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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.

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

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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, *Haidoterminus 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

2.1. Material and repositories

A total of 17 specimens were examined, all originating from amber mines located near Noije 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.

2.2. 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 × 10 × 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 × 8 × 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 × 13 × 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 × 9 × 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 × 8 × 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 measuring 31 × 24 × 6 mm, with a Psocoptera contacting its right hind leg, a tiny parasitic wasp (Hymenoptera) and a beetle (Coleoptera).

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

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

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

LA01. Alate gyne. An exquisitely preserved specimen, without distortion, but missing right antennomeres VII–XII and tarsomeres of left mid leg and hind legs. Exposed in dorsal, profile and full facial views, in a quadrangular piece of clear yellow amber measuring 10 × 8 × 6 mm, with a staphylinid beetle (Coleoptera) and several domichnia (borings) from pholadid bivalves (Smith and Ross, 2018).

RM1. Alate gyne. A complete specimen exposed mostly in right lateroventral view, apparently weakly distorted but largely obscured by small bubbles contacting the body, organic debris floating in amber matrix, and internal fractures crossing the amber piece. In a rounded piece of clear yellow amber measuring 39 × 26 × 8 mm, with a psychodid fly (Diptera) and numerous domichnia (borings) from pholadid bivalves.

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 × 14 × 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 tarsormeres 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).

2.3. 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.

2.4. 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 (1950) 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.

HoL Horn length: in profile, from base of elbow between vertical and horizontal ventral surfaces of horn to anteriormost point of horn; in *Aquilomyrmex*, measured in dorsal view from anteriormost point of eye to anteriormost point of horn.

HW Head width: in dorsal or full-face view, maximum width of head excluding eyes.

MDL Mandibular length: in profile, a straight distance from basal insertion to tip of mandibles.

MDaL Length of apical portion of mandible: in profile, from midpoint of elbow between basal and apical portions to tip of mandible.

MDbL Length of basal portion of mandible: in profile, from basal insertion of mandibles to midpoint of elbow between basal and apical portions of mandible.

MDtL Length of triangular medioventral blade of mandible: in full-face view, from midpoint of elbow between basal and apical portions of mandible to apex of medioventral blade.

PTH Petiole height: in profile, maximum height of petiole excluding subpetiolar process.

PTL Petiole length: in profile or dorsal view, maximum length of petiole.

PTW Petiole width: in dorsal view, maximum width of petiole.

SL Scape length: maximum length of scape excluding condylar neck.

WL Weber's length: in profile, maximum diagonal length of mesosoma.

MDI Mandibular index: MDL/HL × 100.

SI Scape Index: SL/HL × 100 (HL preferred to HW which is often hard to measure on fossils.

OI Ocular Index: EL/HL × 100.

EPI Eye Position Index: in full-face view, l1/l2 × 100 (see l1 and l2 in Fig. 1A).

HoI Horn Index: HoL/SL × 100.

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., 2013a). 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 undoubtably 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 peduncule, nodiform. Gastral constriction

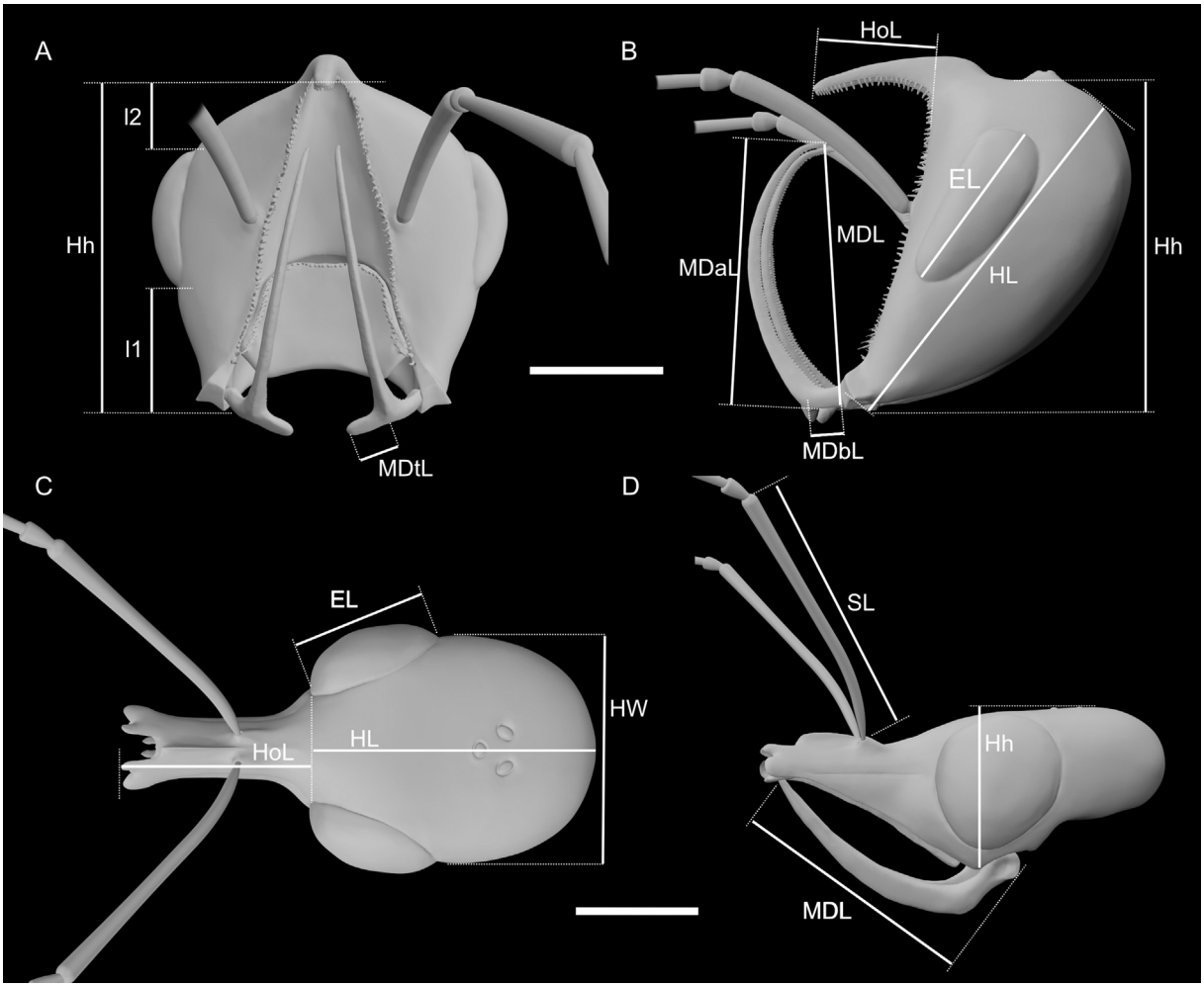

Fig. 1. Measurements of cranial structures shown on 3D models. A, head of *Dhagnathos* gen. nov. in full facial view. B, head of *Dhagnathos* gen. nov. in lateral view. C, head of *Aquilomyrmex* gen. nov. in dorsal view. D, head of *Aquilomyrmex* gen. nov. in lateral view. Scale bars: 1 mm.

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., 2008a; *Haidoterminus* McKellar, Glasier & Engel, 2013; *Linguamyrmex* Barden & Grimaldi, 2017 was described in Barden et al., 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 dorsal (posterior) margin furrowed and serrated; mandibles widely spaced, approximated only apically, with medioventral 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 bulb exposed, inserted within thick annular torulus. Antenna geniculate, filiform; scape short, 0.5 × head length, weakly arched and broadened apically; first funicular article (pedicel) very short, 0.22 × scape length, less than twice as long as wide, broadened apically; flagellomeres unusually slender, funicular article II (antennomere III) about 22 × as long as wide; following antennomeres gradually decreasing in length and width. Posterior clypeal margin apparently fused, while horn is the result of *de novo* medial margin/ridge; anterior clypeal margin broadly rounded. Clypeal horn directed upward for its basal quarter, then bent at a right angle and directed forward for remaining length; horn gently rounded apically, without expanded lobe; dorsal surface of horn convex; ventral surface emarginate, its lateral margins prominent and prolonged basally into raised frontal carinae diverging anteriorly to reach the anterior margin of head, just above insertion of mandibles. Setation of horn consisting, on ventral surface, of a dense brush of short, peg-like denticles at apex; similar peg-like denticles widely spaced and arranged in a single row on each lateral margin, and becoming progressively denser and arranged in 2–3 longitudinal rows along lateral clypeal carinae; dorsal and ventral surfaces of horn sparsely covered by thin, long, erect setae. Labrum well exposed, large, nearly trapezoid, with anterior margin convex, posterior margin slightly emarginate medially, sides unsutured to clypeus so that anterior part of labrum is apparently movable; dorsal surface of labrum rimmed laterally by a longitudinal brush of stiff, spine-like setae, also densely coated by thin, erect setae becoming progressively longer and stiffer along lateral and posterior margins. Mandibles long (MDI 97), scythe-shaped, widely spaced basally and converging apically, with tips curved and acute, nearly reaching the rounded portion of the horn as preserved; basal portion linear, short; apical portion 5 × as long as basal portion, curved dorsally and posteriorly, with dorsal surface concave and rimmed on each margin by row of acute teeth and thin, erect setae directed backwards; medioventral blade between basal and apical portions forming a large, isosceles, blunt tooth perpendicular to apical portion. Palps long (visible on specimen HA03), coated dorsally in fine, tapered setae, maxillary palp with 6 segments, as long as head capsule when combined; labial palp with 5 segments.

Mesosoma. Pronotal colar pronounced, concealing propleuron in dorsal view, separated from remaining pronotal dorsum by a distinct transverse ridge; pronotal dorsum strongly concave immediately anterior to ridge, nearly flat posterior to ridge; promesonotal suture deeply impressed. Mesoscutum as long as pronotum (excluding neck) in dorsal view, about as broad as long; mesoscutal dorsal outline feebly convex, with long parapsidal furrows almost reaching anterior mesonotal margin, converging posteriorly but not touching. Mesoscutellum posteriorly expanded, in dorsal view concealing median portion of metanotum; dorsal and posterior mesoscutellar surfaces concave, their junction forming a sharp angle; dorsal mesoscutellar surface with a deep, broad, transverse groove immediately posterior to scuto-scutellar suture. Metanotum medially as high as long, with posterior surface forming distinct angle with pronotal dorsum. Propodeum 1.25 × as high as long, dorsal and declivitous surfaces meet at pronounced right angle, forming conspicuous ridge; dorsal surface nearly flat, declivitous surface faintly concave; propodeal spiracle slit-like, opening posteriad, at junction of propodeal dorsum and sides; metapleural gland orifice opening laterally, protected by guard setae. Legs long and robust (mostly visible on specimen HA03); mesocoxa distinctly shorter than pro-and metacoxae; small trochantellus present on mid- and hind legs; all femora distinctly swollen in their basal half, tibiae swollen in their apical half; ventral margin of protibia apically with large calcar gently curved, protibia possessing small subapical point, and two straight, stout setae less than half as long as calcar; mesotibia apically with two long, straight, pectinate spurs, and two short, stout setae; metatibia apically with one long, pectinate spur and one long, simple spur; tarsomeres I–IV of all legs with pairs of stout setae along entire ventral surface (8–10 pairs on tI, 4–5 pairs on 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·f2, basal portion of Rs·f3, M·f4, and Cu1 nebulous, all other veins tubular; pterostigma elongate, ca. 6 × as long as broad; a short stub of cross-vein 1r-rs present, nebulous; Rs·f1 half as long as M·f1, both distinctly arched; Rs·f2 and Rs·f3 nearly at right angle, Rs·f2 half as long as M·f2; 2rs-m present, situated beyond apex of pterostigma; discal and subdiscal cells pentagonal; cu-a arising from M+Cu and proximal to M·f1 (Cu·f1 short); vein Cu with both Cu1 and Cu2 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·f1 more than twice as long as 1rs-m; cu-a arising from M+Cu, proximal to fork of M·f1 and Cu (Cu·f1 short); Rs·f2, M·f2, Cu, and A·f2 present, not reaching wing margin.

Metasoma with petiole short-pedunculate, almost 0.6 × 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.

