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1 **Mesomegaloprepidae, a remarkable new damselfly family (Odonata: Zygoptera) from**
2 **mid-Cretaceous Burmese amber**

3

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20

21 **ABSTRACT**

22 *Mesomegaloprepus magnificus* gen. et sp. nov. (Odonata: Zygoptera) is described from more
23 than 14 specimens in eight pieces of mid-Cretaceous (earliest Cenomanian, ca. 99 Ma)
24 Burmite amber from Myanmar. Possible phylogenetic affinities with the Neotropical
25 Latibasaliidae, Thaumatoeuridae, and Pseudostigmatinae are discussed, and a relationship
26 with Pseudostigmatinae considered as possible, but because of conflicting evidence separate

27 family status as Mesomegaloprepidae fam. nov. is tentatively preferred. The remarkable
28 degree of homoplastic conflict in the wing venational similarities indicates that these
29 represent relatively weak evidence for phylogenetic relationships. The palaeoecology,
30 including sexual dimorphism in wing coloration, of the new taxon is discussed, and the large
31 number of inclusions explained with possible breeding behaviour in association with water-
32 filled tree holes (phytotelmata) of the amber tree, similar to extant Pseudostigmatinae. The
33 position of all alleged fossil Thaumatonneuridae are discussed and revised: *Eothaumatoneura*
34 *ptychoptera* Pongracz, 1935 from the Eocene Geiseltal locality is restored in
35 Thaumatonneuridae. Cretaceous *Euarchistigma* and Paleogene *Eodysagrion* are tentatively
36 retained as subfamilies Euarchistigmatinae and Eodysagrioninae in Thaumatonneuridae.
37 Paleogene Dysagrioninae and Petrolestinae are removed from Thaumatonneuridae and
38 attributed to a restored family Dysagrionidae, and Paleocene Latibasaliidae is transferred from
39 Amphipterygoidea to Epallagoidea.

40

41 *Keywords:*

42 Pseudostigmatinae

43 Thaumatonneuridae

44 Latibasaliidae

45 Cenomanian

46 Myanmar

47 Phylogeny

48

49 **1. Introduction**

50

51 Descriptions of fossil damselflies in Cretaceous amber were relatively rare until the
52 recent palaeoentomological studies on the mid-Cretaceous amber from Myanmar, work which
53 has already resulted in the description of seven species from the families Hemiphlebiidae,
54 Perilestidae, Dysagrionidae, Platystictidae, and Platycnemididae (Poinar et al., 2010; Huang et
55 al., 2015; Zheng et al., 2016a, b, c, in press), with further descriptions in preparation by the
56 authors.

57 Here, we describe a remarkable new fossil damselfly taxon, *Mesomegaloprepus*
58 *magnificus* gen. et sp. nov. (Zygoptera: Mesomegaloprepidae fam. nov.) (Fig. 1), from eight
59 amber pieces with more than 14 conspecific inclusions in 99 Ma Burmese amber. This fossil
60 shows curious similarities with the extant tropical families Thaumtoneuridae and
61 Pseudostigmatidae, giving us an occasion to discuss the position of the fossil taxa currently
62 considered in these two clades (see Supplementary material).

63

64 **2. Materials and methods**

65 Fossils were examined and measured using an incident light stereomicroscope
66 (Olympus SZX9) and a stereomicroscope (Nikon SMZ 1500), as well as a Leitz Wetzlar
67 binocular microscope. Photographs were taken using a Zeiss Discovery V20 microscope
68 system. Optical instruments were equipped by camera lucida and digital cameras. The raw
69 digital images were processed with focus stacking software, and figure plates prepared with
70 Adobe PhotoshopTM.

71 We follow the wing venation nomenclature of Riek and Kukalová-Peck (1984),
72 emended by Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant
73 Odonoptera, as well as characters for family diagnoses, are largely based on the
74 phylogenetic system proposed by Bechly (1996, 2003). Several recent works that have

75 addressed the higher phylogeny of Zygoptera (Dumont et al., 2010; Davis et al., 2011;
76 Dijkstra et al., 2013, 2014) have been taken into account.

77

78 *2.1. Burmese amber*

79

80 The specimens are preserved in eight pieces of relatively clear, yellow Burmite amber.
81 The amber pieces were polished before being examined and photographed. The amber piece
82 with paratype NIGP 161753 has been included in a glass coffin with Canada Balsam as
83 medium for better examination. All amber material was legally acquired in Myanmar from
84 local traders with government registration, and legally exported according to the official
85 regulations in Myanmar.

86 Fossil-bearing has mostly been collected from the Hukawng Valley in northern
87 Myanmar (formerly known as Burma). For an overview of the amber deposit and its
88 geological setting see, e.g., Zherikhin and Ross (2000), Grimaldi et al. (2002), Cruickshank
89 and Ko (2003), and Ross et al. (2010). Radiometric U–Pb zircon dating (Shi et al., 2012)
90 recently constrained this amber to a minimum age of 98.79 ± 0.62 Ma, which is equivalent to
91 the mid-Cretaceous (earliest Cenomanian). The original habitat of the amber forest is still
92 controversial, in fact it has originally been assumed to be a tropical araucarian forest
93 (Grimaldi et al., 2002; Poinar et al., 2007), possibly with Dipterocarpaceae as another source
94 for the fossil resin. However, the first detailed report on the macromolecular nature and
95 palaeobotanical affinity of Burmite (Dutta et al., 2011), based on gas chromatography - mass
96 spectrometry, rejected Araucariaceae and Dipterocarpaceae in favour of Pinaceae as the
97 Burmese amber tree. Grimaldi (2016), after Grimaldi and Ross (in press), considered ‘based
98 on the abundant inclusions of leafy shoots’ that it was formed by a conifer, and ‘amber
99 produced possibly by *Metasequoia* (Taxodiaceae) or a close relative’. Even though fossil and
100 extant Pinaceae are generally absent from south of the equator and from tropical rainforests in

101 particular, a notable exception is *Pinus krempfii* from the rainforests of Vietnam (Brodrribb
102 and Feild, 2008).

103 The family, genus, and species are registered in Zoobank under the
104 urn:lsid:zoobank.org:act:CFC6346B-B702-4A83-B436-6D3730E73C9C

105

106 **3. Systematic palaeontology**

107

108 Order Odonata Fabricius, 1793

109 Suborder Zygoptera Selys, 1854

110 Family Mesomegaloprepidae fam. nov.

111

112 *Type-genus. Mesomegaloprepus* gen. nov.

113 *Diagnosis.* As for the genus, since it is presently monotypic (see below).

114

115 Genus *Mesomegaloprepus* gen. nov.

116

117 *Type-species. M. magnificus* sp. nov.

118 *Etymology.* Named after the Mesozoic period and the extant pseudostigmatine genus

119 *Megaloprepus* Rambur, 1842, with which it shares several wing venational similarities

120 including a unique triadic branching of vein MP. The gender of the name is masculine.

121 *Diagnosis.* Male ligula with distal segment modified to form a very long single

122 flagellum; wings with extensive brown colour (as preserved) pattern and very dense wing

123 venation with a several hundreds of cells; secondary antenodal crossveins absent, except for

124 three accessory crossveins between C and ScP distal of Ax2; series of five to seven crossveins

125 in antesubnodal space; nodus in a very basal position, at about 20% of wing length; more than

126 sixty postnodal crossveins; postnodal and postsubnodal crossveins not aligned; discoidal cell

127 rectangular and crossed by a single crossvein; distal side MAb of discoidal cell not oblique or
128 with reversed obliquity; subdiscoidal cell traversed by two crossveins; base of RP2 far distal
129 of subnodus; vein CuP between M+Cu and AA instead of being between M+Cu and A; bases
130 of RP3/4 and IR2 (midfork) basally recessed midway between arculus and nodus (instead of
131 aligned with subnodus); longitudinal wing veins distally distinctly curved to posterior wing
132 margin; CuA long, extending well beyond mid wing level, with numerous curved posterior
133 branches and characteristic triadic branching pattern of CuA and apical part of MP (but not
134 MA, which is unbranched); no intercalary veins between MP and CuA; pterostigma in apical
135 position, short and rectangular (parallel-sided); pterostigmal brace reduced; no lestine oblique
136 vein 'O'; absence of several rows of cells between costal margin, RA, and RP1 near wing
137 apex.

138

139 *Mesomegaloprepus magnificus* sp. nov.

140 Figs. 2–8

141

142 *Etymology.* The specific epithet is after the wonderful colored wings of these
143 damselflies.

144 *Holotype.* Holotype female NIGP 164902, allotype male NIGP161753, deposited at
145 Nanjing Institute of Geology and Palaeontology, P.R. China.

146 *Paratypes.* Female NIGP161754; male NIGP 164903; male NIGP 164904; NIGP
147 164950; NIGP 164951, all deposited at Nanjing Institute of Geology and Palaeontology;
148 SMNS Bu-231 deposited at the State Museum of Natural History Stuttgart, Germany.

149 *Type-locality and stratum.* Tanai Village, Hukawng Valley, Kachin State, northern
150 Myanmar. Burmite, mid-Cretaceous (earliest Cenomanian), ca. 99 Ma (Shi et al., 2012).

151 *Diagnosis.* As for the genus, since it is presently monotypic (*see above*), wings dark
152 brown with a hyaline apex, in males with posterior hyaline patch in distal cubital area, and in
153 females with narrow hyaline transverse band near base of RP2 (sexual dimorphism).

154 *Descriptions.*

155 *Holotype female NIGP 164902.* A head and thorax with three wings attached. Wings
156 basal halves dark brown, then a narrow hyaline transverse zone, followed by a second dark
157 zone and wing apex hyaline; forewing ca. 29.0 mm long (preserved part 26.0 mm long), 8.7
158 mm wide, 3.7 mm wide at nodus level; distance from base to arculus 2.4 mm, from arculus to
159 nodus 3.2 mm; nodus in a basal position, more than 19% of wing length; petiole very short,
160 0.8 mm long, 1.0 mm wide; distance from base to Ax1 1.8 mm, from Ax1 to Ax2 0.8 mm;
161 arculus distinctly basal of Ax2; 3 accessory secondary antenodal crossveins between C and
162 ScP distal of Ax2, but none between ScP and RA; antesubnodal space with a regular series of
163 crossveins; numerous postnodal crossveins not well aligned with postsubnodal crossveins;
164 pterostigma present but not colored, no pterostigmal brace; bases of RP3/4 and IR2 (midfork)
165 basally recessed midway between arculus and nodus; IR2 apparently arising on RP3/4; basal
166 space between RP3/4 and IR2 not narrowed; area between RP and MA between arculus and
167 base of RP3/4 without a crossvein; base of RP2 far distal from subnodus; no oblique
168 crossvein; two secondary longitudinal veins between MA and MP in distal part, both
169 apparently emerging from MP; discoidal cell crossed, rectangular, with MAb of inverted
170 obliquity; subdiscoidal cell traversed by two crossveins; CuP between M+Cu and AA; anal
171 area rather wide with a series of small transverse cells between AA and AP; cubital area
172 broad, CuA long with numerous curved posterior branches and characteristically triadic
173 branching pattern of CuA; area between MP and CuA broader than postdiscoidal area in their
174 basal parts; no intercalary vein between MP and CuA.

175 *Allotype NIGP161753.* The amber piece is 3.5 cm long and 0.5 cm wide. This
176 specimen (Figs. 2-3) features head, thorax, and the four basal abdominal segments, two fore

177 legs, one mid leg, one hind leg, two-third of left forewing and bases of the two hind wings
178 attached. Head transverse, 5.0 mm wide, with eyes well separated, distance between eyes ca.
179 4.0 mm; ocelli disposed in triangle on a low protuberance between eyes. Legs with long
180 spines on femora and tibiae. Abdomen ca. 2.0 mm wide (it is not visible if there is a
181 secondary copulatory apparatus on the second segment or not). Forewing uniformly dark
182 brown owing oxidation; forewing ca. 29.0 mm long (preserved part 26.0 mm long), 8.7 mm
183 wide, 3.7 mm wide at nodus level; distance from base to arculus 2.4 mm, from arculus to
184 nodus 3.2 mm; nodus in a basal position, more than 19% of wing length; petiole very short,
185 0.8 mm long, 1.0 mm wide; distance from base to Ax1 1.8 mm, from Ax1 to Ax2 0.8 mm;
186 arculus distinctly basal of Ax2; 3 accessory secondary antenodal crossveins between C and
187 ScP distal of Ax2, but none between ScP and RA; antesubnodal space with a regular series of
188 crossveins; numerous postnodal crossveins not well aligned with postsubnodal crossveins;
189 pterostigma present but not colored, no pterostigmal brace; bases of RP3/4 and IR2 (midfork)
190 basally recessed midway between arculus and nodus; IR2 apparently arising on RP3/4; basal
191 space between RP3/4 and IR2 not greatly narrowed; area between RP and MA between
192 arculus and base of RP3/4 with a crossvein; base of RP2 far distal from subnodus; no oblique
193 crossvein; two secondary longitudinal veins between MA and MP in distal part, both
194 apparently emerging from MP; discoidal cell crossed, rectangular, with MAb of inverted
195 obliquity; subdiscoidal cell traversed by two crossveins; CuP between M+Cu and AA; anal
196 area rather wide with a series of small transverse cells between AA and AP; cubital area
197 broad, CuA elongate with numerous curved posterior branches and characteristically triadic
198 branching pattern of CuA; area between MP and CuA broader than postdiscoidal area in their
199 basal parts; no intercalary vein between MP and CuA.

200 *Paratype NIGP 161754.* The amber piece with this paratype is 2.6 cm long and 0.5 cm
201 wide. This specimen (Fig. 2e-f) features fragments of thorax with part of head and first basal
202 abdominal segments still attached, plus bases of the two right wings and the basal half of left

203 forewing. The preserved parts of wing are nearly identical in proportions and venation to
204 those of the holotype, documenting the conspecific status. Head transverse with eyes well
205 separated. Thorax ca. 2.8 mm wide and ca. 4.0 mm high. Abdomen 2.0 mm wide; no
206 secondary copulatory apparatus on segments 2-3 (thus a female specimen). Forewing dark
207 brown with a narrow lighter transverse band distal of nodus, near base of RP2, forewing with
208 preserved part ca. 18.0 mm long, 3.3 mm wide at nodus level; distance from base to nodus 4.4
209 mm, nodus in a very basal position; petiole very short, 1.2 mm long; Ax2 about opposite
210 arculus; area between RP and MA between arculus and base of RP3/4 without any crossvein.

211 *Paratype NIGP 164903.* This specimen features a nearly complete abdomen of a male,
212 with a nearly complete hind wing attached to fragments of the thorax and two wing apices, as
213 well as isolated legs with very long spines. It has the same proportions and wing venation as
214 the holotype (including arculus distinctly basal of Ax2); nevertheless its area between RP and
215 MA between arculus and base of RP3/4 is without any crossvein. The wing has a brown
216 colour pattern except for the translucent apex and distal cubital area. This specimen clearly
217 shows the male secondary copulatory apparatus of abdominal segment 2, with a ligula having
218 its distal segment modified to form a very long single flagellum, reaching segment 3; a series
219 of strong spines on the genital lobes; anterior hamuli well developed with a smooth point.

220 *Paratype NIGP 164950.* This specimen features 10 isolated wings of male and female
221 specimens that probably represented a mating group. The wings are largely identical to those
222 of the allotype NIGP 161753 (including arculus distinctly basal of Ax2), except in the area
223 between RP and MA between arculus and base of RP3/4 without any crossvein. The colour
224 pattern is similar to the other specimens. The Pterostigmata are covering 2.5-3.5 narrow cells
225 beneath them.

226 *Paratype NIGP 164951.* This specimen features six isolated wings (probably of a
227 mating pair) without preserved bodies. The wings are also identical to the holotype. The
228 colour patterns are similar to those of the other specimens.

229 *Paratype male NIGP 164904*. This specimen features a male with head, thorax and
230 part of the abdomen, plus wings. The wings are also identical to the holotype. The colour
231 patterns are similar to those of the other specimens.

232 *Paratype SMNS Bu-231*. This specimen features partially preserved bodies of three
233 specimens (incl. male and female), with fragments of all wings and legs bearing very long
234 spines. The wing venations are very similar to those of the allotype (including arculus
235 distinctly basal of Ax2) and the colour pattern is similar to those of the other specimens.
236 Notable differences are: antesubnodal space with seven crossveins but no crossveins in the
237 basal third (right wings of female); midfork (origin of IR2 and RP3/4) is not in midway
238 position between subnodus and arculus but further recessed close to arculus (right hind wing
239 of female); subdiscoidal cell traversed by two crossveins in the forewing, but only one in the
240 hind wing (right wings of female); pterostigma covering three narrow cells beneath it (in the
241 female).

242

243 **4. Discussion**

244

245 *4.1 Phylogenetic relationships*

246 Placement of Mesomegaloprepidae fam. nov. is challenging owing to conflicting
247 evidence. *Mesomegaloprepus* gen. nov. shows venational similarities with three different
248 known family-group taxa of Neotropical damselflies, viz. Latibasaliidae (genus *Latibasalia*
249 Petrulevičius and Nel, 2004), Coenagrionidae-Pseudostigmatinae (esp. genus *Megaloprepus*),
250 and Thaumtoneuridae (esp. genus *Thaumtoneura* McLachlan, 1897).

251

252 *4.1.1 Comparison with Latibasaliidae Petrulevičius and Nel, 2004*

253 Latibasaliidae (Zygoptera: Amphipterygoidea) are an enigmatic fossil family from the
254 Paleogene (Upper Palaeocene) of Argentina (Petrulevičius and Nel 2004, 2007). A potential

255 relationships with the fossil genera *Petrolestes* Cockerell, 1927 and *Congqingia* Zhang, 1992
256 (Amphipterygoidea: Thaumatonneuridae) was discussed in the original description, because
257 they share the absence of secondary antenodal crossveins and the absence of antesubnodal
258 crossveins. However, these characters are very homoplastic and weak. We transfer here
259 Latibasaliidae from Amphipterygoidea to Epallagoidea as sister group of Zacallitidae, because
260 of the shared convex longitudinal intercalary vein in the cubital field as unique putative
261 synapomorphy.

262 *Mesomegaloprepus* shows several similarities with Latibasaliidae: arculus distinctly
263 basal of Ax2; Ax1 and Ax2 close together; very oblique nodal and subnodal veinlets;
264 postnodal crossveins not aligned with postsubnodal crossveins (symplesiomorphy);
265 pterostigmal brace reduced; midfork (origins of IR2 and RP3/4) recessed distinctly basal of
266 subnodus; discoidal cell quadrangular; distal side MAb of discoidal cell with reversed
267 obliquity; cubital space expanded with several rows of cells; longitudinal veins distally
268 strongly curved; secondary intercalary branches between RP3/4 and MA, and between MA
269 and MP; no leistine oblique vein 'O'; wings with dark banded colour pattern.

270 However, *Mesomegaloprepus* differs from Latibasaliidae in several important
271 characters: nodus in more basal position; midfork mid way between arculus and subnodus
272 (instead of being recessed much closer to arculus); basal side of pterostigma not oblique;
273 triadic branchings of CuA. Further potential differences (viz. secondary antenodals between C
274 and ScP distal of Ax2, several antesubnodal crossveins, and subdiscoidal cell divided) are not
275 totally certain, because the corresponding wing areas seem not very well preserved in the
276 known specimens of Latibasaliidae.

277 The mentioned differences in *Mesomegaloprepus* are all derived states that could be
278 autapomorphies; so they would not contradict a relationship with Latibasaliidae. However,
279 many of the similarities are either of uncertain polarity, or symplesiomorphies, or
280 homoplastic, so that the evidence for a relationship is weak and inconclusive. We therefore

281 can neither exclude nor establish a sister group relationship of Mesomegaloprepidae with
282 Latibasaliidae. Nevertheless, the densely reticulated wings with short petiolus, and especially
283 the rectangular shape of the discoidal cell with a distal side MAb with reversed obliquity
284 would support a position in Epallagoidea (new position for Latibasaliidae), and the expanded
285 cubital field would agree with Zacallitidae (here recognized as sister group of Latibasaliidae).
286 Furthermore, the recession of the midfork, the reduced pterostigmal brace and lestine oblique
287 vein 'O', as well as the coloured wings would support a position in Caloptera
288 (Calopterygoidea sensu Dijkstra et al., 2013), if this group is monophyletic at all, which is
289 rather doubtful (Dijkstra et al., 2014).

290

291 *4.1.2 Comparison with Pseudostigmatinae Kirby, 1890 (sensu Dijkstra et al., 2013)*

292

293 Pseudostigmatinae (formerly classified as distinct family Pseudostigmatidae) is a
294 group of mainly Neotropical giant damselflies (also known as helicopter damselflies) that
295 oviposit in phytotelmata, where the dendrolimnetic larvae develop. Adults pluck orb-weaver
296 spiders and their prey from spider webs (Fincke, 1984; Clausnitzer, 2002). The extremely
297 long abdomen is apparently not developed for oviposition in phytotelmata but used as balance
298 while hovering in front of spider webs (Clausnitzer, 2002). The only Pseudostigmatinae
299 outside of the Neotropical realm is the Eastern African *Coryphagrion grandis* Morton, 1924,
300 which was formerly classified in a monotypic separate family Coryphagrionidae Pinhey,
301 1962, but recognized as most closely related to or belonging to Pseudostigmatinae by Bechly
302 (1996, 2003), Clausnitzer and Lindeboom (2002), Rehn (2003), Groeneveld et al. (2007), Yu
303 and Bu (2011), and Ingle et al. (2012). *Coryphagrion* Morton, 1924 is very similar to
304 *Mecistogaster* Rambur, 1842. Like all Neotropical Pseudostigmatinae, it oviposits in
305 phytotelmata and exclusively feeds on spiders and insects picked out of spider webs
306 (Lounibos, 1980; Clausnitzer, 2002; Clausnitzer and Lindeboom, 2002). All Neotropical

307 genera have a more or less reduced pterostigma and males have characteristical hamuli
308 anteriores and a terminal single flagellum on the ligula (Schmidt, 1915; Dijkstra et al., 2014),
309 while *Coryphagrion* has retained a normal pterostigma and lacks the terminal ligula flagellum
310 (Kimmins, 1931; Dijkstra et al., 2014). Morphological and genomic data have shown that the
311 Pseudostigmatinae (incl. *Coryphagrion*) nest deeply within Coenagrionidae and thus should
312 be classified within this family (Ramírez, 1997; Bybee et al., 2008; Carle et al., 2008; Yu and
313 Bu, 2011; Ingley et al, 2012; Dijkstra et al., 2014). Dijkstra et al. (2013) therefore formally
314 sunk the family Pseudostigmatidae in Coenagrionidae, where it forms a subfamily
315 Pseudostigmatinae with three tribes (Bechly, 1996, 2003; Ingley, 2012): Coryphagrionini
316 (only including *Coryphagrion* as sister group to Neotropical pseudostigmatines),
317 Pseudostigmatini (including the two narrow-winged genera *Mecistogaster* and *Pseudostigma*
318 Selys, 1860 with simple longitudinal veins), and Megaloprepini (broad-winged genera
319 *Microstigma* Rambur, 1842, *Anomisma* McLachlan, 1877, and *Megaloprepus* , with
320 characteristic triadic branchings of longitudinal veins MA and CuA). The phylogeny and
321 character distribution shows that narrow wings without triadic branchings represent the
322 plesiomorphic ground plan condition, from which derived broad winged forms evolved
323 (Bechly, 1996, 2003; Ingley, 2012). The extant genus *Megaloprepus* represents the largest
324 known damselfly of all times with a wingspan of up to 19 cm and an abdomen length of 10
325 cm (Groeneveld et al., 2007).

326 Putative synapomorphies of *Mesomegaloprepus* with Pseudostigmatinae (incl.
327 Coryphagrionini) are as follows: similar shape of wing with very dense venation and a large
328 number of cells (also present in *Thaumatoneura*); very basal position of nodus at about 20%
329 of wing length (also present in *Thaumatoneura*), correlated with a basal recession of the
330 midfork at about 25% of wing length, and a high number of postnodal veins and an origin of
331 RP2 far distal of subnodus; discoidal cell elongated (also present in Thaumaturidae); IR2
332 apparently arising from RP3/4 (as in Thaumaturidae); more than two rows of cells

333 between RP1 and RP2 (also present in *Thaumatoneura*), with very long IR1 and a shorter
334 negative intercalary between IR1 and RP1 (very much like Pseudostigmatinae, and unlike
335 *Thaumatoneura*); pterostigma very short, rectangular, and in apical position. Finally the
336 possible association with phytotelmata (*see below*) might represent evidence for a relationship
337 with Pseudostigmatinae (incl. *Coryphagrion*), but also occurs by convergence in some
338 unrelated tropical damselfly and dragonfly taxa. However, the following plesiomorphies of
339 *Mesomegaloprepus* contradict a placement within the crown group of Pseudostigmatinae or
340 even in Coenagrionoidea: much smaller size (all Pseudostigmatinae show gigantism);
341 presence of three accessory secondary antenodal crossveins between C and ScP distal of Ax2
342 (unknown in Coenagrionoidea, but 1-2 present in *Thaumatoneura*); multiple antesubnodal
343 crossveins (unknown in Coenagrionoidea); postnodal and postsubnodal crossveins not aligned
344 (unknown in Coenagrionoidea, but present in *Thaumatoneura*); RA and RP1 not sigmoidally
345 curved at apex, and RP1 and RP2 not converging apically; basal part of space between IR2
346 and RP3/4 not strongly narrowed; only a single row of cells between C and RA at apex (two
347 or more rows in Pseudostigmatinae, except for some but not all specimens of *Coryphagrion*
348 and *Mecistogaster*, but also *Thaumatoneuridae*). *Mesomegaloprepus* differs from nearly all
349 known Coenagrionidae (including all Pseudostigmatinae), with the sole exception of
350 Protoneurinae *s.str.* (subfamily of Coenagrionidae according to Dijkstra et al., 2014), in the
351 rectangular shape of the discoidal cell (as in *Thaumatoneura*, and less developed in
352 *Megaloprepus*). Also *Mesomegaloprepus* differs from all known Coenagrionoidea (including
353 all Pseudostigmatinae) in the position of the arculus distinctly basal of Ax2 (but the polarity
354 of this character is unclear), the recession of the midfork (origins of IR2 and RP3/4) distinctly
355 basal of subnodus (a derived state that never occurs in Coenagrionoidea and
356 *Thaumatoneuridae*, but is typical for Lestoidea and “Calopterygoidea”), and the presence of
357 several secondary (intercalary) longitudinal veins in the median and radial areas (as in
358 *Thaumatoneuridae*).

359 Putative synapomorphies with Neotropical Pseudostigmatinae (Pseudostigmatini +
360 Megaloprepini) are as follows: pterostigmal brace reduced (as in *Thaumatoneura*; still braced
361 in *Coryphagrion*); male secondary genital apparatus with distal segment of ligula modified
362 into a very long single flagellum (absent in *Coryphagrion*). The following plesiomorphies of
363 *Mesomegaloprepus* contradict a placement in the crown group of Neotropical
364 Pseudostigmatinae: RA, RP1, and IR1 not apically strongly curved towards the hind margin
365 and converging to the same point at the hind margin (only reversed in *Anomisma*); only a
366 single row of cells between RP1 and IR1 (like *Coryphagrion*, but unlike all other
367 Pseudostigmatinae and Thaumaturidae); normal pterostigma present (replaced by pseudo-
368 pterostigma in all Neotropical Pseudostigmatinae). The very short parallel-sided pterostigma
369 of *Mesomegaloprepus* could be interpreted as precursor of the further reduction of the
370 pterostigma in Neotropical Pseudostigmatinae, but the presence of a normal pterostigma
371 rather than a pseudo-pterostigma would still exclude any position within the crown group
372 Pseudostigmatinae and especially any closer relationship with *Megaloprepus*.

373 Putative synapomorphies with broad-winged Pseudostigmatinae (Megaloprepini) are
374 as follows: broad shape of wings; CuA very long with numerous curved posterior branches,
375 and triadic branching pattern of CuA (also present in *Thaumatoneura*); furcation of RP into
376 RP1 and RP2 shifted into distal half of wing, thus base of RP2 very far distal of subnodus (as
377 in *Thaumatoneura*). However, the following plesiomorphies of *Mesomegaloprepus* contradict
378 a placement in the crown group of the broad-winged Pseudostigmatinae and thus refute a
379 potential sister group relationship with either *Anomisma* or *Megaloprepus*: pterostigma
380 present; absence of the typical triadic branching of apical MA, and apical furcation of RP3/4;
381 distally only a single row of cells between RA and RP (at least two rows in Megaloprepini,
382 but also at apex of Thaumaturidae); only a single row of cells between RP1/2 and RP3/4
383 between the RP forks (as in Thaumaturidae).

384 Putative synapomorphies with the extant genus *Anomisma* (Pseudostigmatinae:
 385 Megaloprepini) are as follows: discoidal cell divided (unique autapomorphy within
 386 Coenagrionidae, and unlike the undivided discoidal cell in *Thaumatoneura*); subdiscoidal cell
 387 divided by two crossveins (vs only one in *Thaumatoneura*); presence of at least one accessory
 388 secondary antenodal crossvein between C and ScP distal of Ax2 (unique reversal within
 389 Coenagrionidae, also present in *Thaumatoneura*). However, *Anomisma* has a very different
 390 discoidal cell that is very elongate (instead of short), acute (instead of rectangular), and
 391 divided by 2-3 (instead of only one) crossveins. Also, *Anomisma* has only a single accessory
 392 secondary antenodal crossvein instead of three. These differences may suggest a case of
 393 convergence rather than synapomorphy, especially since these two characters are highly
 394 homoplastic within Zygoptera.

395 Putative synapomorphies with the extant genus *Megaloprepus* (Pseudostigmatinae:
 396 Megaloprepini) are as follows: discoidal cell not very acute (contrary to other
 397 Pseudostigmatinae); longitudinal wing veins being distally distinctly curved to the posterior
 398 wing margin (also present in *Thaumatoneura*); more strongly developed triadic branching
 399 pattern of distal part of MP; dark banded colour pattern of wings with sexual dimorphism (as
 400 in *Thaumatoneura*). The absence of intercalary veins between MP and CuA
 401 (symplesiomorphy), and the presence of secondary longitudinal veins in area between MP and
 402 MA apparently emerging from MP (thus possibly a precursor of the triadic branching of MP
 403 in *Megaloprepus*) are characters that would rather support an attribution of
 404 *Mesomegaloprepus* to Pseudostigmatinae close to *Megaloprepus* (MP is apically shortly
 405 forked in *Anomisma* and *Microstigma*, but simple in *Coryphagrion*, *Mecistogaster*, and
 406 *Pseudostigma*).

407 Altogether, the wing venational similarities with Pseudostigmatinae are either very
 408 weak characters (pterostigma short and stigmal brace reduced) or clearly convergences
 409 (similarities with *Megaloprepus*), because a subordinate ingroup position of

410 *Mesomegaloprepus* within Pseudostigmatinae is excluded by its plesiomorphic absence of
411 several derived groundplan characters of Pseudostigmatinae and Megaloprepini (see above),
412 while the similarities between *Mesomegaloprepus* and broad-winged Megaloprepini do not
413 belong to the ground plan of Pseudostigmatinae as documented by the very similar wing
414 venations of the most basal pseudostigmatine genera *Coryphagrion*, *Mecistogaster*, and
415 *Pseudostigma*. The characteristic ligula with single terminal flagellum is a derived similarity
416 of *Mesomegaloprepus* with Neotropical Pseudostigmatini + Megaloprepini, but it is still
417 absent in Coryphagrionini, and is homoplastic in recent damselflies (e.g., present in the
418 unrelated agriolestid genus *Podopteryx* Selys, 1871 according to Kalkman and Theischinger,
419 2013), so that it also represents a weak and conflicting character. Consequently, there is no
420 conclusive evidence to establish a phylogenetic relationship of *Mesomegaloprepus* with the
421 Pseudostigmatinae.

422

423 *4.1.3 Comparison with Thaumtoneuridae Tillyard and Fraser, 1938 (sensu Dijkstra,*
424 *2014)*

425

426 Recent Thaumtoneuridae are endemic to the Neotropics and only include the two
427 genera *Thaumtoneura* McLachlan, 1897 (one species *T. inopinata*) and *Paraphlebia* Selys,
428 1862 (four species) (Dijkstra et al., 2014) from Central America, which all are relatively large
429 damselflies typically found in the vicinity of waterfall habitats (“waterfall damsels”). Females
430 have hyaline wings, while males are typically dimorphic with either hyaline wings or distinct
431 dark colour pattern (Calvert, 1914; González-Soriano and Córdoba-Aguilar, 2003; Romo-
432 Beltrán, 2009).

433 A close relationship of the Recent genera *Thaumtoneura* and *Paraphlebia* was
434 previously suggested based on adult and larval morphology (Novelo-Gutiérrez, 2008;

435 Garrison et al., 2010). It has been confirmed with modern phylogenomic studies (Fogarty et
436 al., 2008; Dijkstra, 2014).

437 Bechly (1996, 2003) considered that the Thaumtoneuridae are related to the
438 Amphipterygoidea within the jewelwing clade Eucaloptera (Calopterygoidea sensu Dijkstra et
439 al., 2013). Dijkstra et al. (2014) suggested a somewhat different phylogeny for
440 Thaumtoneuridae in a clade that comprises several genera previously considered as
441 “Megapodagrionidae”, and this whole clade being sister group of a clade that comprises the
442 Philogeniidae, Amphipterygidae, Lestoideidae, and Epallagidae (= Euphaeidae).

443 The fact that two South East Asian “megapodagrionid” damselfly genera (viz.
444 *Bornargiolestes* Kimmins, 1936 and *Burmargiolestes* Kennedy, 1925) have been proposed by
445 Dijkstra et al. (2014) as closest relatives of Thaumtoneuridae, could suggest that a stem-
446 Thaumtoneuridae from Burmese amber would not be an unlikely discovery.

447 All fossil taxa that previously have been attributed to Thaumtoneuridae are rather of
448 dubious relationship and are revised below.

449 Putative synapomorphies of *Mesomegaloprepus* with extant Thaumtoneuridae
450 (*Paraphlebia* + *Thaumtoneura*) (see Bechly, 1996, 2003) are as follows: dark banded colour
451 pattern of wings with sexual dimorphism (as in *Megaloprepus*); dense wing venation with
452 several hundreds of cells; nodus in very basal position, correlated with large number of
453 postnodal crossveins (as in Pseudostigmatinae); triadic branching of CuA; subdiscoidal cell
454 traversed by a crossvein; discoidal cell elongated (as in Pseudostigmatinae); IR2 apparently
455 arising from RP3/4 (as in Pseudostigmatinae); presence of several secondary (intercalary)
456 longitudinal veins in median and radial area. