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The first representative of Progonocimicidae (Hemiptera: Coleorrhyncha) from mid-Cretaceous Burmese amber

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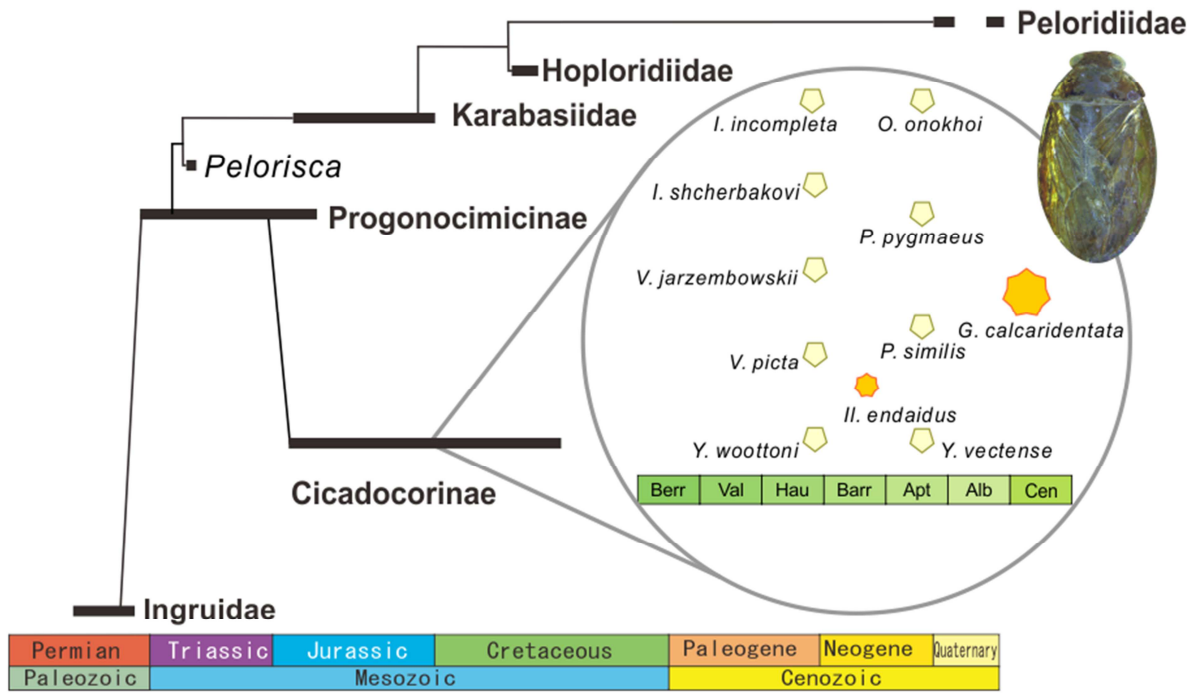
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ACCEPTED MANUSCRIPT

1 **The first representative of Progonocimicidae (Hemiptera:**  
2 **Coleorrhyncha) from mid-Cretaceous Burmese amber**

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22

23 **Abstract**

24 *Gakasha calcaridentata* **gen. et sp. nov.** representing Progonocimicidae:  
25 Cicadocorinae (moss bugs) is described. It is the first record of Coleorrhyncha in  
26 mid-Cretaceous Burmese amber and the second in fossil resins from the Cretaceous  
27 period. The taxonomic position of some taxa placed in the genus *Mesocimex* is  
28 analysed and new placements proposed. The fossil record of Cicadocorinae is  
29 discussed.

30

31 **Key words**

32 Burmese amber; Coleorrhyncha; Progonocimicidae; *Gakasha calcaridentata* **gen. et**

33 **sp. nov.**; synonymy; new combinations

34

35

## 36 **1. Introduction**

37 The hemipteran suborder Coleorrhyncha Myers et China, 1929 is known in the  
38 fossil record since the Permian. These Hemiptera, also known as ‘moss bugs’,  
39 contains four families: the only extant family Peloridiidae Breddin, 1897  
40 (Holocene-recent); and extinct families Karabasiidae Yu. Popov, 1985 (Jurassic,  
41 Sinemurian-Tithonian), Hoploridiidae Yu. Popov et Shcherbakov, 1991 (Cretaceous,  
42 Aptian) and Progonocimicidae Handlirsch, 1906 (Permian (Changhsingian)–  
43 Cretaceous (Aptian)) (Dong et al., 2014; Szwedo, 2018).

44 The extant Peloridiidae comprises 17 genera and 38 described species, distributed  
45 in temperate and subantarctic rain forests of eastern Australia, New Zealand, New  
46 Caledonia and Patagonia, in the Southern Hemisphere, with a classical southern  
47 Gondwanan distribution (Burckhardt, 2009; Burckhardt et al., 2011; Shcherbakov,  
48 2014; Ye et al., 2018). Mainly found in damp moss or on decaying mossy trunks and

49 twigs of *Nothofagus* trees, almost all extant species of Peloridiidae lack hind wings  
50 and are unable to fly. They occasionally feed on moss rhizoids, or even on  
51 wood-destroying fungi or on lichens (Evans, 1982; Popov and Shcherbakov, 1996;  
52 Shcherbakov, 2014; Szwedo, 2011).

53 The family Hoploridiidae was previously considered to be one of the subfamilies  
54 of Karabasiidae (Popov and Shcherbakov, 1991) but recently, Dong et al. (2014)  
55 suggested they to be raised to family rank. Species of Hoploridiidae are characterized  
56 by the large and flattened body, and distinguished from Karabasiidae by the reticulate  
57 venation and wide paranota lacking areolation, two-segmented hind tarsi without an  
58 apical pecten of teeth. The family Karabasiidae was considered to be a transitional  
59 group between Progonocimicidae and Peloridiidae (Jiang J.Q. et al., 2016; Popov and  
60 Shcherbakov, 1991, 1996; Szwedo, 2011; Wang B. et al., 2009).

61 The more ancient family Progonocimicidae was wide spread in Eurasia, Australia,  
62 and South America from the Upper Permian to Upper Cretaceous with more than 20  
63 genera, consisting of two subfamilies: Progonocimicinae Handlirsch, 1906 and  
64 Cicadocorinae Becker-Migdisova, 1958 (Jiang J.Q. et al., 2016; Popov and

65 Shcherbakov, 1991, 1996; Szwedo, 2011; Wang B. et al., 2009). This statement was  
66 undermined by Dong et al. (2014), but based on weak premises. Progonocimicinae  
67 was considered to derive from the Ingruidae (Ingruomorpha Szwedo, 2018) in the late  
68 Permian, and consists the ancestors of Cicadocorinae and Karabasiidae (Popov and  
69 Shcherbakov, 1996). Members of this subfamily were widely dispersed in the Triassic  
70 (eastern part of Australia, Kazakhstan, Kyrgyzstan; the taxa from Argentina need  
71 revision, most probably representing Heteroptera: Archegocimicidae), while in the  
72 Jurassic their records are limited to Europe (Germany, Belgium). Cicadocorinae  
73 appeared in the fossil record in the early Jurassic and persisted at least to  
74 mid-Cretaceous.

75 According to former studies, in the Cretaceous period Progonocimicidae:  
76 Cicadocorinae only occurred in the United Kingdom, Russia (Transbaikalia Krai),  
77 Mongolia and in Lebanon in the southern hemisphere, with 6 genera and 10 species  
78 (Figs 1, 7, Table 1).

79

## 80 **2. Material and method**

81 The amber under study was from an amber mine located near Noiye Bum Village,  
82 Tanaing (Tanai) Town, Kachin State, Myanmar (Jiang T. et al., 2018: fig. 1A-C; Kania  
83 et al., 2015: fig. 1A-D). The U-Pb dating of zircons from the volcanoclastic matrix of  
84 the amber has provided a refined age estimate of  $98.79 \pm 0.62$  Ma for the deposit (Shi  
85 et al., 2012), although some traces of re-deposition suggested that the amber might be  
86 reworked and the age of the amber should be older than the deposits (Ross, 2015;  
87 Wang B. et al., 2016; Wang B. et al., 2015; Zhang et al., 2017). *Domicchnia* (crypts) of  
88 *martesiine* bivalves (Pholadidae: *Martesiinae*) boring into amber pieces suggested  
89 than the age of the amber is older than the deposit, but recent study of bivalves has  
90 shown that some of them were boring into the resin while it was still soft indicating  
91 than the amber is contemporaneous with the age of the deposit (Ross, 2018; Smith  
92 and Ross, 2018).

93 The amber deposit is located in the West Burma terrane, which collided with the  
94 Sibumasu terrane in the Eurasian continental margin at around 80 Ma, in the low  
95 latitude tropical zone (Broly et al., 2015; Heine and Müller, 2005; Seton et al., 2012).  
96 This suggests some island or archipelago environments for at least part of the



97 amberiferous area at time of resin formation and deposition (Jiang et al., 2018;  
98 Rasnitsyn and Öhl-Kühlme, 2018). The depositional environment was suggested to be  
99 a nearshore marine setting close to deltas, with marine fossils found in the deposits  
100 (Cruikshank and Ko, 2002; Thu and Zaw, 2017).

101 The specimen was prepared in the Laboratory of Evolutionary Entomology and  
102 Museum of Amber Inclusions, University of Gdańsk, Poland, and was observed under  
103 a stereoscopic microscope with varying illumination and filters to increase contrast of  
104 pigmentation and morphological details. Drawings were prepared under a Nikon  
105 microscope (SMZ1000) with a drawing tube attached, and photographs were taken  
106 using a Zeiss AXIO Zoom.V16 microscope system, in the Nanjing Institute of  
107 Geology and Palaeontology, Chinese Academy of Sciences. Photographs and  
108 drawings were adjusted using CorelDraw X8 and CorelPhoto-Paint X8 packages. All  
109 taxonomic acts established in the present work have been registered in ZooBank.

110 The nomenclature of the wing venation used in this paper is based on the general  
111 scheme for Paraneoptera (Nel et al. 2012), modifying the interpretations of  
112 Kukalová-Peck (1991), Popov and Shcherbakov (1991) and Szwedo (2011). Cell

- 113 nomenclature is adopted from Bourgoin et al. (2015). Abbreviations:
- 114 PC – precosta
- 115 CA – costa anterior
- 116 CP – costa posterior
- 117 bScP – basal portion of subcosta posterior
- 118 dScP – distal portion of subcosta posterior
- 119 dScP+RA<sub>1</sub> – common branch of distal portion of subcostal posterior fused with
- 120 first branch of radius anterior; Popov and Shcherbakov (1991) interpreted this vein as
- 121 free distal portion of subcosta
- 122 R – radius
- 123 RA – radius anterior
- 124 RP – radius posterior; RS according to Popov and Shcherbakov (1991)
- 125 MP – media posterior; according to Kukalová-Peck (1991) vein MA in
- 126 Paraneoptera is completely fused with R
- 127 MP<sub>1+2</sub> – common stalk of MP<sub>1</sub> and MP<sub>2</sub>
- 128 MP<sub>1</sub> – first terminal of Media posterior

- 129 MP<sub>2</sub> – second terminal of media posterior
- 130 MP<sub>3+4</sub> – common terminal of third and fourth branch of media posterior
- 131 CuA – cubitus anterior
- 132 CuA<sub>1</sub> – first terminal of cubitus anterior
- 133 CuA<sub>2</sub> – second terminal of cubitus anterior; ambient vein according to Popov and  
134 Shcherbakov (1991)
- 135 CuP – cubitus posterior (claval fold, claval suture is parallel and adjacent to CuP;  
136 in former papers these two structures were treated as “claval fracture”; claval fracture  
137 according to Popov and Shcherbakov, 1991)
- 138 Pcu – postcubitus
- 139 A<sub>1</sub> – first anal vein; veins Pcu and A<sub>1</sub> are fused at apical portion of clavus forming  
140 common stalk Pcu+A<sub>1</sub>
- 141 *rp-mp* – transverse veinlet connecting radius posterior and media posterior
- 142 *mp-cua* – transverse veinlet connecting media posterior and cubitus anterior
- 143 *icu* – veinlet connecting cubitus posterior with claval margin or tornus
- 144 costal area – area between veins of costal complex, i.e. CA and PC+CP (veins of

- 145 costal complex are termed precostal carina by Popov and Shcherbakov, 1991)
- 146 costal cell – area of corium between costal complex and stem ScP+R
- 147 radial cell – area of corium between stems ScP+R and MP
- 148 medial cell – area of corium between stems MP and CuA
- 149 cubital cell – area of corium between stem CuA and claval suture (CuP)
- 150 Cell C0 – area delimited by forking of ScP+RA<sub>1</sub> and RA<sub>2</sub> ('stigmatal area' in  
151 Sternorrhyncha and Fulgoromorpha)
- 152 Cell C1 – area delimited by forking of RA and RP
- 153 Cell C2 – area between branches RP and MP/MP<sub>1+2</sub>, proximally and distally  
154 delimited by radiomedial transverse veinlet *rp-mp*<sub>1</sub>
- 155 Cell C3 – area between first fork of stem MP, i.e. between branches MP<sub>2</sub> and  
156 MP<sub>3+4</sub>
- 157 Cell C3a – area between branches MP<sub>1</sub> and MP<sub>2</sub>
- 158 Cell C4 – area between branches MP<sub>3+4</sub> and CuA<sub>1</sub>
- 159 Cell C5 – the areola postica, the cell delimited by the first fork of stem CuA, i.e.  
160 branches CuA<sub>1</sub> and CuA<sub>2</sub>.

161

162 **3. Systematic palaeontology**

163

164 Order Hemiptera Linnaeus, 1758

165 Suborder Coleorrhyncha Myers et China, 1929

166 Superfamily Progonocimicoidea Handlirsch, 1906

167 Family Progonocimicidae Handlirsch, 1906

168 Subfamily Cicadocorinae Becker-Migdisova, 1958

169 2012 Ciadococinae [sic!] Becker-Migdisova, 1958: Dong et al., p. 74.

170 2013 Ciadococinae [sic!] Becker-Migdisova, 1958: Dong et al., p. 34.

171

172 Genus: *Gakasha* **gen. nov.**

173 Type species: *Gakasha calcaridentata* sp. nov., by present designation and monotypy.

174

175 LSID: urn:lsid:zoobank.org:act:D8594277-ED94-444E-B4F1-6E3D62F61DAB

176

177 *Etymology.* Generic name is derived from the word ‘ga kasha’ meaning “a minute  
178 insect” in Kachin language. Gender: feminine.

179

180 *Diagnosis.* In general shape of tegmen resembling Cretaceous genera *Onokhoia* Yu.  
181 Popov, 1988 and *Ilahulgabalus* Szwedo, Azar et Ziadé, 2011 (tegmen elongated, not  
182 broadly rounded as in *Yuripopovia* Jarzembowski, 1991, *Valdiscytina* Yu. Popov, 1993  
183 in Klimaszewski and Popov, 1993, *Ildavia* Yu. Popov, 1993 in Klimaszewski and  
184 Popov, 1993 and *Popovus* Özdikmen et Demir, 2007). Posterior margin of tegmen  
185 rounded (more truncate in *Onokhoia* and *Ilahulgabalus*); bScP reaching nearly to  
186 apex of basal cell (bScP not reaching half of basal cell in *Ilahulgabalus*); dScP+RA<sub>1</sub>  
187 separating from stem R at level of Pcu+A<sub>1</sub> intersection with claval fold and CuP  
188 (dScP+RA<sub>1</sub> separating from stem R at level of claval veins Pcu and A<sub>1</sub> junction in  
189 *Onokhoia*; dScP+RA<sub>1</sub> separating from stem R slightly apicad of claval veins junction  
190 in *Ilahulgabalus*); basal cell closed with longer stalk of MP+CuA, and shorter CuA  
191 stalk (basal cell closed by subequal stalks MP+CuA and CuA in *Onokhoia*; basal cell  
192 closed at point by stalk MP+CuA in *Ilahulgabalus*); short, oblique veinlet *rp-mp*<sub>1</sub>

193 present (absent in *Onokhoia* – branches RP and MP<sub>1</sub> connected at point; longer, not so  
194 oblique veinlet *rp-mp* in *Ilahulgabalus*). Hind wing with a short common terminal  
195 CuP+Pcu (similar to *Absoluta* Becker-Migdisova, 1962; common terminal CuP+Pcu  
196 longer in *Ilahulgabalus*). Metatibia with two movable lateral spurs (no armature of  
197 metatibia in *Onokhoia*; single movable lateral spur in *Ilahulgabalus*), and four apical  
198 spurs (two external ones longer).

199

200 *Description.* Head with compound eyes narrower than pronotum (ca. 0.61), about 4  
201 times as wide as long in midline. Vertex between compound eyes about twice as wide  
202 as long in mid line, wider at anterior and posterior margins; anterior margin slightly  
203 arcuate, posterior margin subparallel, elevated; disc of vertex with delicate  
204 puncturation. Lateral ocelli distinct, at half of compound eyes length, adpressed to  
205 compound eyes. Supraantennal ridge straight; median ocellus just above the ridge.  
206 Postclypeus slightly swollen, longer in mid line than wide at base, subtriangular,  
207 wider in upper margin, tapering ventrad; anteclypeus shorter than postclypeus, convex,  
208 subtriangular, about as long in mid line as wide; loral plates semilunar, with upper

209 angles reaching upper margin of postclypeus, lower angles at level of lower margin of  
210 postclypeus, reaching lateral margins of anteclypeus at about its upper  $\frac{1}{2}$ . Maxillary  
211 plate and genae narrow. Clypellus about three times as long as wide at base. Bases of  
212 antennae between margin of clypeus and lower margin of compound eyes; antenna  
213 3-segmented, scapus short, pedicel twice as long as wide, flagellum longer than  
214 pedicel, thick, tapered, annulate, with 7 annuli, each annulus provided with two longer  
215 and thicker setae (some shorter, irregular setae present on basal annuli), three basal  
216 pairs about as long as annulus width, apical with setae longer than length of annulus,  
217 terminal one with four longer apical setae, two apical and two subapical ones.  
218 Rostrum with basal segment short, apical segment reaching mesocoxae.

219 Pronotum subhexagonal, wider than mesonotum, about 2.5 times as wide as long  
220 in midline; anterior margin arcuate; anterolateral angles widely angulate; posterior  
221 margins straight, diverging posteriad, posterolateral margins acutely angulate,  
222 posterolateral margin arcuate, posterior margin shallowly arcuately concave. Disc of  
223 pronotum delicately transversely wrinkled. Lateral margin of pronotum carinate,  
224 lateroventral lobes tuck, reaching prothoracic katapisternum.



225 Mesonotum triangular, about 1.5 times as wide as long in mid line. Disc of  
226 mesonotum delicately transversely wrinkled.

227 Left tegmen overlapping right tegmen. Tegmen membranous, with venation  
228 distinct, nodal line thick, oblique, veins on corium thickened, to less extent on  
229 membrane, elevated. Tegmen about 3.25 times as long as wide at claval apex, about  
230 2.3 times as long as maximal width. Apex of clavus slightly distad of  $\frac{1}{2}$  of tegmen  
231 length. Costal margin arcuate, anterolateral angle widely arcuate, apex between  
232 terminals RP and MP<sub>1</sub>, posterior margin slightly arcuate, posterolateral margin  
233 broadly rounded, tornus and claval margin arcuate. Costal area narrow, distinctly  
234 narrower than costal cell (less than  $\frac{1}{5}$ <sup>th</sup>), thickened, slightly widened at very base,  
235 horizontally carinate, reaching MP<sub>3+4</sub>. Basal cell about 2.5 times as long as wide,  
236 closed posteriorly by stalks MP+CuA and CuA; bScP slightly shifted from main stem  
237 R+MP+CuA, reaching nearly to apex of basal cell. Stem R arcuate, subparallel to  
238 costal margin, longer than dScP+RA<sub>1</sub> branch; dScP+RA<sub>1</sub> oblique, reaching costal  
239 margin posteriad of claval apex; terminal RA<sub>2</sub> slightly longer than terminal ScP+RA<sub>1</sub>,  
240 subparallel to terminal RP; terminal RP slightly arcuate anteriad, as prolongation of

241 nodal line. Stem MP leaving basal cell separately, arcuate, subparallel to stem R; first  
242 fork at nodal line, stalk  $MP_{1+2}$  short, in nodal line, terminal  $MP_1$  thinner than stem MP  
243 and  $MP_{1+2}$  stalk, straight, shorter than terminal  $MP_2$ ; terminal  $MP_2$  straight, thinner,  
244 parallel to terminal  $MP_1$ ; terminal  $MP_{3+4}$  longest, longer than  $MP_2$ , straight, thinner,  
245 parallel to terminal  $MP_2$ . Stem CuA leaving basal cell separately, arcuate, adhering to  
246 claval suture (CuP) in basal portion, then directed mediad, forked at nodal line;  
247 terminal  $CuA_1$  in line prolonging stem CuA, straight reaching margin posteriad of  
248 tegmen apex; terminal  $CuA_2$  straight, subparallel to  $CuA_1$ . Claval veins Pcu and  $A_1$   
249 fused at about  $\frac{2}{3}$ <sup>rd</sup>s of claval suture length, in apical portion of clavus; free portion of  
250  $A_1$  about  $\frac{1}{3}$ <sup>rd</sup> of claval suture length. Veinlet  $rp-mp_1$  short, oblique, thickened, placed  
251 at nodal line; veinlet  $mp_{3+4}-cua_1$  subperpendicular to CuA, about as long as stalk  
252  $MP_{3+4}$ , thickened, placed at nodal line; very short  $icu$  intersecting the prolongation of  
253 CuP on thickened margin of tornus. Costal cell at widest point about as wide as radial  
254 cell; radial cell longer than medial cell, acute at apex, closed by RP stalk,  $rp-mp_1$ ,  $MP_1$   
255 stalk and  $MP_{1+2}$  stalk; medial cell lanceolate, closed obtusely apicad by  $MP_{3+4}$  stalk  
256 and  $mp_{3+4}-cua$  veinlet, slightly narrower than radial cell. Costal cell at widest point as

257 wide as radial cell at widest point. Cell C0 elongate, obliquely diamond-shaped;  
258 longer than cell C1, about as long as cell C3a; cell C3 subrectangular, longer than cell  
259 C3a and cell C5; cell C5 subrectangular, merely wider apically, about as wide as  
260 appendix.

261 Hindwing with short common terminal of CuP+Pcu.

262 Procoxa slightly elongate, protrochanter elongate, subconical. Proleg short,  
263 profemur shorter than protibia; protibia subquadrangular in cross section, with rows  
264 of short setae along margins and at apex; basiprotarsomere shorter than apical one,  
265 elongately cup-shaped; apical protarsomere about twice as long as basiprotarsomere,  
266 tarsal claws distinct, arolium fan-shaped, wide. Mesoleg short; mesofemur shorter  
267 than mesotibia; mesotibia slightly longer than protibia, subquadrangular in cross  
268 section, with rows of short setae along margins; mesotarsus two-segmented.

269 Metacoxae conical, adpressed to each other, metatrochanters ring-like. Metatibia  
270 elongated, with two movable lateral spurs, first subbasal and second slightly basad of  
271 half of metatibia's length, and row of apical teeth and four movable spurs. Lateral  
272 spurs narrow basally, rounded at anterior margin, flattened at posterior margin, with

273 row of about 30 small spinules; two external apical spurs almost as long as lateral  
274 spurs, slightly flattened at internal margins, provided with row of small spinules  
275 ventrally, third and fourth spurs (subexternal ones) shorter, about half of lateral spur  
276 length, elongately leaf-shaped, with lateroventral carinations provided with row of six  
277 spinules; row of apical teeth between spurs composed of 6 elongate ones; metatarsus  
278 long, about 0.8 of metatibia length; basimetatarsomere longer than combined length  
279 of mid- and apical metatarsomeres, widening apicad, with row of 11 apical teeth;  
280 midmetatarsomere about as long as apical metatarsomere, with oblique row of 11  
281 apical teeth. Tarsal claws distinct, arolium fan-shaped, wide.

282 Abdomen wide, flattened, 4<sup>th</sup> abdominal segment the widest, subsequent segments  
283 narrowing posteriad, hypopleurites 3<sup>rd</sup> to 7<sup>th</sup> distinct, spiracles placed in middle of  
284 their length, shifted mediad towards sternites; female 7<sup>th</sup> sternite large with distinctly  
285 arcuate posterolateral margin, anterior margin straight; hypopleurite 8<sup>th</sup> (paratergite)  
286 distinctly elongate caudally, with tapered process, not exceeding tip of ovipositor,  
287 with rows of short setae dispersed along mediolateral carination. Anal tube short,  
288 about as long as wide, covered with short setae. Gonoplasts tube-like, elongate,

289 opened ventrally, covering gonapophyses VIII and IX and covered with row of  
290 elongate setae; in ventral view exceeding length of anal tube about 3 times.

291

292 *Gakasha calcaridentata* **sp. nov.**

293 (Figs 2–5)

294

295 LSID: urn:lsid:zoobank.org:act:62DD87F7-C459-4264-B452-4DED028D3FD0

296

297 *Etymology.* Specific epithet is derived from Latin calcar (spur) and dens, ~tis (tooth),  
298 and refers to row of small denticles on posterior margin of metatibial lateral and  
299 lateroapical spurs.

300

301 *Material.* Holotype, female. Burmese amber, oval piece,  $19 \times 16 \times 3.5$  mm, weight  
302 0.88 g. The inclusion of the taxon described here was cut out from the lump, polished  
303 and preserved as a microscopic slide in Canada balsam. Specimen No.  
304 NIGP154576-A, deposited in Nanjing Institute of Geology and Palaeontology,

305 Chinese Academy of Sciences, Nanjing.

306 Dorsal side well displayed, ventral side partly visible, obscured by cracks filled with

307 hard sediment (partly removed) and internal impurities (decay gases) and resin layers.

308 Syninclusions: an unidentified Cixiidae-like planthopper (Hemiptera: Fulgoromorpha);

309 Hymenoptera Apocrita, Hymenoptera Apocrita Parasitica; Coleoptera; Diptera

310 Nematocera.

311

312 *Diagnosis.* Vertex between compound eyes twice as wide as long in mid line.

313 Pronotum in mid line 2.5 times as long as vertex in mid line, about 2.8 times as long

314 as wide. Tegmen membranous, transparent. Stem CuA at base very close to claval

315 suture; segment between first fork of ScP+R and RA<sub>2</sub> fork about ½ as long as stem

316 ScP+R. Cell C0 elongately diamond-shaped, more than 3 times as long as wide;

317 apical cells elongate, cell C1 about 7 times as long as wide; cell C3 longer than

318 median cell. Appendix as wide as cell C5. Angle between claval margin and tornus

319 (tangents) ca. 135°. Metatibio-metatarsal formula 2+2+6 : 11 : 11. Anal tube in female

320 about as long as wide.

321

322 *Description.* Body total 4.16 mm long, 2.32 mm wide. Head transverse, distinctly  
323 shorter (0.28 mm) in mid line than wide with compound eyes (1.13 mm), about  $\frac{1}{2}$  as  
324 wide as pronotum. Lateral ocelli distinct, on the crown, adhering compound eyes,  
325 median ocellus adjacent to supraantennal ledge. Pronotum 1.8 mm wide and 0.65 mm  
326 long in mid line. Mesonotum about 1.26 mm wide at base and 0.85 mm long in mid  
327 line. Tegmen 3.27 mm long, about 1 mm wide at claval apex, maximal width 1.37 mm,  
328 veins on corium thickened, carinate, nodal line veins thick, carinate, terminal RP thick,  
329 terminals of MP and CuA thinner, not distinctly carinate. Cubital cell very narrow at  
330 base then widening to nodal line. Vein Pcu at base adhering claval suture, then  
331 diverging, vein  $A_1$  and Pcu+ $A_1$  shifted from claval margin. Margin of tornus arcuate,  
332 strengthened at very base by prolongation of CuP (fused with Pcu+ $A_1$ ?).

333 Protibia setigerous, 0.55 mm long, external rows of setae longer than internal ones;  
334 protarsus two-segmented, 0.37 mm long. Mesotibia 0.84 mm long, mesotarsus 0.37  
335 mm long. Metatibia about 1.1 mm long, with 2 long lateral spurs, first slightly basad  
336 of knee, second, slightly apicad of  $\frac{1}{2}$  of metatibia length, lateral spurs ca. 0.38 mm

337 long; basimetatarsomere 0.57 mm long, midmetatarsomere 0.28 mm long, apical  
338 metatarsomere 0.28 mm long, 0.33 mm long with tarsal claws.

339 Anal tube of female ca. 0.18 mm long (dorsal view). Ovipositor (portion visible in  
340 ventral view, gonoplacs) ca. 0.35 mm long.

341

#### 342 **4. Discussion**

##### 343 *Taxonomic and nomenclatorial problems within Cicadocorinae*

344 The oldest members of Cicadocorinae come from the Late Triassic deposits of  
345 England (Popov et al., 1994), and they were considered to originate from some early  
346 Progonocimicinae. Cicadocorinae diversified markedly in the Jurassic and distributed  
347 worldwide in the Early Cretaceous (Bechly and Szwedo, 2007; Szwedo, 2011). The  
348 subfamily Cicadocorinae comprises the genera *Absoluta* Becker-Migdisova, 1962,  
349 *Archicercopis* Handlirsch, 1939, *Cicadocoris* Becker-Migdisova, 1958, *Mesocimex*  
350 Hong, 1983, *Ilahulgabalus* Szwedo, Azar et Ziadé, 2011, *Ildavia* Yu. Popov, 1993,  
351 *Onokhoia* Yu. Popov, 1988, *Valdiscytina* Yu. Popov, 1993 and *Yuripopovia*  
352 Jarzembowski, 1991 (Heads et al., 2018; Popov and Shcherbakov, 1991). After



353 synonymisation of most of the species of the genus *Olgamartynovia*  
354 Becker-Migdisova, 1958 by Popov and Shcherbakov (1991), *Cicadocoris* and  
355 *Mesocimex* became the largest genera of Cicadocorinae. They have been suggested to  
356 be synonyms by most of the former studies (Dong et al., 2014; Jiang J.Q. et al., 2016),  
357 but this synonymisation seems to be premature. Popov and Shcherbakov (1991)  
358 presented sets of characters separating these genera, based mainly on venational  
359 characters; however, some species can present transitional combinations. Most of the  
360 species ascribed to these two genera are in need of urgent revisionary studies to  
361 resolve their taxonomic position. A graphical summary of generic synonymies is  
362 presented on figure 6. One of the obstacles hampering the clarification of taxonomy  
363 and classification within Cicadocorinae is dissymmetry of some veins on left and  
364 right tegmina, and a new approach to this problem, already addressed by Popov and  
365 Shcherbakov (1991), is necessary.

366 The genus *Olgamartynovia* Becker-Migdisova, 1958, *sensu stricto* was  
367 synonymized under *Cicadocoris* (Popov and Shcherbakov, 1991), with some species  
368 moved to *Cicadocoris*, other to *Mesoscytina* Hong, 1983, and a few remaining of

369 uncertain position (Fig. 6). Thus the genus *Cicadocoris* comprises the type species  
370 and some five more. Some of the species placed in *Cicadocoris* should be  
371 synonymized, because the differences between left and right tegmina were formerly  
372 interpreted as specific ones (Popov and Shcherbakov, 1991). A provisional list of  
373 species comprised in the genus is as follows: *Cicadocoris kuliki* Becker-Migdisova,  
374 1958 (type species) **stat. resurr.** and *C. affinis* (Yu. Popov, 1982) **stat. resurr.**, *C.*  
375 *arcuatus* (Yu. Popov, 1982) **stat. resurr.**, *C. assimilis* Dong, Yao et Ren, 2013, *C.*  
376 *frater* (Yu. Popov, 1982) **stat. resurr.** The taxonomic placement of the following  
377 species is not certain, and these are only tentatively placed within the genus  
378 *Cicadocoris*: ?*C. admotus* (Yu. Popov, 1982), ?*C. complexus* (Yu. Popov, 1982), ?*C.*  
379 *confinis* (Yu. Popov, 1982), ?*C. conjunctus* (Yu. Popov, 1982), ?*C. distans* (Yu. Popov,  
380 1982), ?*C. ignoratus* (Yu. Popov, 1982), ?*C. parallelus* (Yu. Popov, 1982), ?*C. similis*  
381 (Yu. Popov, 1982), ?*C. sogjutensis* (Yu. Popov, 1982), ?*C. turanicus*  
382 (Becker-Migdisova, 1958).

383 Venational characters of *Cicadocoris parvus* Jiang et Huang, 2017 match to the set  
384 proposed by Popov and Shcherbakov (1991) for the genus *Mesocimex*, therefore we

385 propose a new combination *Mesocimex parvus* (Jiang et Huang, 2017) **comb. nov.**  
386 Jiang J-Q. and Huang (2017) suggested that *Cicadocoris varians* Dong, Yao et Ren,  
387 2012 is probably a junior synonym of *Mesocimex sinensis* because of taphonomic  
388 deformation; therefore we propose a new combination *Mesocimex varians* (Dong, Yao  
389 et Ren, 2012) **comb. nov.** The other species originally described in *Olgamartynovia*  
390 merit generic separation: '*Olgamartynovia*' *rigida* Yu. Popov, 1982 =  
391 '*Olgamartynovia*' *paula* Yu. Popov, 1982; '*Olgamartynovia*' *beckermigdisovae* Yu.  
392 Popov, 1982, '*Olgamartynovia*' *nana* Yu. Popov, 1982; '*Olgamartynovia*'  
393 *transbaikalica* Yu. Popov, 1985; '*Olgamartynovia*' *distincta* Yu. Popov, 1982 as  
394 already suggested by Popov and Shcherbakov (1991), and sustained by Dong et al.  
395 (2013), and Heads et al. (2018). This action is not followed here, as the original  
396 material needs to be revised prior to taxonomic decisions, and more substantiated  
397 characters and data on the diversity and disparity within Cicadocorinae should be  
398 gathered. Therefore, we propose to conserve the formal generic name  
399 '*Olgamartynovia*' for these taxa with: ?'*Olgamartynovia*' *rigida* Yu. Popov,  
400 1982; ?'*Olgamartynovia*' *beckermigdisovae* Yu. Popov, 1982; ?'*Olgamartynovia*'

401 *nana* Yu. Popov, 1982; ?*Olgamartynovia* *transbaikalica* Yu. Popov, 1985  
402 and ?*Olgamartynovia* *distincta* Yu. Popov, 1982.

403 The generic name *Mesocimex* Hong, 1983 was resurrected from synonymy for the  
404 reasons given in Wang B. et al. (2009). Jiang J.Q. et al. (2015) proposed to  
405 synonymise *Mesocimex lini* Wang, Szwedo et Zhang, 2009 under *Mesocimex*  
406 *brunneus* (Hong, 1983), referring to text-figure 51 (Hong, 1983: p. 66) and figures 1  
407 and 2 of plate 11. However, these photos are a taxon named *Mesocimex sinensis* Hong,  
408 1983. A photograph of *M. brunneus* is presented on plate 11, figure 3. According to  
409 this photo *M. brunneus* is characterised by vertex in mid line about as long as wide,  
410 and in *M. lini* it is  $\frac{1}{2}$  of vertex width; the same ratio is visible in specimens figured by  
411 Jiang J.Q. et al. (2014: Fig. 2A, B, C) as *C. brunneus*. Before this problem will be  
412 solved, we propose to treat *Mesocimex lini* Wang, Szwedo et Zhang, 2009 **stat. resurr.**  
413 as a valid name.

414 A nomenclatorial combination *Cicadocoris sinensis* (Hong, 1983) was proposed  
415 first by Dong et al. (2014); Jiang J.Q. et al. (2015), referring to the original  
416 description of *Mesocimex sinensis* and fig. 50 in Hong (1983: p. 65), but mistakenly

417 listed fig. 3 of plate 11; the original paper refers to figs. 1 and 2 of plate 11. Jiang J.Q.  
418 et al. (2015) proposed to synonymise *Cicadocoris anisomeridis* Dong, Yao et Ren,  
419 2014 under *C. sinensis*. The venation of *C. anisomeridis* is very close to specimens  
420 identified as *C. sinensis* by Jiang J.Q. et al. (2015, fig. 3 B, C, D, fig. 4), but according  
421 to a photo of *C. anisomeridis* in Dong et al. (2014: fig. 1A-D) the head of it presents a  
422 vertex about as long as wide, while in some *C. sinensis* specimens figured in Jiang  
423 J.Q. et al. (2015, fig. 3A, B) the vertex is about twice as wide as long in mid line.  
424 According to Hong (1983) *M. sinensis* had 'head small', and any other details could  
425 be found in descriptions and inferred from photos. Venational characters in  
426 Cicadocorinae species seem to be very conservative or could be homoplastic, so  
427 probably not very informative for nomenclatorial purposes. Therefore the above  
428 mentioned synonyms should be treated with some reservations and they need to be  
429 revised. Hence, we propose the names *Mesocimex sinensis* Hong, 1983 **stat. resurr.**  
430 and *Cicadocoris anisomeridis* Dong, Yao et Ren, 2014 **stat. resurr.** as valid until the  
431 material will be checked.

432 The genus *Cicadocoris* comprises 14 (to 19) currently recognised species level

433 taxa, distributed mainly in Kyrgyzstan and north China in the Early and Middle  
434 Jurassic (Dong et al., 2012). The *Mesocimex* species come also from the Early to  
435 Middle Jurassic, and mainly occur in Kyrgyzstan, Russia, north China and the United  
436 Kingdom (Dong et al., 2013; Wang B. et al., 2009).

437

438 *Morphological features and peculiarities of Gakasha gen. nov.*

439 The above described genus *Gakasha* **gen. nov.** can be placed in Cicadocorinae by  
440 the following characters: tegmen with costal area horizontal, base of costal area  
441 narrow; stem R continued by branch RP, dScP+RA<sub>1</sub> convex and free portion of A<sub>1</sub>  
442 shorter than half of claval suture. It is the second genus known from the fossil resins  
443 of the Cretaceous, differing from *Ilahulgabalus* by characters of the tegmen venation,  
444 armature of metatibia and metatarsus. Regarding the tegmen shape and ratio, it  
445 resembles the genus *Onokhoia* from Transbaikalia, but differs in details of venation  
446 and metatibia armature. *Gakasha* **gen. nov.** is for the moment the most completely  
447 preserved specimen, presenting much more details, often not available from  
448 compression/impression fossils. The newly described genus presents a number of

449 peculiar features, not known up to date among Cicadocorinae and Progonocimicidae.

450 For the first time, the lateral ocelli are clearly observed – Popov and Shcherbakov

451 (1991) mentioned that ocelli were untraceable among known fossils, with supposed

452 position at anterior margin of the head. In *Gakasha* **gen. nov.**, ocelli are placed on the

453 crown, adhering compound eyes, but more posteriad, not on the margin. In

454 Peloridiidae, ocelli are small, sometimes inconspicuous, placed at anterior margin of

455 the head, close to compound eye (Popov and Shcherbakov, 1996; Spangenberg et al.

456 2013). Another feature of *Gakasha* **gen. nov.** is presence of 3-segmented antennae,

457 with terminal segment slightly incrassate, tapering apicad. This character is

458 characteristic for Peloridioidea Breddin, 1897; Progonocimicoidea are

459 characteristically with antennae 4-7 segmented, setaceous or incrassate (Popov and

460 Shcherbakov, 1991). The flagellum of the antenna in *Gakasha* **gen. nov.** is annulate,

461 with seven recognisable annuli, each provided with some setae, shorter at base, but

462 distinctly longer in apical annuli, with the longest setae on the terminal one. In

463 *Hackeriella veitchi*, the scapus is longer than pedicel (in *Gakasha* **gen. nov.** it is

464 opposite, scapus is short, and pedicel distinctly longer) and flagellum not annulated,

465 and lacks setae (Spangenberg, 2013); a similar, non-annulate, and lacking distinct  
466 setae, flagellum is present in other Peloridiidae (Burckhardt, 2009). The postclypeus  
467 and anteclypeus in *Gakasha* **gen. nov.** seem to be fused, but separated by a groove.  
468 The postclypeus is more inflated, anteclypeus convex and loral plates wide,  
469 resembling the situation present in *Mesocimex*. The general venation pattern of  
470 *Gakasha* **gen. nov.** is typical of Cicadocorinae; it differs clearly from *Ilahulgabalus*  
471 by the shape of the nodal line and width of appendix; the nodal line of *Gakasha* **gen.**  
472 **nov.** is formed by terminal RP, oblique veinlet  $rp\text{-}mp_1$ , stalk of  $MP_1$ , stalk of  $MP_{1+2}$ ,  
473 stalk of  $MP_{3+4}$ ; veinlet  $mp_{3+4}\text{-}cua_1$ , stalk  $CuA_2$  and veinlet *icu*. Such a model is unique  
474 among Cicadocorinae genera; in *Onokhoia*, the anterior portion of the nodal line is  
475 formed by fused veins RP and  $MP_1$ ; in the other genera by terminal  $MP_1$ . Two lateral  
476 movable spurs are present in *Mesocimex* and *Cicadocoris*, at least in some species  
477 ascribed to the genus *Mesocimex* (*M. lini* **stat. resurr.**); in this species, the base of the  
478 spur seems to be distinctly wider than in *Gakasha* **gen. nov.** and there are no  
479 elongated spurs/teeth at the metatibial apex (Wang B. et al., 2009). The genus  
480 *Onokhoia* is characteristically lacking lateral movable spurs; in *Ilahulgabalus* is there



481 a single lateral spine and four of the apical teeth are enlarged. Four distinct lateral  
482 (movable) spurs, provided with row of denticules, at the tip of the metatibia seem to  
483 be a unique feature of *Gakasha* **gen. nov.** The basimetatarsomere and  
484 midmetatarsomere in *Gakasha* **gen. nov.** are provided with an apical row of teeth,  
485 similar to most Cicadocorinae – in *Ilahulgabalus*, the basimetatarsomere is provided  
486 with a row of small apical teeth and the midmetatarsomere is spatulate, elongate in the  
487 middle, with a lateral tooth (or two lateral teeth). The midmetatarsomere is about as  
488 long as the apical metatarsomere in *Gakasha* **gen. nov.**, while in *Ilahulgabalus* it is  
489 shorter. These differences could be related to the jumping abilities of these  
490 Cicadocorinae. Strongly armed metatibiae, with long lateral spurs and four apical  
491 spurs, together with long tarsus with apical teeth on basi- and midmetatarsomeres of  
492 *Gakasha calcaridentata* **gen. et sp. nov.** infer advanced jumping abilities in this  
493 species (Bonsignori et al., 2013; Burrows, 2007a, b, 2009b; Clemente et al., 2017). A  
494 single apical metatibial spur is a unique feature of the planthopper family Delphacidae  
495 Leach, 1815 (Fulgoroidea Latreille, 1807) (Asche, 1985; Bartlett et al., 2014; Wilson  
496 2005). According to Metcalfe (1969), it appears to have developed from an apical

497 tibial spine, and represents a sequence of primitive to advanced states, i.e., thick and  
498 spike-like to thin and flattened, which is also reflected in the ontogeny of delphacids,  
499 and is of evolutionary and classification importance (Wilson and McPherson, 1981).  
500 The exact role of this spur during jumping is not studied yet, but it could be assumed  
501 that it prevents legs from slipping on the surface when preparing to jump on the one  
502 hand, and on the other, could serve as part of a sensory mechanism responsible for  
503 jump mechanics and co-ordination. Membranized episterna in front of the metacoxae  
504 and legs modified for jumping, with apical pectens of macrosetae bearing teeth on the  
505 metatibia and on enlarged basi- and midmetatarsomeres, were postulated as  
506 symplesiomorphies of Coleorrhyncha (Popov and Shcherbakov, 1996). Cicadocorinae  
507 are believed to be the best hoppers among the Coleorrhyncha, their decline in the  
508 mid-Cretaceous being synchronous with the rise of another groups of small, jumping  
509 Hemiptera (Popov and Shcherbakov, 1996), the modern planthoppers (Fulgoroidea  
510 Latreille, 1807) and leafhoppers (Cicadelloidea Latreille, 1802); probably also the  
511 first jumping psyllids (Psylloidea Latreille, 1807). The modern Peloridiidae are also  
512 able to jump (Burrows et al., 2007), but their metatibia lack any lateral spurs or

513 enlarged apical teeth, so the jumping mechanism in Cicadocorinae was probably  
514 different. The only family in which the apical movable spur on the metatibia is  
515 developed is Delphacidae: alas the exact jumping mechanics of these planthoppers is  
516 still unknown. Data about jumping abilities in representatives of Fulgoromorpha  
517 Evans, 1946 (Burrows, 2009, 2014a, b) and Cicadomorpha Evans, 1946 –  
518 froghoppers (Burrows, 2003, 2006a, b; Gorb, 2004; Sutton and Burrows, 2010),  
519 leafhoppers (Burrows, 2007a, b) and treehoppers (Burrows, 2013) suggest some  
520 similarities and differences in structure of body parts engaged in jumping, power  
521 amplification mechanisms, neural control and jumping mechanisms (Bräunig and  
522 Burrows, 2008; 2006a, b, 2007c, 2009a, 2010, 2013, 2014a, b; Burrows and Bräunig,  
523 2010; Burrows and Sutton, 2013; Burrows et al., 2008, 2011, 2014; Siwanowicz and  
524 Burrows, 2017; Sutton and Burrows, 2010). In recent Peloridiidae, the hind coxae are  
525 set more closely together, and may touch each other towards their most dorsal medial  
526 edges where some tubercles (microtrichia) are present (Burrows et al., 2007). They  
527 are not tightly linked together by attachment devices in contrast to the situation in  
528 froghoppers (Burrows, 2006b; Gorb, 2004) or leafhoppers (Burrows, 2007a). The

529 metacoxae of Cicadocorinae are tightly placed close to each other, similar to the  
530 situation in Cicadomorpha, and probably present some attachments. In the  
531 Heteroptera Latreille, 1810 (Saldidae Amyot et Audinet-Serville, 1843 and Miridae  
532 Hahn, 1831) two distinct jumping strategies are used (Burrows, 2009b, Burrows and  
533 Dorosenko, 2017), and it seems that in the case of Cicadocorinae, in which the  
534 hindwings are well developed, but metatibiae not extremely elongated, the addition of  
535 wing movements to the propulsive movements of the legs has made their jumping  
536 performance more effective.

537 Jumping ability is often treated as a single character (Hennig, 1981; Shcherbakov  
538 and Popov, 2002); however, this ability was actually achieved by a combination of  
539 many structural modifications of the legs and thorax, including those of muscles,  
540 muscle attachments, and associated sclerites involving energy storage and the locking  
541 system, among others (Gorb, 2004). Ogawa and Yoshizawa (2017), after detailed  
542 studies of metathoracic muscular characters suggested that almost all apomorphic  
543 conditions associated with jumping ability evolved independently in Cicadomorpha  
544 and Fulgoromorpha. Thus, regarding particular morphological structures in

545 Cicadorinae, i.e. closed metacoxae, elongated metatibiae, presence of apical spurs  
546 preventing slipping, elongate tarsal segments with apical rows of teeth, we can also  
547 assume that jumping mechanisms and adaptation details in Cicadorinae could differ  
548 from those observed in modern hemipterans.

549 The abdomen of *Gakasha* **gen. nov.** differs from females of other Cicadorinae  
550 with the 3<sup>rd</sup> abdominal segment being longer laterally than the following segments 4<sup>th</sup>  
551 to 7<sup>th</sup> (the abdominal segments are homonomous in lateral length). In this, it more  
552 resembles the situation in the female abdomens of modern Peloridiidae (Burckhardt,  
553 2009, Sweet, 1996) with the first two abdominal segments narrowed and diminished.  
554 Distinct hypopleurites (3<sup>rd</sup> to 7<sup>th</sup>) with spiracle placed mediad and close to the margin  
555 also resemble the situation in Peloridiidae. A unique feature of *Gakasha* **gen. nov.** is  
556 the enlarged female 7<sup>th</sup> abdominal sternite, covering the base of the ovipositor, as it is  
557 observable among Cicadellidae. Another peculiar feature of *Gakasha* **gen. nov.** is the  
558 presence of the enlarged 8<sup>th</sup> hypopleurites (paratergites) forming the elongate, tapered  
559 caudad processes. An ovipositor with gonoplacs fused dorsally, covering the 8<sup>th</sup> and  
560 9<sup>th</sup> gonapophyses, with a ventral slit, is peculiar and also resembles more the so-called

561 saw-case present in Cicadellidae. In known Cicadocorinae, the 9<sup>th</sup> abdominal segment  
562 of the females seems to be rather barrel-shaped, with obtuse posterior margin; it is  
563 small in *Gakasha* **gen. nov.**, flattened, only with posterolateral angles visible.  
564 Karabasiidae have a 9<sup>th</sup> abdominal segment broadly emarginate apically, embracing  
565 the base of anal tube; in Hoploridiidae, the 9<sup>th</sup> segment is wider than long, with  
566 distinctly truncate lateral lobes (Popov and Shcherbakov, 1991). Unlike in  
567 Peloridiidae, in *Gakasha* **gen. nov.** the base of anal tube of the female is not  
568 concealed by lateral lobes of the 9<sup>th</sup> abdominal segment. The details of the genital and  
569 paragenital structures of Cicadocorinae are still poorly known, but seem to be variable,  
570 and could provide important phylogenetic information.

571 Morphology-based cladistic analyses, with revised morphological observations and  
572 including Coleorrhyncha, supported the relationship of Coleorrhyncha+Heteroptera  
573 (Friedemann et al., 2014) as clade Prosorrhyncha (Szwedo, 2018); this opinion was  
574 also supported by molecular phylogenetic studies based on 18S rRNA (Campbell et  
575 al., 1995; Ouvrard et al., 2000; Wheeler et al., 1993) and multiple gene regions (Cryan  
576 and Urban, 2012). Recent phylogenomic study of Hexapoda that incorporated data

577 from >1,400 gene regions (Misof et al., 2014) casted doubt on this view. A sister  
578 group relationship between Coleorrhyncha and Heteroptera was also refuted by recent  
579 mitochondrial phylogenomic analyses (Cui et al., 2013; Wang Y. et al., 2015).  
580 Moreover, recent studies of wing base structure (Yoshizawa et al., 2017) suggested  
581 that Coleorrhyncha could be more closely related to Cicadomorpha and  
582 Fulgoromorpha than to Heteroptera. Therefore, an apparent conflict between various  
583 morphological and molecular data and their interpretations has arisen in the placement  
584 of Coleorrhyncha. Regarding the fossil record of the group, the Coleorrhyncha  
585 appeared in the Late Permian, as descendants of Ingruidae (Fig. 7) – the group close  
586 to highly diversifying early Cicadomorpha during the Permian (Popov and  
587 Shcherbakov, 1996; Shcherbakov and Popov, 2002; Szwedo, 2018). Coleorrhyncha is  
588 monophyletic lineage, divided into two main clades. The family Progonocimicidae  
589 seems not to be a monophylum, contrary to the opinion of Dong et al. (2014), based  
590 on a very limited number of taxa examined. Cicadocorinae seems to form a single  
591 lineage, but the status of Progonocimicinae is not clear. Placement of the genus  
592 *Pelorisca* Popov et Shcherbakov, 1991 in this subfamily is controversial (Popov and

593 Shcherbakov, 1991). The family Karabasiidae seems to be the monophyletic sister  
594 group to Hoploridiidae + Peloridiidae (Fig. 7). The ancient history of the  
595 Coleorrhyncha, together with the high specialization and relictual character of its  
596 recent representatives could be one of the sources of incongruences in phylogenetic  
597 proposals.

598

599 *Distributional pattern of Cretaceous Cicadocorinae*

600 The Cretaceous representatives of Cicadocorinae present interesting distributional  
601 pattern, with *Ildavia*, *Yuripopovia* and *Valdiscytina* from the Lower Cretaceous  
602 deposits of the United Kingdom, *Popovus* from the Lower Cretaceous of western  
603 Mongolia, *Onokhoia* from the Lower Cretaceous of Transbaikalia (Russia), and two  
604 genera from more southern latitudes – *Ilahulgabalus* from the Lower Cretaceous  
605 amber of Lebanon and *Gakasha* **gen. nov.** from mid-Cretaceous Burmese amber  
606 (Table 1; Figs. 1 and 7). According to palaeoclimatic reconstructions for the Early  
607 Cretaceous (Skalton, 2003; Chumakov, 2004), Cicadocorinae were mainly distributed  
608 in the temperate warm humid zone (Hauterivian to Aptian), except *Ilahulgabalus*,



609 present much more south in the tropical equatorial dry zone in the lower Barremian  
610 (Maksoud et al., 2017), but with the climate more mild and humid (Azar et al., 2003,  
611 2010). *Gakasha* **gen. nov.** dates from earliest Cenomanian times, from the equatorial  
612 humid zone, but according to palaeotopographic data, with arid influence caused by  
613 elevated areas nearby (Li, et al. 2018; Skelton, 2003; Wu et al., 2017). By the mid  
614 Cretaceous, extensive outgassing of carbon dioxide due to magmatic eruptions at  
615 oceanic ridges and vast outpourings of lava and volcanic activity, rising sea level  
616 (lowering albedo), and the continuing breakup of Pangea had led to long-term global  
617 warming (~20°–22°C). Therefore the global climate was one of the warmest in  
618 Earth's history (Hay, 2017; Hay and Floegel, 2012). The data from palaeoclimatic  
619 reconstructions (Chumakov, 1995, 2004; Chumakov et al., 1995; Zhou et al., 2012)  
620 suggest that the Equatorial-Tropical arid belts associated with the descending limbs of  
621 the Hadley cells were extensive in the Early Cretaceous, becoming more restricted in  
622 the warmer Late Cretaceous, and that vegetation spread to warm high latitudes and  
623 cool low latitudes in a warm climate with a high level of CO<sub>2</sub> (Zhou et al., 2012),  
624 similar to the pattern of modern vegetation (Bonan, 2008). The find of Cicadocorinae

625 in Burmese amber put a new question to the reconstruction of Burmese amber forests  
626 biota, as the Cicadocorinae more probably inhabited rather humid environments.  
627 Palaeoenvironmental details and palaeoecological reconstructions for the Burmese  
628 amber forest have not been fully elaborated yet. Palynological study suggests a humid  
629 warm temperate climate (Cruickshank and Ko, 2003) for resin production and amber  
630 deposition. Both pollen and plant fossils identified so far, suggest that the  
631 amberiferous forest was placed in the equatorial floristic realm (Vakhrameev, 1988).

632

### 633 **5. Concluding remarks**

634 Summary of taxonomic changes: *Mesocimex lini* Wang, Szwedo et Zhang, 2009  
635 **stat. resurr.** from *Cicadocoris brunneus* (Hong, 1983); *Cicadocoris kuliki*  
636 Becker-Migdisova, 1958 **stat. resurr.** from *Mesocimex kuliki* (Becker-Migdisova,  
637 1958); *Cicadocoris affinis* (Yu. Popov, 1982) **stat. resurr.** from *Mesocimex affinis* (Yu.  
638 Popov, 1982); *Cicadocoris arcuatus* (Yu. Popov, 1982) **stat. resurr.** from *Mesocimex*  
639 *arcuatus* (Yu. Popov, 1982). *Cicadocoris frater* (Yu. Popov, 1982) **stat. resurr.** from  
640 *Mesocimex frater* (Yu. Popov, 1982). Incertae sedis taxa within the genus  
641 *Cicadocoris*: ?*C. admotus* (Yu. Popov, 1982), ?*C. complexus* (Yu. Popov, 1982), ?*C.*  
642 *confinis* (Yu. Popov, 1982), ?*C. conjunctus* (Yu. Popov, 1982), ?*C. distans* (Yu. Popov,  
643 1982), ?*C. ignoratus* (Yu. Popov, 1982), ?*C. parallelus* (Yu. Popov, 1982), ?*C. similis*

644 (Yu. Popov, 1982), ?*C. sogjutensis* (Yu. Popov, 1982), ?*C. turanicus*  
645 (Becker-Migdisova, 1958). Conserved collective '*Olgamartynovia*' with  
646 '*Olgamartynovia rigida* Yu. Popov, 1982; '*Olgamartynovia beckermigdisovae* Yu.  
647 Popov, 1982; '*Olgamartynovia nana* Yu. Popov, 1982; '*Olgamartynovia*'  
648 *transbaikalica* Yu. Popov, 1985 and '*Olgamartynovia distincta* Yu. Popov, 1982.  
649 Incertae sedis taxa within the genus *Mesocimex*: ?*M. admotus* (Yu. Popov, 1982) **stat.**  
650 **resurr.**, ?*M. complexus* (Yu. Popov, 1982) **stat. resurr.**, ?*M. confinis* (Yu. Popov,  
651 1982) **stat. resurr.**, ?*M. conjunctus* (Yu. Popov, 1982) **stat. resurr.**, ?*M. distans* (Yu.  
652 Popov, 1982) **stat. resurr.**, ?*M. ignoratus* (Yu. Popov, 1982) **stat. resurr.**, ?*M.*  
653 *parallelus* (Yu. Popov, 1982) **stat. resurr.**, ?*M. parvus* (Jiang et Huang, 2017) **comb.**  
654 **nov.**, ?*M. similis* (Yu. Popov, 1982) **stat. resurr.**, ?*M. sogjutensis* (Yu. Popov, 1982)  
655 **stat. resurr.**, ?*M. turanicus* (Becker-Migdisova, 1958) **stat. resurr.**, ?*M. varians*  
656 (Dong, Yao et Ren, 2012) **comb. nov.**

657 *Gakasha calcaridentata* **gen. et sp. nov.** described above is the first representative  
658 of Cicadocorinae: Progonocimicidae found in Burmese amber. It is the second know  
659 taxon in amber, the latest known representative of the family, and the second known  
660 cicadocorine from the equatorial belt. *Gakasha calcaridentata* **gen. et sp. nov.** is very  
661 peculiar in morphological features, presenting a high level of morphological  
662 specialization. Apart generally uniform body structure and venation shared by most of  
663 Cicadocorinae, the new taxon presents specialized form in the antennae, highly

664 modified armature of the hind legs (probably related to its jumping ability), and  
665 specialized female genital structures (with tubular ovipositor). *Gakasha*  
666 *calcaridentata* **gen. et sp. nov.**, with its morphological peculiarities also casts some  
667 light on the taxonomic and nomenclatorial problems within Cicadocorinae, giving  
668 new pointers to the disparity of Cicadocorinae.

669 The relationships within the group and systematics of Cicadocorinae remain  
670 obscure. The venational characters of the genera and species seems to be reliable only  
671 to some extent, so new characters and a new approach to the available data are  
672 necessary to resolve nomenclatorial and systematic problems within Cicadocorinae  
673 and Progonocimicidae. Finding a well-preserved specimen entombed in amber gives a  
674 new opportunity to better understand the evolutionary history of the group including  
675 its diversity and morphological disparity.

676

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691

692 **References**

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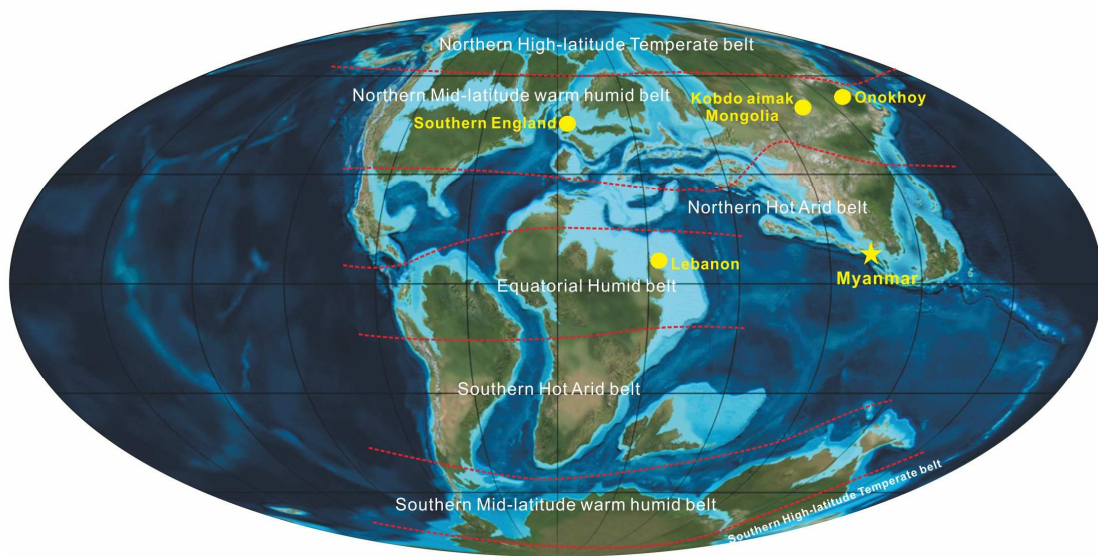
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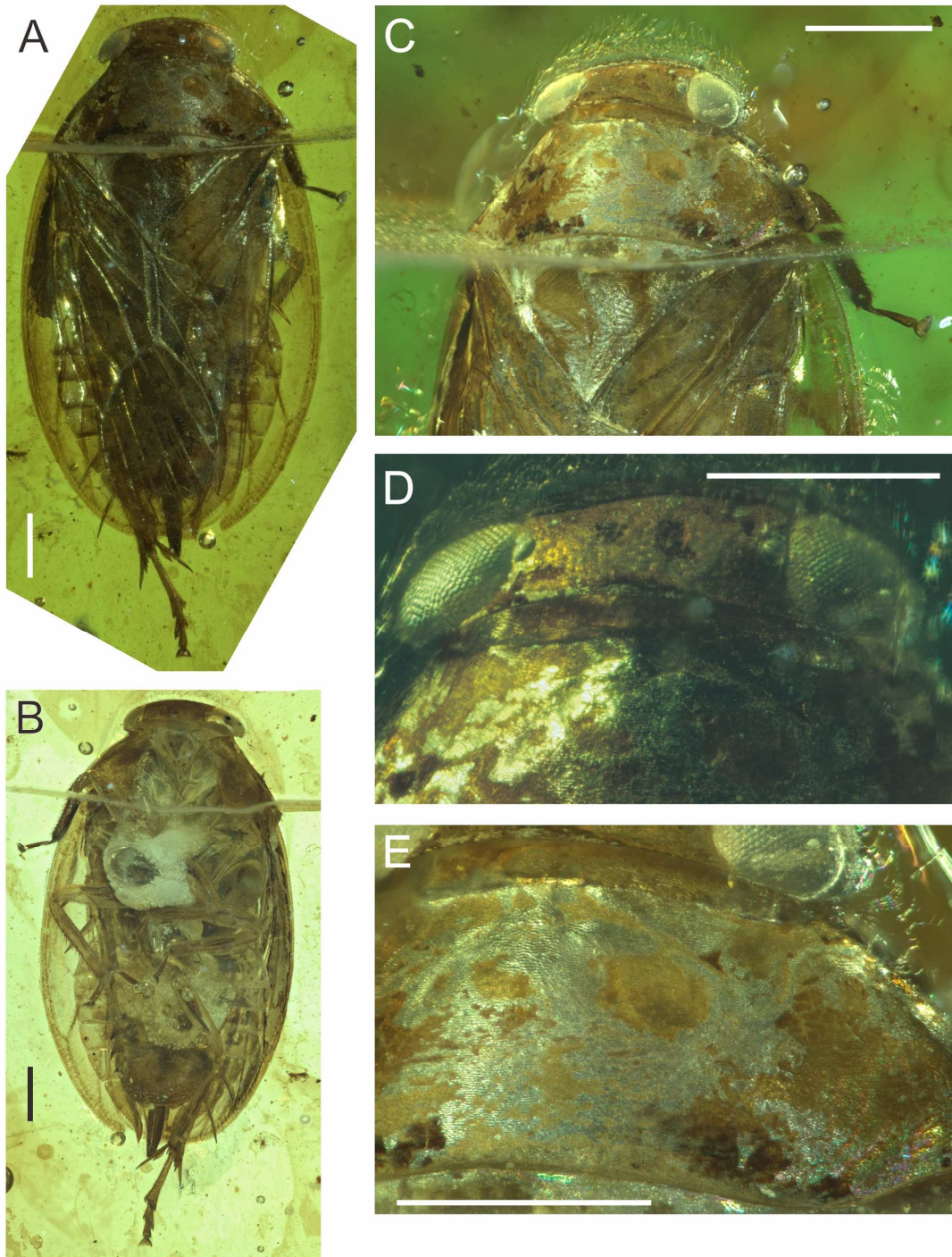
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1026 Captions to figures



1027

1028 Fig. 1. Distribution map of known Cretaceous Progonocimicidae: Cicadocorinae,  
 1029 palaeogeographic reconstruction for 105 Ma, courtesy of Professor Ron Blakey  
 1030 (Colorado Plateau Geosystems, Inc.); climatic belts after Skelton (2003) and  
 1031 Chumakov (2004).



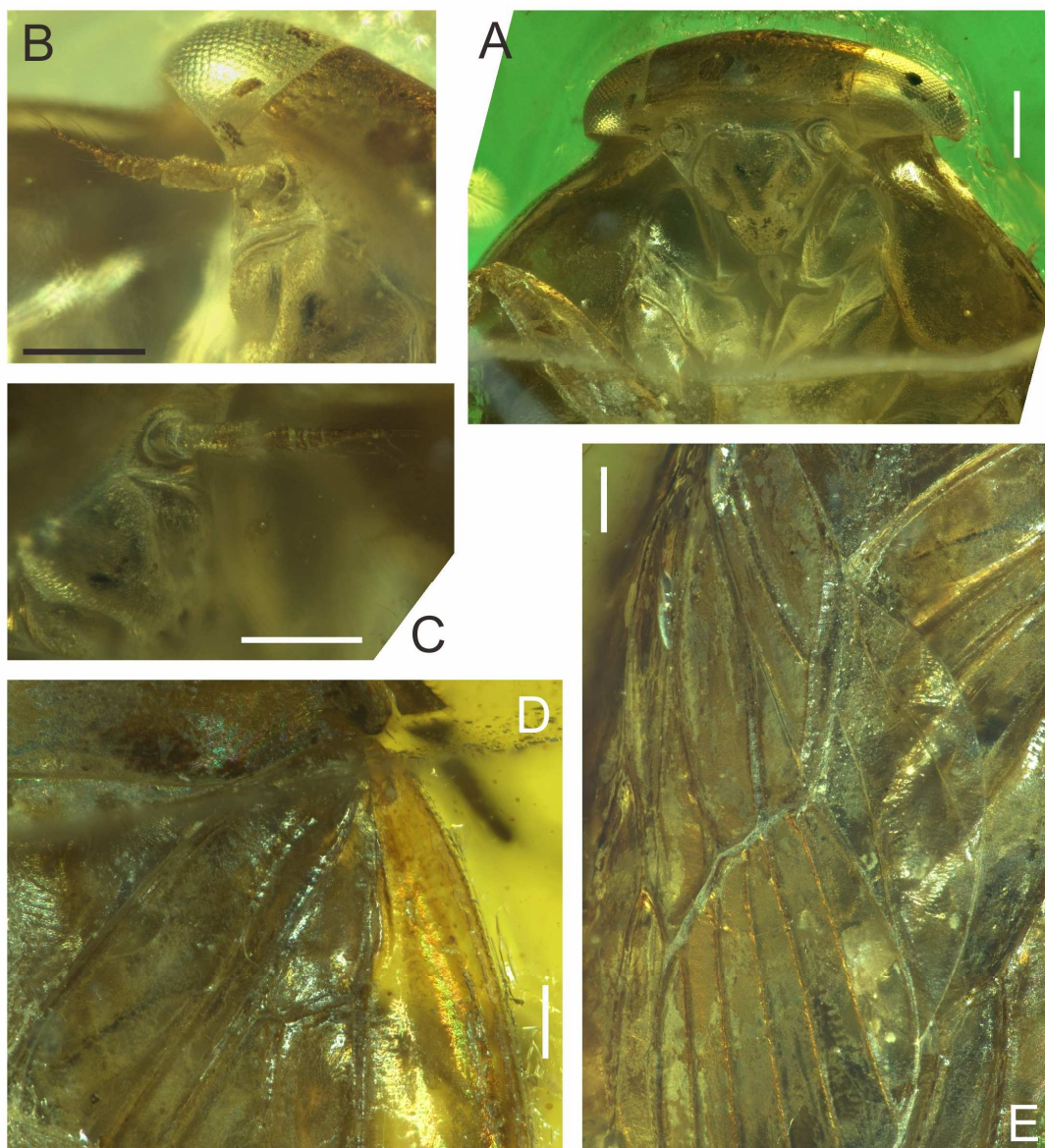
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1033 Fig. 2. *Gakasha calcaridentata* **gen. et sp. nov.** A. General dorsal view of the

1034 specimen. B. Ventral view of the specimen. C. Anterior portion of body. D. Head in

1035 dorsal view. E. Sculpture of pronotum. Scale bars: 0.5 mm.





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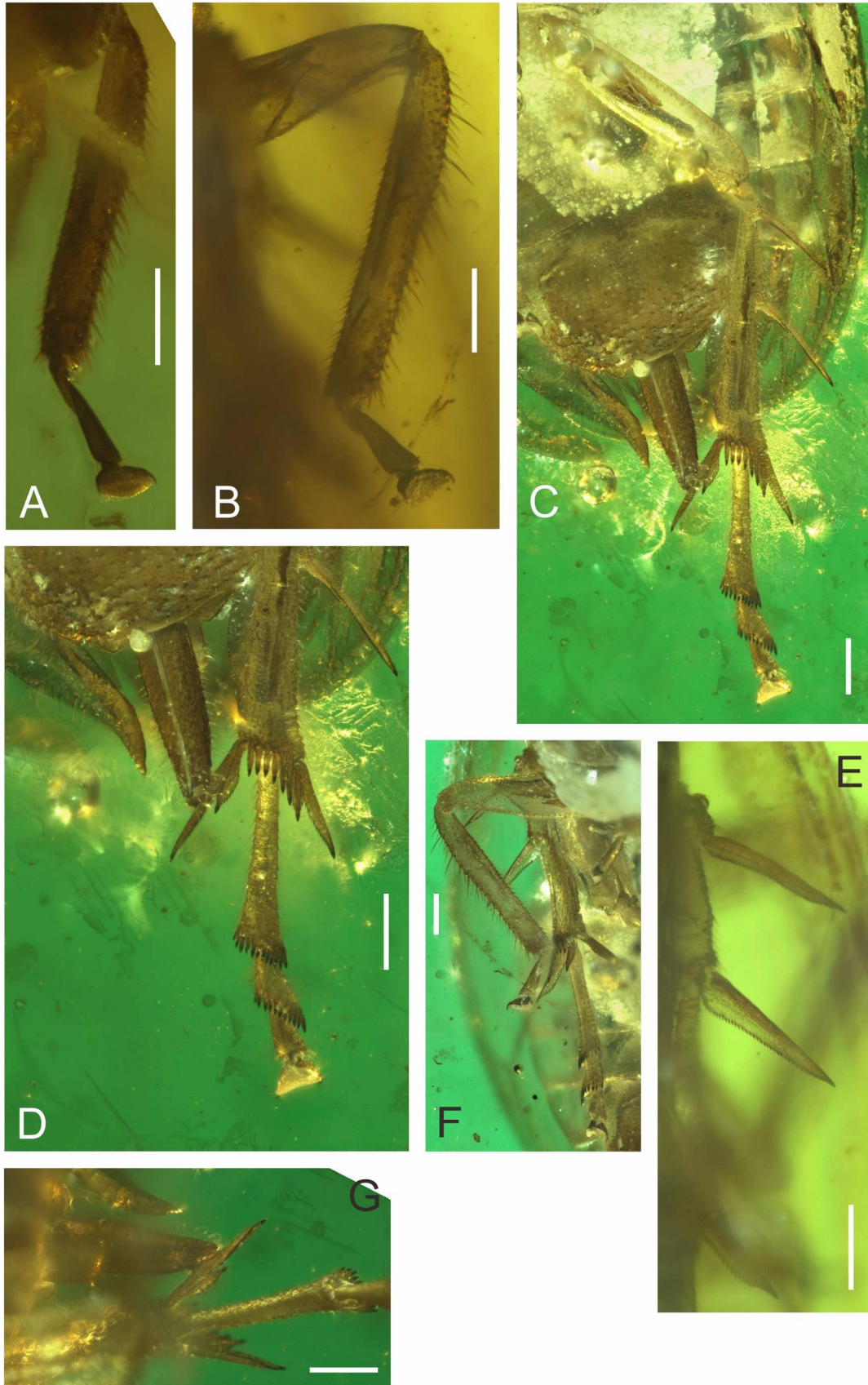
1037 Fig. 3. *Gakasha calcaridentata* **gen. et sp. nov.** A. Head in ventral view. B. Right

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antenna. C. Left antenna. D. Basal cell of right tegmen. E. Claval margin, tornus,

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nodal line of left tegmen and posterior part of left hind wing.

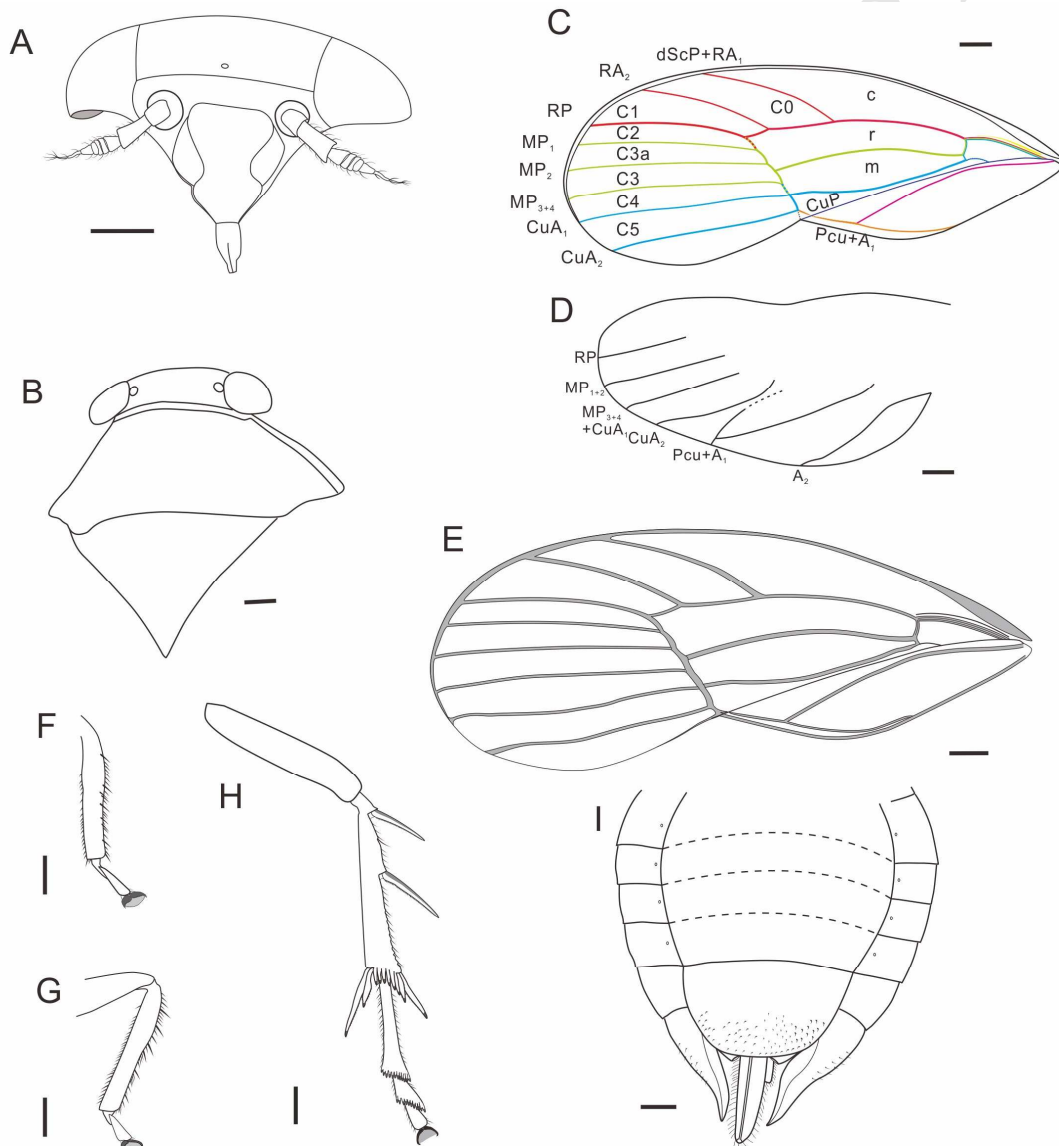


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1041 Fig. 4. *Gakasha calcaridentata* **gen. et sp. nov.** A. Protibia and protarsus. B;



1042 Mesofemur, mesotibia and mesotarsus; C. Left metatibia. D. Left metatarsus,  
 1043 female genital plate, ovipositor and anal tube, ventral view. E. Lateral spurs of  
 1044 left metatibia. F. Right metatarsus, ventral view. G. Anal tube, ovipositor and  
 1045 left metatarsus, dorsal view through the tegmen membrane.

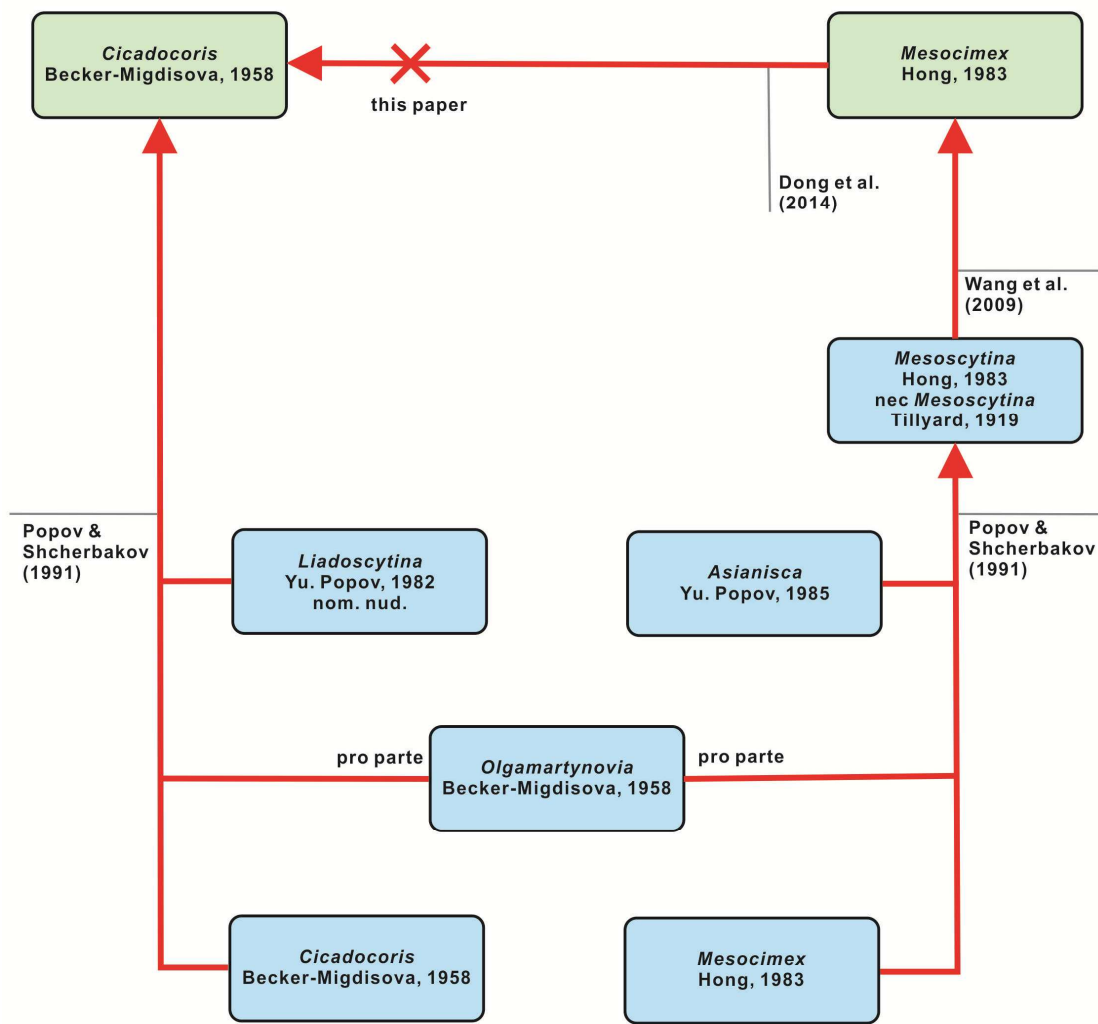


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1047 Fig. 5. *Gakasha calcaridentata* gen. et sp. nov. A. Head in anteroventral view. B.

1048 Outline of head, pronotum and mesonotum, dorsal view. C. Left tegmen, pattern of

1049 venation and cell nomenclature, c - costal cell, r - radial cell; m – median cell. D.  
 1050 Hindwing venation pattern. E. Left tegmen. F. Protibia and protarsus; G. Mesoleg.  
 1051 H. Metaleg. I. Female abdomen and genital structures, ventral view. Scale bars: 0.2  
 1052 mm.



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1054 Fig. 6. Graphical summary of taxonomic decisions and synonyms of the genera

1055 *Cicadocoris* and *Mesocimex*.



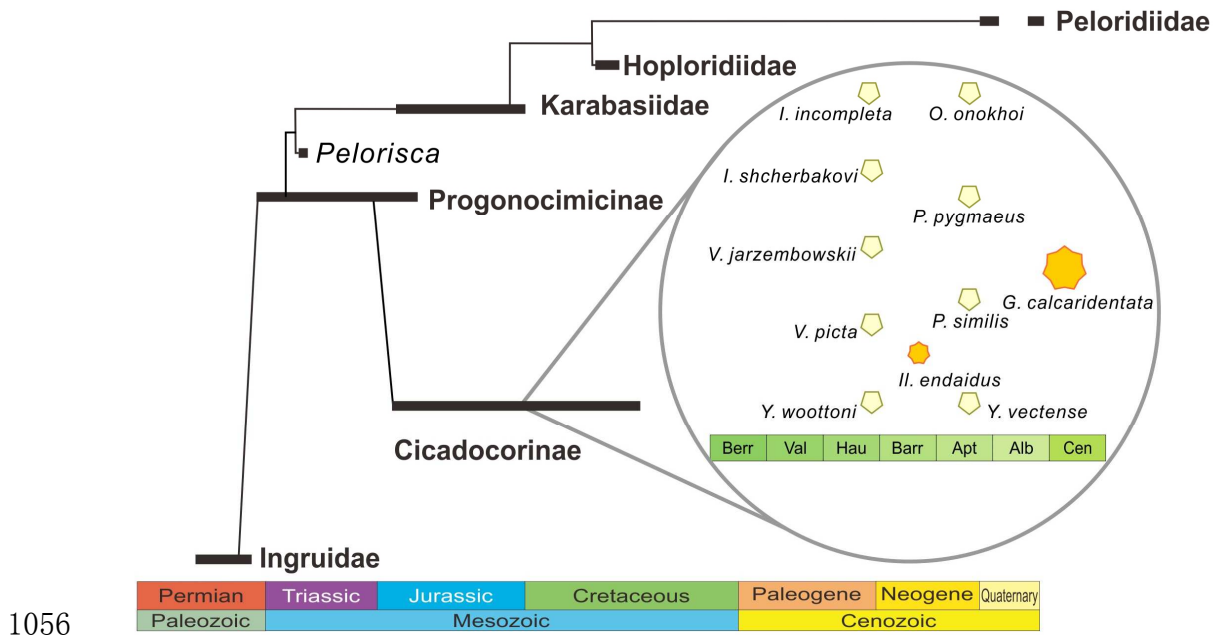


Fig. 7. Evolutionary outline of main Coleorrhyncha lineages with more detailed reference to the Cretaceous Cicadocorinae. Note that Progonocimicinae as recently understood seems not to form a monophyletic lineage.

Table 1. List of species of Progonocimicidae in Cretaceous

Species	Locality	Geological age
<i>Gakasha calcaridentata</i> gen. et sp. nov.	Noije Bum Hill, Burmese amber	Cenomanian (ca. 99.8 Ma)
<i>Onokhoia onokhoiensis</i> Popov, 1988	Onokhoy, Transbaikal Krai, Russia	Aptian (125.45-112.6 Ma)
<i>Popovus pygmaeus</i> (Yu. Popov, 1986)	Kobdo aimak, Mongolia	Aptian (125.5-112.6 Ma)
<i>Popovus similis</i> (Yu. Popov, 1986)	Kobdo aimak, Mongolia	Aptian (125.5-112.6 Ma)
<i>Yuripopovia vectense</i> Heads, 2008	Atherfield, Isle of Wight, United Kingdom	Aptian (125.45-122.46 Ma)
<i>Ilahulgabalus endaidus</i> Szwedó, Azar et Ziadé, 2011	Daychouniyyeh, Lebanon	Barremian (130-125.45 Ma)
<i>Ildavia incompleta</i> Yu. Popov, 1993	Keymer Tile Works, United Kingdom	late Hauterivian (136.4-130 Ma)
<i>Valdiscytina picta</i> Yu. Popov, 1993	Keymer Tile Works, United Kingdom	late Hauterivian (136.4-130 Ma)
<i>Ildavia shcherbakovi</i> Yu. Popov, 1993	Clockhouse Brickworks, United Kingdom	late Hauterivian (136.4-130.0 Ma)
<i>Valdiscytina jarzembowskii</i> Yu. Popov, 1993	Clockhouse Brickworks, United Kingdom	late Hauterivian (136.4-130.0 Ma)
<i>Yuripopovia woottoni</i> Jarzembowski, 1991	Clockhouse Brickworks, United Kingdom	late Hauterivian (136.4-130.0 Ma)

## Highlights

- First Coleorrhyncha: Progonocimicidae: Cicadocorinae was described from Burmese amber
- It is the complete specimen and presents peculiar morphological characters
- It inhabited equatorial climatic zone, during the warm times of the mid-Cretaceous