



Li, Y-D., Liu, Z-H., Jarzembowski, E. A., Yin, Z-W., Huang, D-Y., & Cai, C-Y. (2019). Early evolution of Cupedidae revealed by a mid-Cretaceous reticulated beetle from Myanmar (Coleoptera: Archostemata). *Systematic Entomology*, 44(4), 777-786.  
<https://doi.org/10.1111/syen.12355>

Peer reviewed version

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[10.1111/syen.12355](https://doi.org/10.1111/syen.12355)

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1 **Early evolution of Cupedidae revealed by a mid-Cretaceous reticulated beetle from Myanmar**  
2 **(Coleoptera: Archostemata)**

3

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22 This published work has been registered in ZooBank,

23 <http://zoobank.org/urn:lsid:zoobank.org:pub:313565C2-4F42-48BD-8720-F379DE202868>.

24

25 **Abstract.**

26 Cupedidae, the most species-rich family of the archaic suborder Archostemata, were abundant, diverse and  
27 widespread in the Mesozoic, yet little is known about the early evolution and biogeography. This stems, in  
28 part, from a lack of exceptionally preserved fossils from the Mesozoic and of formal phylogenetic study of

29 both extant and extinct taxa. Here we describe and illustrate a new fossil from mid-Cretaceous Burmese amber,  
30 and provide a phylogeny combining both fossils and all known extant genera of Archostemata. A dataset of 43  
31 in-group taxa and 4 out-group taxa based on 110 morphological characters was analyzed under parsimony.  
32 The results indicate that *Priacma* LeConte and *Paracupes* Kolbe, as well as the Cretaceous genera  
33 *Barbaticupes* Jarzembowski *et al.* and *Mallecupes* Jarzembowski *et al.*, together form a sister clade to the rest  
34 of Cupedidae. *Priacma megapuncta* **sp.n.** is attributed to the relict North American *Priacma* by the presence  
35 of distinct subtruncate elytral apices, lateral elytral margins with two rows of sharp teeth, and peculiar fixing  
36 epipleural folds near the elytral apices. Our discovery of the first fossil species of *Priacma* in Burmese amber  
37 reveals the antiquity and wider distribution of the genus in the late Mesozoic.

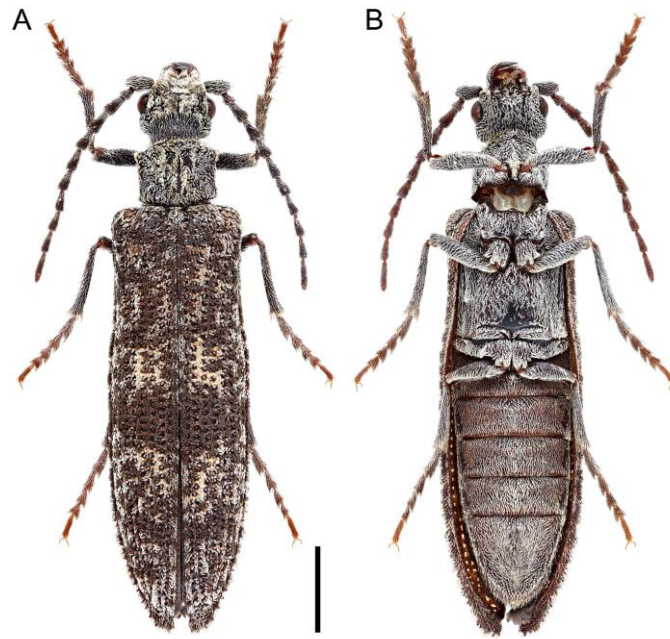
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## 39 **Introduction**

40 The beetle suborder Archostemata is currently a comparatively small group of Coleoptera, with 45 species  
41 occurring in South America, North America, Europe, Asia, and Australia (Hörschemeyer, 2016). Compared  
42 to their extant fauna, archostematans were abundant and diverse in the fossil record, especially from the  
43 Mesozoic era (Hörschemeyer, 2016; Kirejtshuk *et al.*, 2016). The earliest-known beetles from the Permian  
44 are superficially like Archostemata (Ponomarenko 1969), but represent stem-group Coleoptera (Beutel &  
45 Friedrich, 2008; Hörschemeyer, 2016). Archostemata currently comprises Cupedidae, Ommatidae,  
46 Micromalthidae, Crowsoniellidae, and possibly Jurodidae (Hörschemeyer, 2016), but the interrelationships  
47 among them remain unsettled, as phylogenies based on morphological characters and molecular data have  
48 yielded inconsistent topologies (e.g., Beutel *et al.*, 2008; Hörschemeyer, 2009; Lawrence *et al.*, 2011;  
49 McKenna *et al.*, 2015; Linard *et al.*, 2018). It is noteworthy that some authors adopted a broader concept of  
50 Cupedidae, regarding the family Ommatidae as a subfamily within Cupedidae *sensu lato* (e.g., Ponomarenko,  
51 2000; Kirejtshuk *et al.*, 2016).

52 Among extant archostematan families, Cupedidae (or reticulated beetles), characterized by a widened  
53 subapical tarsomere and capitate galea, is the most species-rich group with thirty-one extant species attributed  
54 in nine genera (Hörschemeyer, 2009; Hörschemeyer & Yavorskaya, 2016). A comprehensive  
55 morphology-based phylogenetic analysis by Hörschemeyer (2009) indicated that the species-poor genera  
56 *Priacma* LeConte and *Paracupes* Kolbe together comprise the sister clade to the rest of crown-group

57 Cupedidae. Although Cupedidae is the most diverse archostematan family today, fossils belonging to  
58 Cupedidae appear to be much more abundant and diverse in the Mesozoic than in the present (Kirejtshuk *et al.*,  
59 2016). Fossil cupedids are mainly preserved as compressions, of which many key characters are usually not  
60 well preserved or simply missing, obscuring reliable interpretation. Mesozoic cupedids are of great significant  
61 for understanding the origin and early diversification of this family, but the systematic positions of Mesozoic  
62 cupedids have never been tested in a formal phylogenetic analysis (e.g., Tan & Ren, 2009; Kirejtshuk *et al.*,  
63 2016). This stems, in part, from insufficient preservation of morphological features in the previously described  
64 compression fossils. Unlike compression fossils, amber, or fossilized resin, can preserve astonishingly fine  
65 details of bioinclusions with high fidelity. The mid-Cretaceous Burmese amber deposit in northern Myanmar  
66 is one of the most prolific and extensively studied sources of Mesozoic exceptional faunas (e.g., Grimaldi *et*  
67 *al.*, 2002; Shi *et al.*, 2012; Cai *et al.*, 2017; Cai *et al.*, 2018; Xing *et al.*, 2018). Recent years have witnessed  
68 exciting discoveries of an increasing number of archostematan beetles from this mid-Cretaceous Burmese  
69 amber. Most described archostematans are represented by members of the extant Southern Hemisphere family  
70 Ommatidae (Jarzembowski *et al.*, 2016, 2017a, 2017b, 2018a, 2018b; Jarzembowski & Wang, 2016; Liu *et al.*,  
71 2017; Yamamoto, 2017). By contrast, only three species, *Barbaticupes combertiae* Jarzembowski *et al.*, 2017c,  
72 *Mallecupes qingqingae* Jarzembowski *et al.*, 2017d and *M. clevelyi* Jarzembowski *et al.*, 2017e, have been  
73 assigned to the family Cupedidae *sensu stricto* (= Cupedinae *sensu* Kirejtshuk *et al.*, 2016). Based on our  
74 observation of more than 23,000 pieces of fossiliferous Burmese amber in our collection, cupedids appear to  
75 be rather rare when compared to other common archostematan species that can be placed in extant *Omma*  
76 Newman (Ommatidae). Here we report on the discovery of a novel cupedid species from Burmese amber.  
77 This fossil can be placed in the extant genus *Priacma* (Fig. 1), and provides insights into the early evolution of  
78 Cupedidae.



79

80 **Fig. 1.** *Priacma serrata*, the sole extant representative of *Priacma* from North America. Scale bars, 2 mm.

81

## 82 **Material and methods**

### 83 *Material and photography*

84 The Burmese amber specimen containing the new species studied here is derived from the Hukawng Valley in  
85 Tanai Township, Myitkyina District of Kachin State, Myanmar. The holotype (NIGP168831) is deposited in  
86 the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The  
87 amber piece was trimmed with a small table saw, ground with emery papers of different grain sizes, and  
88 finally polished with polishing powder. The holotype is a nearly completely preserved adult, with almost all  
89 morphological details visible, but the apical six antennomeres of the right antenna were polished away. Three  
90 previously published cupedid species were also re-examined, including *Barbaticupes combertiae*  
91 (NIGP166314 & NIGP166315, Fig. S1), *Mallecupes qingqingae* (NIGP157008 & NIGP164791, Fig. S2) and  
92 *M. clevelyi* (NIGP164792, Fig. S3).

93 Observations and photographs were taken under incident light using a camera-attached to a Zeiss  
94 Discovery V20 stereo microscope, a Leica M205 C stereo microscope and a Canon EOS-1D X camera with a  
95 Canon MP-E 65mm f/2.8 1–5x macro lens. Epifluorescence images were obtained with Zeiss Axio Imager 2  
96 light microscope combined with fluorescence imaging systems. Images were stacked with CombineZP,

97 Helicon Focus 6 and Adobe Photoshop CC. The morphological terminology follows Hörnschemeyer (2009)  
98 and Hörnschemeyer & Yavorskaya (2016). The measurements were taken as follows: body length from apex  
99 of mandible to elytral apex; head length from mandibular apex to anterior margin of pronotum (from dorsal  
100 view); head width as maximum width of head across eyes; pronotal length as maximum length of pronotum;  
101 pronotum width as maximum width of pronotum; elytral length from anterior margin to apex; elytral width as  
102 maximum width of each elytron.

103

#### 104 *Taxa sampling, characters and phylogenetic analyses*

105 Taxon selection was mainly derived from a previously published work by Hörnschemeyer (2009). Exemplars  
106 included: (i) four outgroup taxa: *Blattella germanica* (Linnaeus) (Blattodea), *Sialis lutaria* (Linnaeus)  
107 (Megaloptera: Sialidae), *Trachypachus* sp. (Adephaga: Trachypachidae) and *Elateroides dermestoides*  
108 (Linnaeus) (Polyphaga: Lymexylidae); (ii) a total of 39 extant species of all extant genera of the families  
109 Cupedidae, Ommatidae, Micromalthidae and Crowsoniellidae; and (iii) four mid-Cretaceous cupedids from  
110 Burmese amber, including *B. combertiae*, *M. cleevelyi*, *M. qingqingae* and *P. megapuncta* **sp.n.**

111 The morphological data matrix was mainly modified from the dataset for extant archostematan  
112 phylogeny (Hörnschemeyer, 2009). We removed the enigmatic species, *Sikhotealinia zhiltzovae* Lafer, from  
113 the data matrix, because its subordinal placement remains contentious (Yan *et al.*, 2014, and references  
114 therein). An obscure and poorly defined character (median protuberances, character #14 in Hörnschemeyer,  
115 2009) was removed in our analyses. Specifically, the description of median protuberances (P3) on the head of  
116 some extant cupedids conflicted with what has been scored in the matrix. For example, P3 of *Ascioplaga*  
117 *mimeta* (Neboiss) was indicated in the labelled figure (Fig. 5 in Hörnschemeyer, 2009), whereas this character  
118 was coded as absent in the data matrix (Hörnschemeyer, 2009). In addition, a new character, the presence or  
119 absence of a fixing epipleural fold at the elytral apex, was added.

120 Parsimony analyses were performed with the program TNT version 1.5 (Goloboff *et al.*, 2008) assigning  
121 equal and implied weights. In the implied weighting analysis, the concavity value (*K*) was set to 12, which has  
122 been proven to yield a better topology against homoplastic characters (Goloboff *et al.*, 2018). Most parameters  
123 were set as default in the “new technology search”, while the value for “find min. length” was changed from 1  
124 to 1000. For each analysis, a majority-rule consensus was calculated, and non-parametric bootstrap analysis

125 was implemented by 10,000 pseudoreplicates. Character states were mapped onto the trees with WinClada  
126 version 1.0 (Nixon, 2002). Trees were drawn with the online tool iTOL version 4.2.3 (Letunic & Bork, 2016)  
127 and graphically edited with Adobe Illustrator CC 2017.

128

## 129 **Results**

### 130 *Systematic palaeontology*

131 Order Coleoptera Linnaeus, 1758

132 Suborder Archostemata Kolbe, 1908

133 Family Cupedidae Laporte, 1836 *sensu stricto*

134 Genus *Priacma* LeConte, 1861

135

136 †*Priacma megapuncta* Li & Cai sp.n. (Figs 2, 3, S4)

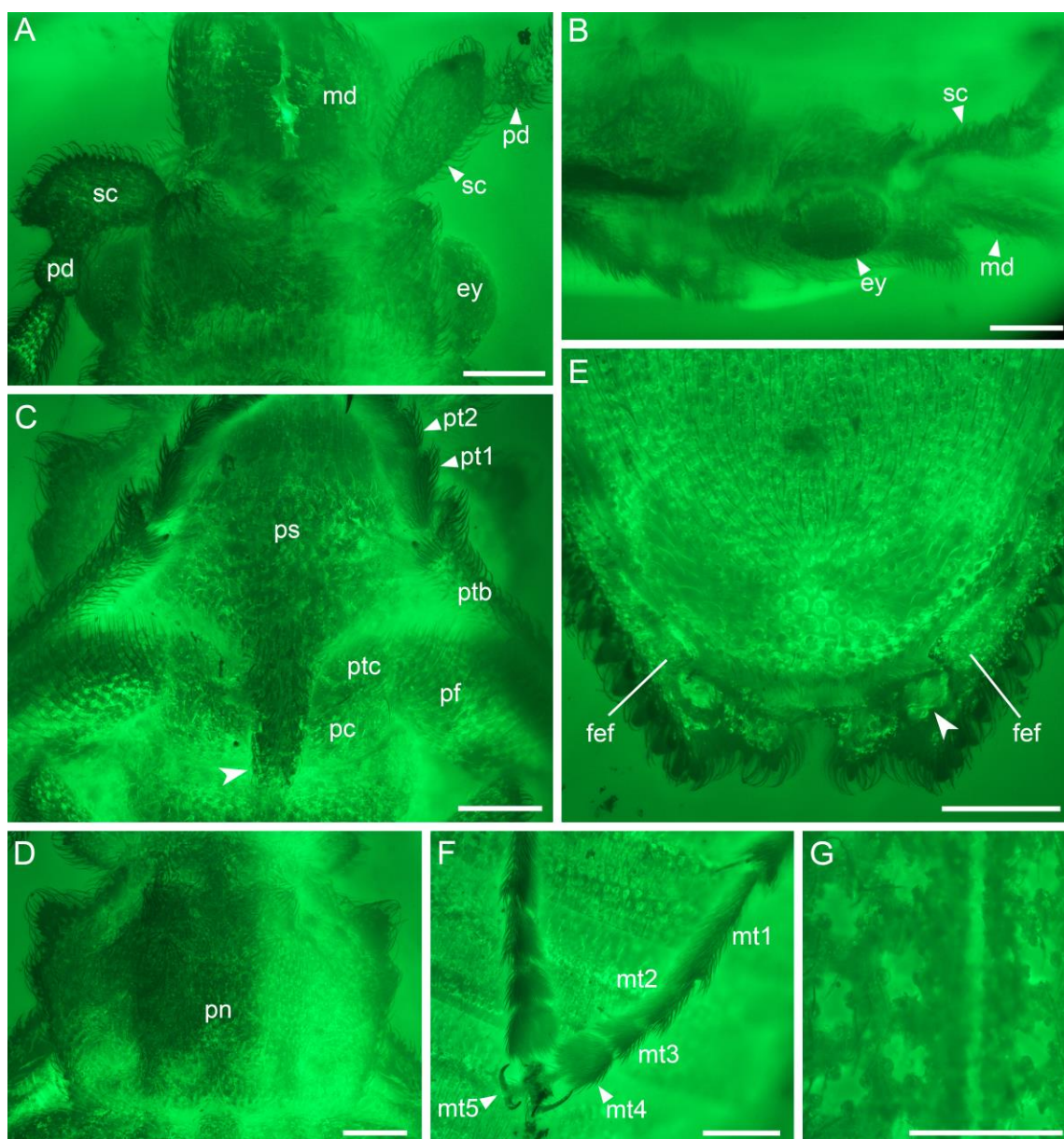
137 <http://zoobank.org/urn:lsid:zoobank.org:act:3495A03B-EECE-4120-B5CF-73268DFB39AC>.



138

139 **Fig. 2.** General habitus of *Priacma megapuncta* sp.n., holotype, NIGP168831. A, dorsal view. B, ventral view.

140 C, lateral view. Scale bars, 1 mm.



142

143 **Fig. 3.** Details of *Priacma megapuncta* sp.n., holotype, NIGP168831, under epifluorescence. A, B, head. A,  
 144 dorsal view. B, lateral view. C, D, prothorax. C, ventral view, showing the prosternal process extending  
 145 beyond the posterior margin of conical procoxae (arrowhead). D, dorsal view. E. elytral apices in ventral view,  
 146 showing the large window puncture (arrowhead) and fixing epipleural fold present at the elytral apices. F,  
 147 metatarsi. G, maculated window punctures on the elytra. Abbreviations: ey, compound eye; fef, fixing  
 148 epipleural fold; md, mandible; mt1–5, metatarsomeres 1–5; pc, procoxa; pd, pedicel; pf, profemur; pn,  
 149 pronotum; ps, prosternum; pt1,2, protarsomeres 1,2; ptb; protibia; ptc, protrochanter; sc, scape. Scale bars,  
 150 400  $\mu$ m.



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*Etymology.* The specific epithet is a combination of the Latin “*mega-*” and “*puncta*”, referring to the unusually large window puncture at the apex of each elytron.

*Material.* Holotype, NIGP168831. The fossil beetle is a well-preserved adult, with some body parts slightly polished away, including the apical antennomeres of the right antenna and the apex of the left mandible.

*Locality and horizon.* Amber mine located near Noiye Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, upper Albian or lower Cenomanian.

*Diagnosis.* The new species *P. megapuncta* can be separated from other *Priacma* species by the following combination of features: antennae slightly longer than half of the body length; pronotum with double tips at anterior corners; prosternal process extending beyond posterior margin of procoxae; and elytra with a single larger window puncture near elytral apex.

*Description.* Body elongate, 11.79 mm long, flattened, covered with short setae; scales absent; cuticle tuberculate. Head (Fig. S4A) subtriangular, 2.0 mm long (including mandibles) and 2.1 mm wide; dorsal protuberances (supraantennal and supraocular tubercles) on head inconspicuous, similar to that of *P. serrate*, inconspicuous. Compound eyes elliptical (not round as in *P. serrata* (LeConte)) from lateral view (Fig. 3B). Temples narrower than eyes, prominent. Antennae (Figs 3A; S4A, C) long, inserted laterally, reaching mid length of body, with 11 antennomeres, filiform; scape broad, flattened and curved, with serration on the edge; pedicel short; flagellomeres progressively becoming thinner distad with similar length, although apical antennomere slightly longer than others. Mandibles (Figs 3A; S4A, B) large and flattened; inner part of the dorsal surface blackened; inner margin also with wide and blunt teeth. Maxillary palpi reaching the mandible tip (Fig. S4B). Galeae capitate (Fig. S4B). Gular sutures not visible. Prementum reduced; ligula missing; mentum, submentum and head capsule fused. Pronotum (Fig. 3C) subtrapezoidal, 1.85 mm long and 2.36 mm wide, slightly wider than head but narrower than elytra combined, with double tips at anterior corners; anterior

179 tip subtriangular; posterior tip blunt; anterior margin convex medially, completely covering neck constriction  
180 from dorsal view; lateral margins serrated. Prosternal process extending beyond the posterior margin of  
181 conical procoxae (Figs 3D; S4D). Metacoxae large, subtriangular. Trochanters small. Femora stout;  
182 metafemora not extending beyond lateral edge of hind body. Tibiae thinner and longer than corresponding  
183 femora. Tarsi 5-segmented; tarsomere 4 distinctly bilobed; meso- and metatarsi (Fig. 3F) with elongated  
184 tarsomere 1; basal four tarsomeres with dense and dark setae ventrally, and tarsomere 5 with sparse setae.  
185 Claws simple. Elytra elongate, 7.95 mm long and each 1.51 mm wide, with ten rows of irregular and rounded  
186 window punctures with 4–5 maculae (Fig. 3G) as well as a single larger maculated window puncture near  
187 apex (Figs 3E; S4E, G); difference between primary veins and secondary veins inconspicuous; elytral apices  
188 emarginate (Figs 3E; S4E, G); notch extending beyond apex of abdomen; two rows of teeth well developed  
189 along distal five-sixths of lateral margins of elytra (Fig. S4F); fixing epipleural fold present at elytral apices  
190 (Figs 3E, S4G). Abdomen elongate, apex acute, rounded, with five visible ventrites; ventrite 5 twice as long as  
191 ventrite 4; all ventrites except the first markedly depressed anteriorly and overlapping the successors from  
192 below.

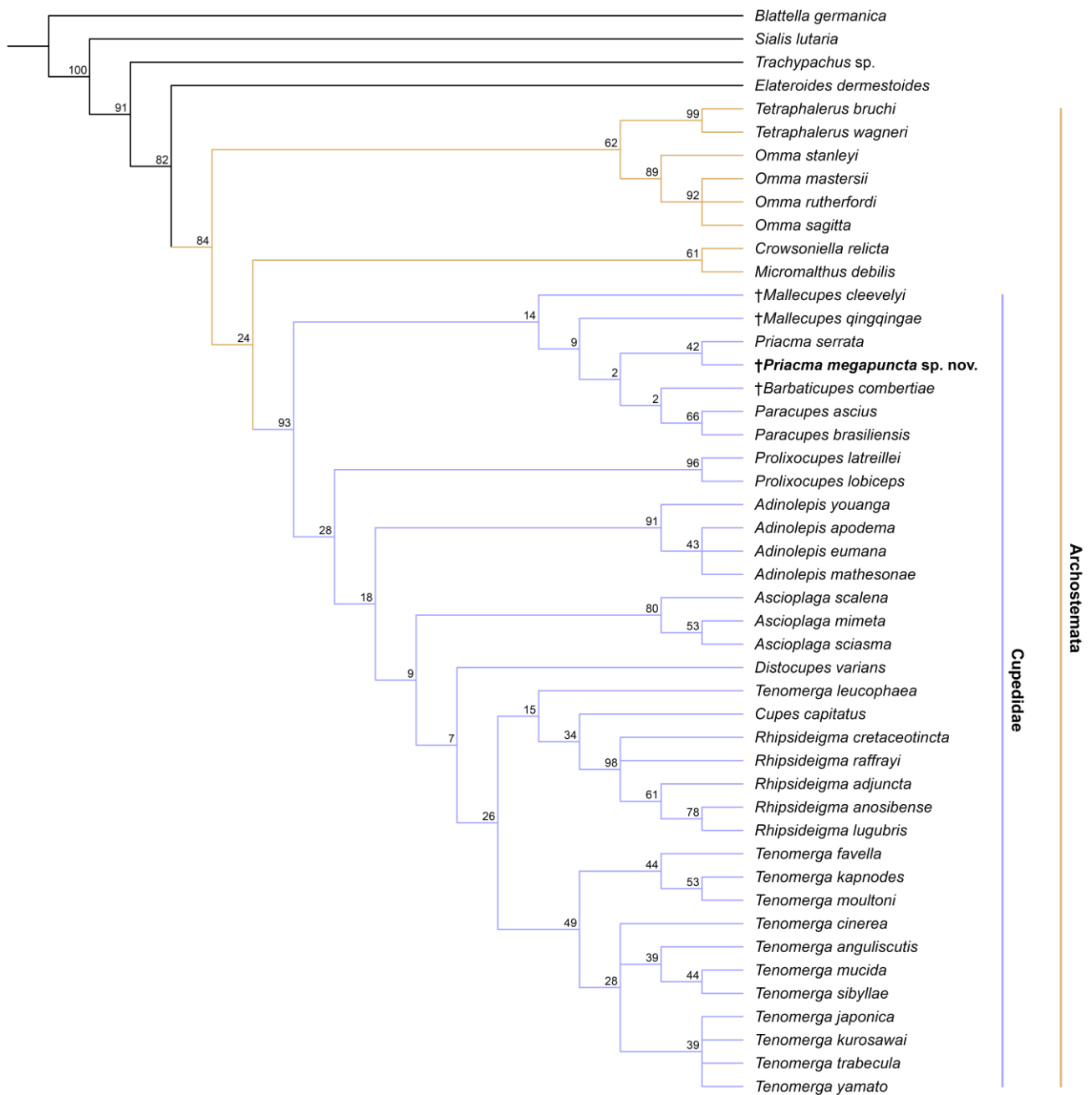
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194 *Remarks.* The overall body shape of *P. megapuncta* **sp.n.** is superficially similar to that of extant  
195 *Paracupes* species from South America, but it differs from the latter by many significant features (see  
196 discussion below). The fossil can be assigned with confidence to the *Paracupes*-related genus *Priacma* as  
197 evidenced by the distinct subtruncate elytral apices, the peculiar rows of sharp teeth along the lateral elytral  
198 margins (also found in *Paracupes* and *Mesocupes admotus* (Ponomarenko); Kirejtshuk *et al.*, 2016), and the  
199 presence of fixing epipleural folds near elytral apices (a synapomorphy of *Priacma*). All characters are  
200 distinctive among all extant cupedids, and they have been regarded as important diagnostic features for  
201 *Priacma* (Kirejtshuk *et al.*, 2016). In addition, *P. megapuncta* has widely separated antennae (distance  
202 between antennal insertions more than half the distance between eyes), and elongate and robust mandibles.  
203 Both characters are supportive of such a placement, although they may also be interpreted as plesiomorphies  
204 of Cupedidae.

205

206 *Phylogenetic assessment of Priacma megapuncta sp.n.*

207 Parsimony analyses using equal weights yielded 672 most parsimonious trees (280 steps long), in which  
208 Archostemata (excluding Jurodidae), Ommatidae and Cupedidae were all recovered as monophyletic groups,  
209 with moderate to strong support (Fig. S5). Micromalthidae and Crowsoniellidae were clustered together with  
210 relatively low support (bootstrap value = 52), and together were placed as the sister clade to the rest of  
211 Archostemata. The implied weighting analysis ( $K = 12$ ) yielded three most parsimonious trees, and most  
212 clades supported under equal weights were also recovered, though Micromalthidae and Crowsoniellidae were  
213 placed as the sister group of Cupedidae (Fig. 4). Regarding the systematic position of the fossil species *P.*  
214 *megapuncta* **sp.n.**, both results under parsimony, using equal weights and implied weighting, indicated *P.*  
215 *megapuncta* as sister to *P. serrata* (bootstrap values = 27 and 42, respectively).



216

217 **Fig. 4.** Majority-rule consensus tree of three equally shortest trees (280 steps, CI = 0.62, RI = 0.83) from TNT  
 218 implied weighting parsimony analysis.

219

220 *Phylogeny of Cupedidae*

221 In both parsimony analyses, the monophyly of Cupedidae was recovered with strong supporting values (Figs 4,  
 222 S5). Similarly, a close relationship between *Priacma* and *Paracupes* was supported in both analyses, and the  
 223 two extant genera, together with the Cretaceous *Barbaticupes* Jarzembowski *et al.* and *Mallecupes*  
 224 Jarzembowski *et al.*, formed a sister clade to the rest of crown-group Cupedidae. Considering the extant taxa,

225 this result is consistent with that recovered in Hörnschemeyer (2009), but not in Beutel *et al.* (2008), in which  
226 they suggested *Priacma* as a sister group to the remaining genera. Among the ‘derived group’, *Prolixocupes*  
227 Neboiss was recovered in both analyses as sister to the remaining cupedid genera, including *Adinolepis*  
228 Neboiss, *Ascioplaga* Neboiss, *Cupes* Fabricius, *Distocupes* Neboiss, *Rhipsideigma* Neboiss and *Tenomerga*  
229 Neboiss. The relationships among *Adinolepis*, *Ascioplaga* and *Distocupes* were not well resolved, because the  
230 supporting values were generally very low. The clade including the genera *Cupes*, *Rhipsideigma* and  
231 *Tenomerga* was recovered in both analyses, although the *Tenomerga* is not monophyletic as found in  
232 Hörnschemeyer (2009). The peculiar species *T. leucophaea* (Newman), together with *Cupes* and *Rhipsideigma*,  
233 formed a clade. And this monophylum represented the sister group of the remaining species of *Tenomerga*.

234 Apomorphies of selected clades based on the implied weighting parsimony analysis are presented in Fig.  
235 S6. The monophyly of Cupedidae is supported by four apomorphic characters: tips of P1 blunt and rounded,  
236 blunt and conical, or acute and conical (ch. 10), anterior corners of pronotum not rounded (ch. 41), subapical  
237 tarsomere wider than apical tarsomere (ch. 46), and parameres with apical hooks (ch. 76). *Priacma*,  
238 *Paracupes* and the Cretaceous genera *Barbaticupes* and *Mallecupes* formed a monophyletic group as defined  
239 by a single non-homoplasious character: presence of large and elongated mandibles (ch. 24). A sister  
240 relationship between *P. megapuncta* **sp.n.** and *P. serrata* is supported by the obvious fixing epipleural fold at  
241 the elytral apex (ch. 57). The remaining cupedids, excluding *Priacma*, *Paracupes*, *Barbaticupes* and  
242 *Mallecupes*, are supported by dense, thick and inflated scales on the head (ch. 4), 3 to 4 basal antennomeres  
243 with special scales (ch. 21), ventral surface of mandible with at least two differently structured areas separated  
244 by a ridge or a groove (ch. 27), and the characteristic of the scales covering window punctures (ch. 50). Most  
245 supported groups in this clade are consistent with the result of Hörnschemeyer (2009). However, *Adinolepis*  
246 and *Ascioplaga* were not recovered as sister groups. The clade comprising *Ascioplaga*, *Distocupes*, *Cupes*,  
247 *Rhipsideigma*, and *Tenomerga* was supported by the shape of the anterior tip of protuberances P2 (ch. 12).

248

#### 249 *Phylogenetic relationships among archostematan families*

250 As originally defined in Lawrence & Newton (1995), Archostemata includes four extant families: Cupedidae,  
251 Ommatidae, Micromalthidae, and Crowsoniellidae. The enigmatic Jurodidae is excluded in this study, because  
252 it seems to intermingle features belonging to Adephaga, Archostemata and Polyphaga (Yan *et al.*, 2014). The

253 results under parsimony, using both equal weights and implied weighting, recovered the monophyly of  
254 Cupedidae and Ommatidae (Figs S5, 4). The monophyly of Ommatidae is moderately supported (bootstrap  
255 values = 62 and 62), whereas it is strongly supported for Cupedidae (bootstrap values = 95 and 93). A close  
256 relationship between Crowsoniellidae and Micromalthidae is supported in the parsimony analyses, but the  
257 bootstrap values are relatively low. The relationships among these four families are not well resolved.

258

## 259 **Discussion**

260 The extant genus *Priacma* has a sole species, *P. serrata*, confined to the west of the Rocky Mountains (North  
261 America), including California, Oregon, Washington, Idaho, Montana, and British Columbia (Kirejtshuk *et al.*,  
262 2016). Our discovery of a fossil species of *Priacma* from the mid-Cretaceous Burmese amber represents the  
263 first definite representative of this relict genus in the fossil record. The exceptional preservation of *P.*  
264 *megapuncta* **sp.n.** allows for a new interpretation of the evolution of morphological characters. In *P. serrata*,  
265 setae covering both dorsal and ventral sides are white and scale-like, making its cuticle invisible. However,  
266 the fossil species *P. megapuncta* does not have such scales, and setae are sparse. All extant cupedids and some  
267 ommatids have more or less scales, whereas *Crowsoniella* Pace (Crowsoniellidae) and *Micromalthus* LeConte  
268 (Micromalthidae) are glabrous (Hörschemeyer *et al.*, 2002). Hörschemeyer *et al.* (2002) suggested that the  
269 presence of scales in Ommatidae and Cupedidae is probably plesiomorphic, and *Crowsoniella* and  
270 *Micromalthus* secondarily lost them. However, given the absence of obvious scales in *P. megapuncta* and  
271 *Mallecupes clevelyi* (Cupedidae), as well as *Brochocoleus zhiyuani* Liu *et al.*, 2017 and *Stegocoleus caii*  
272 Jarzembowski & Wang, 2016 (Ommatidae), it is more likely that the scales originated independently in both  
273 families. A recent molecular-based study indicated Ommatidae (*Tetraphalerus* Waterhouse) as a sister group to  
274 Micromalthidae (*Micromalthus*), and they together being sister to Cupedidae (McKenna *et al.*, 2015). This  
275 phylogenetic result also suggests that scales in Ommatidae and Cupedidae probably evolved independently.

276 In extant Cupedidae except for *P. serrata*, antennal insertions are narrowly separated by less than one  
277 diameter of the compound eye (or two diameters of the scapus; Hörschemeyer, 2009; Hörschemeyer &  
278 Yavorskaya, 2016). By contrast, the distance between antennal insertions of *P. serrata* and most other  
279 archostematan species are longer than the diameter of the eye (Hörschemeyer, 2009; Hörschemeyer &  
280 Yavorskaya, 2016). Similar to *P. serrata*, the distance is large in *P. megapuncta*, and fossil species *M. clevelyi*

281 and *M. qingqingae* from the same amber locality also have widely separated antennal insertions, although the  
282 antennae of the third Burmite species, *Barbaticupes combertiae*, are relatively closer to each other. The  
283 antennae of *P. serrata* are distinctly short among cupedids, not reaching the mid length of the body (Bouchard,  
284 2014), whereas in *P. megapuncta* and other cupedids the antennae are longer. The protuberances on the head  
285 are important features for generic-level identification of Cupedidae (Hörschemeyer *et al.*, 2006;  
286 Hörschemeyer, 2009). Most cupedids bear conspicuous dorsal protuberances, but the protuberances in some  
287 cupedids such as *Priacma* and *Paracupes*, are relatively low. Our fossil species has inconspicuous  
288 supraantennal (P1) and supraocular (P2) protuberances on the head, suggesting it belongs to this group of  
289 Cupedidae. Indeed species of *Mallecupes* even possess no posterior protuberances. However, *B. combertiae*,  
290 which was recovered as the sister group of *Paracupes* in our analyses, has distinctive head protuberances,  
291 which may raise an important issue that head protuberances in different genera could be homoplasious. All  
292 extant archostematan species except *Crowsoniella* and *Micromalthus* possess a prementum (Hörschemeyer,  
293 2009). For example, the prementum in *P. serrata* is triangular with a ligula on it (Hörschemeyer *et al.*, 2002),  
294 but this structure is reduced in *P. megapuncta*, a feature unique among all known cupedids. In *Mallecupes*, the  
295 prementum and ligula are also not visible, however, due to the relatively poor preservation state and limits of  
296 observational methods; whether prementum and ligula are indeed reduced or not in *Mallecupes* still requires  
297 further study. There are two tips at the anterior corners of the pronotum in *P. megapuncta*, whereas only a  
298 single tip is developed in *P. serrata* (Hörschemeyer, 2009). In *P. serrata*, the prosternal process is short, only  
299 reaching (or slightly extending beyond) the posterior margins of the procoxae (Hörschemeyer, 2009).  
300 However, the prosternal process of *P. megapuncta* is comparatively long, obviously extending beyond the  
301 posterior margins of the procoxae, similar to *Paracupes* and many other derived cupedids. The length of the  
302 prosternal process may vary within the genus *Priacma*, but it may be considered as a diagnostic feature at a  
303 species level. We propose that this character cannot be taken as a diagnostic feature of *Priacma* as previously  
304 adopted by Tan *et al.* (2006a).

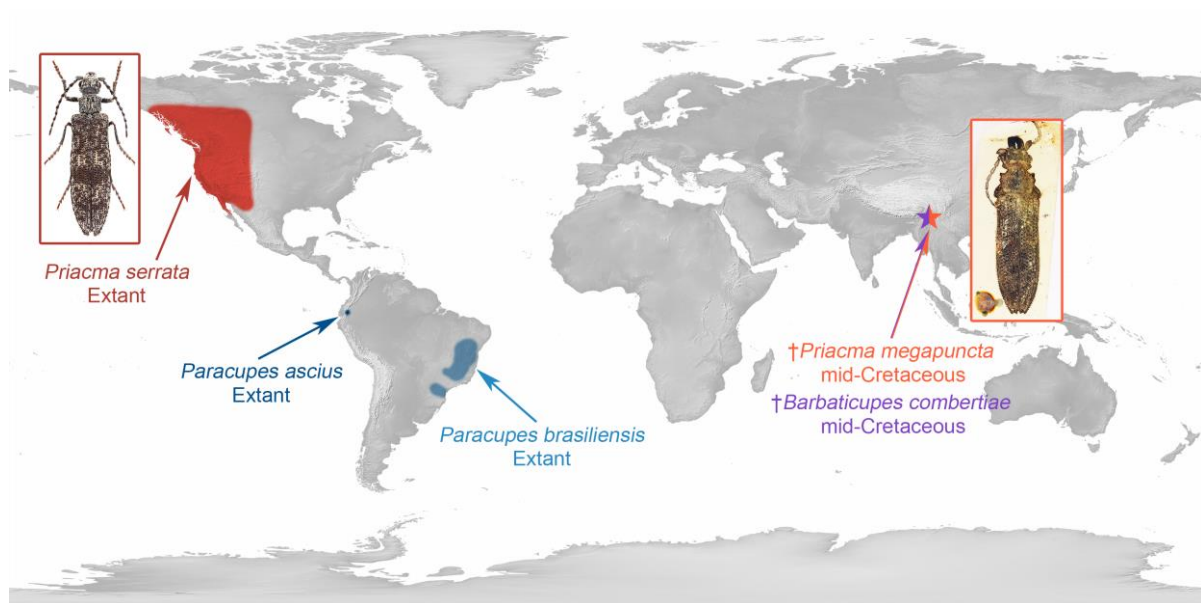
305 The most unusual character of *P. megapuncta* is the presence of a large window puncture near the apex of  
306 each elytron. To our knowledge, there is no such a modification of elytra in other extant or extinct cupedids.  
307 The well-developed fixing epipleural fold near the elytral apex in *P. serrata* is unique among extant cupedids  
308 (Kirejtshuk *et al.*, 2016), so the close affinity of *P. serrata* to the fossil species *P. megapuncta* is strongly

309 supported by this potential synapomorphy of the genus. This is the first evidence indicating that the largely  
310 unnoticed fixing epipleural fold on the ventral side of the elytra can be fossilized in amber, although it has  
311 been suggested that it is not possible to trace this feature in fossils (Kirejtshuk *et al.*, 2016). The exact function  
312 of the fixing epipleural folds remains elusive, but they may function in the fixation of the abdomen and elytra,  
313 which has been provisionally interpreted as an adaptation to aquatic or wet conditions (Kirejtshuk *et al.*, 2016).  
314 Another intriguing feature of *P. megapuncta* is the toothed elytral margins. As in extant *P. serrata* and *Pa.*  
315 *brasiliensis* Kolbe, the elytral margin bears two stripes of sharp teeth, whereas such stripes are greatly reduced  
316 in *M. qingqingae* and *Pa. ascius* Neboiss, and absent in other derived cupedids (Kirejtshuk *et al.*, 2016).

317 Our phylogenetic analyses indicate that *Priacma* and *Paracupes*, as well as the Cretaceous genera  
318 *Barbaticupes* and *Mallecupes*, together represent an early branching clade of Cupedidae, which may be  
319 defined as a monophyletic tribe Priacmini. Hörnschemeyer & Yavorskaya (2016) suggested that *P. serrata* is  
320 the sister group to all other cupedid genera, but they did not provide any supporting evidence. It is probable  
321 that such a hypothesis was based on the results by Beutel *et al.* (2008), in which they focussed on the  
322 phylogeny of both extant and extinct families of Archostemata. Notably, in one of the analyses (with fossil  
323 taxa excluded) by Beutel *et al.* (2008), the relationships among *Priacma*, *Paracupes* and other genera are  
324 unresolved. Both *Priacma* and *Paracupes* are very small genera; *P. serrata* has a relatively wide distribution  
325 in western North America (Bouchard, 2014; Kirejtshuk *et al.*, 2016), while the two extant species of  
326 *Paracupes* are restricted to South America: *Pa. brasiliensis* from eastern Brazil, and *Pa. ascius* from Ecuador  
327 (Neboiss, 1989; Hörnschemeyer & Yavorskaya, 2016). Our discovery of a new fossil species belonging to  
328 extant *Priacma* has important biogeographic implications (Fig. 5). It indicates that *Priacma* also occurred in  
329 the ancient tropical forest where later became today's southeastern Asia, with a likely subsequent move into  
330 North America where the extant member of the genus is now found. Recent molecular dating analyses  
331 indicated that stem-group Cupedidae originated in the Late Jurassic, approximately 157.82 million years ago  
332 (McKenna *et al.*, 2015). By contrast, another molecular dating of beetles by Zhang *et al.* (2018) suggested an  
333 Early Triassic age for the origin of Cupedidae. The former result conflicts with the fossil record of Cupedidae,  
334 because diverse cupedids have been reported from the Middle Jurassic Daohugou beds (ca. 165 Ma) in  
335 northeastern China (Tan *et al.*, 2006b, 2007; Tan & Ren, 2009; Kirejtshuk *et al.*, 2016). Therefore, it is  
336 appropriate to suggest that Cupedidae probably had a much longer history, at least as far back as the Middle



337 Jurassic, which is more consistent with the hypothesis by Zhang *et al.* (2018). Unfortunately, the precise  
338 systematic positions of the Jurassic cupedids from Daohugou have never been tested in a phylogenetic context.  
339 Indeed, many key features can be extracted from those fossils: they have widely separated antennae as in  
340 *Priacma*, but unlike *Priacma* and *Paracupes*, they have small mandibles and smooth (non-toothed) elytral  
341 margins (Tan *et al.*, 2006b, 2007) as found in more derived extant cupedids (Hörschemeyer, 2009). As such,  
342 the relationship between the Jurassic fossils and extant cupedids remains a mystery. New discoveries of  
343 phylogenetically-informative cupedids from Cretaceous ambers (e.g., mid-Cretaceous Burmese amber, Early  
344 Cretaceous Spanish amber and Lebanese amber) and other exceptional faunas will hopefully help to  
345 reconstruct the evolutionary dynamics of this archaic family, which has likely suffered from severe extinction  
346 events during its long geological history.



347  
348 **Fig. 5.** Geographic distribution of several basal cupetid genera: *Priacma*, *Paracupes* and *Barbaticupes*. World  
349 map was made with Natural Earth (NaturalEarthData.com).

350  
351 The monophyly of the suborder Archostemata is strongly supported by our phylogenetic results, and by  
352 many other works based on both morphological (e.g., Beutel *et al.*, 2008; Hörschemeyer *et al.*, 2006;  
353 Hörschemeyer, 2009; Lawrence *et al.*, 2011) and molecular data (Bocak *et al.*, 2014; McKenna *et al.*, 2015;  
354 Kusy *et al.*, 2018; Linard *et al.*, 2018). However, the relationships among all extant archostematan families  
355 remain elusive. The phylogenies based on morphological characters (both larval and adult) are unable to

356 confidently resolve the relationships among extant archostematan families. In particular, as shown in  
357 Hörnschemeyer (2009), different phylogenetic methodologies using parsimony and Bayesian inference yield  
358 slightly conflicting topologies in deeper nodes. When the fossil species were added, the relationships among  
359 Cupedidae were not well resolved as well. Lawrence *et al.* (2011) provided a phylogenetic tree of Coleoptera  
360 based on 516 adult and larval characters. According to their result under implied weighting parsimony, both  
361 Cupedidae and Ommatidae were recovered as polyphyly. However, our Bayesian analysis (using the discrete  
362 Markov k model) of the same dataset strongly supported the monophyly of the two families (Cai, unpublished  
363 result). The molecular-based phylogenetic studies are promising for elucidating the interrelationships in  
364 Archostemata, but published results appear limited by insufficient taxon and gene sampling, and the effects of  
365 missing data (Bocak *et al.*, 2014; McKenna *et al.*, 2015; Kusy *et al.*, 2018; Linard *et al.*, 2018). One of the  
366 challenges we are facing is that *Crowsoniella relictata* Pace (Crowsoniellidae) has not been sequenced because  
367 so far only three specimens are known. Despite the uncertainties in both morphology and molecular based  
368 phylogenetic studies of Archostemata, the monophyly of Cupedidae is well supported by almost all published  
369 trees (e.g., Beutel *et al.*, 2008; Hörnschemeyer, 2009; McKenna *et al.*, 2015) except the one by Lawrence *et al.*  
370 (2011). A re-discovery of new material of *C. relictata* (and the puzzling *Sikhotealinia zhiltzovae*) and further  
371 DNA-based phylogenetic studies will be of great significance of reconstructing the backbone phylogeny of the  
372 suborder Archostemata.

373

## 374 **Conclusions**

375 Our discovery of a new species belonging to Cupedidae from the mid-Cretaceous Burmese amber represents  
376 the fourth record of the family in this fossil locality. It highlights the palaeodiversity and morphological  
377 disparity of Cupedidae in the late Mesozoic. Phylogenetic analyses demonstrated that *Priacma megapuncta*  
378 **sp.n.** is a sister group to the extant peculiar species *P. serrata* from North America, indicating that *Priacma* is  
379 an ancient genus and was once much more widespread in the Cretaceous. Many interesting features of *P.*  
380 *megapuncta*, including large mandibles, toothed elytral margins, and elytral apices with fixing epipleural folds,  
381 are important for understanding the early evolution of Cupedidae. Further discoveries of fossil cupedids from  
382 Mesozoic exceptional faunas, as well as robust molecular-based phylogenies based on a more extensive  
383 sampling of extant taxa and molecular markers, will contribute to elucidating the long evolutionary history of

384 Cupedidae.

385

### 386 **Supporting Information**

387 Additional supporting information may be found online in the Supporting Information section at the end of the  
388 article.

389

390 **Fig. S1.** Details of *Barbaticupes combertiae*, under epifluorescence. A, B, D, NIGP166315. A, head and  
391 prothorax in dorsolateral view. B, head in ventrolateral view, showing the gula. D, distal part of right elytron,  
392 dorsolateral view, showing the elytral scales confined to primary veins. C, NIGP166314, aedeagus in ventral  
393 view. Abbreviations: ah, apical hook; ey, compound eye; p1,2, supraantennal and supraocular protuberances,  
394 respectively; gu, gula; mxp, maxillary palpi; pm, paramere; sc, scape; v5, ventrite 5. Scale bars: 400  $\mu\text{m}$  in A;  
395 200  $\mu\text{m}$  in B–D.

396

397 **Fig. S2.** Details of *Mallecupes qingqingae*, under epifluorescence. A, C, D, NIGP157008. A, head and  
398 prothorax in ventrolateral view. C, distal parts of elytra, ventrolateral view. D, middle part of right elytron,  
399 lateral view, showing the outermost row of large maculated window punctures. B, NIGP164791, maculated  
400 window punctures on the elytra. Abbreviations: ey, compound eye; gu, gula; md, mandible; ps, prosternum; sc,  
401 scape. Scale bars: 400  $\mu\text{m}$  in A, C; 200  $\mu\text{m}$  in B, D.

402

403 **Fig. S3.** Details of *Mallecupes clevelyi*, NIGP164792, under epifluorescence. A, head in ventral view. B,  
404 prothorax in ventral view, showing the prosternal process not extending beyond the posterior margin of  
405 conical procoxae (arrowhead). C, maculated window punctures on the elytra. D, distal parts of abdomen and  
406 left elytron, ventral view. Abbreviations: ey, compound eye; fl1, flagellomere 1; md, mandible; mxp,  
407 maxillary palpi; pc, procoxa; pd, pedicel; pf, profemur; ps, prosternum; sc, scape; v5, ventrite 5. Scale bars:  
408 200  $\mu\text{m}$ .

409

410 **Fig. S4.** Details of *Priacma megapuncta* sp.n., holotype, NIGP168831, under incident light. A, B, head. A,  
411 dorsal view. B, ventral view, showing the mouthparts. C, proximal portion of the left antenna. D, prothorax in

412 ventral view, showing the prosternal process extending beyond the posterior margin of conical procoxae  
413 (arrowhead). E–G, distal parts of elytra. E, G, dorsal and ventral, respectively, showing emarginate elytral  
414 apices and the large window punctures. F, lateral view, showing the double stripes of teeth. Abbreviations:  
415 fl1,2, flagellomeres 1,2; gl, galeae; lbp, labial palpi; mxp, maxillary palpi; pd, pedicel; sc, scape. Scale bars:  
416 500  $\mu\text{m}$  in A–E, G; 1 mm in F.

417

418 **Fig. S5.** Majority-rule consensus tree of 672 equally shortest trees (280 steps, CI = 0.62, RI = 0.83) from  
419 equally weighted parsimony analysis using TNT.

420

421 **Fig. S6.** Majority-rule consensus tree from implied weighting parsimony analysis, with character state labeled.  
422 A, Archostemata. B, Cupedini. Black circles indicate non-homoplasious changes; white circles indicate  
423 homoplasious characters; numbers above the branches of the strict consensus tree indicate character numbers.

424

425 **File S1.** List of characters used in the phylogenetic analyses.

426

427 **File S2.** Morphological dataset (47 taxa and 110 morphological characters) used for the analyses.

428

## 429 **Acknowledgements**

430 We are grateful to Chen-Kun Jiang for technical help in photography, and to Dr. Thomas Hörnschemeyer for  
431 providing 3D models of some extant archostematans. Financial support was provided by the Strategic Priority  
432 Research Program (B) (XDB26000000, XDB18000000), the National Natural Science Foundation of China  
433 (41688103, 41602009), the Natural Science Foundation of Jiangsu Province (BK20161091), and a Newton  
434 International Fellowship from the Royal Society. Y.-D.L. acknowledges support from the Training Plan of the  
435 National Basic Subject Top-Notch Talent. This is a Leverhulme Emeritus Fellowship contribution for E.A.J.

436 The authors declare no competing interests.

437

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