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

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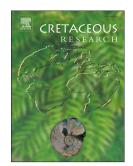
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Journal Pre-proof	

1	A revision of Haidomyrmex cerberus Dlussky (Hymenoptera:
2	Formicidae: Sphecomyrminae) from mid-Cretaceous Burmese
3	amber
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20	
21	ABSTRACT
22	The type species of the genus Haidomyrmex Dlussky, 1996 is revised. Haidomyrmex
23	cerberus was originally described based on a partial worker specimen only, which
24	was later re-figured with some erroneous characters. Two worker specimens

- 25 assignable to this species were recently discovered in the collection of Burmese amber
- 26 from the Capital Normal University of Beijing. A revised description and comparison
- with the two other known species of *Haidomyrmex* are provided, and the diagnoses of 27
- 28 the genus and species are emended.
- 29
- 30 Key words:
- Journal Pression Haidomyrmecini 31
- 32 stem-group ants
- 33 Myanmar
- trap-jaw ants 34
- 35 hell-ants.

36

37 1. Introduction

38

Fossils are unique records of the past diversity of life, providing the only evidence 39 on stem groups or extinct lineages that vanished millions of years ago. Some 40 fossils that are exquisitely preserved can provide a myriad of morphological and 41 ecological data on an extinct taxon. But there are a lot of species known and 42 43 described from a single fossil individual that is incompletely preserved, thus remaining only partially informative. In 1996, Dlussky described Haidomyrmex 44 cerberus, the first ant species ever found in Burmese amber and a highly intriguing 45 ant with a bizarre cranio-mandibular morphology. Unfortunately, the type and unique 46 47 specimen was only partially preserved, missing parts of the antennae, legs and gaster. 48 Some characters, especially those of the head, were also obscured due to the turbidity of the amber piece and the position in which the specimen was exposed. Still, Dlussky 49 50 provided a rather detailed description including some hardly visible features, and he suggested this ant to be analogous to the modern trap-jaw ants, but placed the genus in 51 the extinct Sphecomyrminae (Dlussky, 1996). This placement was followed by Bolton 52 (2003) who erected a new tribe Haidomyrmecini for this genus. Engel and Grimaldi 53 (2005: figs. 7-8), however, proposed a re-interpretation of the holotype and modified 54 55 the generic diagnosis. In contrast to the features described by Dlussky (1996), Engel and Grimaldi (2005) could not see the inner tooth on the mandibles, the long trigger 56 setae on the clypeus, the stiff seta on the third antennomere, the remnant ocelli, and 57 the subpetiolar process. They also suggested that the mandibles were not preserved in 58 their natural position but significantly distorted, and erroneously noted similarities 59 with the genus Brownimecia Grimaldi, Agosti & Carpenter, 1997, from New Jersey 60 amber. But the discovery of *Haidomyrmodes* Perrichot et al., 2008, a genus closely 61

62 similar to Haidomyrmex, later revealed that Dlussky (1996) had correctly interpreted the mandibles (Perrichot et al., 2008). The haidomyrmecines' bauplan was further 63 confirmed by the subsequent discoveries of the genera Haidoterminus McKellar, 64 Glasier & Engel, 2013, Ceratomyrmex Perrichot, Wang & Engel, 2016, and 65 Linguamyrmex Barden & Grimaldi, 2017 (McKellar et al., 2013; Perrichot et al., 66 2016; Barden et al., 2017). But some confusion remains on the strict definition of 67 Haidomyrmex and the Haidomyrmecini, since two additional species of Haidomyrmex 68 were described with 12 antennal segments while depicted with only 11 segments 69 (Barden and Grimaldi, 2012: fig. 4), and the presence of the trigger setae, reduced 70 ocelli and inner mandibular tooth was confirmed on the holotype of H. cerberus 71 72 (Perrichot et al., 2016: supplemental information).

73 Finally, despite the discovery of several hundreds of additional specimens of Haidomyrmex in Burmese amber during the last decade, it is striking that none could 74 be assigned to H. cerberus again (Perrichot, pers. data from various institutional and 75 private collections). Instead, they largely belong to *H. scimitarus* Barden & Grimaldi, 76 2012, more rarely to H. zigrasi Barden & Grimaldi, 2012, the two other species 77 described more recently (Barden and Grimaldi, 2012). A reason for this could be that 78 the type specimen of *H. cerberus*, although described in 1996, originated from an 79 early collection of Burmese amber that was sent to Cockerell by Swinhoe in 1920 80 81 (Ross and York, 2000; Zherikhin and Ross, 2000). Thus, the holotype might have been collected from a locality and/or geological stratum that was potentially distinct 82 from the current localities from where Burmese amber were mined for the last decade. 83 However, in a study of 250 ants from the Burmese amber collection that was recently 84 established at the Capital Normal University of Beijing, two out of nine Haidomyrmex 85 are assignable to *H. cerberus*. This discovery allows for a complemental description 86

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

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89 2. Material and methods

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91 Depository, horizon, and specimen handling

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This study is based on new amber material from Hukawng Valley in Kachin State of 93 northern Myanmar located at the north end of Noije Bum, at 26°15'N, 96°34'E, some 94 18 km south-west of the town of Tanai. This deposit is dated to 98.79 ± 0.62 Mya 95 based on radiometric uranium-lead dating (Shi et al., 2012), and the recent finding of 96 an ammonite embedded in amber and assignable to Puzosia (Bhimaites) supports a 97 Late Albian-Early Cenomanian age of the amber (Yu et al., 2019). The amber is 98 housed in the Key Lab of Insect Evolution & Environmental Changes, Capital Normal 99 100 University, Beijing, China. (CNUB; Dong Ren, Curator)

Specimen No. CNU-HYM-MA2019051 is complete, without apparent distortion, 101 and preserved in a piece of yellow amber containing a suspension of bubbles and 102 organic fragments. Specimen No. CNU-HYM-MA2019052 is almost complete, 103 missing only the left antenna beyond scape and left foreleg beyond femur, and is only 104 weakly distorted. It is preserved in a piece of clear yellow amber with stellate hairs, 105 fragments of a spider web and organic debris, and has tiny bubbles or dust covering 106 the cuticle in places. Both amber pieces were ground and polished to form small 107 cabochons prior to acquisition, but a further polishing in the CNU Lab was made 108 using silicon carbide papers for us to inspect the specimens in optimal views. 109

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

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

118 The type specimen NHM-In.20182 was examined and photographed at the 119 Sackler Lab of the Natural History Museum of London in 2013. The photographs are 120 available on AntWeb (at <u>www.antweb.org</u>).

121

122 **3. Systematic palaeontology**

123

124 Family Formicidae Latreille, 1809

125 Subfamily Sphecomyrminae Wilson & Brown, 1967

126 Tribe Haidomyrmecini Bolton, 2003

127 Genus Haidomyrmex Dlussky, 1996

128

129 *Type species. Haidomyrmex cerberus* Dlussky, 1996: 451, fig. 1. See also: Engel and

130 Grimaldi, 2005: 11, figs. 7–8; Perrichot et al., 2016: fig. S3D.

131

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

137 flagellomeres; clypeus posteriorly developed into an elevated setose lobe just below antennal insertions, the lobe coated by a brush of stiff spines and bearing a pair of 138 fine, long trigger setae around anterolateral corners; frontal triangle prominent, 139 positioned just behind clypeal lobe, anteriorly with tuft of stiff setae; face and gena 140 distended; mandible scythe or L-shaped, with short, straight basal portion and long 141 apical portion curved upward; inner surface of mandibles shallowly concave, the 142 ventral corner between basal and apical portions with a triangular blade pointing 143 inward; mandibles apparently moving vertically and laterally; when closed, mandibles 144 145 parallel and vertically aligned, with inner blades overlapping and tips of apical portion meeting clypeal brush; pronotum with narrow neck; thoracic sutures oblique; legs 146 long and slender; pretarsal claw with small subapical tooth; propleuron very well-147 developed; propodeum with shallow or steep declivity; petiole nodiform, with short 148 anterior peduncle, subpetiolar process present; gaster without constriction between 149 first and second segments; sting large and entirely retractable. 150

151

152 Haidomyrmex cerberus Dlussky, 1996

153 Figs. 1–3

154

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

159

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

162 1.4 times of pedicel length, F2 longest of basal three flagellar articles, ca. 2.2 times of 163 pedicel length; clypeal lobe coated by stiff setae evenly arranged in rows, those on 164 ventral margin longer and thicker; mandibles scythe shaped, elbowed at right angle, 165 with anterior margin of inner blade bearing a longitudinal row of 7–8 spine-like setae, 166 apical portion with acute tip but without serration; mesonotum with scutellum 167 distinctly convex; propodeum gradually sloped; subpetiolar process keel-like, with 168 anterior surface nearly vertical.

169

Description of new material. Based on CNU-HYM-MA2019051, with differential 170 characters from CNU-HYM-MA2019052 in brackets. All measurements are in 171 millimeters (mm). Total body length ca. 4.50 [4.90]. Head, mesosoma and petiole 172 sparsely covered by thin erect setae; legs (except coxae and trochanters) and outer 173 surface of mandibles more densely covered by thin setae; pygidium and hypopygium 174 setulose [antenna and outer surface of mandibles densely covered by fine decumbent 175 setae; remaining body sparsely covered by thin, short erect setae]. Height of head 176 capsule (from anterior clypeal margin to highest point of vertex) 0.80; length (from 177 anterior surface of clypeal lobe to occipital margin) 0.52. Ocelli absent [reduced to 178 pit-like traces]. Length/width of compound eyes 0.30/0.20. Antenna inserted between 179 compound eyes and flanking prominent frontal triangle; total length of antenna 2.55; 180 scape ca. 4 times as long as pedicel, F1 ca. 1.4 times length of pedicel [1.3x]; FII ca. 181 2.2 times length of pedicel; lengths of antennomeres: scape 0.53, pedicel 0.12; 182 flagellomeres F1–F10: 0.16, 0.23, 0.22, 0.20, 0.20, 0.22, 0.18, 0.17, 0.16, 0.21; apex 183 of scape slightly broadened, its ventral margin bearing short erect setae; FI with stiff, 184 erect seta on ventral surface (Fig. 2B). Clypeal process a small hemispheric lobe 185 (maximal diameter 0.12) moderately elevated, dorsal surface coated by brush of stiff 186

187 spine-like setae gradually longer and thicker toward ventral margin of lobe, ventral surface with one visible pair of trigger setae [two pairs visible] flanking tips of 188 mandibles; trigger seta length 0.31. Anterior clypeal margin concave, bearing 4 erect 189 190 stiff setae (Fig. 2C). Mandibles (Fig. 2C) parallel and close to each other, basal portion 0.51 in length (ignoring slight curvature), curved apical portion 0.67 in length; 191 curved portion gradually tapered to an acute point, apex nearly reaching to tip of 192 clypeal process, ventral margin of curved portion coated in dense setae from base to 193 terminal quarter; inner surface of mandibles concave, particularly from inner 194 triangular blade to apical two thirds of curved portion; anterior margin of triangular 195 blade with a row of 7–8 spine-like setae directed inward (Fig. 2C); triangular blades 196 overlapping posteriorly, apparently symmetrical and each with a single minute tooth. 197 Maxillary palps (Fig. 2D) long, exposed length 0.53, with 5 visible articles (basal 198 article mostly concealed between mandibles). Labial palps (Fig. 2D) short, exposed 199 length 0.08, with only 2 apical articles visible (but palp formula should be 5:3 200 201 according to undescribed specimens of *Haidomyrmex* with palpomeres fully exposed; Perrichot, pers. data from various institutional and private collections). 202

Mesosoma. Long and slender; depth (greatest dorso-ventral distance) 0.45, length 203 (including neck) 1.98. Neck narrow and long, pronounced in lateral view. Pronotum 204 elongate; pronotal dorsal outline feebly convex in its anterior third, flat and sloped in 205 its posterior two thirds (Fig. 1A, B; Fig. 2A). Mesosomal length 0.38; mesonotum 206 convex (Fig. 1A, B), maximum width 0.12 and 0.08 in height. A distinct metanotal 207 sclerite posteriorly to this bulging mesoscutellum. Propodeum longer than high, 208 gradually sloping posteriorly; metapleural gland opening semicircular, facing 209 posteroventrad; metapleural bulla developed, roughly hemispherical. Legs long and 210 slender. Length of procoxa 0.65, mesocoxa 0.39, metacoxa 0.32. Length of meso- and 211

212 metatrochanters 0.20. Length of pro- and mesofemur ca.1.00, metafemur 1.84. Length of protibia 0.86, mesotibia 0.91, metatibia 1.67. Protibia apically with one long 213 pectinate spur (calcar) and two short simple spurs. Mesotibia with two simple spurs, 214 215 metatibia with one large pectinate spur and one short simple spur (Fig. 1D). Several short and stiff setae also present apically on hind tibia. Total length of pro-, meso-, 216 and metatarsi 1.10, 1.37, 1.90, respectively. Basal tarsomere longest, remaining four 217 tarsomeres shortening gradually, length of metatarsal segments I-V: 0.87, 0.46, 0.30, 218 0.18, 0.20. Surface of tarsomeres covered with fine setae. Pretarsal claws with distinct 219 220 subapical tooth, arolium well-developed.

Metasoma. Petiole (Fig. 1C) with short anterior peduncle, dorsal margin broadly 221 rounded, strongly narrowed posteriorly; petiole length 0.58, maximal height 0.32. 222 Subpetiolar process (Fig. 1C) 0.06 at greatest height, in profile a small triangle with 223 posterior margin distinctly longer than anterior margin. Lateral sulcus visible running 224 anteroposteriorly along petiole. First gastral segment with helcium pronounced, 225 forming a narrow post-petiolar peduncle. Gaster 1.45 in length (excluding sting), with 226 gastral segment I 0.48, segment II 0.57; sutures between tergite and sternite of 227 segments I and III distinct; distal part of gastral segment V (pygidium and 228 hypopygium) setulose. Sting long, robust; externalized part enclosed by 229 gonostyli/third valvulae. 230

231

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

234

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

237 following antennomeres combined (vs. scape distinctly longer in H. scimitarus and H. 238 zigrasi), and with F1 ca. 1.2 times the length of pedicel, F2 ca. twice the length of 239 pedicel (vs. F1 twice as long as pedicel, F2 4 times the length of pedicel in H. 240 scimitarus; F1 slightly shorter than pedicel, F2 as long as pedicel in H. zigrasi). 241 Finally, the body covered by dense patches of erect setae, combined with the dense 242 pubescence of the basal antennomeres and outer surface of the mandibles, are 243 characteristic of *H. cerberus*, but absent in the other two species. 244

245

4. Conclusion 246

247

The present discovery confirms that all species of Haidomyrmex possess similar 248 mandibles with the inner surface armed with a triangular blade, and paired trigger 249 setae ventrally on the clypeus. It is likely that they all have the inner surface of 250 mandibles concave and with a ventral row of stiff setae, although these characters 251 could not be assessed for *H. zigrasi* since the only know specimen has the mandibles 252 tightly closed. The specimen CNU-HYM-MA2019052 is preserved with the 253 mandibles entirely aligned and their triangular blades overlapping, suggesting that the 254 inner concavities form a tube-like channel. Similar concave mandibles forming a 255 channel were observed on *Linguamyrmex*, another genus of haidomyrmecine ants that 256 might have used this system to feed on liquid (Barden et al., 2017). Some extant ants 257 feed on honeydew or hemolymph (Hölldobler and Wilson 1990; Saux et al. 2004). It 258 indicates that Haidomyrmex might have fed on liquid too, as maybe all members of 259 the Haidomyrmecini, or so-called "hell ants". This tribe currently contains seven 260 species within five genera of potentially highly specialized predators, and 261

262 encompassing most of the Late Cretaceous: Haidomyrmex (3 sp.), Ceratomyrmex (1 sp.) and Linguamyrmex (1 sp.), from Burmese amber; Haidomyrmodes (1 sp.) from 263 Albian-Cenomanian French amber; and Haidoterminus (1 sp.) from Campanian 264 Canadian amber (Perrichot et al., 2008, 2016; Barden and Grimaldi, 2012; McKellar 265 et al., 2013; Barden et al., 2017; Barden, 2017: table. 1). Indeed, all female 266 haidomyrmecines share long sickle to L-shaped mandibles that uniquely moved in a 267 vertical plane aligned with the longitudinal axis of the body, and a clypeus elongate 268 and posteriorly with a prominent setose pad (vs. short mandibles transversely aligned 269 270 and moving laterally, and clypeus transverse and anteriorly setose in the remaining Sphecomyrminae). 271 10.4

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Acknowledgments 273

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291 **References**

- 292
- Barden, P., 2017. Fossil ants (Hymenoptera: Formicidae): ancient diversity and the
 rise of modern lineages. Myrmecological News 24, 1–30.
- Barden, P., Grimaldi, D.A., 2012. Rediscovery of the bizarre Cretaceous ant
 Haidomyrmex Dlussky (Hymenoptera: Formicidae), with two new species.
- American Museum Novitates 3755, 1–16. doi: 10.1206/3755.2
- Barden, P., Herhold H.W., Grimaldi, D.A., 2017. A new genus of hell ants from the
 Cretaceous (Hymenoptera: Formicidae: Haidomyrmecini) with a novel head
 structure. Systematic Entomology 42, 837–846. doi: 10.1111/syen.12253
- Bolton, B., 2003. Synopsis and classification of Formicidae. Memoirs of the
 American Entomological Institute 71, 1–370.
- Bolton, B., 2019. AntCat An online catalogue of the ants of the world. Available
 from <u>http://www.antcat.org/</u> (accessed 9 May 2019)
- Dlussky, G.M., 1996. Ants (Hymenoptera: Formicidae) from Burmese amber.
 Paleontological Journal 30 (4), 449-454. Translated from Paleontologicheskii
 Zhurnal 1996(3), 83–89.
- Engel, M.S., Grimaldi, D.A., 2005. Primitive new ants in Cretaceous amber from
 Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). American
 Museum Novitates 3485, 1–23.
- 311 Grimaldi, D., Agosti, D., Carpenter, J. M., 1997. New and rediscovered primitive ants

	Journal Pre-proof
312	(Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their
313	phylogenetic relationships. American Museum Novitates 3208, 1-43.
314	Hölldobler, B., Wilson, E.O., 1990. The Ants. Harvard University Press, Cambridge.
315	630 pp.
316	McKellar, R.C., Glasier, J.R.N., Engel, M.S., 2013. A new trap-jawed ant
317	(Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous
318	amber. The Canadian Entomologist 145, 454–465. doi:10.4039/tce.2013.23
319	Perrichot, V., Nel, A., Néraudeau, D., Lacau, S., Guyot, T., 2008. New fossil ants in
320	French Cretaceous amber (Hymenoptera: Formicidae). Naturwissenschaften 95,
321	91–97. doi: 10.1007/s00114-007-0302-7
322	Perrichot, V., Wang, B., Engel, M.S., 2016. Extreme morphogenesis and ecological
323	specialization among Cretaceous basal ants. Current Biology 26, 1468-1472.
324	doi: 10.1016/j.cub.2016.03.075
325	Ross, A.J, York, P.V., 2000. A list of type and figured specimens of insects and
326	other inclusions in Burmese amber. Bulletin of the Natural History Museum,
327	London (Geology) 56, 11–20.
328	Saux, C., Fisher, B., Spicer, G.S., 2004. Dracula ant phylogeny as inferred by nuclear
329	28S rDNA sequences and implications for ant systematics (Hymenoptera:
330	Formicidae: Amblyoponinae). Molecular Phylogenetics and Evolution, 33, 457-
331	468. doi: 10.1016/j.ympev.2004.06.017
332	Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Wang, M., Lei, W., Li, Q.,
333	Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons.
334	Cretaceous Research 37, 155–63. doi:10.1016/j.cretres.2012.03.014
335	Yu, T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F, Zhang, H., Wang, B.,
336	Dilcher, D., 2019. An ammonite trapped in Burmese amber. Proceedings of the

- 337 National Academy of Sciences of the U.S.A. 116, 11345–11350. doi:
 338 10.1073/pnas.1821292116
- 339Zherikhin, V.V, Ross, A.J., 2000. A review of the history, geology and age of Burmese
- amber (Burmite). Bulletin of the Natural History Museum, London (Geology)

341 56, 3–10.

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Journal Prevention

Figure Captions

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

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

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

