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1 The oldest malachite damselfly (Odonata: Synlestidae) from the Lower Cretaceous of China

2

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11

12 ABSTRACT

13 The synlestid damselfly, *Cretaphylolestes cretacicus* gen. et sp. nov., is described from the
14 Lower Cretaceous Shouchang Formation (lower Aptian) of Zhejiang Province, Eastern China.
15 It is the oldest Synlestidae, as we exclude the Late Jurassic–Early Cretaceous genus
16 *Gaurimacia* from this family. The clade Lestiformia is currently represented in the Mesozoic
17 by two Early Cretaceous genera of its stem group, a Perilestidae from the mid-Cretaceous
18 Burmese amber and this newly described Synlestidae. This group remains under-represented
19 in the Cretaceous, compared to the other zygopteran subclades. It probably diversified during
20 the Late Cretaceous and the Paleocene, as the Lestidae are frequent and diverse in the
21 Oligocene and more recent periods.

22

23 *Keywords:* Zygoptera; Lestiformia; Shouchang Formation; paleodiversity

24

25

26 **1. Introduction**

27 Until recently, the Mesozoic record of the Zygoptera (Odonata) was poor compared to
28 that of its sister group Eiproctophora. But the works of Jarzembowski et al. (1998), Bechly
29 (2007), etc. on compression fossils from the Early Cretaceous of UK and Brazil, and
30 especially those on the mid-Cretaceous Burmese amber Odonata have filled this gap (Zheng,
31 2021). But these discoveries mainly concern the Caloptera Belyshev & Haritonov, 1983,
32 Coenagrionomorpha Bechly, 1996, and the Hemiphlebiidae Tillyard, 1926 in the
33 Lestomorpha Bechly, 1996 (= Hemiphlebiidae + Lestiformia Bechly, 1996) (= Lestoidea
34 Calvert, 1901, sensu Dijkstra et al., 2014). Only three or four Mesozoic Lestiformia (=
35 Cretacoenagrionidae Bechly, 1996 & Perilestidae Tillyard & Fraser, 1938 & Synlestidae
36 Tillyard, 1917 & Lestidae Calvert, 1901) are known, while the Lestidae are present in the
37 middle Eocene (A.N., pers. obs.) and frequently found in the Oligocene and the Miocene
38 lacustrine deposits (Nel & Paicheler, 1994).

39 Here we described a new Synlestidae from the Lower Cretaceous Shouchang
40 Formation at the Shouchang Township, Zhejiang Province, East of China. We also discuss the
41 position of the Mesozoic Russian genus *Gaurimacia* Vasilenko, 2005, originally considered
42 as belonging to this family.

43

44 **2. Material and method**

45

46 The present described fossil material was collected from the Lower Cretaceous
47 Shouchang Formation near the Shanghujia Village, Shouchang Township, Jiande City,
48 Zhejiang Province (Fig. 1). The age of the Shouchang Formation was argued by different
49 authors to assign to Barremian or Aptian. **Biostratigraphic research suggests the Shouchang**
50 **Formation belongs to** the lower Barremian (e.g., Chen, 2000) or middle Aptian (Xi et al.,

51 2019). However, some isotopic studies indicated **that** the age of the Shouchang Formation
52 should be early Aptian, 122 Ma or 125-121 Ma (Li et al., 1988; Li et al., 2011). Recent
53 chronostratigraphy revealed the series U-Pb zircon dating of the Shouchang Formation at the
54 Shouchang area, Jiande City as 123.8 ± 1.0 Ma at middle section, and 129.3 ± 1.7 Ma,
55 126.3 ± 1.4 Ma, 127.1 ± 1.1 Ma at the lower sections respectively (Li et al., 2018). The bottom
56 of overlapped Hengshan Formation got the U-Pb zircon dating as 120.9 ± 1.2 Ma at the same
57 section (Li et al., 2018). Therefore, the Shouchang Formation at the Shouchang area mainly
58 rang from the early Barremian to early Aptian. The present material was collected from
59 middle section of the Shouchang Formation thus **representing** an early Aptian age.

