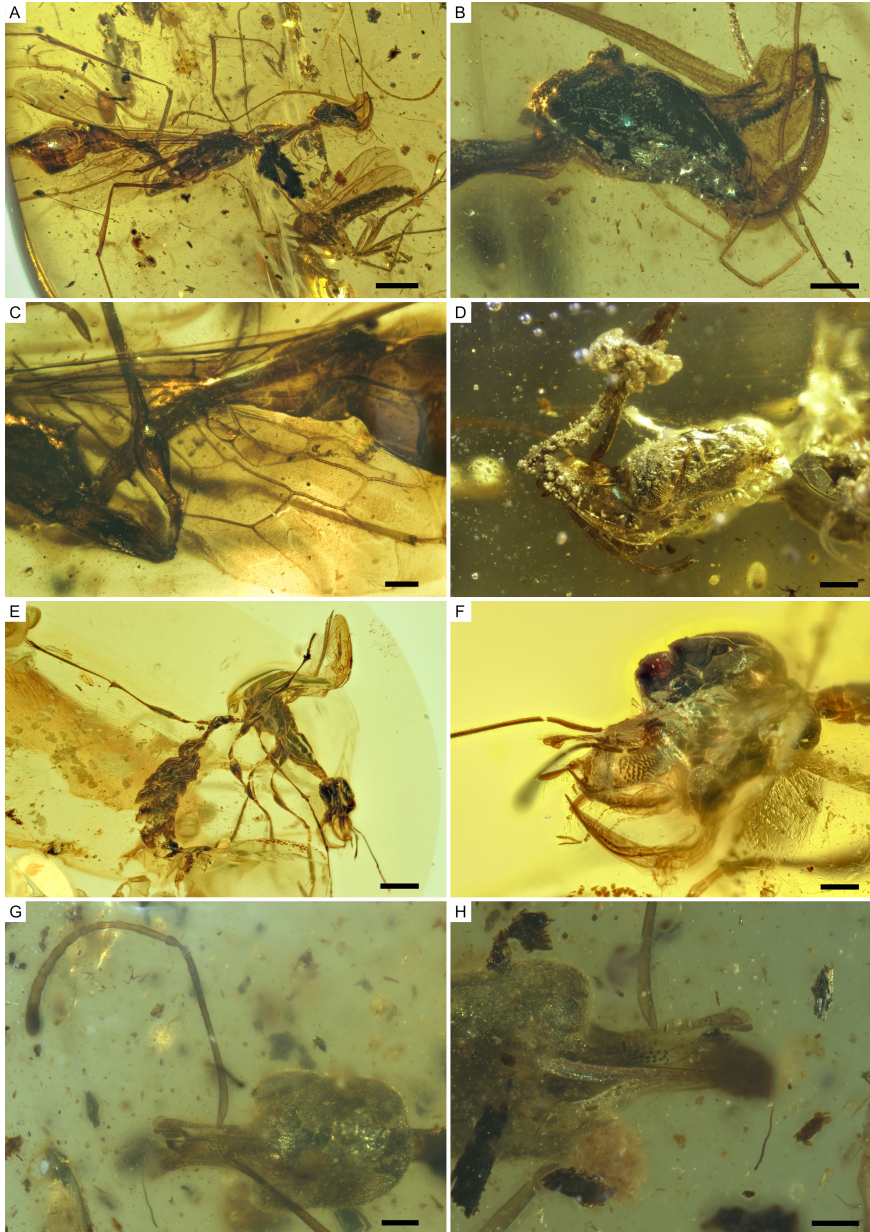


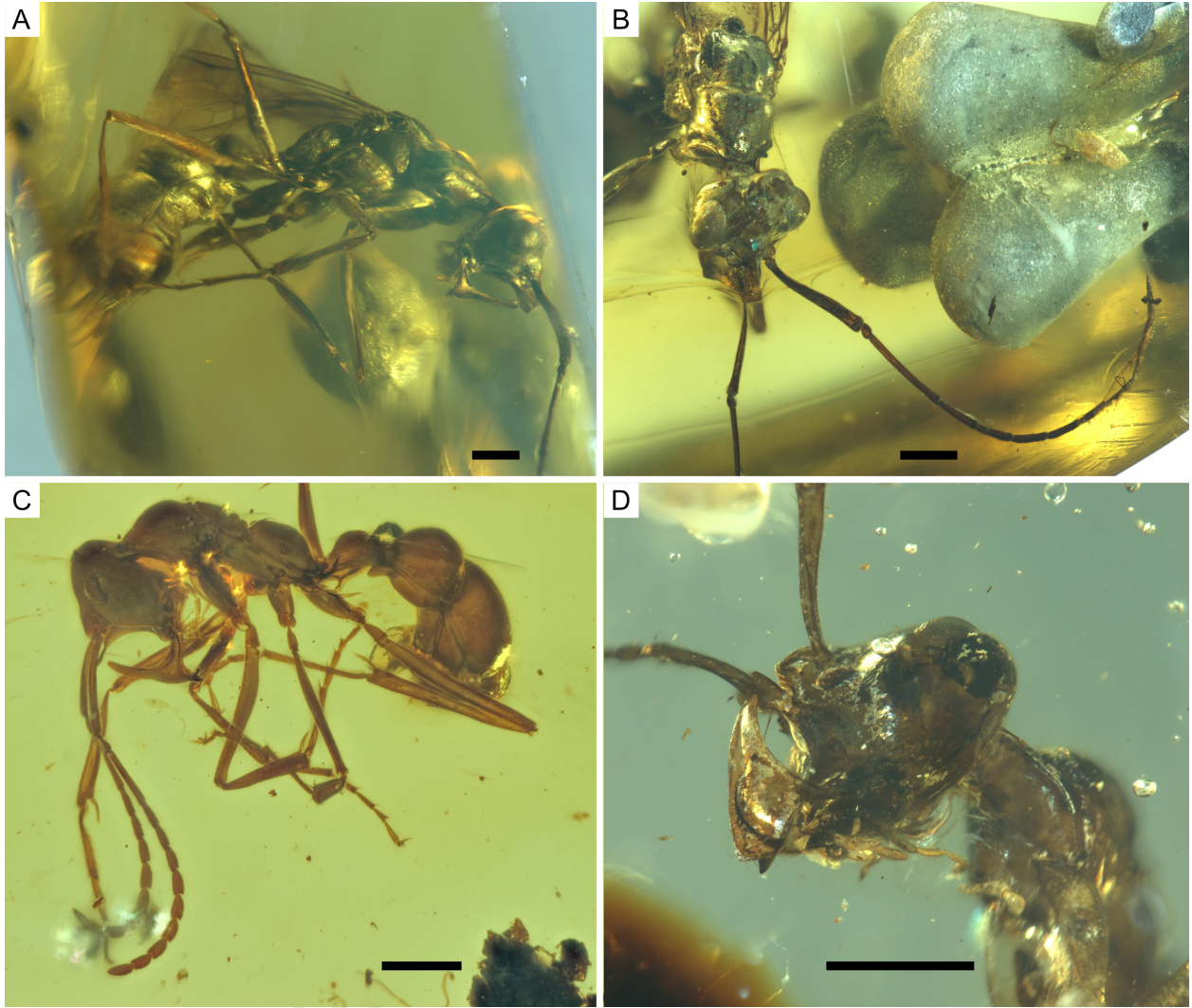


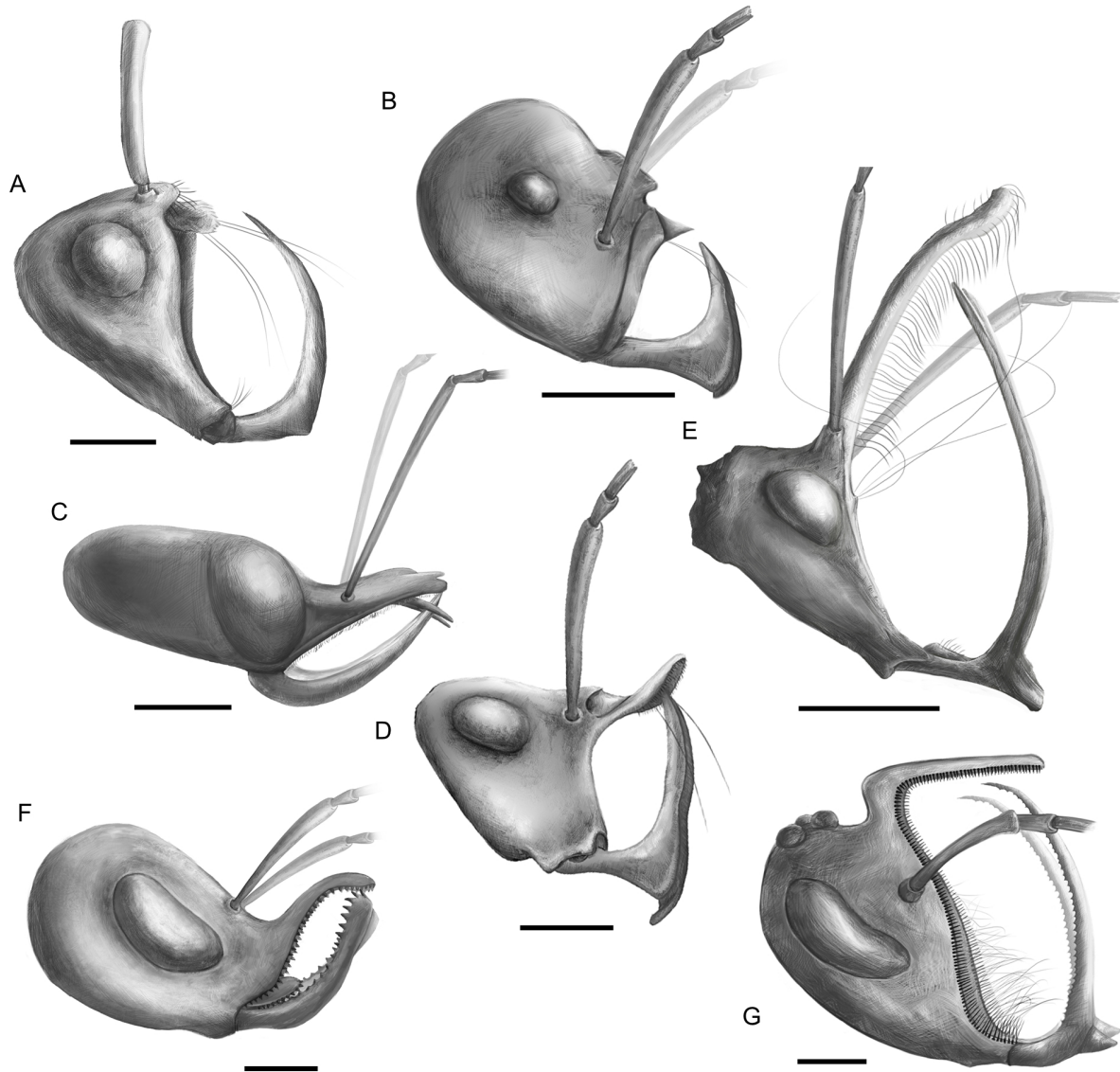












Author statement

Vincent Perrichot, Bo Wang: Conceptualization; **Vincent Perrichot, Phillip Barden:** Data curation, Writing- Original draft preparation. **Vincent Perrichot, Bo Wang, Phillip Barden:** Investigation. **Vincent Perrichot, Phillip Barden:** Writing- Reviewing and Editing.

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: