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Vincent Perrichot, Bo Wang, Phillip Barden. New remarkable hell ants (Formicidae: Haidomyrmecinae stat. nov.) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 2020, 109, pp.104381. <10.1016/j.cretres.2020.104381>. <insu-02439287>

HAL Id: insu-02439287

<https://insu.hal.science/insu-02439287v1>

Submitted on 14 Jan 2020

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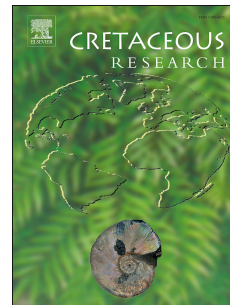


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PII: S0195-6671(19)30460-4

DOI: <https://doi.org/10.1016/j.cretres.2020.104381>

Reference: YCRES 104381

To appear in: *Cretaceous Research*

Received Date: 29 October 2019

Revised Date: 24 December 2019

Accepted Date: 6 January 2020

Please cite this article as: Perrichot, V., Wang, B., Barden, P., New remarkable hell ants (Formicidae: Haidomyrmecinae stat. nov.) from mid-Cretaceous amber of northern Myanmar, *Cretaceous Research*, <https://doi.org/10.1016/j.cretres.2020.104381>.

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

3
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15
16 **Abstract**

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

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

31

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

33

34

35 **1. Introduction**

36

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

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

52 with muted astonishment, stating that *Haidomyrmex* differed “from all known Formicidae,
53 both recent and fossil, by the very peculiar structure of the cranio-mandibular system.”
54 Dlussky was referencing the unique scythe-like mandibles and elongated head capsule that
55 characterize the many species of hell ants known today. The sole specimen worked by
56 Dlussky was reexamined by Engel and Grimaldi (2005), who refigured *H. cerberus* and
57 stressed the enigmatic nature of its morphology (see also Perrichot et al., 2016 and Cao et al.,
58 2020 for additional figures and a redescription). Additional haidomyrmecine material was
59 subsequently described as *Haidomyrmodes mammuthus* Perrichot et al., 2008, in Albian-
60 Cenomanian age French amber, which confirmed that the unique cranial morphology of hell
61 ants was present in more than one species (Perrichot et al., 2008a). Incidentally, because the
62 inclusions present in French amber spanned both workers and alates, these haidomyrmecines
63 also represent the earliest direct evidence of reproductive division of labor in ants (Perrichot
64 et al., 2008b). Aside from *H. mammuthus*, the majority of hell ants are recovered from
65 Burmese amber, however, *Haidotermis cippus* McKellar, Glasier & Engel, 2013 from
66 Campanian-age Canadian amber in Alberta, extends the temporal range of haidomyrmecines
67 at least 20 million years (McKellar et al., 2013a). A total of nine genera and 14 species are
68 now described. All but two genera and three species have been discovered in the last ten
69 years, and four genera and five species are described here for the first time.

70

71 **2. Material and methods**

72

73 *Material and repositories.* A total of 17 specimens were examined, all originating from
74 amber mines located near Noiye Bum Village, Tanai Town, Myitkina District of Kachin
75 State, northern Myanmar (see locality in Kania et al., 2015: fig. 1; or Grimaldi and Ross,
76 2017: fig. 2). A radiometric dating of zircons from the amber-bearing bed gave a maximum

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

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

89
90 *Condition of studied material.* Details on the respective condition of the specimens are as
91 follows:

92 IGR.BU-003. Alate gyne. Preserved without distortion, but missing right antennomeres
93 XI–XII, left antennomeres IV–XII, apical portion of fore wings, portion of all right legs
94 beyond femur, portion of left fore leg beyond tarsomere II and left hind leg beyond
95 trochanter, and apico-dorsal portions of gaster beyond AIV. The amber piece is crossed by an
96 internal fracture running obliquely to the head through the left compound eye, scapes,
97 medioapical portion of the horn, and lower portion of the right gena. The piece broke at the
98 level of this fracture during polishing, so the two fragments were immediately glued together.
99 Originally preserved with a thrips (Thysanoptera), now in a separate fragment measuring
100 $14.4 \times 10 \times 6$ mm.

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

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

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

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

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

121 NIGP172003. Alate gyne. A specimen exposed in right anterolateral view, without
122 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

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

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

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

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

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

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

166

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

175

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

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

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

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

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

215 **3. Systematic paleontology**

216

217 Order Hymenoptera Linné, 1758

218 Family Formicidae Latreille, 1809

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

220

221 Haidomyrmecini Bolton, 2003: 74, 261.

222

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

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

243 *Diagnosis* (females). Mandibles scythe- or sickle-shaped, with linear basal portion leading to
244 an elongate and dorsally curved apical portion tapering, with inner margin usually developed
245 in a triangular blade pointing medially and ventrally (exception in *Aquilomyrmex* where the
246 inner margin is simple); mandibles uniquely articulating in a vertical plane oblique to
247 longitudinal axis of body, in addition to a moderate lateral opening. Clypeus elongate, with
248 anterior margin broadly concave, smooth, and lateral margins leading posteriorly to an
249 elevated brushy lobe just ventral to antennal insertion, or to a horn expanded anteriorly
250 between toruli. Antennae 12-segmented, filiform, usually with third antennomere longest of
251 basal three flagellomeres (exceptions are in *Haidomyrmex* where fourth antennomere is
252 longest, and in *Haidomyrmodes* where basal flagellomeres are of equal length). Petiole with a
253 short anterior peduncle, nodiform. Gastral constriction between AIII and AIV generally
254 present, faintly to deeply impressed. Pygidium simple, unarmed. Sting robust, dorsally
255 curved. Legs with procoxa distinctly longer than meso- and metacoxae, with trochantellus
256 present on mid- and hind legs; tibial spur formula 1-2-2, rarely 1-1-2, and tibiae additionally
257 with 1–4 subapical, stout setae. In gynes, the fore wing with 8 closed cells, with cross-vein
258 1r-rs absent or incomplete (present as a short tubular or nebulous stub not reaching Sc+R);
259 cross-vein 2rs-m present, tubular; and cross-vein cu-a arising from M+Cu or Cu. Hind wing
260 with jugal lobe present, with costal, basal and subbasal cells enclosed by tubular veins.

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

265 *Distribution.* Canada, France, Myanmar; Cretaceous, Uppermost Albian to Campanian (100-
266 79 Ma).

267

268 Genus *Dhagnathos* gen. nov.

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

270 Type species: *Dhagnathos autokrator* sp. nov.

271

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

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

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

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

291

292 *Dhagnathos autokrator* sp. nov.

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

294 Figs. 2A–C, 3, 8G

295

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

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

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

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

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

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

307 Head only slightly longer than high and wide. Vertex and posteroventral surface rounded,
308 anterior surface relatively flat, and genae shorter than eyes and projecting anteroventrally
309 above mandible insertion into a cheek-like lobe. Ocelli present near top of vertex,
310 conspicuous, ocellar diameter slightly larger than width of first antennomere; interocellar
311 distance about half of ocellar diameter. Compound eyes bulging, reniform, 2.4× as long as
312 wide, situated posteriorly on head (EPI 440). Antennae inserted between compound eyes
313 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

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

366 Fore wing with Rs·f2, basal portion of Rs·f3, M·f4, and Cu1 nebulous, all other veins
367 tubular; pterostigma elongate, ca. 6× as long as broad; a short stub of cross-vein 1r-rs present,
368 nebulous; Rs·f1 half as long as M·f1, both distinctly arched; Rs·f2 and Rs·f3 nearly at right
369 angle, Rs·f2 half as long as M·f2; 2rs-m present, situated beyond apex of pterostigma; discal
370 and subdiscal cells pentagonal; cu-a arising from M+Cu and proximal to M·f1 (Cu·f1 short);
371 vein Cu with both Cu1 and Cu2 present. Hind wing with jugal lobe present; anterior margin
372 with 5 median and 22 distal hamuli; vein C present; vein R present, reaching distal wing
373 margin; Rs·f1 more than twice as long as 1rs-m; cu-a arising from M+Cu, proximal to fork of
374 M·f1 and Cu (Cu·f1 short); Rs·f2, M·f2, Cu, and A·f2 present, not reaching wing margin.

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

387 *Measurements* (holotype IGR.BU-003; in mm). HL 2.50; HoL ca. 1.70; EL 1.20; ocelli
388 diameter 0.20; MD_bL 0.40, MD_tL 0.55, MD_aL 2.00; length/width of antennomeres: I (scape)

389 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
390 preserved) 6.35 (7.90 on specimen DHA4); PL 1.84, PH 1.00, PW 0.67.

391

392 Genus *Chonidris* gen. nov.

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

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

395

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

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

409

410 *Chonidris insolita* sp. nov.

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

412 Figs. 2D–F, 4, 8F

413

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

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

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

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

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

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

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

496 *Measurements* (in mm) (holotype NIGP171998), [paratype NIGP172003], {specimen RM2}.
497 HL [1.42] {1.68}; HoL [0.86] {0.658}; EL [0.72]; MDL [1.44] {1.10}; length of
498 antennomeres: I (scape) [1.00] {0.96}, II (pedicel) [0.17] {0.21}, III [1.42] {0.92}; WL
499 (3.66) {3.30}; FWL (5.2) {5.50}; PL (1.33), PH (excluding process) (1.12).

500

501 Genus *Aquilomyrmex* sp. nov.

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

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

504

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

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

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

522

523 *Aquilomyrmex huangi* sp. nov.

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

525 Figs. 2G–H, 5, 8C

526

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

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

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

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

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

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

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

537 Head prognathous, dorsoventrally flattened; in dorsal view, with lateral margins slightly
538 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× scape length, less than twice as long as wide, broadened
552 apically; antennomere III and XII longest flagellomeres, AIII cylindrical, about 3.6× 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

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

616 *Measurements* (in mm) (holotype NIGP172000), [specimen RM3]. HL (1.40) [1.33], HW
617 (1.05), Hh (0.50); HoL (0.86); EL (0.56 in dorsal view); MDL (ca. 1.00); length of
618 antennomeres: I (scape) (1.47) [1.80], II (pedicel) (0.16) [0.18], III-XII (0.25, 0.18, 0.16,
619 0.13, 0.13, 0.16, 0.13, 0.13, 0.13, 0.25); WL [3.50]; PL (0.61).

620

621 Genus *Protoceratomyrmex* gen. nov.

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

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

624

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

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

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

642

643 *Protoceratomyrmex revelatus* sp. nov.

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

645 Figs. 6A–B, 8B

646

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

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

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

653 *Diagnosis*. As for the genus by monotypy.

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

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

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

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

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

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

706 *Measurements* (in mm) (holotype NIGP172002). HL 0.82; EL 0.20; HoL ca. 0.09; MDbL
707 0.36, MDtL 0.09, MDaL 0.41; length of antennomeres: I (scape) 0.42, II (pedicel) 0.08, III–
708 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.

709

710 Genus *Linguamyrmex* Barden & Grimaldi, 2017

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

712

713 *Linguamyrmex brevicornis* sp. nov.

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

715 Figs. 6C–E, 7

716

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

719 *L. vladi*.

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

721 *Additional specimens.* LA01, alate female (Figs. 6D, 7A–B), and RM4, worker (Figs. 6E,
722 7C).

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

725 *Diagnosis* (females). Closely similar to *L. vladi*, but differs from this species by having a
726 shorter clypeal horn (horn index HoI = 31–34 in *L. brevicornis*, 56 in *L. vladi*), with stalk
727 much reduced, slightly broader than long, with the setose pad more hexagonal and aligned
728 with stalk (circular and with a distinct bend between stalk and clypeal pad in *L. vladi*), and
729 with clypeal pad coated in stout setae. It is also differentiated by the mandibles with two teeth
730 on ventral corner of medioventral blade (teeth absent in *L. vladi*) and, in workers, with the
731 apical mandibular portion shorter than basal portion (apical portion longer in *L. vladi*). In
732 addition to the difference in the proportion of the mandible, the female castes of *L.*

733 *brevicornis* differ by their size (body length ca. 7 mm in gyne, 4 mm in worker), by the
734 antennae with flagellomeres compact in worker, more elongate in gyne, and by subpetiolar
735 process present in worker.

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

739 Head. As in *Linguamyrmex vladi*, but with compound eyes slightly reniform, emarginate
740 in middle of posterior margin. Ocelli distinct, positioned on a prominent cuticular triangle, in
741 dorsal view, with posterior margin of lateral ocelli aligned with posterior margin of eyes.
742 Antenna filiform, with flagellomeres elongate, cylindrical except apical one, which has acute
743 tip; third antennomere twice as long as following one. Antennal sockets immediately flanking
744 a medial frontal triangle that is sharply expanded anteriorly above clypeal horn, and
745 connecting ventrally with dorsal surface of horn by a cleared, laterally flattened cuticle;
746 frontal triangle projection terminates anteriorly at approximately same length as clypeal horn
747 with slight indentation just dorsad clypeal horn, giving the appearance of a second, small,
748 broadly rounded horn. Clypeal horn originating at base of frontal triangle, short and straight,
749 in profile view almost perpendicular to longest axis of head. Horn paddle-shaped, with short,
750 compact stalk and hexagonal, setose pad; stalk apparently glabrous, 0.10 mm in length, 0.12
751 mm in width; setose pad 0.26 mm in length, 0.20 mm at greatest diameter, with anterior
752 margin straight, transverse; dorsal surface of setose pad glabrous, ventral surface densely and
753 uniformly coated with very short, velcro-like vestiture; trigger hairs not visible. Lateral
754 clypeal margins extending from above mandibular insertions toward horn as gently curved
755 lines. Anterior clypeal margin broadly concave. Labrum visible. Mandible scythe-shaped;
756 basal portion linear, short, meeting apical curved portion nearly at right angle; medioventral
757 triangular blade bearing one large apical tooth and one small preapical tooth, with concave
758 dorsal surface coated with pointed setae; apical portion of mandible posterior to medioventral
759 blade 1.6× as long as blade, with tip broadly rounded. Mandibles preserved in closed position
760 (with tips of apical portion reaching nearby clypeal setose pad), almost entirely parallel and
761 closely approximated, except ventral corners of blades overlapping and tips slightly
762 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.

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

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

805

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

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

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

821 *Measurements* (in mm) (worker holotype NIGP172001) [worker specimen RM4] {gyne
822 specimen LA01}. HL [0.82] {0.82}; EL [0.21] {0.42}; HoL [0.17] {0.36}; MDL [0.59]
823 {0.80}; length of antennomeres: I (scape) (0.57) [0.67] {1.04}, II (pedicel) (0.09) [0.12]
824 {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,
825 0.32, 0.31, 0.30, 0.30, 0.32, 0.32, 0.35}; WL [1.29] {2.29}; PL {0.70}.

826

827 *Key to genera and species of Haidomyrmecinae:*

828

829 1. Clypeus posteriorly with a slightly elevated setose lobe positioned just ventrad or
830 between antennal insertion 2
831

832 ▶ Clypeus posteriorly projecting forward into a cephalic horn arising ventrad, between, or
833 dorsad antennal insertion 5

834 2. Antenna compact, with flagellomeres short (<2× as long as broad); first flagellomere as
835 long as or longer than second one

- 836 3
- 837 ▶ Antenna elongate, with flagellomeres long (>2× 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 *Haidoterminus 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,

- 911 2019
- 912 9. Body and legs robust; mandibles scythe-shaped, with medioventral triangular blade
 913 present; in frontal view, the outline of apical portion of mandibles aligned with clypeal
 914 lateral ridges; clypeal horn gradually tapering to rounded tip; genae elongate, the
 915 mandibles inserted far from compound eyes
 916 10
- 917 ▶ Body and legs gracile; mandibles sickle-shaped, with medioventral triangular blade
 918 absent; clypeal horn and labrum protruding horizontally, their tip with a deep median
 919 notch; apical lateral margins of horn bilobed; genae strongly reduced, the mandibles
 920 inserted close to compound eyes *Aquilomyrmex*
 921 *huangi* gen. et. sp. nov.
- 922 10. Mandibles with apical curved portion much longer than basal portion and entirely serrate
 923 along dorsal margin; with medioventral blade an isosceles tooth not projecting beyond
 924 mandibular elbow (labrum and clypeal surface below horn entirely exposed when
 925 mandibles closed); ocelli large, antennomeres and compound eyes distinctly elongate
 926 *Dhagnathos autokrator* gen. et. sp. nov.
- 927 ▶ Mandibles with apical curved portion not distinctly longer than basal portion; with
 928 medioventral blade a large triangle gradually tapering to tip of apical portion (labrum and
 929 clypeal surface below horn entirely concealed when mandibles closed); dorsal margin of
 930 mandibles serrate along distal half of medioventral projection, bidentate apically; ocelli,
 931 antennomeres, and compound eyes more reduced *Chonidris insolita* gen. et. sp. nov.

932

933 **4. Discussion**

934

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

955

956 **5. Concluding remarks**

957

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

960 haidomyrmecines as a stem-group lineage that diverged from modern ants prior to the most
961 common recent ancestor of all living ants (Barden and Grimaldi, 2016; Barden et al.,
962 submitted). This phylogenetic placement, molecular divergence estimates (Moreau and Bell
963 2013) and the presence of crown ants in Cretaceous amber (Grimaldi and Agosti, 2000;
964 McKellar et al., 2013b; Zheng et al., 2018; Perrichot, 2019) indicate that hell ants and early
965 members of extant lineages overlapped for tens of millions of years. The extinction of
966 haidomyrmecines following their diversification remains an outstanding question in ant
967 evolution, as is the function and evolutionary history responsible for this striking expansion
968 into unparalleled phenotypic space.

969

970 **Acknowledgements**

971 We are grateful to Fangyuan Xia (Shanghai), Yiren Huang (Taiwan), Edward Liu (Hong
972 Kong), Yan Liu (Jinan) for access to specimens from their collection. We thank Sieghard
973 Ellenberger (Kassel, Germany) and Tyler Janovitz (Massachusetts, USA) for authorization to
974 use the photograph of specimen TJ41-020; Martina Decker, Oliver Budd, Jackson Fordham,
975 and Victor Nzegwu at the New Jersey Institute of Technology (NIJT) for 3D model
976 reconstruction used in figure 1; and Dinghua Yang (NIGPAS) for artistic reconstruction of
977 heads. We are also thankful to Michael Engel and an anonymous reviewer for their insightful
978 comments of the manuscript, as well as to Eduardo Koutsoukos, for his input as editor. This
979 research was supported by the Strategic Priority Research Program of the Chinese Academy
980 of Sciences (XDB26000000 and XDA19050101) and the National Natural Science
981 Foundation of China (41688103).

982

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1079 **Figures legends**

1080

1081 **Fig. 1.** Measurements of cranial structures shown on 3D models. A, head of *Dhagnathos* gen.
1082 nov. in full facial view. B, head of *Dhagnathos* gen. nov. in lateral view. C, head of
1083 *Aquilomyrmex* gen. nov. in dorsal view. D, head of *Aquilomyrmex* gen. nov. in lateral view.
1084 Scale bars: 1 mm.

1085

1086 **Fig. 2.** Representative alate females of *Dhagnathos autokrator* gen. et sp. nov. (A–C,
1087 holotype IGR.BU-003), *Chonidris insolita* gen. et sp. nov. (D–F), and *Aquilomyrmex huangi*
1088 gen. et sp. nov. (G–H). Habitus (A), head in lateral (B) and frontal (C) views. Habitus of
1089 holotype NIGP171998 (D), head of paratype NIGP172003 (E) in anterolateral view, head of
1090 specimen HA04 (F) in frontal view. Habitus of holotype NIGP172000 (G), head of specimen
1091 TJ41-020 (H) in lateral view. Scale bars: 1 mm (A, D, G), 0.5 mm (B, C, H), 0.2 mm (E, F).

1092

1093 **Fig. 3.** Overview and details of alate females (gynes) of *Dhagnathos autokrator* gen. et sp.
1094 nov. Specimen HA03 (A), specimen XA01 (B), specimen RM1 (C–D), and holotype
1095 IGR.BU-003 (E–G). Habitus (A, B, C), fore wing (D), mandibles, clypeus and labrum in
1096 lateral views (E, F), wings, propodeum and petiole (G). Abbreviations: cc, lateral clypeal
1097 carina; cd, clypeal denticles; cp, clypeal process (horn); lss, labral spine-like setae; mib,
1098 mandibular inner blade; mp, mesal process of 1st gastral sternite; pdr, propodeal ridge; spp,
1099 sub-petiolar process. Scale bars: 2 mm (A–C), 1 mm (D, G), 0.5 mm (E, F).

1100

1101 **Fig. 4.** Overview and details of alate females (gynes) of *Chonidris insolita* gen. et sp. nov.
1102 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).

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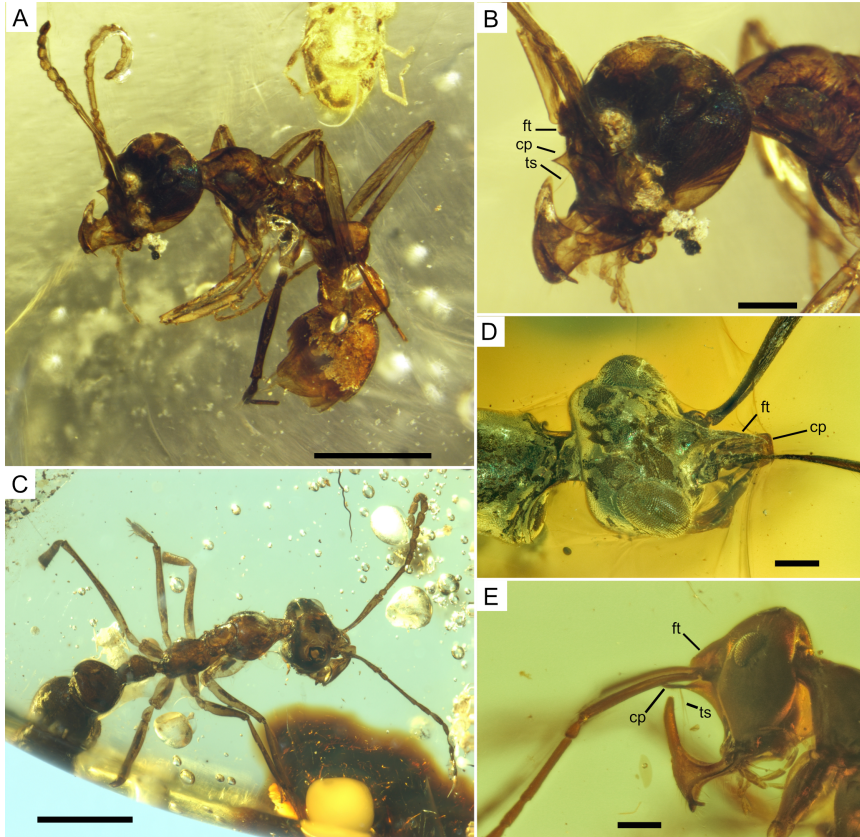
1112 **Fig. 6.** Representative females of *Protoceratomyrmex revelatus* gen. et sp. nov. (A–B) and
 1113 *Linguamyrmex brevicornis* gen. et sp. nov. (C–E). Habitus (A) and head (B) of worker
 1114 holotype NIGP172002. Habitus of worker holotype NIGP172001 (C), head of gyne specimen
 1115 LA01 in dorsal 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).

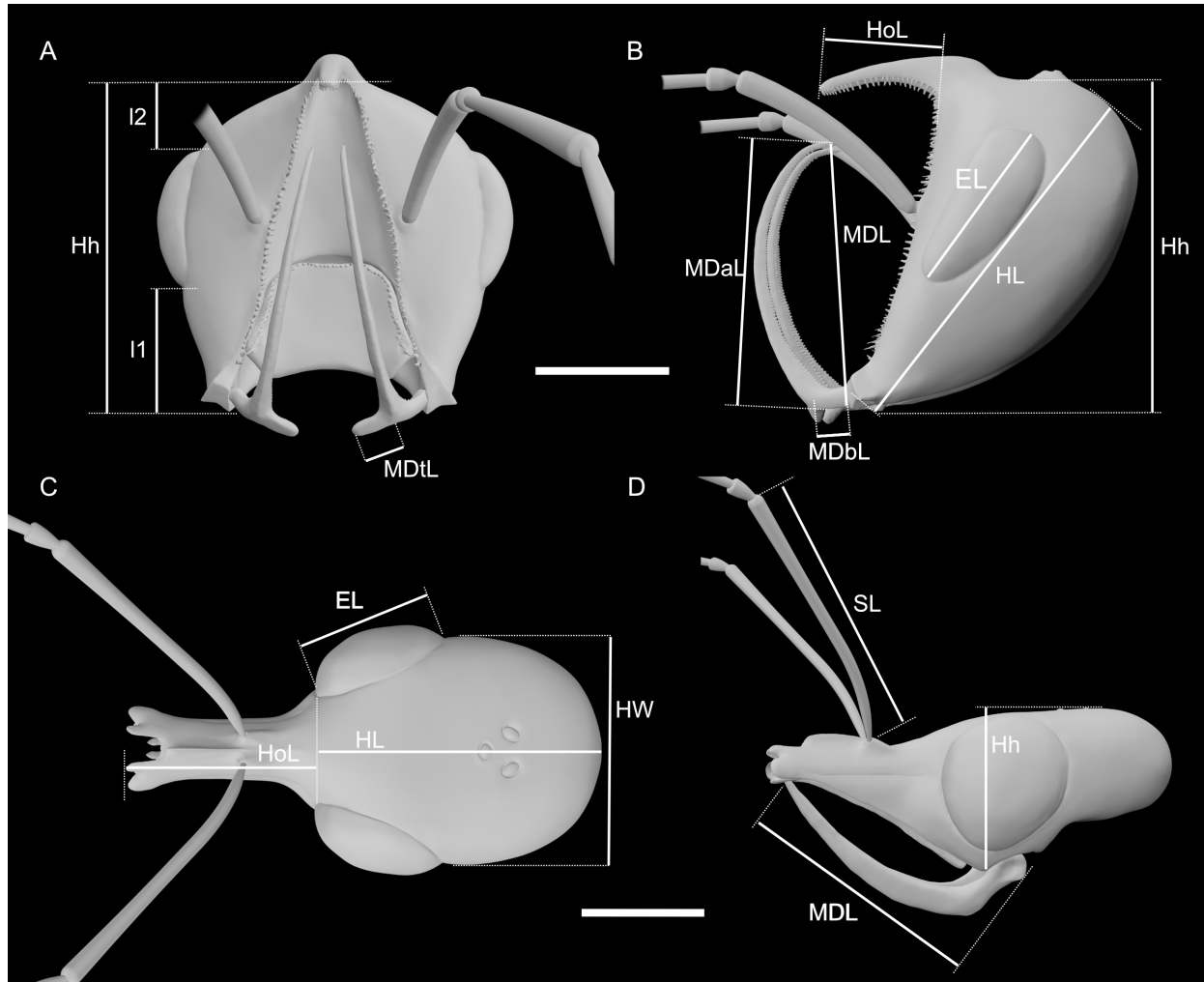
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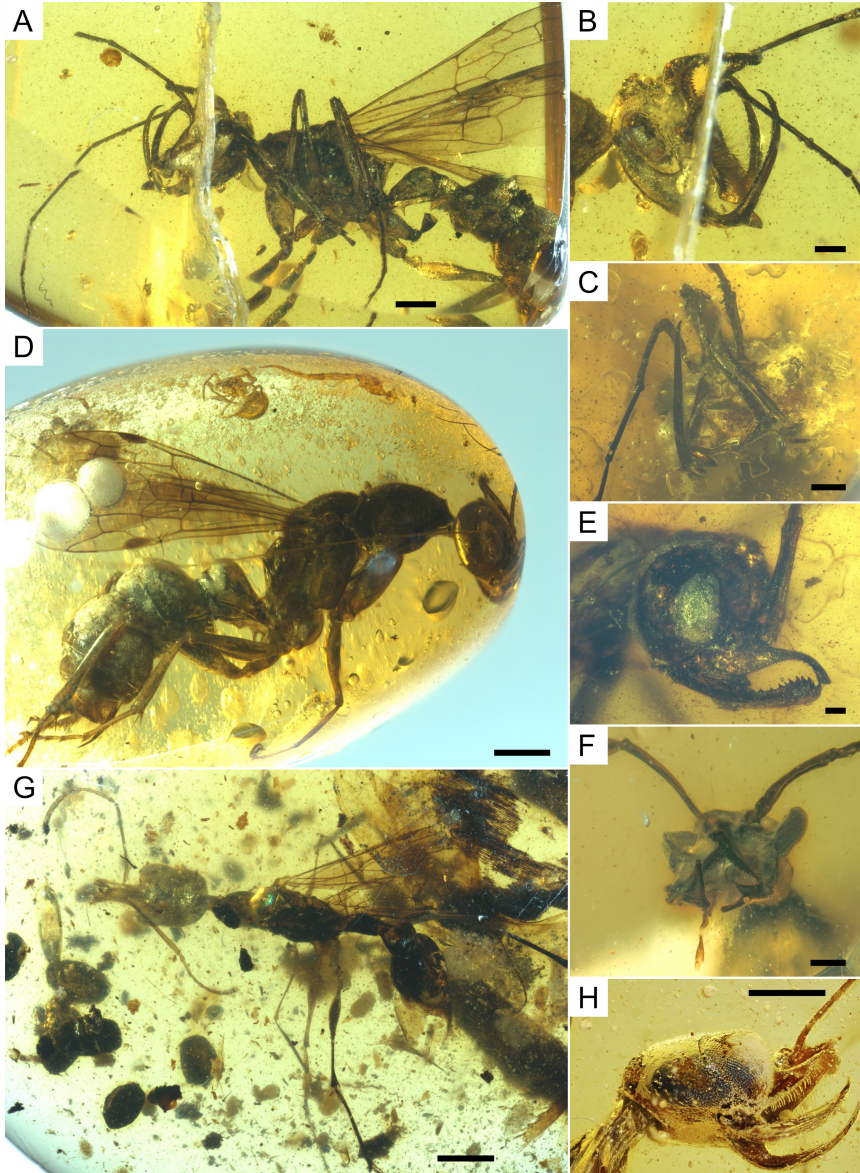
1119 **Fig.7.** Overview and details of females of *Linguamyrmex brevicornis* gen. et sp. nov. Gyne
 1120 specimen LA01 (A–B), worker specimen RM4 (C), worker holotype NIGP172001 (D).
 1121 Habitus (A, C), head and mesosoma in dorsal view (B), head in ventrolateral view (D). Scale
 1122 bars: 0.5 mm.