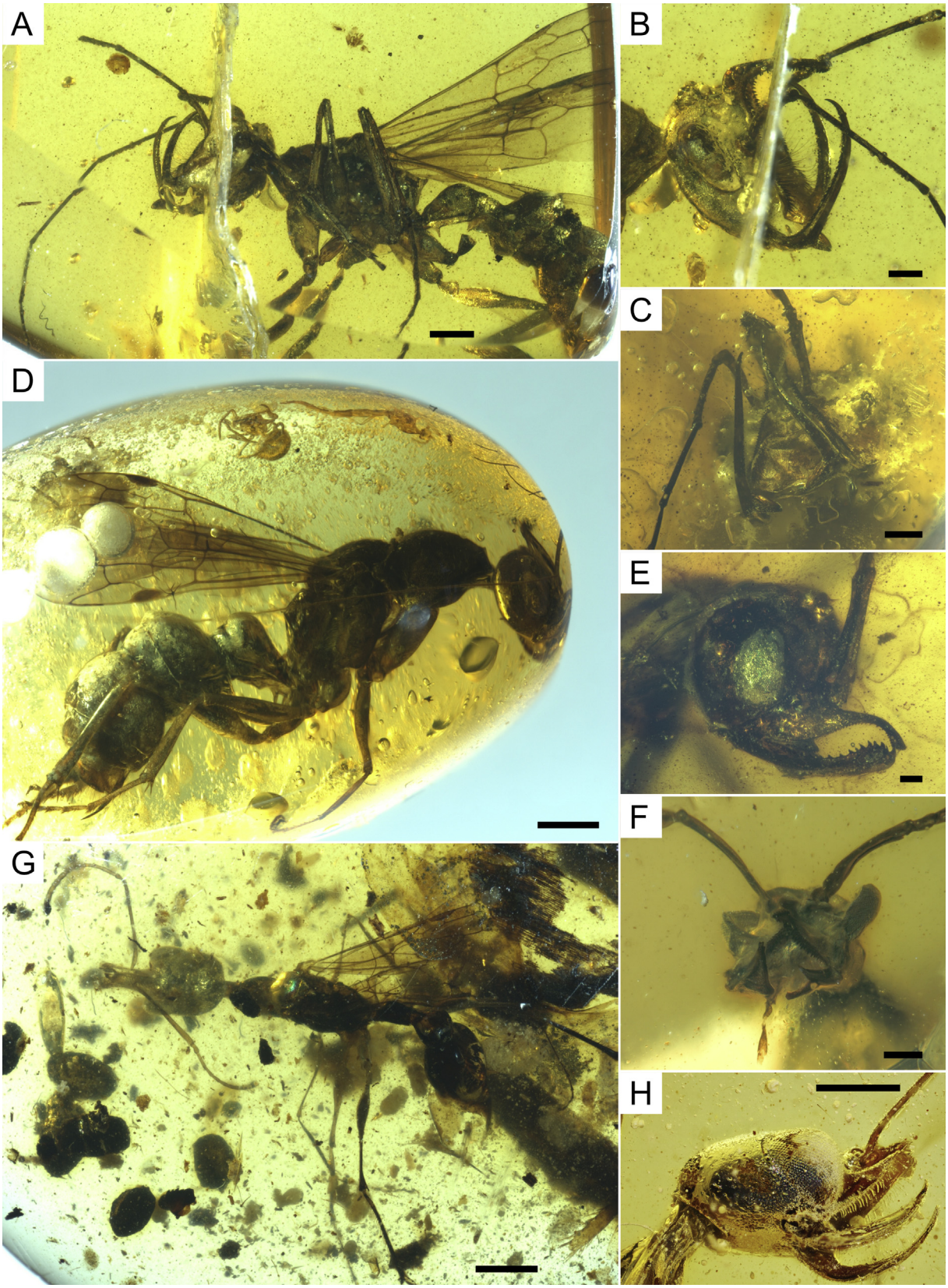

Fig. 2. Representative alate females of *Dhagnathos autokrator* gen. et sp. nov. (A–C, holotype IGR.BU-003), *Chonidris insolita* gen. et sp. nov. (D–F), and *Aquilomyrmex huangi* gen. et sp. nov. (G–H). Habitus (A), head in lateral (B) and frontal (C) views. Habitus of holotype NIGP171998 (D), head 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).

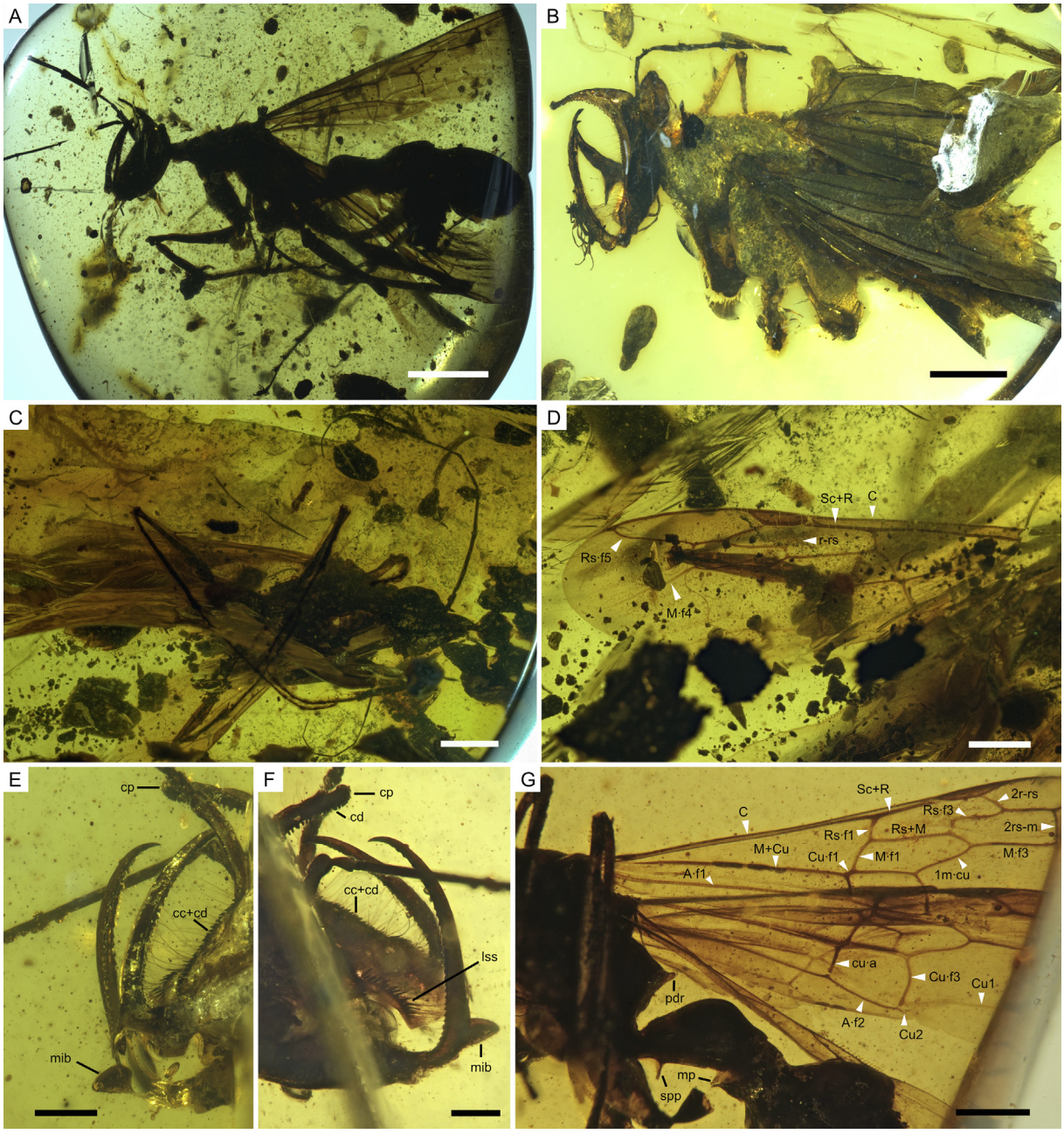

Fig. 3. Overview and details of alate females (gynes) of *Dhagnathos autokrator* gen. et sp. nov. Specimen HA03 (A), specimen XA01 (B), specimen RM1 (C–D), and holotype IGR.BU-003 (E–G). Habitus (A, B, C), fore wing (D), mandibles, clypeus and labrum in lateral views (E, F), wings, propodeum and petiole (G). Abbreviations: cc, lateral clypeal carina; cd, clypeal denticles; cp, clypeal process (horn); lss, labral spine-like setae; mib, mandibular medioventral 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).

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.

Holotype. NIGP171998, alate female (Figs. 2D, 4H).
Paratype. NIGP172003, alate female (Figs. 2E, 4F–G).
Additional specimens. HA04 and RM2, two alate females (Figs. 2F, 4A–E).
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 *insolitus* (Latin, meaning 'strange'), and refers to the unusual accommodation of the mandibles within the clypeus.
Diagnosis. As for the genus, by monotypy.
Description (gyne). Body length around 10 mm. Cuticle smooth, densely covered by short adpressed setae; additionally with long, thin, erect setae sparsely covering head capsule, mesosoma, legs, and apical portions of gastral segments I–III, setae more densely covering pygidium.

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

Wing venation as in *Dhagnathos* except, in fore wing, the pterostigma 3 × as long as broad, cross-vein Rs·f1 not arched, short stub of 1r-rs tubular, M·f2 extremely short (1m-cu almost arising at level of Rs·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 exserted, distinctly arched dorsally.

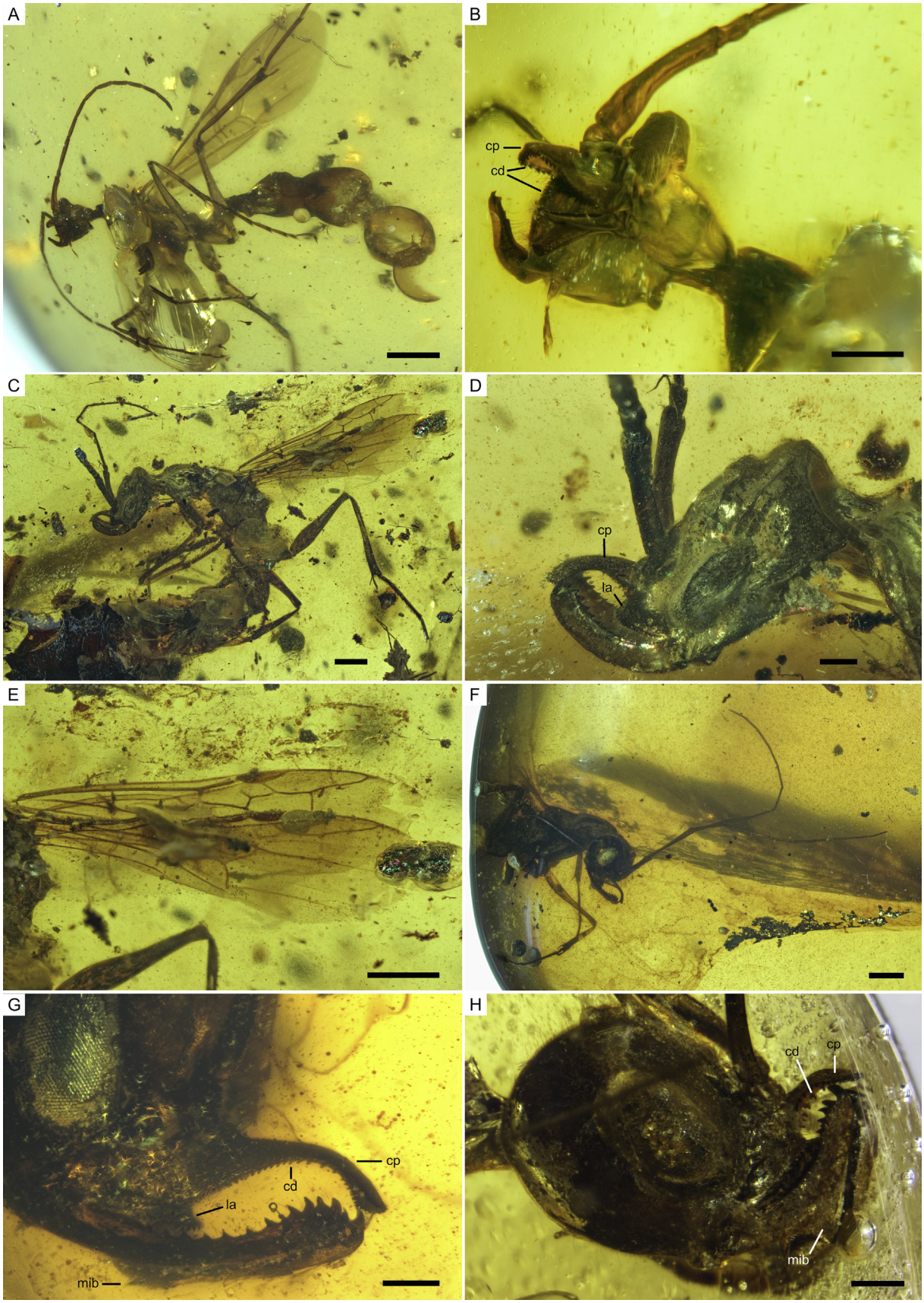

Fig. 4. Overview and details of alate females (gynes) of *Chonidris insolita* gen. et sp. nov. Specimen HA04 (A–B), specimen RM2 (C–E), paratype NIGP172003 (F–G), and holotype NIGP171998 (H). Habitus (A, C, F), heads (B, D, H), wings in lateral view. Scale bars: 1 mm (A, C, E, F), 0.25 mm (B, D, G, H).

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*** gen. 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 elongate, nearly flat. Ocelli forming a small, weakly prominent triangle situated on vertex far posteriorly to posterior eye margins. Compound eyes large, oval, with outer margin only feebly extending beyond side of head laterally, situated dorsolaterally near anterior margin of head. Genae much reduced. Antennae inserted anteriorly to anterior margin of compound eyes, dorsally to base of clypeal horn, and immediately flanking lateral edges of a prominent frontal shelf; frontal shelf is distributed into a three-pronged projection comprising a median membranous support stalk, flanked by strong, turreted toruli partially concealing antennal bases in dorsal view; membranous stalk is flattened laterally, appearing as a slender line in dorsal view; in lateral view, stalk appears broad with conspicuous medial hole (potentially arising from desiccation; however, present in holotype and paratype), lower portion of stalk with ventral margin fused to the dorsal margin of the clypeal horn. Base of antenna with basal bulb exposed. Antenna geniculate, 12-segmented; scape long (SI 140), weakly arched in its basal half; pedicel short, 0.10 × scape length, less than twice as long as wide, broadened apically; antennomere III and XII longest flagellomeres, AIII cylindrical, about 3.6 × as long as wide, following flagellomeres gradually (weakly) increasing in width, apical flagellomere with rounded apex. Clypeal horn dorsoventrally flattened, protruding anteriorly (HoI 50), gently curved dorsally toward apex; with dorsal surface convex in profile view, ventral surface apparently concave; terminus of membranous horn bifurcated widely, with each bifurcation terminating in a subsequent bilobed pad; each pad with a small, medial, rounded lobe and a larger, lateral, rounded lobe, with tapered setae present along these lobes; lateral margins of horn connecting obliquely with anteroventral angles of head, just above mandibular insertion, by a cleared vertical cuticle, rimmed by short, thin, erect setae and occasional serrations. Labrum situated ventrally to horn, with to horn in size and shape except for apex only bifid (not each bifurcation bilobed; i.e., with the form of a snake tongue); ventral surface coated by short, darkened, thick, peg-like denticles on its basal half, additionally with sparse, long, fine, erect setae throughout. Mandibles sickle-shaped, inserted very close to compound eyes, lateral to hypostoma in ventral view; weakly spaced basally and converging apically, with tips acute and reaching to horn's apex between anterior median notch of labrum and clypeal horn; basal portion linear, directed ventrally; apical portion about 3 × as long as basal portion, curved dorsally approximately at 45° from basal portion, with dorsal surface apparently concave and smooth. Palps short, not reaching to occipital margin; maxillary palp with 5 visible segments, labial palp with 3 visible segments.

