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1 **First boganiine beetle in mid-Cretaceous amber from northern Myanmar (Coleoptera:**
2 **Boganiidae)**

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18

19 ABSTRACT

20 *Cretoboganium gei* gen. et sp. nov., a new amber inclusion of the cucujoid family Boganiidae is
21 described and figured based on a well-preserved adult from the mid-Cretaceous Burmese amber
22 (Hukawng Valley, northern Myanmar), some 99 million years ago. Based on the presence of a pair of
23 pronotal callosities, *Cretoboganium* can be firmly placed in the extant subfamily Boganiinae, a small
24 group currently comprising two small austral genera. Our discovery represents the first fossil record
25 for Boganiinae. It also demonstrates another example that an apparently austral group may have its
26 sister group occurred in today's northern hemisphere. Together with the other fossil boganiid known
27 from the Middle Jurassic of China, the finding suggests that Boganiidae is an ancient and relict
28 group. Moreover, the present biogeographic distribution of Boganiinae is indicative of an earlier
29 origin of this subfamily, which likely originated before the breakup of the Gondwanan
30 supercontinent.

31

32 **Keywords:**

33 Cucujoidea

34 Cenomanian

35 Burmese amber

36 Austral fauna

37 taxonomy

38

39 **1. Introduction**

40 With only 15 extant species placed in 6 extant genera, the cucujoid family Boganiidae is a small and
41 distinctive beetle group, currently restricting to Australia, New Caledonia and southern Africa
42 (Lawrence and Ślipiński, 2010; Escalona et al., 2015). All extant adults and larvae of Boganiidae
43 seem to be pollenophagous. For example, *Boganium malleense* Escalona et al., belonging to the
44 subfamily Boganiinae, occur in the flowers of *Eucalyptus gracilis* F. (Myrtaceae), and adults of
45 *Athertonium* Crowson are collected in the blossoms of Myrtaceae, Elaeocarpaceae, Cunionaceae,
46 Meliaceae and Lauraceae (Escalona et al., 2015). Although the phylogenetic relationships between
47 Boganiidae and other cucujoid families remains unsettled, both morphological and molecular data
48 indicate it as a member of the superfamily Cucujoidea (Lawrence et al., 2011; McKenna et al., 2015).

49 Fossil boganiids are very sparse. The first described fossil species, *Palaeoboganium jurassicum*
50 Liu et al., is from the Middle Jurassic Daohugou beds (Inner Mongolia, northeastern China), some
51 165 million years old (Liu et al., 2018). *Palaeoboganium jurassicum* was suggested as a potential
52 pollinator of Jurassic cycads based on phylogenetic evidence (Liu et al., 2018). As such, our
53 knowledge about the early evolutionary history and historical biogeography of this small peculiar
54 family is lacking. Here we reported the first amber-entombed boganiid beetle with exquisite
55 morphological details preserved in the Cretaceous amber from northern Myanmar.

56 57 **2. Material and Methods**

58 The fossil species is described and figured based on a sole specimen preserved in Upper Cretaceous
59 Burmese amber (Hukawng Valley, northern Myanmar; ca. 99 Ma). Observations and photographs
60 were made using a Zeiss Discovery V20 stereo microscope and a Zeiss Axio Imager 2 light
61 microscope with a digital camera attached respectively. The Zeiss Axio Imager 2 microscope was
62 equipped with a mercury lamp and specific filters for DAPI, eGFP and rhodamine.

63 Photomicrographs with a green background were taken under the eGFP mode, and those with a red

64 background were under the rhodamine mode. Extended depth of field images were digitally
65 compiled using a Zerene Stacker v.1.0.4 software, and arranged in Adobe Photoshop CS5. The
66 publication LSID is: urn:lsid:zoobank.org:pub:F9E63684-8BB6-40FE-AC61-D48C3FA3504F.

67

68 **3. Systematic Palaeontology**

69 Order: Coleoptera Linnaeus, 1758

70 Family: Boganiidae Sen Gupta and Crowson, 1966

71 Subfamily: Boganiinae Sen Gupta and Crowson, 1966

72

73 Genus: *Cretoboganium* gen. nov.

74 ZooBank LSID: urn:lsid:zoobank.org:act:4A3787D5-34FF-48A3-8485-700A7117593D.

75 *Type species. Cretoboganium gei* sp. nov.