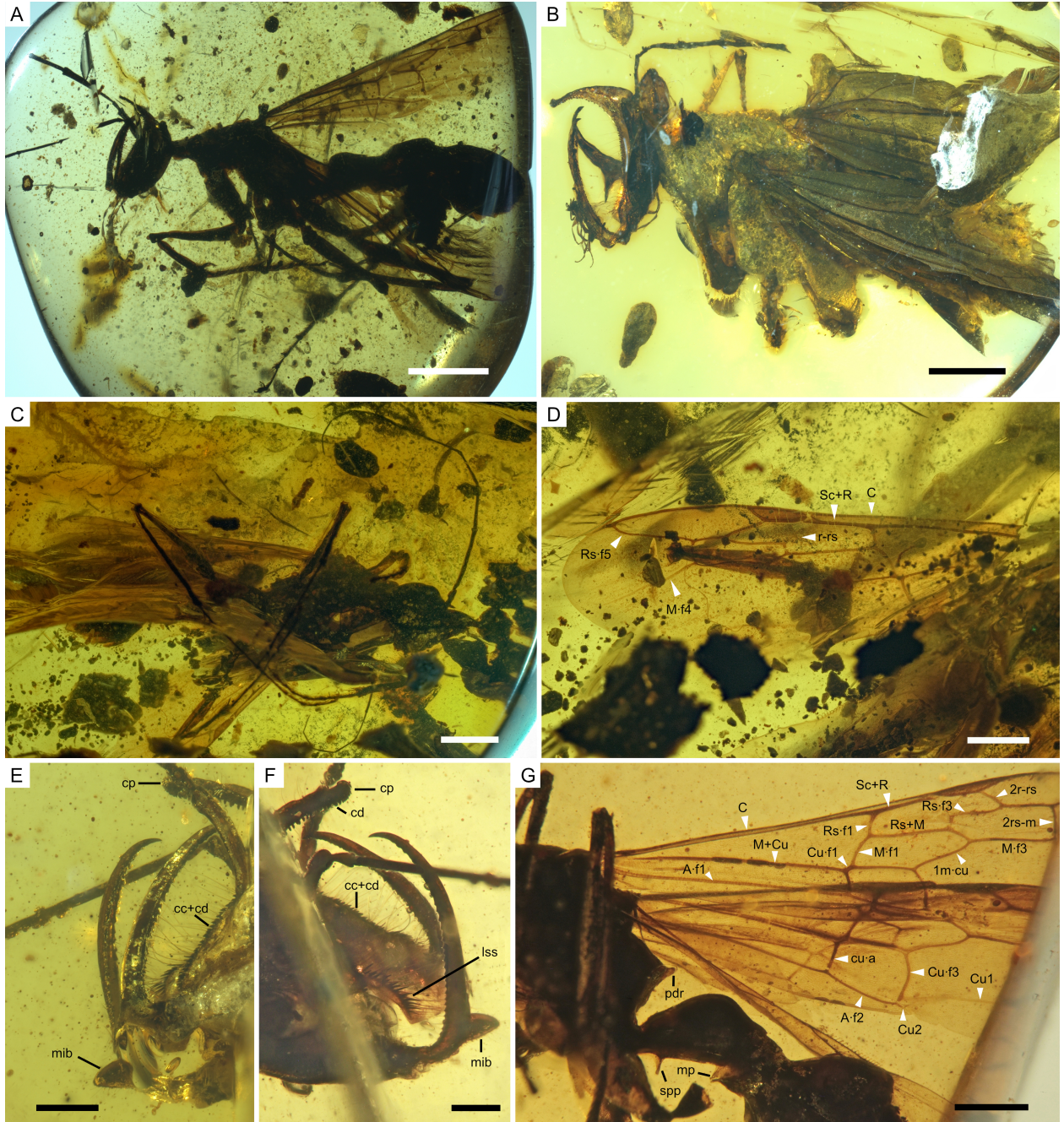
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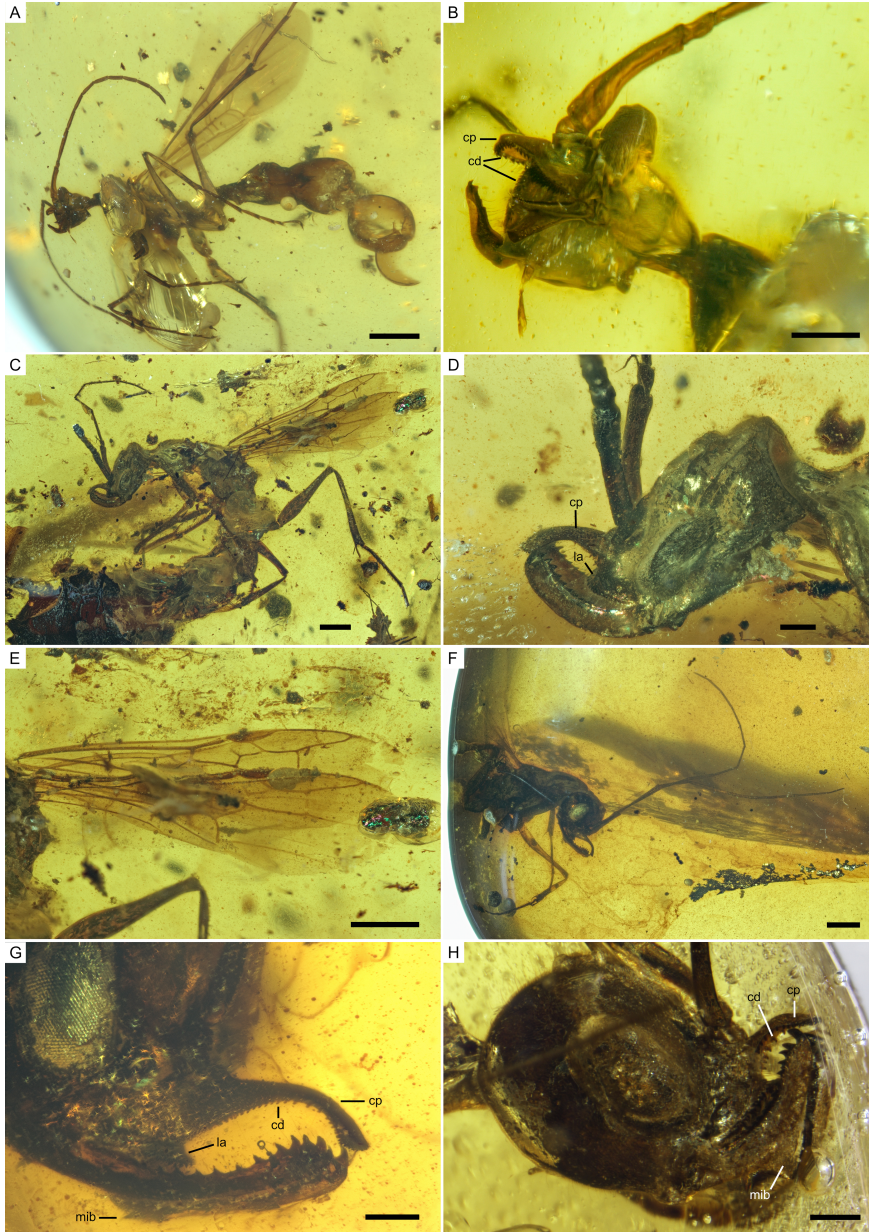
1124 **Fig. 8.** Artistic reconstructions of the heads of hell ants in lateral view, with mandibles
 1125 closed. A, *Haidomyrmex*. B, *Protoceratomyrmex* gen. nov. C, *Aquilomyrmex* gen. nov. D,
 1126 *Linguamyrmex*. E, *Ceratomyrmex*. F, *Chonidris* gen. nov. G, *Dhagnathos* gen. nov. Scale
 1127 bars: 0,5 mm.

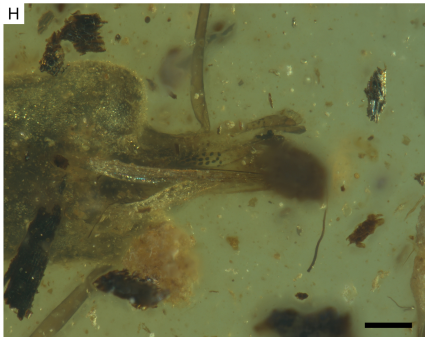
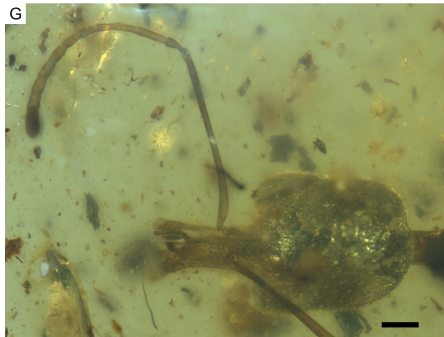
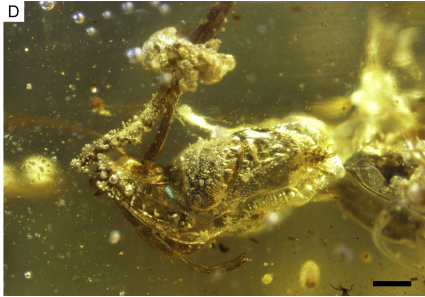
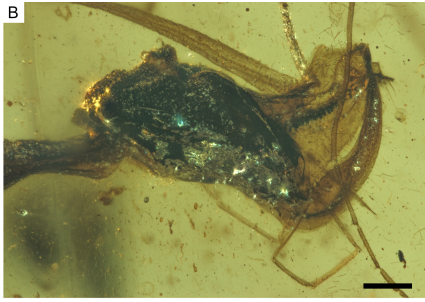
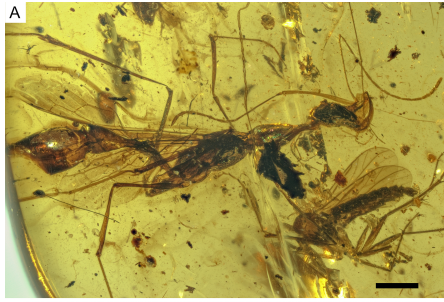


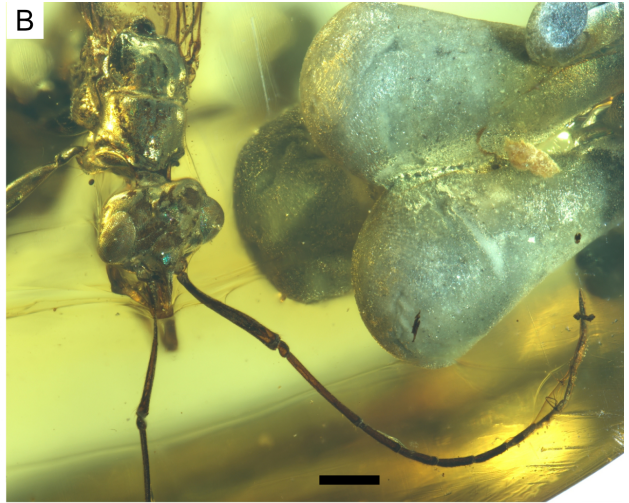
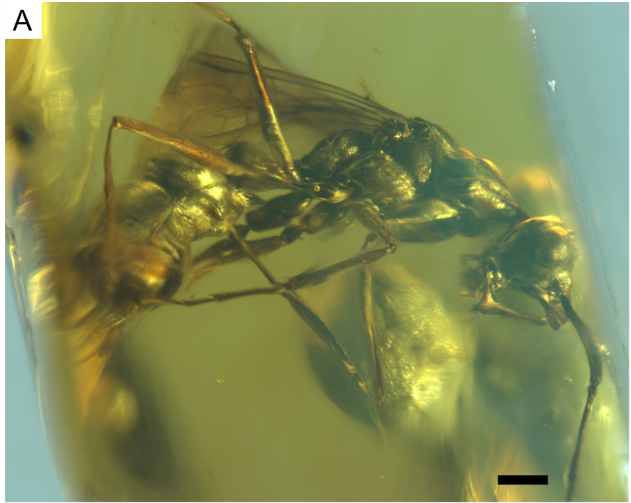


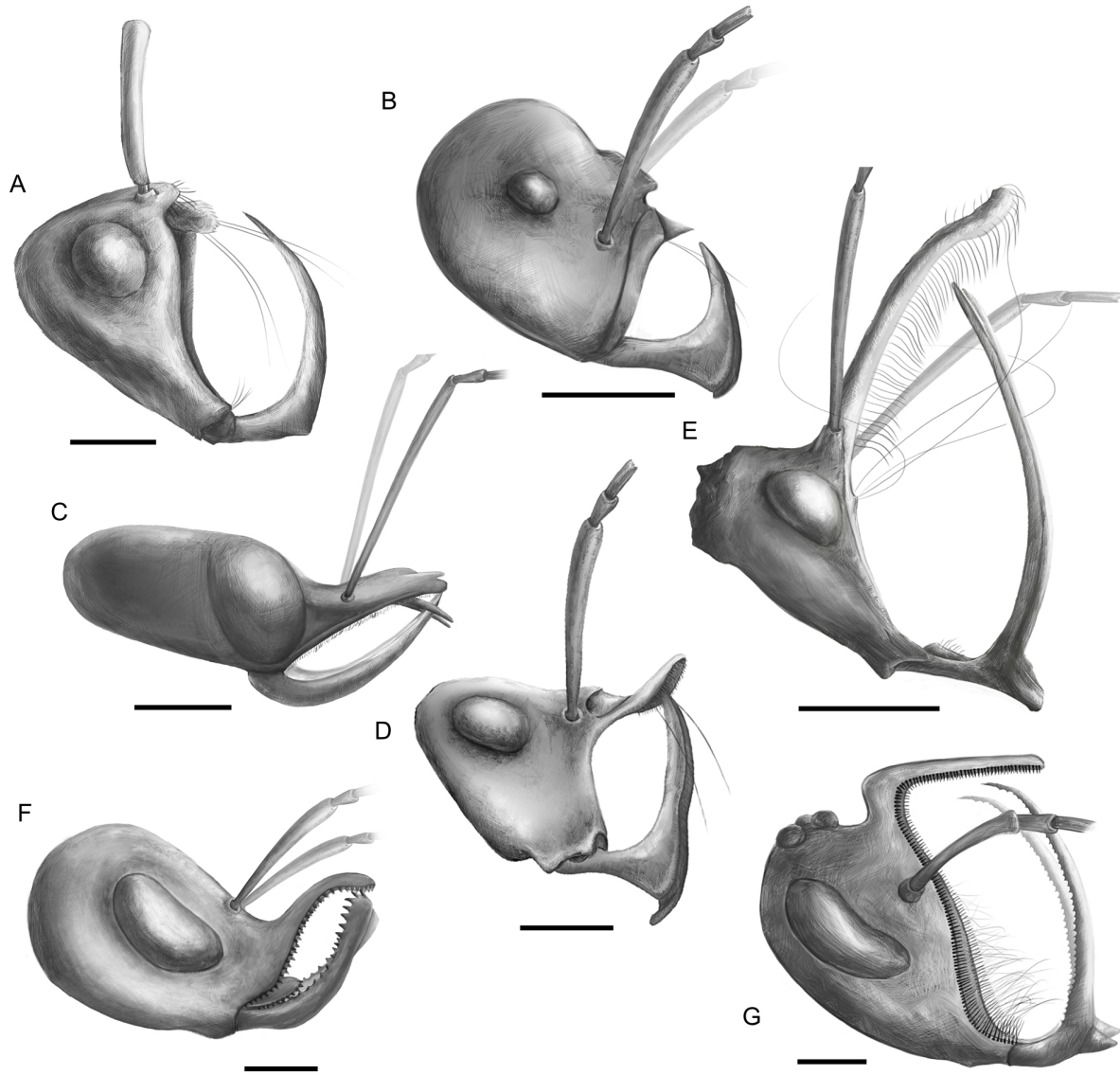












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Vincent Perrichot, Bo Wang: Conceptualization; **Vincent Perrichot, Phillip Barden:** Data curation, Writing- Original draft preparation. **Vincent Perrichot, Bo Wang, Phillip Barden:** Investigation. **Vincent Perrichot, Phillip Barden:** Writing-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

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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:

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