Mesosoma elongate, distinctly longer than high and wide. Pronotal neck pronounced, about as long as wide, 0.4 × as wide as maximal width of pronotal dorsum; pronotal dorsum distinctly lower than remaining mesosomal dorsum, with posterior margin strongly concave. Promesonotal suture present, complete. Mesoscutum in dorsal view shorter than pronotum (excluding neck), shorter than broad, with a distinct oblique anterior face forming a sharp angle with pronotal dorsum. Mesoscutal dorsal outline strongly convex, with faint parapsidal furrows converging posteriorly, almost reaching posterior mesoscutal margin. Mesoscutellum anteriorly flat, posteriorly strongly convex; anterior half bordered on each side by sharp carina converging posteriorly toward posterior convexity. Metanotum medially exposed in dorsal view, about half as long as mesoscutum. Propodeum convex, about as high as long, dorsal and declivitous surfaces forming a continuous curve; propodeal spiracle slit-like, situated high on sides, opening posteriad. Metapleural gland orifice a circular concavity at posteroventral margin of propodeum. Legs very long, slender. Mesocoxa only slightly shorter than procoxa, half as long as metacoxa. Small trochantellus present on mid- and hind legs. All femora distinctly swollen in their basal half, more than twice as broad as apical portion; ventral margin of each femur apically with two flange-like cuticular lobes flanking the base of tibia, these lobes increasingly larger from fore-to hind legs. Tibiae gradually increasing in width apicad. Dorsal surface of mid- and hind tibiae with a longitudinal row of 18–20 short, erect, stiff setae, and a paired row of long, erect, fine setae. Ventral margin of protibia apically with large calcar gently curved and one stout seta less than half as long as calcar; additionally the dorsal margin with three small, stiff setae. Mesotibia apically with two small, simple spurs; dorsal margin with 4 short, stiff setae. Metatibia apically with one

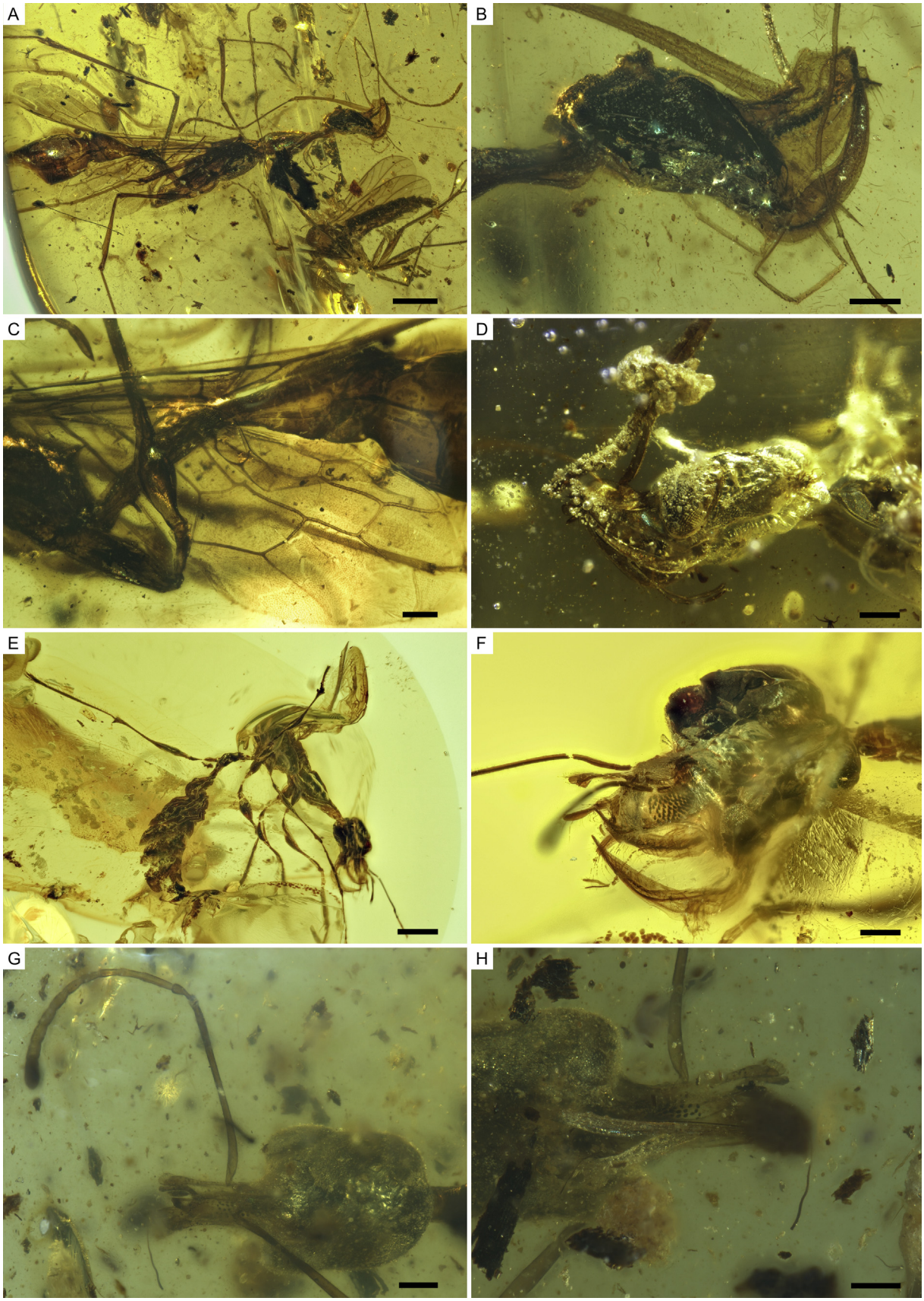

Fig. 5. Overview and details of alate females (gynes) of *Aquilomyrmex huangi* gen. et sp. nov. Specimen RM3 (A–C), specimen HA06 (D), paratype NIGP171999 (E–F), and holotype NIGP172000 (G–H). Habitus (A, E), heads (B, D), hind leg and first metasomal segments (C) in lateral view. Head in dorsolateral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

long, pectinate spur and one short, simple spur; dorsal margin with 2 stiff setae. Tarsomere I of all legs elongate, longer than combined length of following tarsomeres II–V; tarsomere I of fore leg coated with longitudinal row of stiff setae on dorsal margin, and dense, short, fine, erect setae throughout; tarsomere I of hind leg very long, 0.8 × as long as tibia. Pretarsal claws 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 14 distal hamuli, jugal lobe not visible, base of hind wing lost.