76

77 *Diagnosis. Cretoboganium* can be readily distinguished from all known extant and extinct genera of
78 Boganiidae by the following combination of characters: frontoclypeal suture strongly curved
79 (possible apomorphy); clypeal base not constricted; antennae short, with distinct 3-segmented
80 antennal club; maxillary palp short; pronotum with a pair of large callosities; prosternal process
81 distinctly dilated at apex; and elytra with regular puncture rows.

82

83 *Etymology.* Combination of the Latin word *creta*, meaning chalk, and the generic name *Boganium*; it
84 is neuter in gender.

85

86 *Description.* Body (Fig. 1) comparatively large for Boganiidae (ca. 3 mm long), elongate, slightly
87 flattened, subglabrous.

88 Head (Fig. 2A) strongly transverse, not declined. Occipital region without transverse ridge.

89 Frontal region without median endocarina. Eyes (Fig. 2B) large, entire, strongly laterally
90 protuberant, coarsely faceted, without interfacetal hairs. Antennal insertions (Fig. 2B) slightly
91 concealed from above. Frontoclypeal suture distinctly impressed, curved; base of clypeus not
92 impressed laterally, its anterior edge rounded, without teeth. Labrum concealed beneath clypeus.
93 Antennae (Fig. 2B) with eleven antennomeres, with distinct, 3-segmented club (Fig. 3D). Mandible
94 small. Maxilla (Fig. 2C) with setose galea; maxillary palp short.

95 Pronotum (Fig. 2A) setose, strongly transverse, about 0.65 times as long as wide, widest slightly
96 before middle; sides strongly curved, not explanate; lateral pronotal carinae complete, simple, visible
97 for their entire lengths from above, with raised margin; anterior angles rounded, with prominent
98 callosities containing gland openings (Fig. 2B); posterior angles sharp and distinct; posterior edge
99 weakly bisinuate, well margined; pronotal disc without sublateral carinae. Prosternum (Fig. 2C) in
100 front of coxae slightly longer than shortest diameter of procoxal cavity. Prosternal process (Fig. 2C)
101 complete, distinctly expanded apically; apex nearly truncate. Protrochantins exposed. Procoxal
102 cavities strongly transverse, narrowly separated, externally broadly open. Scutellar shield not
103 abruptly elevated, anteriorly simple, laterally expanded and rounded, posteriorly broadly rounded.

104 Elytra (Fig. 2D) about 1.6 times as long as wide and 2.9 times as long as pronotum, finely
105 setose, with several indistinct rows of small punctures. Elytral apices meeting at the suture.
106 Mesocoxal cavities moderately separated, subcircular. Metacoxae narrowly separated, not extending
107 laterally to meet elytra. Hind wing, if present, not visible. Trochanterofemoral joint strongly oblique;
108 tibial apices gradually widened at apex; tarsal formula 5-5-5 (Fig. 3A–C); penultimate tarsomere
109 distinctly reduced and one preceding tarsomere lobed beneath (Fig. 3A–C); pretarsal claws usually
110 simple.

111 Abdomen with five free ventrites; intercoxal process acute.

112

113 *Cretoboganium gei* sp. nov. (Figs. 1–4)

114 ZooBank LSID: urn:lsid:zoobank.org:act:6C581C66-8FDD-49AC-8A1F-DD937B0EA407.

115

116 *Etymology.* In honor of Mr. Chang Ge for his effort in sharing knowledge of Burmese amber and
117 donating the holotype for our study.

118

119 *Material.* Holotype, NIGP167701, sex undetermined; deposited in the Nanjing Institute of Geology
120 and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Mid-Cretaceous amber (earliest
121 Cenomanian or late Albian; Ross et al., 2010; Shi et al., 2012), Hukawng Valley in Tanai, Kachin
122 State, northern Myanmar.

123

124 *Diagnosis.* Body relatively large (ca. 3 mm long), black; antenna short; and pronotal callosities very
125 large.

126

127 *Description.* Body 3.09 mm long (measured from anterior margin of head to abdominal apex); black
128 throughout the body.

129 Head strongly transverse; head surface glabrous. 0.44 mm long and 0.79 mm wide (across
130 eyes). Eye large. Mandible small, not visible from above, apparently without teeth. Anterior margin
131 of clypeus with dense anteriorly-directed setae. Antenna short, nearly asymmetric, with apical three
132 antennomeres forming a distinct club; surface of antennomeres densely setose; antennomere 1
133 elongate and broad, antennomere 2 subquadrate, narrower than antennomere 1, antennomere 3 longer
134 than wide, antennomeres 4–8 almost in the same length and width, antennomere 9 nearly twice as
135 long as antennomere 8, antennomere 10 in the same width and shape as antennomere 9, antennomere
136 11 subconical, slightly narrower than antennomere 10. Maxillary palp short, palpomere 2 elongate,
137 palpomere 3 very short, palpomere 4 fusiform, much longer than palpomere 3.

138 Pronotum strongly transverse, 0.68 mm long and 1.05 mm wide. Surface without punctures or

139 setae. Pronotal callosities located near the anterior pronotal angles, prominent from above. Apex of
140 prosternal process dilated apically, with dense posteriorly-directed setae. Elytra complete, 2.0 mm
141 long and each 0.64 mm wide, with regularly arranged rows of small punctures. Humeral callus well
142 developed. Legs moderately long; tibiae setose, expanded at apex, apical tibial edges fringed with
143 spines; tarsomeres 1–3 successively shortened, tarsomere 4 much shorter and smaller than the rest,
144 tarsomere 5 long, as long as tarsomeres 2–4 combined; ventral side of pro- and mesotarsomeres 1–3
145 covered with dense setae. Pretarsal claws long, curved. Genitalia not visible.

146

147 **4. Discussion**

148 The new genus *Cretoboganium* can be confidently attributed to the extant cucujoid family
149 Boganiidae based on the following combination of morphological features: 1) head with distinct
150 frontoclypeal suture; 2) protrochantins well developed; 3) all coxae narrowly separated; 4) tarsi 5-
151 segmented, with tarsomere 4 reduced; and 5) abdomen with five ventrites (Lawrence and Ślipiński,
152 2010; Escalona et al., 2015). Another important diagnostic character for modern Boganiidae,
153 mandible with dorsal setose cavity, is unfortunately not visible from the holotype. Moreover,
154 *Cretoboganium* can be referred to the extant subfamily Boganiinae as strongly evidenced by the
155 presence of paired pronotal callosities and the comparatively short and somewhat fusiform apical
156 maxillary palpomere (Escalona et al., 2015). The subfamily Boganiinae currently comprises only two
157 extant genera: *Afroboganium* Endrödy-Younga & Crowson (South Africa and Namibia) and
158 *Boganium* Sen Gupta & Crowson (South Australia, Victoria, Tasmania and southeastern Western
159 Australia) (Escalona et al., 2015). *Cretoboganium* can be easily recognized from these extant genera
160 by a strongly curved frontoclypeal suture, striate elytra, compact antennae with an abrupt antennal
161 club, and very large pronotal callosities.

162 The most distinctive feature of *Cretoboganium* is the strongly curved frontoclypeal suture. The
163 frontoclypeal suture of modern boganiid beetles are all straight or nearly so (Lawrence and Ślipiński,

164 2010; Escalona et al., 2015). To our knowledge, a strongly curved frontoclypeal suture in Boganiidae
165 is confined to two extinct genera: *Cretoboganium* presented here and *Palaeoboganium* Liu et al.
166 from the Middle Jurassic Daohugou beds (Liu et al., 2018). As in the Jurassic *Palaeoboganium*, the
167 clypeal base of *Cretoboganium* is not constricted at base, a character also found in one of the two
168 extant genera: *Afroboganium*. By contrast, the clypeal base of the Australian *Boganium* is more
169 deeply constricted (Escalona et al., 2015). Although *Cretoboganium* shares with the older
170 *Palaeoboganium* the curved frontoclypeal suture and unconstricted clypeal base, *Cretoboganium*
171 differs significantly from the latter by having strongly clubbed antennae, well-developed pronotal
172 callosities, and much smaller body size (11 mm long in *Palaeoboganium* v.s. 3 mm long in
173 *Cretoboganium*).

174 Another interesting character of *Cretoboganium* is the striate and finely setose elytra. Among all
175 extant Boganiidae, this character is absent in the subfamily Boganiinae, but it can be found in one of
176 three genera of the other subfamily Paracucujinae, i.e., *Metacucujus* Endrödy-Younga and Crowson.
177 The paracucujine genus *Paracucujus* Sen Gupta and Crowson also bears regularly striate elytra, but
178 the elytra lack fine setae (Escalona et al., 2015). The Jurassic *Palaeoboganium*, as a sister group to
179 *Paracucujus* + *Metacucujus*, appears to have glabrous and regularly striate elytra (Liu et al., 2018).

180 The discovery of *Cretoboganium* from the mid-Cretaceous Burmese amber (approximately 99
181 million years ago) stands for the first fossil member of the extant austral subfamily Boganiinae. Such
182 an old and comparatively precise age of this clade is of great importance for further phylogenetic
183 analysis and divergence time estimation in future. This discovery represents another example that
184 current southern hemisphere endemic group may have its sister group apparently occurred in what is
185 now the northern hemisphere (e.g., Thayer et al., 2012; Cai et al., 2012; Krishna et al., 2013; Cai and
186 Huang, 2017a, b). There is high-resolution aeromagnetic data indicating that the eventual breakup
187 (formation of first true ocean floor) between the Antarctic Peninsula and southernmost South
188 America occurred at about 147 Ma (König and Jokat, 2006). This happened before the separations

189 between Africa and South America, and between Antarctic and Australia (Jokat et al., 2003; König
190 and Jokat, 2006). Therefore, it is very likely that Boganiinae first originated before the breakup of the
191 Gondwanan supercontinent, at least about 147 million years ago. The previous find of a mid-Jurassic
192 boganiid species from northeastern China (Liu et al., 2018) indicated Boganiidae as a very ancient
193 group of Cucujoidea (Labandeira, 2000), and it was much more widespread in the Jurassic. Although
194 there are no fossil boganiids documented from the Mesozoic of the southern hemisphere, we can
195 expect such discoveries from the fossil deposits in the Gondwanan landmasses, such as the Late
196 Jurassic of Australia (Talbragar fish beds; Cai et al., 2013; Ashman et al., 2015) and/or the Early
197 Cretaceous of Brazil in the future.

198

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206

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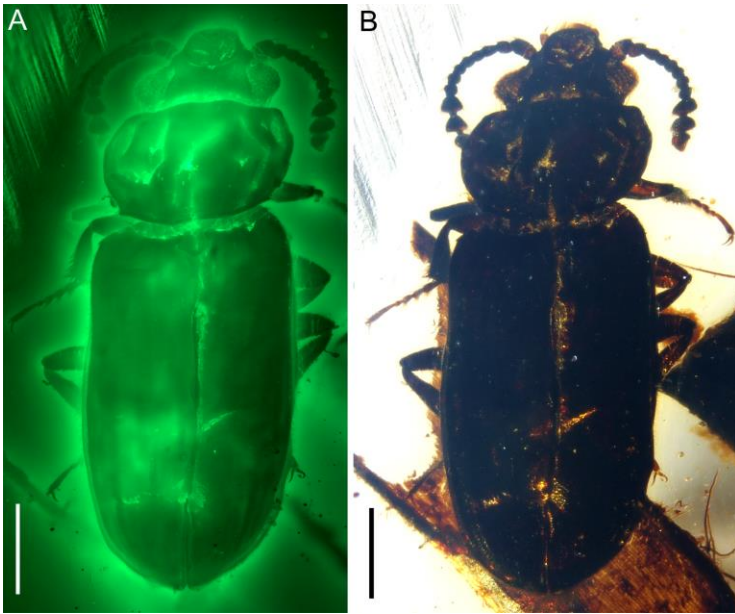
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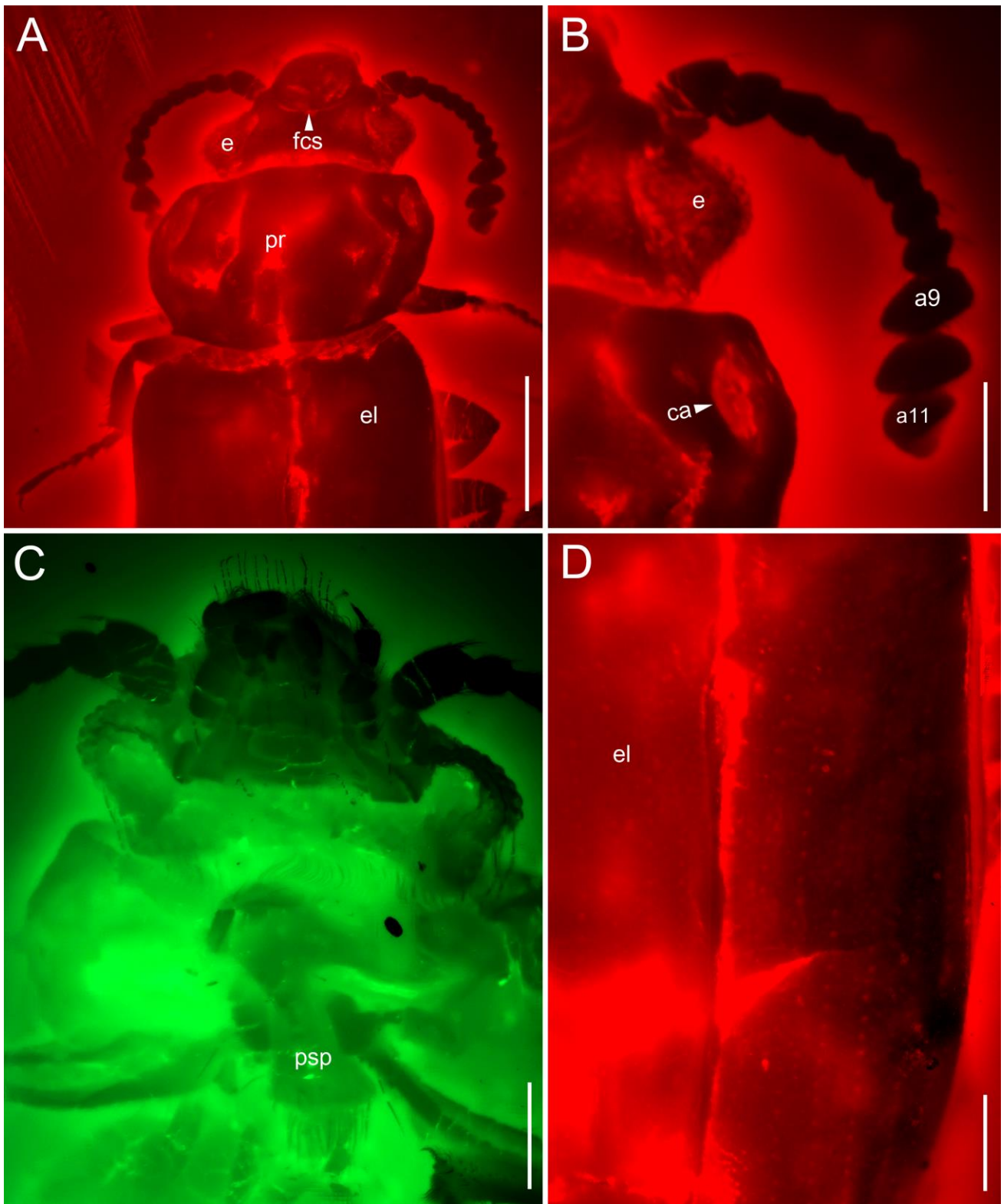
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260



261

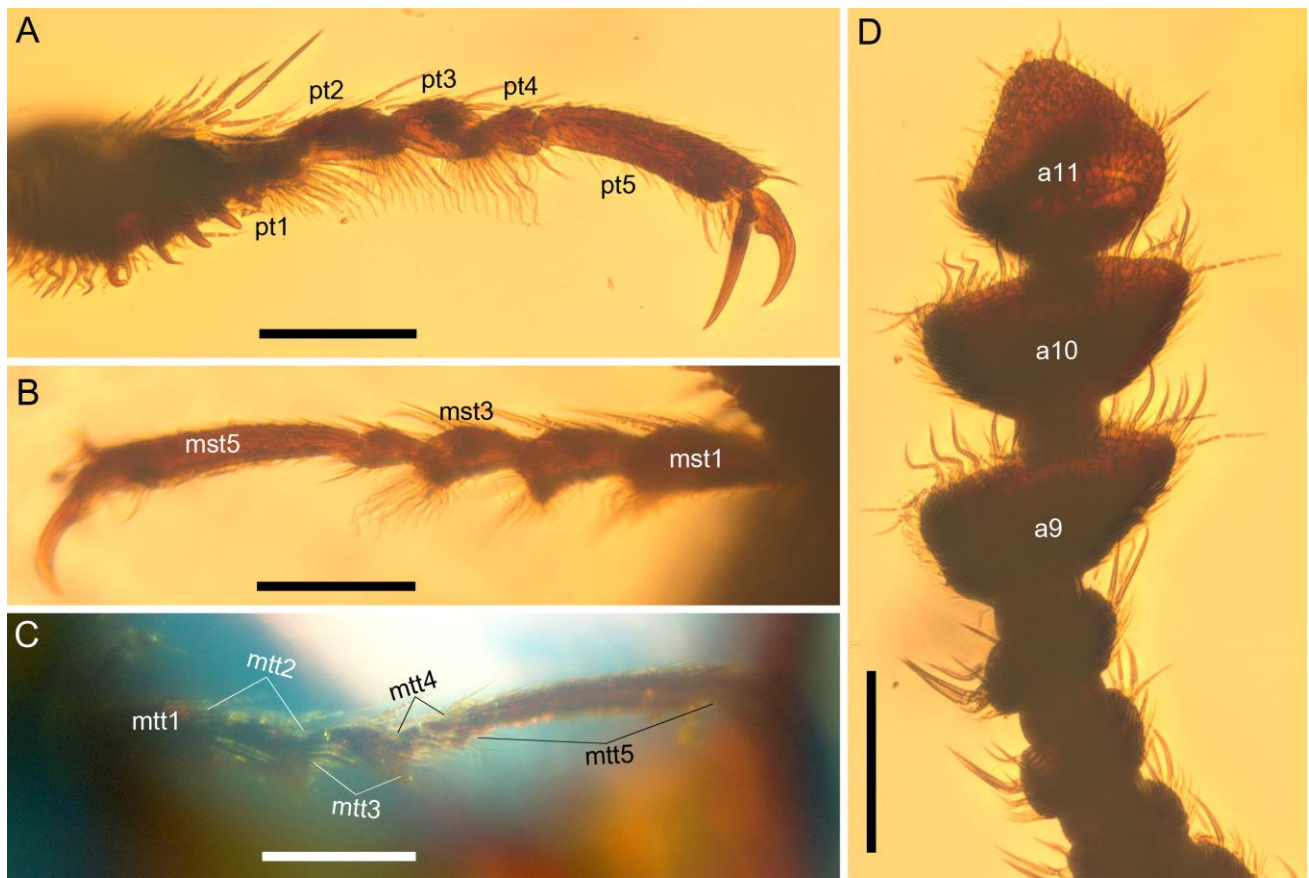
262 **Fig. 1.** Microphotographs of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov. from
263 Upper Cretaceous Burmese amber. A. dorsal view, under green fluorescence; B. dorsal view, under
264 normal reflected light. Scale bars: 500 μ m.



265

266 **Fig. 2.** Enlargements of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov., under
 267 fluorescence. A. dorsal view of head, pronotum and partial elytra; B. enlargement of A, showing
 268 details of eye, antenna and pronotal callosity; C. ventral view of head and prothorax; D. dorsal view
 269 of elytra, showing regular puncture rows. Abbreviations: a, antennomere; ca, callosity; e, eye; el,

270 elytron; fcs, frontoclypeal suture; pr, pronotum; psp, prosternal process. Scale bars: 500 μm in A, 200
271 μm in others.



272

273 **Fig. 3.** Enlargements of holotype (NIGP167701) of *Cretoboganium gei* gen. et sp. nov., under
274 transmitted light. A–C. pro-, meso- and metatarsus, showing reduced tarsomere 4; D. apical six
275 antennomeres of right antenna, showing strongly clubbed antenna. Abbreviations: a, antennomere;
276 mst, mesotarsomere; mtt, metatarsomere; pt, protarsomere. Scale bars: 100 μm .



277

278 **Fig. 4.** Dorsal reconstruction of *Cretoboganium gei* gen. et sp. nov.