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1 The first fossil Perilestidae (Odonata: Zygoptera) from mid-Cretaceous Burmese
2 amber

3

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22

23 A B S T R A C T

24 *Palaeoperilestes electronicus* gen. et sp. nov. is the first perilestid damselfly
25 described from mid-Cretaceous Burmese amber. This new damselfly can be attributed
26 to the family Perilestidae by the midfork being distal of the subnodus and the base of
27 IR2 quite near to the base of RP2, both features found in the extant genera *Perilestes*
28 and *Perissolestes*. *Palaeoperilestes electronicus* gen. et sp. nov. has a strongly
29 zigzagged IR1, however, differing from *Perilestes* and *Perissolestes* which have a
30 straight IR1. The discovery not only adds to the diversity of damselflies in Burmese
31 amber, but also puts the origin of Perilestidae back to at least the mid-Cretaceous.

32
33 Key words: Perilestidae, Zygoptera, Odonata, Cenomanian, Cretaceous, Burmese
34 amber

35
36 **1. Introduction**

37 The Perilestidae Kennedy, 1920 is a family of small damselflies, often called
38 shortwings or twigtails, characterized by short wings (20–25 mm) and very long,
39 slender and colour-banded abdomens (40–56 mm) (Williamson and Williamson 1924;
40 Haber and Wagner, 2014). The adults often perch on plant stems or dead twigs near
41 streams and frequent the understory and glades within dense forest, thus making them
42 easily overlooked in the field. Perilestidae now consists of two Neotropical genera:
43 *Perilestes* Hagen in Selys-Longchamps, 1862 and *Perissolestes* Kennedy, 1941, with
44 the former consisting of eight species while the later comprises 11 species (Dijkstra et

45 al., 2011, 2014; Schorr and Paulson, 2015; Machado, 2015). The African endemic
46 genus *Nubiolestes* Fraser, 1944 was previously attributed to this family (Bechly, 1996;
47 Neiss and Neusa, 2010); however, it is the sister genus of the Perilestidae sensu stricto
48 in the phylogenetic analysis of Dijkstra et al. (2014). In the present paper, a new
49 damselfly, *Palaeoperilestes electronicus* gen. et sp. nov., is described from the
50 mid-Cretaceous Burmese amber. This is the first fossil representative of the extant
51 family Perilestidae. The new discovery increases our knowledge about these unique
52 damselflies.

53

54 **2. Material and methods**

55 The specimen described herein was collected from the Hukawng Valley of
56 Kachin Province, Myanmar (locality in Kania et al., 2015: fig. 1). The age of Burmese
57 amber is radiometrically dated at 98.79 ± 0.62 Ma (earliest Cenomanian; Cohen et al.,
58 2013) based on U–Pb zircon dating of the volcanoclastic matrix (Shi et al., 2012).

59 The amber containing the damselfly is yellow and transparent. The damselfly is
60 preserved together with a big horsefly. The damselfly wings are close to the amber
61 surface and are slightly curved towards the horsefly. This makes it difficult for further
62 polishing and obtaining clear photomicrographs. Photomicrographs were taken using
63 a Zeiss Stereo Discovery V16 microscope system and Zen software. In most instances,
64 incident and transmitted light were used simultaneously. All images are digitally
65 stacked photomicrographic composites of approximately 40 individual focal planes
66 obtained using the free software Combine ZP for a better illustration of the 3D

67 structures. The line drawings were prepared from photographs using image-editing
68 software (CorelDraw X7 and Adobe Photoshop CS6). The specimen is housed in the
69 Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences
70 (NIGPAS). All taxonomic acts established in the present work have been registered in
71 ZooBank (see below), together with the electronic publication LSID:
72 urn:lsid:zoobank.org:pub:28289195-14CB-4434-92CD-6D6F5865ABBF.

73 The nomenclature of the odonatan wing venation used in this paper is based on
74 the interpretations of Riek (1976) and Riek and Kukalová-Peck (1984), as modified
75 by Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant
76 Odonatoptera, as well as family and generic characters followed in the present work,
77 are based on the phylogenetic system proposed by Bechly (1996) and Dijkstra et al.
78 (2014) for the phylogeny of extant Zygoptera. Wing abbreviations are as follows:
79 CuA, cubitus anterior; IR, intercalary radial veins; MA, median anterior; MP, median
80 posterior; N, nodus; Pt, pterostigma; RA, radius anterior; RP, radius posterior; Sn,
81 subnodal crossvein. All measurements are given in mm.

82 83 **3. Systematic palaeontology**

84 Order: Odonata Fabricius, 1793

85 Suborder: Zygoptera Selys-Longchamps, 1854

86 Family: Perilestidae Kennedy, 1920

87 Type genus. *Perilestes* Hagen in Selys-Longchamps, 1862

88 New genus. *Palaeoperilestes* gen. nov.

89 (urn:lsid:zoobank.org:act:08EA6631-83A4-4EBA-8BEC-A6932257A86B)

90 Type species. *Palaeoperilestes electronicus* sp. nov.

91 *Etymology*. Named from the Greek word παλαιός for ‘old’ and the type genus

92 *Perilestes*. Gender unknown.

93 *Diagnosis*. Wing characters: hindwing midfork (base of RP3/4) shifted distal of N;

94 IR1 strongly zigzagged and shortened, originating basal of Pt base; IR2 distinctly

95 shortened, arising on base of RP2 in forewing but one cell basal of that in hindwing;

96 IR2 two cells distal of midfork in hindwing; hindwing MP long and reaching posterior

97 wing margin slightly distal of base of IR1; CuA short and ending on posterior wing

98 margin near base of IR2; postnodal and postsubnodal crossveins somewhat aligned;

99 all intercalary veins (except IR1 and IR2) suppressed; longitudinal veins RA, IR1,

100 RP1, IR2, and RP2 strongly converging to wing apex; Pt one cell long and well

101 braced.

102

103 *Palaeoperilestes electronicus* sp. nov.

104 (urn:lsid:zoobank.org:act:15000F2A-E86C-451F-8857-45BA86B873F6)

105 Figs. 1–5

106

107 *Etymology*. Named after the Greek word electron for ‘amber’.

108 *Holotype*. NIGP163955. The distal two third of two wings, probably a forewing and a

109 hindwing because of their respective positions; deposited in the Nanjing Institute of

110 Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

111 *Locality and Horizon.* Hukawng Valley, Kachin Province, Myanmar; lowermost

112 Cenomanian, Upper Cretaceous.

113 *Diagnosis.* As for genus.

114 *Description.* Forewing incomplete (Figs 2A, 3A). Preserved wing length 6.81 mm,
115 maximum width 2.36 mm, length from base of RP2 to Pt 3.8 mm, from Pt to wing
116 apex 1.87 mm. Five postnodal crossveins and six postsubnodal crossveins present
117 distal of N and basal of Pt, with two basal rows aligned but three distal rows not
118 aligned. Three postnodal and postsubnodal crossveins present distal of Pt, not aligned.
119 IR2 slightly zigzagged, arising from RP2 and slightly distal of base of RP2, lying 0.25
120 mm distally. IR1 strongly zigzagged, three cells and 2.45 mm distal of base of RP2,
121 and two cells basal of Pt base. RP1 with a slight angle below Pt brace. MA distally
122 zigzagged and long. CuA ending on posterior wing margin just below base of IR2. Pt
123 one cell long (Fig. 4), 0.6 mm long and 0.35 mm wide, well braced; star- or
124 pyramid-like microstructures distributed on Pt surface; Pt brace in same orientation to
125 base of Pt. All intercalary veins (except IR1 and IR2) suppressed. Longitudinal veins
126 RA, IR1, RP1, IR2, and RP2 strongly converging to wing apex.

127 Hindwing incomplete (Figs 2B–C, 3B), resembling forewing except for
128 following differences. Preserved wing length 9.01 mm, maximum width 2.37 mm,
129 length from base of RP3/4 to base of RP2 2.7 mm, from base of RP2 to Pt 3.32 mm,
130 from Pt to wing apex 1.57 mm. Seven postnodal crossveins and eight postsubnodal
131 crossveins present before Pt, somewhat aligned. Five postnodal crossveins and five
132 postsubnodal crossveins present distal of Pt, non-aligned. Midfork present distal of N.

133 Base of IR2 two cells and 1.99 mm distal of midfork. Base of RP2 one cell distal of
134 base of IR2, lying 0.7 mm distally. IR1 strongly zigzagged, two cells and 1.38 mm
135 distal of base of RP2, and two cells basal of Pt base. MA long, basally straight but
136 strongly zigzagged distally, ending on posterior wing margin slightly basal of Pt brace.
137 MP long, basally straight but slightly zigzagged distally, ending on posterior wing
138 margin slightly distal of base of IR1. CuA ending on posterior wing margin slightly
139 basal of base of IR2.

140 Three fragmentary legs preserved (Fig. 5), paired long spines present on tibia and
141 tarsi; tibia armed with about seven or eight pairs of spines; tarsi three segmented with
142 third tarsomere length equal to first two tarsomeres, and armed with about five or six
143 pairs of spines; apical claws symmetrical.

145 **4. Discussion**

146 The absence of the wing bases makes the attribution of this damselfly rather
147 difficult. However, *Palaeoperilestes* has a star like microstructures distributed on the
148 surface of the pterostigma (Fig. 4), a derived type for the superfamily Lestoidea
149 Calvert, 1901 (Bechly, 2016), indicating the strong relationship between
150 *Palaeoperilestes* and Lestoidea. Besides, *Palaeoperilestes* has the base of IR2 shifted
151 several cells distal of the midfork. This unique character is only shared by a few
152 zygopteran taxa, i.e., Chorismagrionidae Tillyard and Fraser, 1938, Perilestidae
153 Tillyard and Fraser, 1938, Nubiolestinae Bechly, 1996 and the "megapodagrionid"
154 genus *Arrhenocnemis* Lieftinck, 1933 (according to Bechly, 2016).

155 *Arrhenocnemis* was reassigned to Megapodagrionidae by Lieftinck, (1971);
156 however, it was later attributed to the Paltynemididae: Calicnemiinae (see Gassmann,
157 2005; Orr and Kalkman, 2010). *Arrhenocnemis* consists of three species, viz., *A.*
158 *sinuatipennis* Lieftinck, 1933, *A. amphidactylis* Lieftinck, 1949, and *A. parvibullis*
159 Orr and Kalkman, 2010, all from New Guinea. *Palaeoperilestes* resembles
160 *Arrhenocnemis* in having the base of RP2 one cell distal of the base of IR2, and the
161 base of IR1 being three cells distal of the base of RP2. However, any affinity of
162 *Palaeoperilestes* with *Arrhenocnemis* can be excluded by the presence of crenulated
163 distal wing margins, the midfork being aligned with Sn, and a non-zigzagged IR1 in
164 *Arrhenocnemis*.

165 Chorismagrionidae comprise the relict species *Chorismagrion risi* Morton, 1914
166 (Fig. 6), only recorded in Australia. Fraser (1957) considered the Chorismagrionidae
167 as ‘an annectant between the families Perilestidae and Chlorolestidae’, but Dijkstra et
168 al. (2014) placed *Chorismagrion* in the Synlestidae. The open discoidal cell in
169 *Chorismagrion* cannot indicate affinities between these two groups, since this
170 character has evolved several times within Zygoptera and Epiproctophora (Bechly,
171 2016). The absence of wing base characters makes it more difficult to distinguish
172 *Palaeoperilestes* from *Chorismagrion*. The new specimen shares with *Chorismagrion*
173 a strongly zigzagged IR1. However, *Chorismagrion* has a midfork aligned with Sn,
174 the base of IR2 more cells basal of the base of RP1, the base of IR1 nearer to the base
175 of RP2 than to the base of Pt, and Pt covering two cells, obviously differing from the
176 new specimen.

177 Nubiolestinae Bechly, 1996 comprises the relict genus *Nubiolestes* (type species:
178 *Nubiolestes diotima* (Schmidt, 1943, Fig. 6), recorded in tropical Africa and restricted
179 to Cameroon (Dijkstra and Vick, 2004). *Palaeoperilestes* resembles *Nubiolestes* in the
180 base of IR2 being near to the base of RP2 and the base of IR1 being basal of Pt. The
181 differences of *Palaeoperilestes* from *Nubiolestes* are: the midfork is distal of the
182 subnodus instead of being aligned as in *Nubiolestes*, IR1 is quite zigzagged instead of
183 being straight, and the base of IR2 is two cells distal of the midfork instead of six cells
184 (Schmidt, 1943; Fraser, 1944).

185 *Palaeoperilestes* has IR2 distinctly shortened, arising on RP2 in the forewing and
186 one cell basal of base of RP2 in the hindwing. These structures resemble the situation
187 in the extant family Perilestidae. *Palaeoperilestes* shares with *Perilestes* and
188 *Perissolestes* (Fig. 6) the midfork distal of the subnodus, the base of IR2 quite near to
189 the base of RP2, but differs from them in having a quite zigzagged IR1 (straight IR1
190 in *Perilestes* and *Perissolestes*).

191 In conclusion, *Palaeoperilestes electronicus* cannot be attributed to any known
192 genus. However, *Palaeoperilestes* resembles *Perilestes* and *Perissolestes* more than
193 any of the other genera discussed above. Thus we suggest a new genus provisionally
194 attributed to the family Perilestidae (Fig. 6).

195 It should be noted that the family Austroperilestidae Petrulevičius and Nel, 2005
196 (*Austroperilestes hunco* Petrulevičius and Nel, 2005), described from the Lower
197 Eocene of Argentina, was considered to be related to Perilestidae (Petrulevičius and
198 Nel, 2005). However, *A. hunco* can be easily differentiated from *P. electronicus* by the

199 presence of a 'lestine' oblique vein, IR2 being opposite the subnodus, RP3/4 being
200 basal of the nodus, a long pterostigma and a very dense wing venation.

201

202 **5. Conclusions**

203 The first fossil representative of the extant family Perilestidae, *Palaeoperilestes*
204 *electronicus* gen. et sp. nov., is described from mid-Cretaceous Burmese amber. The
205 new discovery adds to the diversity of damselflies in the mid-Cretaceous amber.
206 Gondwana was considered to be the ancestral area of the Lestoidea (van Tol et al.,
207 2009), and the recent Perilestidae only occurs in the Neotropical region. The new
208 discovery puts the appearance of perilestid damselfly back to at least the
209 mid-Cretaceous in India.

210

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221

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334

335 **Figure captions**

336 **Fig 1.** *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955,
337 photomicrograph of specimen.

338 **Fig 2.** *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955. A,
339 photomicrograph of forewing; B, photomicrograph of mid hindwing; C,
340 photomicrograph of distal part of hindwing.

341 **Fig 3.** *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955, line
342 drawing showing wing venation.

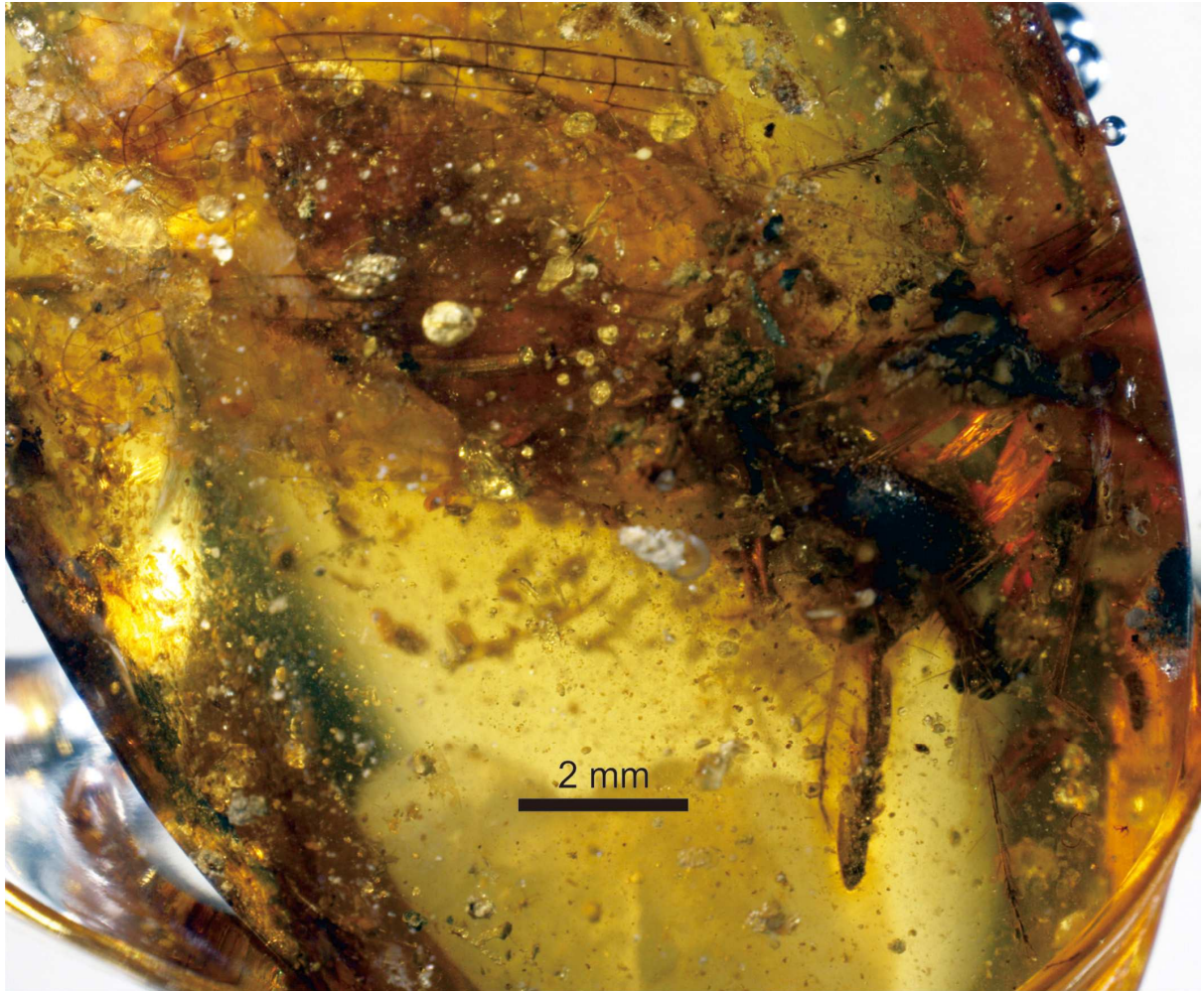
343 **Fig 4.** *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955,
344 photomicrograph showing details of Pt.

345 **Fig 5.** *Palaeoperilestes electronicus* gen. et sp. nov., holotype, NIGP163955,
346 photomicrograph showing leg details.

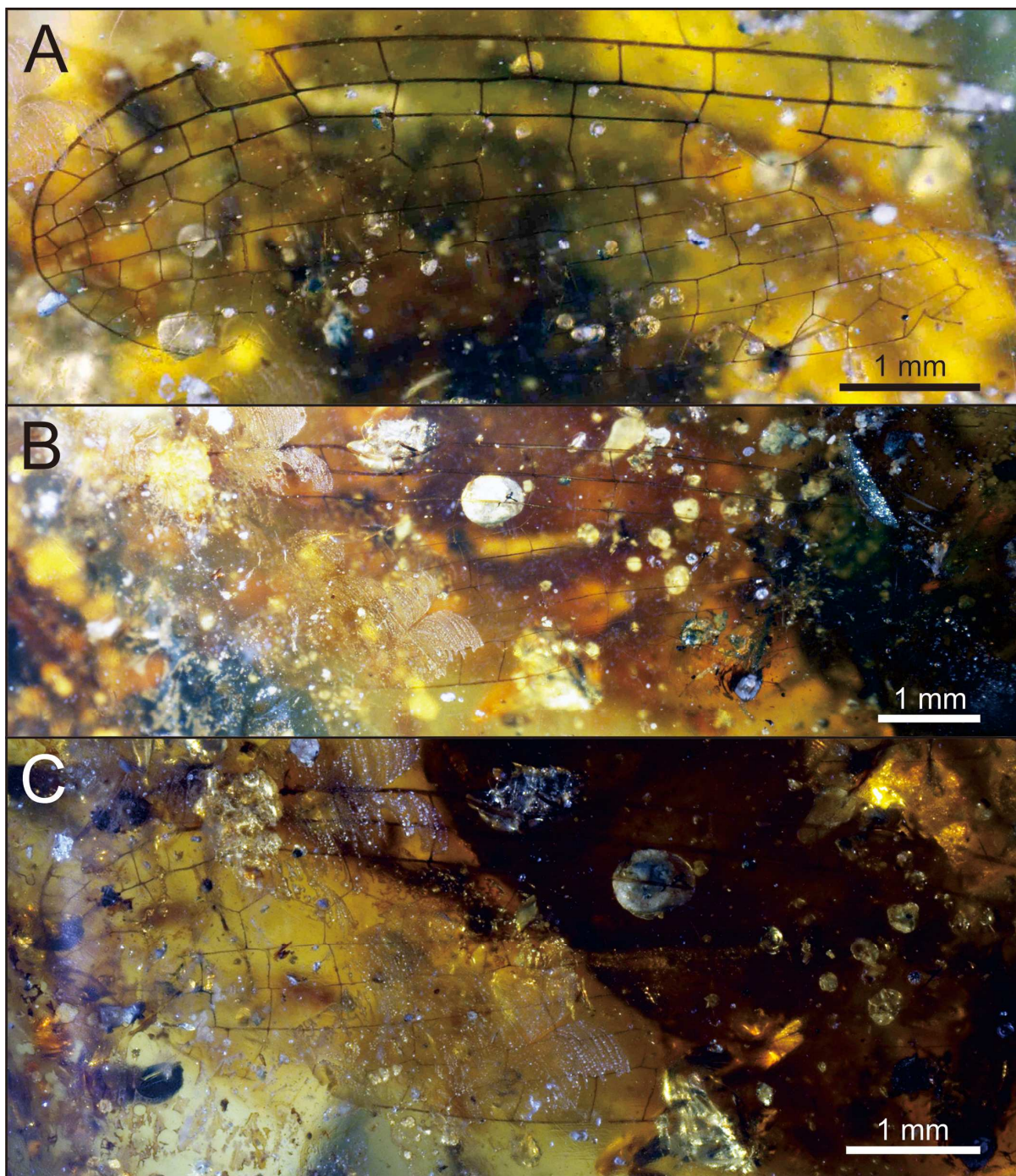
347 **Fig 6.** Putative position of *Palaeoperilestes* gen. nov. in phylogenetic tree of
348 Zygoptera. All line drawings are based on forewings except for *Palaeoperilestes* gen.
349 nov. from a more complete hindwing (Cladogram based on Dijkstra et al. 2014, line
350 drawing of *Chorismagrion risi* Morton, 1914 after Fraser, 1960; line drawing of
351 *Nubiolestes diotima* Schmidt, 1943 after Fraser, 1944; line drawings of *Perilestes*
352 *gracillimus* Kennedy, 1941 and *Perissolestes remotus* Williamson & Williamson,

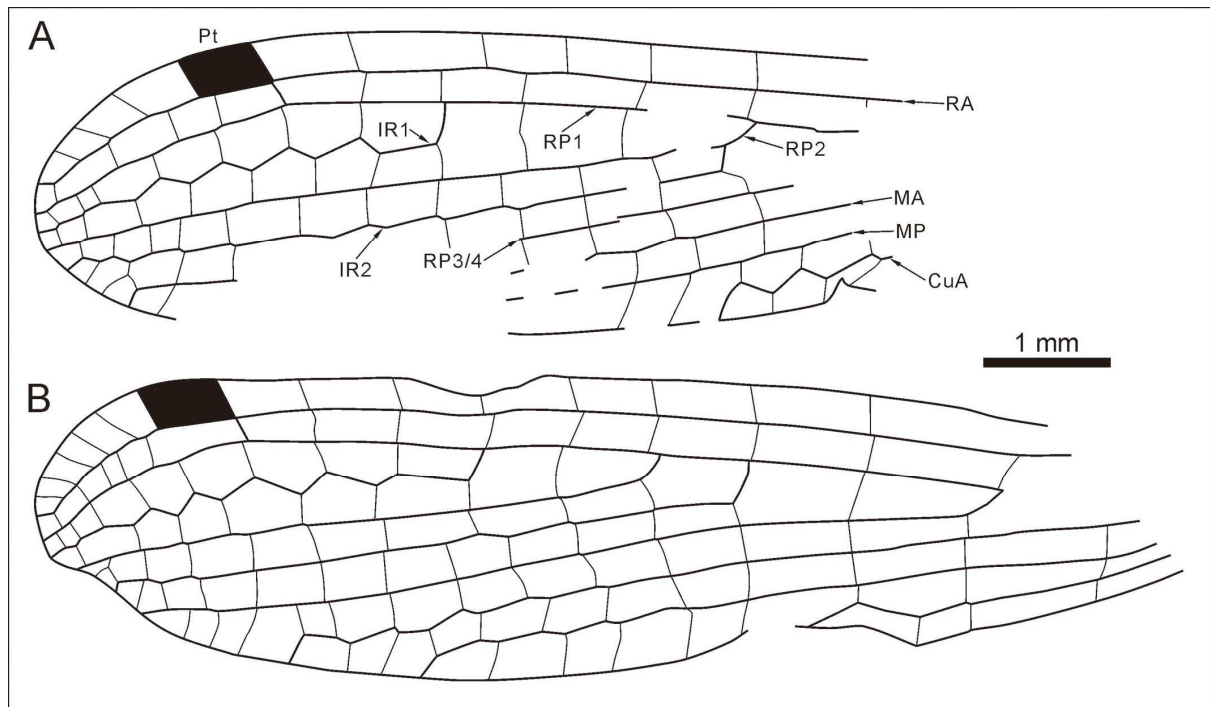
353 1924 after Kennedy, 1941).

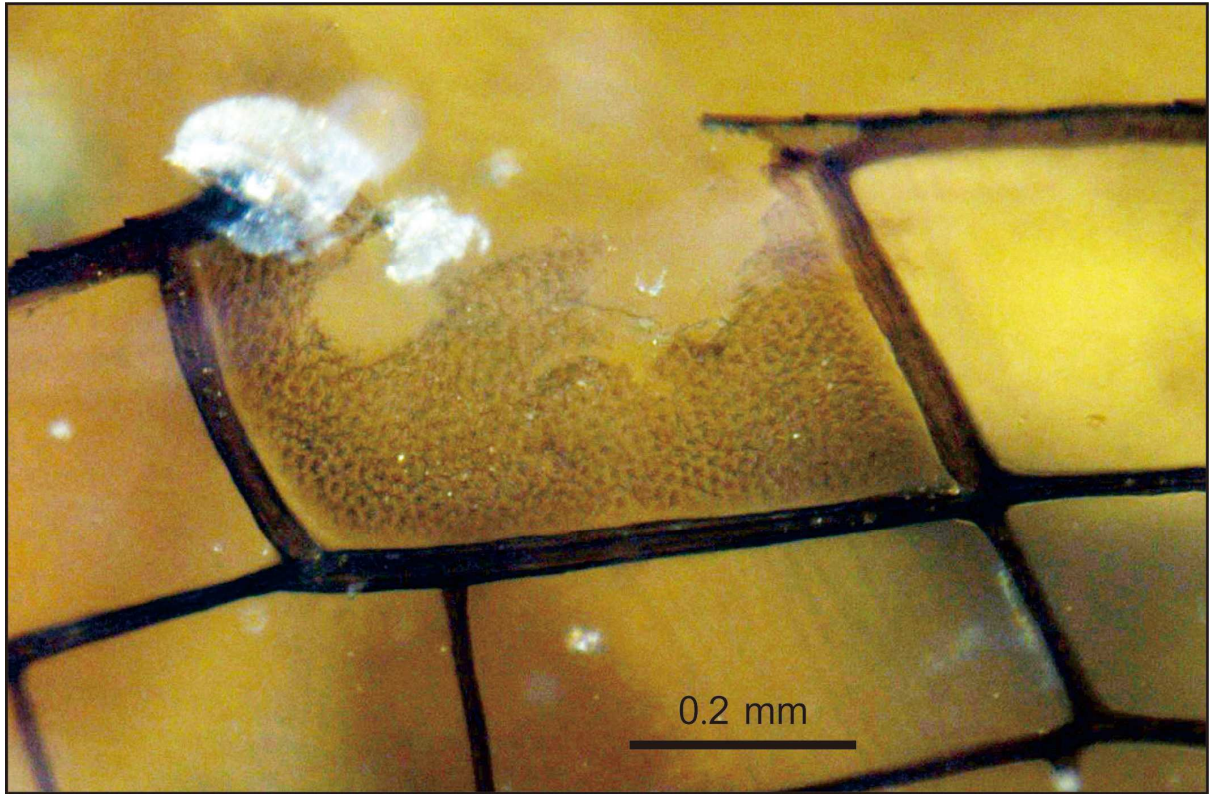
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