60 The fossil insects have been yielded from the Shouchang Formation with relative poorly-
61 studied. From the previously studies, the most fossil insects were collected from the lower
62 parts of the formation that represent a typical *Ephemeropsis* entomofauna (Gu, 1980; Ding et
63 al., 1989; Jiang et al., 1993). For example, the representative species *Ephemeropsis trisetalis*
64 is widely distributed in the Lower Cretaceous of north China, Mongolia and Trans Baikal of
65 Russian though a detailed study for their specific homogeneity is still necessary.
66 *Ephemeropsis* is a representative insect fossil in Jehol biota **with an age range of ~135-120**
67 **Ma (Zhang et al., 2010)** that would be consistency with that of the Shouchang Formation
68 (e.g., Swisher et al., 1999).

69 Only one specimen of the new damselfly was collected from the fine laminated green-
70 grayish shales at the middle part of the Shouchang Formation at 2020. The fossil preserved as
71 dark film with part and counterpart that both split to two pieces. The specimen was carefully
72 prepared using a sharp knife under a stereo microscope. Photograph was taken with a digital
73 camera attached to a Zeiss Discovery V16 microscope; the raw digital image was processed
74 with Helicon Focus 7.0.2 to increase the depth of field; line drawing was drafted with Adobe

75 Illustrator CC 2018 graphic software. The specimens are deposited in the Nanjing Institute of
76 Geology and Palaeontology, Nanjing, China.

77 The nomenclature of the odonatan wing venation used in this paper is based on the
78 interpretations of Riek and Kukalová-Peck (1984), as modified by Nel et al. (1993) and
79 Bechly (1996). The higher classification of fossil and extant Odonatoptera, as well as family
80 and generic characters followed in the present work, is based on the phylogenetic system
81 proposed by Bechly (1996) and Dijkstra et al. (2014) for the phylogeny of extant Zygoptera.
82 Wing abbreviations are as follows: AA, analis anterior; CuA, cubitus anterior; CuP, cubitus
83 posterior; IR, intercalary radial veins; MAa, first branch of median anterior; MAb second
84 branch of median anterior; MP, median posterior; N, nodus; 'O', oblique crossvein between
85 RP2 and IR2; Pt, pterostigma; RA, radius anterior; RP, radius posterior; Sn, subnodal
86 crossvein.

87 [urn:lsid:zoobank.org:pub:488442F4-A9EE-46F7-960C-71515A3383DD](https://doi.org/10.3896/BI.2024.488442F4-A9EE-46F7-960C-71515A3383DD)

88

89 **3. Systematic palaeontology**

90 Order Odonata Fabricius, 1793

91 Suborder Zygoptera Selys-Longchamps, 1854

92 Family Synlestidae Tillyard, 1917

93 *Cretaphylolestes* gen. nov.

94 [urn:lsid:zoobank.org:act:1C5CC3DC-4384-4E11-B01B-914D170CF674](https://doi.org/10.3896/BI.2024.1C5CC3DC-4384-4E11-B01B-914D170CF674)

95 Type species: *Cretaphylolestes cretacicus* sp. nov.

96 *Etymology*. Named after the Cretaceous period and the genus *Phylolestes*.

97 *Diagnosis*. Wing venation only. Bases of RP3/4 and IR2 close to subnodus, IR1 very long,
98 basally zigzagged and distally strongly curved; an oblique crossvein 'O'; base of RP very
99 close to that of arculus; curved stem of MA; long secondary longitudinal veins between IR1

100 and RP2, and RP2 and IR2; RP1 not kinked at insertion of pterostigmal brace vein; distal
101 postnodals and postsubnodals not aligned; pterostigma two-cells long; pterostigmal brace not
102 oblique; MP curved at its base in distal angle of discoidal cell; posterior margin of
103 subdiscoidal cell not fused with posterior wing margin; very long and straight veins RP3/4,
104 IR2 and RP2.

105

106 *Cretaphylolestes cretacicus* sp. nov.

107 (Figs 2–4)

108 [urn:lsid:zoobank.org:act:F2C3BF56-6560-4732-A74B-52961D3EAF79](https://doi.org/10.31233/osf.io/zt9qf)

109 *Etymology*. Named after Cretaceous period.

110 *Material*. Holotype NIPG175591 (imprint and counterimprint of an adult damselfly showing
111 the head, thorax, with fragments of legs, bases of a forewing and a hind wing and apex of a
112 wing), stored at the Nanjing Institute of Geology and Palaeontology, China.

113 *Occurrence*. Lower Aptian, Lower Cretaceous; Shouchang Formation at Shouchang, Zhejiang
114 Province, China.

115 *Diagnosis*. As for the genus.

116 *Description*. Head 2.5 mm wide, 2.0 mm long, clearly deformed due to projection of
117 mouthparts in front of head; compound eye 1.6 mm long, 0.8 mm wide, 1.0 mm apart; ocelli
118 present; thorax 4.0 mm long, 2.8 mm wide; legs poorly preserved, without preserved spurs;
119 preserved parts of fore- and hind wings identical; forewing ca. 17.9 mm long; petiole 1.8 mm
120 long; distance from base to arculus 2.9 mm, from arculus to nodus 3.0 mm, from nodus to
121 pterostigma 8.4 mm; from base to Ax1 1.8 mm, between Ax1 and Ax2 1.1 mm; arculus
122 opposite Ax2; no secondary antenodal crossveins; antesubnodal space free; basal part of area
123 between RP and MAa up to base of RP3/4 free; terminal kink of CP reduced at nodus; nodal
124 furrow reduced; nodal crossing Cr and subnodus moderately oblique; base of RP very close to

125 base of arculus; stem of MA distinctly curved, 0.3 mm long; basal preserved part of MAa
126 straight; stem of MA slightly shorter than MAb, MAb 0.5 mm long; making an acute angle
127 with MP+CuA; MP curved at its base in distal angle of discoidal cell; discoidal cell basally
128 closed, but crossvein between MA and MP+CuA incompletely preserved; subdiscoidal cell
129 narrow elongate; base of AA and CuP opposite Ax1; base of RP3/4 situated at 2/3 of distance
130 between arculus and nodus, closer to nodus; base of IR2 situated below base of subnodus; 10
131 postnodal crossveins preserved, three more distal ones not aligned with corresponding
132 postsubnodals; pterostigma elongate, 1.8 mm long, 0.85 mm wide, covering two complete
133 cells; pterostigmal brace weakly defined, not stronger than postnodals and nearly
134 perpendicular to RA and RP1; six crossveins between C and RA distal of pterostigma; base of
135 IR1 4.2 mm basal of pterostigma (five cells) and 3.5 mm distal of base of RP2 (three cells),
136 elongate, basally zigzagged and distally strongly curved, with one row of cells between it and
137 RP1; base of RP2 two cells and a half distal of subnodus, RP2 straight up to wing margin with
138 a supplementary zigzagged longitudinal vein between it and IR1; a supplementary zigzagged
139 longitudinal vein between RP2 and IR2; a weakly oblique crossvein 'O' between RP2 and
140 IR2, four cells distal from base of RP2; IR2 and RP3/4 straight in their main parts and weakly
141 curved near wing margin, with one row of cells in-between.

142

143 **4. Discussion**

144

145 Following Bechly (1996, 2016), *Cretaphylolestes* gen. nov. falls in the Zygoptera
146 because of the following putative synapomorphies: both pairs of wings of identical shape and
147 venation, distinctly stalked, with a petiolus longer than broad; terminal kink of the CP reduced
148 at nodus; nodal furrow reduced. Also, affinities with the Epiproctophora are excluded because

149 the arculus is shifted basally in a position between the two primary antenodal brackets Ax1
150 and Ax2.

151 Affinities with the Mesozoic Steleopteridae Handlirsch, 1906 are excluded because
152 the bases of RP3/4 and IR2 are not midway between arculus and nodus, IR1 is well-defined,
153 and there is no trace of specialized cells as in this family (Fleck et al., 2001). Affinities with
154 the Cenozoic Sieblosiidae Handlirsch, 1907 are unlikely because the nodus is not traversed by
155 ScP and the discoidal cell is narrow with postero-apical angle acute. Affinities with the
156 Liassic Eosagrionidae Handlirsch, 1920 are excluded because of the absence of secondary
157 antenodals and antesubnodals (Handlirsch, 1920: fig. 140). But *Cretaphylolestes* gen. nov.
158 shares with these families the presence of an oblique crossvein 'O', also present in the
159 Epiproctophora, the 'basal' odonatan family Tarsophlebiidae and many Lestoidea. This
160 character is possibly a symplesiomorphy of the Odonata. *Cretaphylolestes* gen. nov. shares
161 with some Dysagrionidae (e.g. *Dysagrion*) a vein MAb longer than the stem of MA, but it has
162 an oblique crossvein 'O', unlike all the Dysagrionidae (either Mesozoic and Cenozoic)
163 (Archibald et al., 2021; Nel & Zheng, 2021). The Whetwhetaksidae are also excluded for the
164 same reason (Archibald et al., 2021).

165 The shape of the discoidal cell and the midfork not basally recessed exclude affinities
166 with the Caloptera. The following putative synapomorphies support a position in the
167 Euzygoptera Bechly, 1996: longitudinal veins rather straight and long; only the two primary
168 antenodal brackets Ax1 and Ax2 retained in antenodal space; antesubnodal space without any
169 crossveins; no antefurcal crossveins present in the space between RP and MA from arculus to
170 midfork. These characters are also present in the Caloptera Pseudolestidae, but
171 *Cretaphylolestes* gen. nov. differs from this family in the bases of RP3/4 and IR2 closer to
172 subnodus than to arculus, a curved stem of MA, a different shape of the discoidal cell, and the
173 presence of vein 'O' (Münz, 1919: pl. 7, fig. 38).

174 Within the Euzygoptera, affinities with the Coenagrionomorpha are unlikely because
175 of the following characters: pterostigma not shortened; postnodal and postsubnodal crossveins
176 not well-aligned; lesterine oblique vein present; no tendency towards the formation of pseudo-
177 transverse veins in the distal part of the wing.

178 In the Lestomorpha, affinities with the Hemiphlebiidae Tillyard, 1926 are excluded
179 because of the presence of vein 'O', RP1 not kinked at the insertion of the pterostigmal brace
180 vein; presence of intercalary veins between the branches of RP. Nevertheless,
181 *Cretaphylolestes* gen. nov. shares with the Hemiphlebiidae the **most** distal postnodals and
182 postsubnodals not aligned. *Cretaphylolestes* gen. nov. shares with the early Cretaceous
183 Cretacoenagrionidae the bases of RP3/4 and IR2 below subnodus and similar pterostigma, but
184 differs from *Cretaceonagrion* Jarzembowski, 1990 in the curved stem of MA, the presence of
185 vein 'O', very different IR1, and distal postnodals incomplete (Jarzembowski, 1990: fig. 1).
186 The vein MP is curved at its base in the distal angle of the discoidal cell, a putative
187 synapomorphy of the Eulestiformia Bechly, 1996. Affinities with *Chorismagrion* Morton,
188 1914 (in Chorismagrionidae Tillyard & Fraser, 1938 or in Synlestidae) are excluded because
189 the base of IR2 is below subnodus, not shifted distally (**a symplesiomorphy**). *Cretaphylolestes*
190 gen. nov. has a venation very similar to those of the extant Synlestidae, except in the distinctly
191 curved stem of MA, MP less curved at its base, and the presence of the oblique vein 'O'
192 (Münz, 1919: figs 63, 66; Kennedy, 1920; Barnard, 1937, Bechly, 2016; To and Phan, 2018).
193 **In several Synlestidae, a weakly inclined pterostigmal brace is present, unlike in**
194 ***Cretaphylolestes* gen. nov., but some have an inconspicuous pterostigmal brace (e.g.**
195 ***Ecchlorolestes* Barnard, 1937) (Belyshev & Haritonov, 1977: fig. 200).**

196 Notice that Dijkstra et al. (2014) indicated that the 'Perilestidae and Synlestidae were
197 paraphyletic [in respect to the Lestidae] in many analyses but in BI/ML 28S+16S+COI, the

198 two combined were monophyletic with low support and a well-supported monophyletic
199 Perilestidae was embedded in Synlestidae' (see their figure 2).

200 Affinities with the Perilestidae are excluded because the base of IR2 is below
201 subnodus in *Cretaphylolestes* gen. nov., not shifted distally (Zheng et al., 2016). The Eocene
202 family Austroperilestidae Petrulevičius & Nel, 2005, possibly related to the Perilestidae,
203 strongly differs from *Cretaphylolestes* gen. nov. in the nodus shifted in basal fourth of the
204 wing, the very short stem of MA, and the elongate pterostigma (Petrulevičius & Nel, 2005).

205 A majority of Synlestidae have the posterior margin of the subdiscoidal cell fused with
206 the posterior wing margin, unlike *Cretaphylolestes* gen. nov. But the extant genera *Megalestes*
207 Selys-Longchamps, 1862, *Nubiolestes* Fraser, 1945, and *Phylolestes* Christiansen, 1947 have
208 a posterior margin of the subdiscoidal cell not fused with the posterior wing margin,
209 especially in the forewing (Christiansen, 1947: fig. 1; Simaika et al., 2020: fig. 2). *Megalestes*
210 has an oblique vein 'O' but much more pronounced than in *Cretaphylolestes* gen. nov., and
211 the bases of its veins RP3/4 and IR2 are closer to arculus than to nodus, as in the Lestidae
212 (Münz, 1919: fig. 41). Notice that Nel & Fleck (2014: 303) indicated that the type specimen
213 of '*Megalestes*' *anglicus* Cockerell, 1915 is 'a Zygotera Lestiformia, or a
214 Coenagrionomorpha of uncertain affinities'. The Eocene genus *Eolestes* Cockerell, 1940 has
215 the preserved part of its venation very similar to that of *Megalestes*, especially in the bases of
216 veins RP3/4 and IR2 far basally to the nodus (Fraser, 1945; Nel & Paicheler, 1994). Affinities
217 with *Nubiolestes* are unlikely because this genus has a base of RP3/4 just below the subnodus.
218 But *Phylolestes* has a wing venation very similar to that of *Cretaphylolestes* gen. nov.,
219 especially in the very particular shape of the vein IR1, zigzagged at its base and with a strong
220 anterior curvature distally, and a weak oblique vein 'O' (Christiansen, 1947: fig. 1; Westfall
221 & May, 1996: fig. 25). *Cretaphylolestes* gen. nov. and *Phylolestes* also share very long and
222 straight veins RP3/4, IR2 and RP2, and a MAb slightly longer than MA.

223 Few fossil damselflies are currently included in the Synlestidae. The Eocene genera
224 *Madres* Petrulevičius, 2018 and *Inacayalestes* Petrulevičius, 2015 shares with
225 *Cretaphylolestes* gen. nov. an oblique vein 'O', but they have a posterior margin of the
226 subdiscoidal cell fused with the posterior wing margin (Petrulevičius, 2015: fig. 4, 2018: fig.
227 2). The late Jurassic-early Cretaceous genus *Gaurimacia* was included in the Synlestidae
228 without clear argument, as this author only compared it to the genera *Megalestes*, *Phylolestes*
229 and *Orolestes* (that belongs to the Lestidae). The nodus shifted at the proximal fifth of the
230 wing is quite abnormal for a Synlestidae or even a Lestoidea, and is rather found in the
231 Caloptera. It has also a basally opened discoidal cell, unlike all Synlestidae (Vasilenko, 2005).
232 There is no argument supporting a position of *Gaurimacia* in this family. Kohli et al. (2016)
233 did not include any fossil synlestid damselfly that could be used for a divergence time
234 analysis. Also they did not discussed on the position of *Gaurimacia* even if they cited
235 Vasilenko (2005) for *Mersituria ludmilae* Vasilenko, 2005 (Hemiphlebiidae). They also
236 ignored *Inacayalestes*.

237

238 **5. Conclusion**

239

240 The precise placement of *Cretaphylolestes* gen. nov. remains somewhat uncertain
241 because of the presence of homoplasies affecting several characters in the Lestomorpha, e.g.
242 presence vs. absence of the oblique vein 'O', position of the base of RP3/4 close to arculus vs.
243 nodus. Nevertheless, the available characters strongly supports a position in the Synlestidae,
244 probably in the stem group of the family because of the incomplete most distal postnodals and
245 of the presence of a vein 'O', as in *Madres* and *Inacayalestes*, absent in the extant synlestid
246 genera. *Cretaphylolestes* gen. nov. can be considered as the oldest record of this family, as
247 *Gaurimacia* is not a Synlestidae and probably not a Lestoidea.

248 If several Early to mid-Cretaceous Hemiphlebiidae are known (Zheng, 2020), the
249 clade (Perilestidae & Synlestidae & Lestidae) is clearly under-represented in the Mesozoic.
250 The mid-Cretaceous Burmese *Palaeoperilestes electronicus* Zheng et al., 2016 is the current
251 oldest record of the Perilestidae. *Cretaceonagrion* and the enigmatic *Cretalestes martinae*
252 Jarzembowski et al., 1998, from the Lower Weald Clay in UK, probably belong to the stem
253 group of the clade (Perilestidae & Synlestidae & Lestidae) (Jarzembowski, 1990;
254 Jarzembowski et al., 1998). The synlestid *Cretaphylolestes* gen. nov. is the fourth Mesozoic
255 record of this clade. No Mesozoic Lestidae is currently known. The Paleocene *Lestes*
256 *zalesskyi* Piton, 1940 is based on a lost specimen, with a very uncertain original description
257 and figure. Nel & Paicheler (1994) considered that its attribution to the Lestidae is very
258 uncertain. The oldest accurate record of the Lestidae is an undescribed fossil *Lestes* from the
259 Eocene of China (Xia et al., under review). It seems that clade (Perilestidae & Synlestidae &
260 Lestidae) mainly diversified during the Late Cretaceous and/or the Paleocene. The extant
261 Synlestidae are present in China, India, Australia, Africa, and South America, while they are
262 known from the Eocene of South and North America. The Perilestidae are known by two
263 extant South American genera and a Cretaceous Burmese representative. Such disjunctive
264 distributions suggest a rather great antiquity for these two groups, congruent with their
265 records in the Lower Cretaceous.

266

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272

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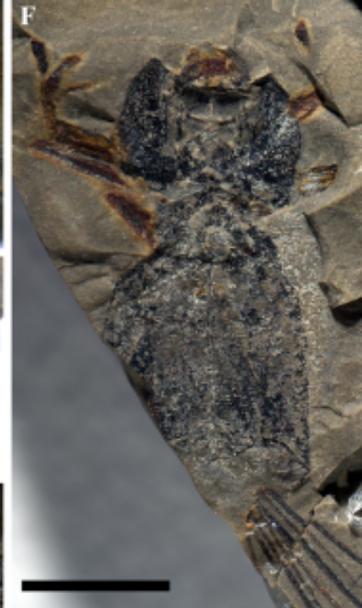
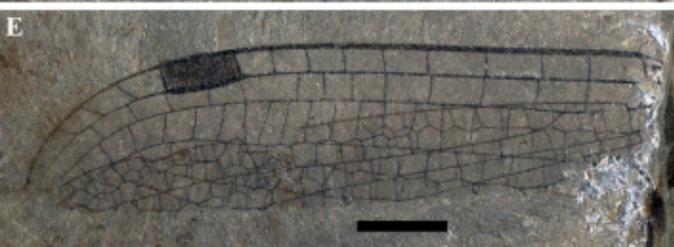
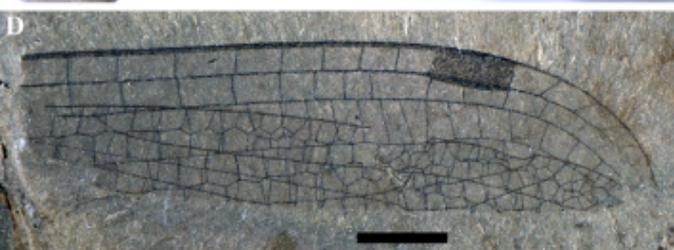
424 **Fig. 1.** Map of area with fossil site.

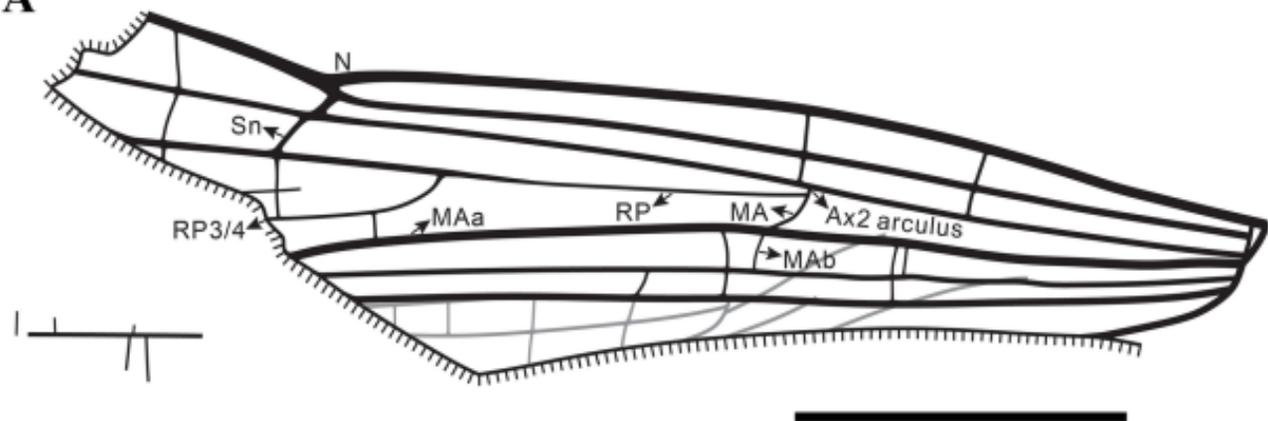
425 **Fig. 2.** *Cretaphylolestes cretacicus* gen. et sp. nov., holotype NIPG175591. Photographs. A.
426 Habitus, imprint. B. Habitus, counterimprint. C. Bases of wings. D. Wing apex,
427 counterimprint. E. Wing apex, imprint. F. Body, counterimprint, dry. G. Body,
428 counterimprint, under alcohol. Scale bars: 1 mm (A-C), 2 mm (D-G).

429 **Fig. 3.** *Cretaphylolestes cretacicus* gen. et sp. nov., holotype NIPG175591. Reconstructions.
430 A. Bases of wings. B. Wing apex. Scale bars: 1 mm.

431 **Fig. 4.** *Cretaphylolestes cretacicus* gen. et sp. nov., holotype NIPG175591. Photograph.
432 Discoidal area (arrowheads base and apex of Mab). Scale bar: 2 mm.





A**B**