Metasoma. Petiole short-pedunculate, twice as long as broad; petiolar tergite a broadly convex node, with anterior and posterior surfaces subequal in length; posterior surface oblique in its basal half, horizontal in its distal half; broadly attached to base of first gastral tergite; subpetiolar process reduced to a small, laterally flattened rectangle present ventrally to petiole node ascent. First gastral segment bell-shaped; first tergite with helcium pronounced, forming a post-petiolar peduncle, with anterior surface posterior to helcium high, oblique, and dorsal surface strongly convex, short. Deep, girdling constriction between first and second gastral segments (abdominal segments III and IV). Second gastral segment 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*, *Haidoterminus*, *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 × 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 × 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

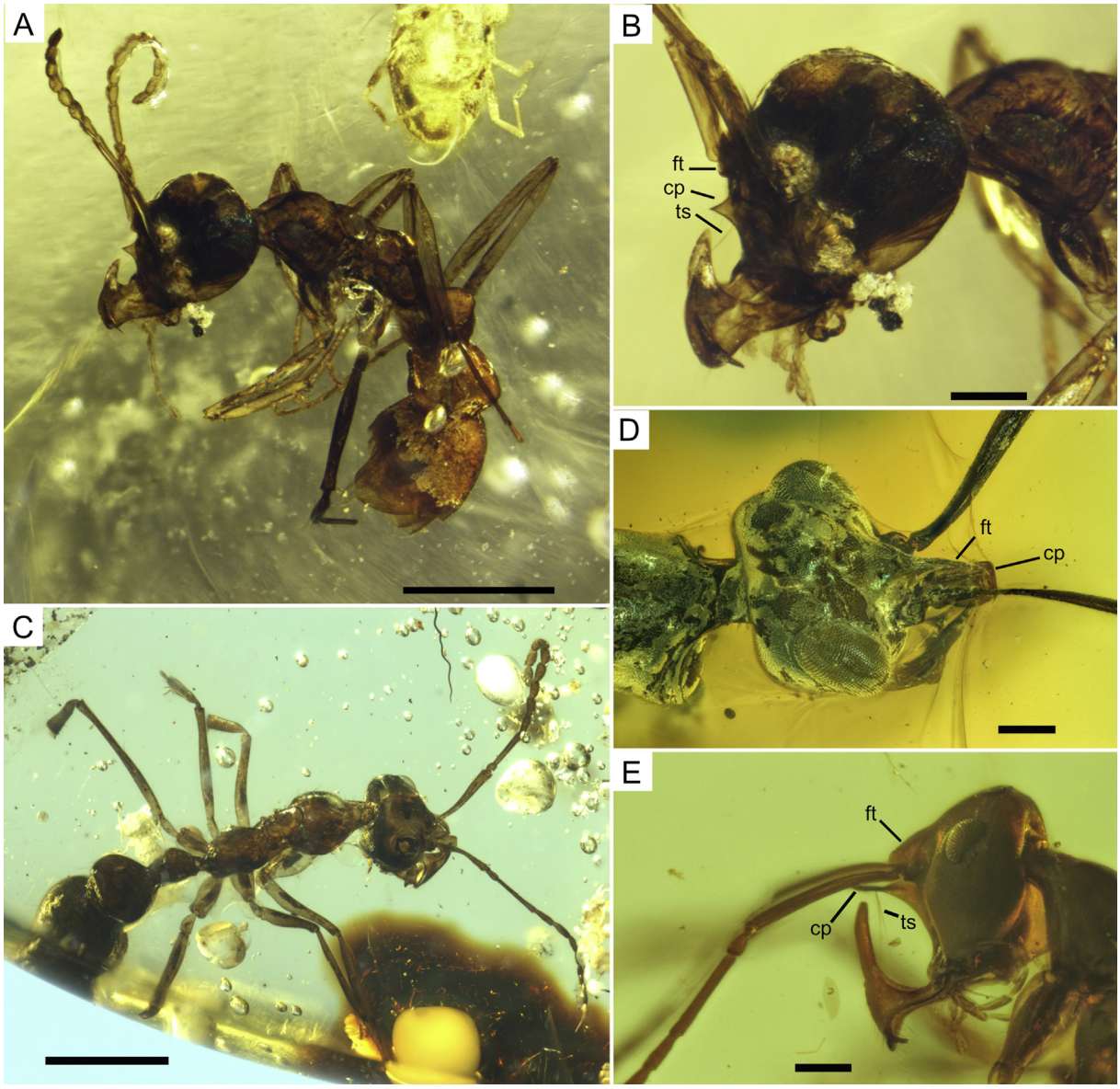

Fig. 6. Representative females of *Protoceratomyrmex revelatus* gen. et sp. nov. (A–B) and *Linguamyrmex brevicornis* gen. et sp. nov. (C–E). Habitus (A) and head (B) of worker holotype NIGP172002. Habitus of worker holotype NIGP172001 (C), head of gyne specimen LA01 in dorsal view (D), head of worker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

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 *Linguamyrmex* Barden & Grimaldi, 2017.
Type species: *Linguamyrmex vladi* Barden & Grimaldi, in Barden et al., 2017: 839.

Linguamyrmex 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 = 31–34 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

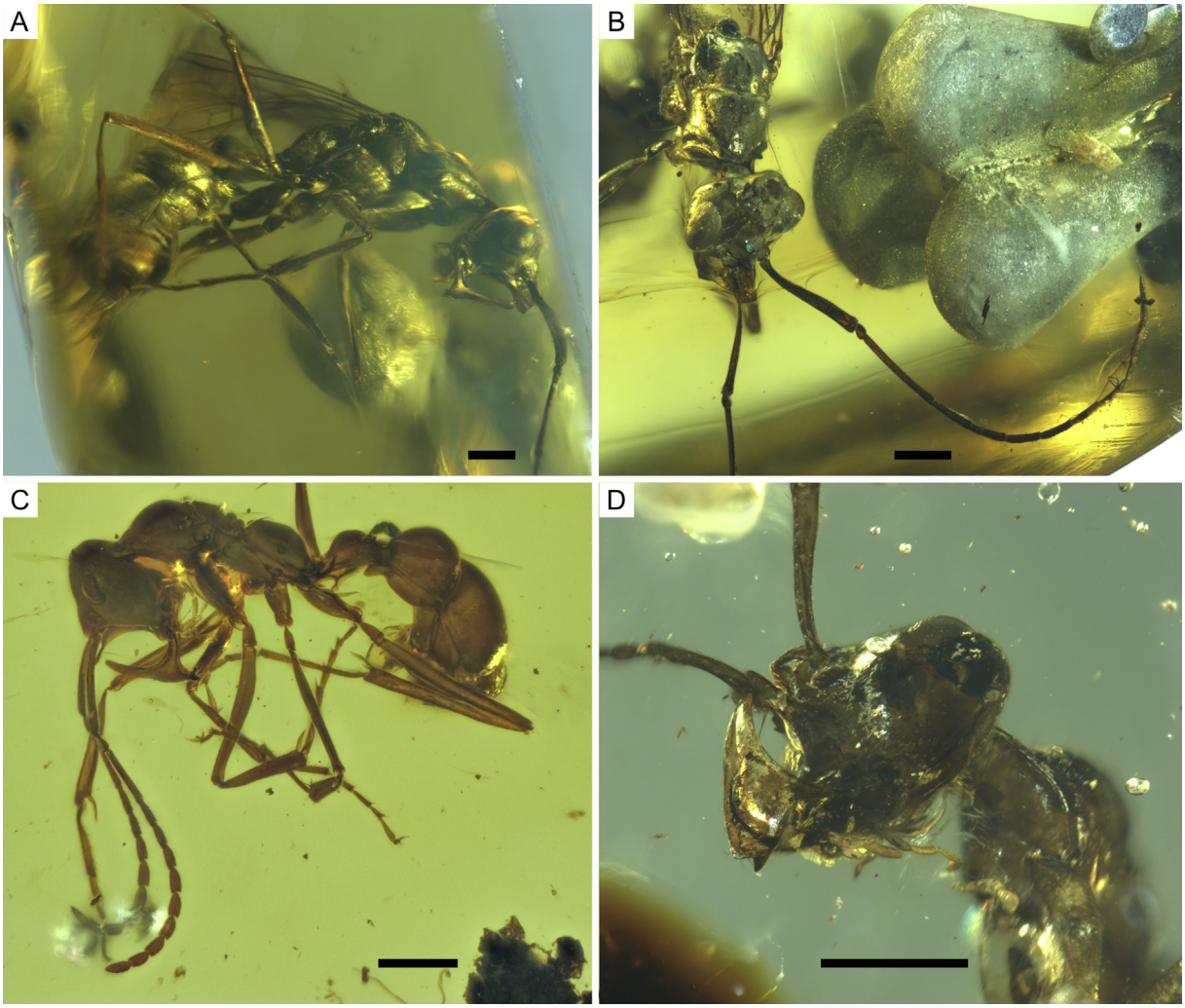

Fig. 7. Overview and details of females of *Linguamyrmex brevicornis* gen. et sp. nov. Gyne specimen LA01 (A–B), worker specimen RM4 (C), worker holotype NIGP172001 (D). Habitus (A, C), head and mesosoma in dorsal view (B), head in ventrolateral view (D). Scale bars: 0.5 mm.

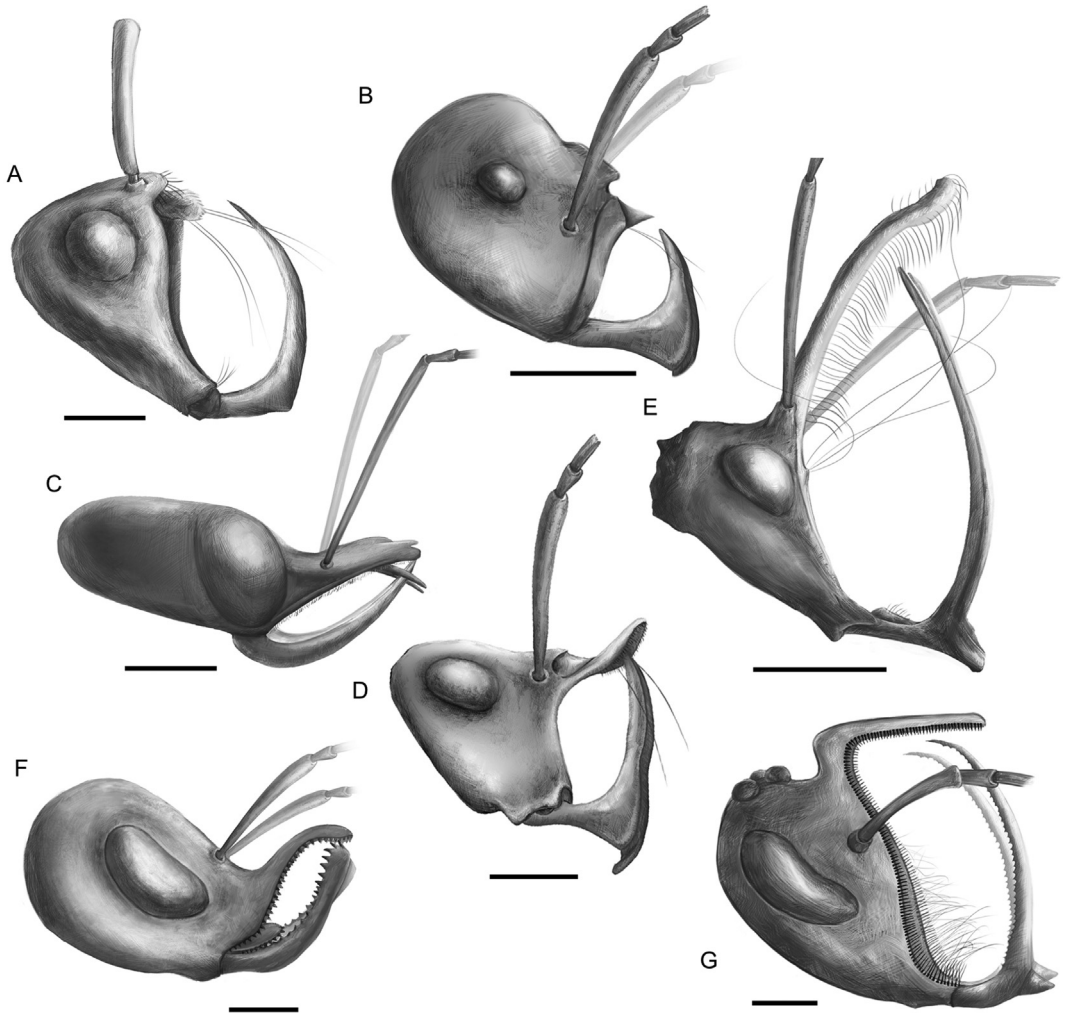

Fig. 8. Artistic reconstructions of the heads of hell ants in lateral view, with mandibles in closed position. A, *Haidomyrmex*. B, *Protoceratomyrmex* gen. nov. C, *Aquilomyrmex* gen. nov. D, *Linguamyrmex*. E, *Ceratomyrmex*. F, *Chonidris* gen. nov. G, *Dhagnathos* gen. nov. Scale bars: 0.5 mm.

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.

Mesosoma. Pronotal colar pronounced but not concealing entire propleuron in dorsal view; pronotal dorsum weakly convex. Promesonotal suture present, complete. In dorsal view, mesoscutum as long as pronotum (excluding neck), about as broad as long, with lateral and posterior margins carinate; posterior mesoscutal margin broadly concave; dorsal mesoscutal surface with long parapsidal furrows almost reaching anterior mesonotal margin, converging posteriorly but not touching. In profile view, pronotal dorsal outline feebly convex, mesoscutal dorsal outline nearly flat. Mesoscutellum prominent posteriorly; posterior mesoscutellar surfaces concave, their junction forming a sharp angle; dorsal mesoscutellar surface with a deep, broad, transverse groove immediately posterior to scuto-scutellar suture. Metanotum medially as high as long, with posterior surface forming distinct angle with pronotal dorsum. Propodeum 1.3 × as high as long; in profile view, propodeal dorsum distinctly lower than pronotal dorsum; propodeal dorsum nearly flat, declivitous surface feebly convex, their junction broadly rounded. Propodeal spiracle slit-like, oriented posteriad. Metapleural gland opening circular, gaping. Legs long and robust, mesocoxa distinctly shorter than pro- and metacoxae; small trochantellus present on mid- and hind legs; all femora distinctly swollen in their basal half, tibiae swollen in their apical half; ventral margin of protibia apically with large calcar and two simple, stout setae less than half as long as calcar; mesotibia apically with two long, straight, pectinate spurs, and two short, straight, stout setae; metatibia apically with one long, pectinate spur and one long, simple spur. Tarsomeres I–IV of all legs with pairs of stout setae along entire ventral surface (8–10 pairs on tarsomere I, 4–5 pairs on tarsomere II, 3 pairs on tarsomere III, 2 pairs on tarsomere IV), 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 fine, erect setae; pretarsal claws 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 3
- Antenna elongate, with flagellomeres long (>2 × as long as broad); first flagellomere shorter than second one ..... *Haidomyrmex* species: 4
3. All flagellomeres nearly of same length; clypeal setose pad positioned anterior to antennal insertion; ocelli present; two metatibial spurs ..... *Haidomyrmodes mammuthus* Perrichot et al., 2008.
- Flagellomere I longest of basal four flagellar articles; clypeal setose pad positioned slightly posterior to antennal insertion; ocelli absent; one metatibial spur ..... *Haidoterminus cippus* McKellar, Glasier & Engel, 2013 .
4. Flagellomere II longest of basal three flagellar articles; frontal triangle moderately elevated; vertex, ventral margin of mandibles, and antennomeres densely setose; mandibles with medioventral blade bearing at least one large apical tooth, with tip of apical portion tapered to acute point, smooth; ocelli reduced to pit-like traces; subpetiolar process present ..... *Haidomyrmex cerberus* Dlussky, 1996
- Flagellomere II longest; frontal triangle strongly elevated; vertex, ventral margin of mandibles, and antennomeres mostly glabrous; mandibles with medioventral blades asymmetrical, left one bearing three small teeth, right one bearing two larger teeth; tip of apical portion tapered to sharp point, smooth; ocelli and subpetiolar process absent ..... *Haidomyrmex scimitarus* Barden & Grimaldi, 2012
- Apical flagellomere longest; frontal triangle feebly elevated; vertex, ventral margin of mandibles, and antennomeres mostly glabrous; mandibles with medioventral blade bearing a single apical tooth, with tip of apical portion tapered to blunt point and minutely serrate; ocelli absent; subpetiolar process a minute tooth ..... *Haidomyrmex zigrasi* ..Barden & Grimaldi, 2012.
5. Posterior clypeal projection not furrowed ventrally (= without lateral ridges), forming a pointed or paddle-shaped horn; long, paired trigger setae present, arising from base of clypeal process or ventral surface of apical setose pad; peg-like denticles absent or present only on ventral setose pad; labrum not obviously exposed..... 6
- Posterior clypeal projection distinctly furrowed ventrally, with lateral ridges originating above mandible insertions, and converging posteriorly to form the lateral margins of a horn; paired trigger setae absent; peg-like denticles present along lateral clypeal ridges, or on labrum, or both; labrum exposed ventrally of horn 9
6. Clypeal horn a small triangulate cuticular elevation; one pair of trigger setae positioned at base of horn; compound eyes small (OI 24); ocelli absent; flagellomeres II–X compact, barely longer than wide ..... *Protoceratomyrmex revelatus* gen. et. sp. nov.
- Clypeal horn paddle-shaped, comprising basal stalk and apical setose pad; compound eyes small to large (OI 26–39); ocelli present; flagellomeres II–X elongate, distinctly longer than wide 7
7. Clypeal horn and curved apical portion of mandibles extremely long, reaching high above vertex (HoI 140; MDI 130); peg-like denticles present on ventral setose pad; 2 pairs of trigger setae positioned at base of horn's stalk; frontal triangle fused with horn, not distinguishable; gastral constriction between AIII and AIV at most faintly impressed ..... *Ceratomyrmex ellenbergeri* Perrichot, Wang & Engel, 2016

- Clypeal horn and curved apical portion of mandibles distinctly shorter, not reaching above vertex (MDI 70); peg-like denticles absent; 1 pair of trigger setae positioned on ventral surface of apical setose pad; frontal triangle connecting with horn by cleared cuticular membrane; gastral constriction between AIII and AIV deeply impressed……. *Linguamyrmex* species: 8

8 Clypeal horn reduced (HoI 25–35), with stalk almost indistinct and apical setose pad hexagonal, as broad as (worker) or smaller than (gyne) compound eye's length (EL); mandibles with medioventral blade bearing two teeth and, in worker, surpassing midlength of apical curved portion; compound eyes small in worker (OI 25); propodeum higher than long ……..…… *Linguamyrmex brevicornis* gen. et. sp. nov.

- Clypeal horn conspicuous (HoI 56), with stalk short, not surpassing frontal triangle in dorsal view, and apical setose pad circular, broader than EL in worker; mandibles with medioventral blade smooth and not reaching to midlength of apical curved portion; compound eyes large in worker (OI 39); propodeum longer than high …… ……..… *Linguamyrmex vladi* Barden & Grimaldi, 2017.
- Clypeal horn enormous (HoI 95–105), with apical setose pad circular, nearly as broad as head in dorsal view, and stalk about as long as pad; mandibles with medioventral blade smooth and, in worker, not reaching to midlength of apical curved portion; compound eyes large in worker (OI 44); propodeum longer than high …… …….. *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*, *Haidoterminus*, *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 (Figures 4 and 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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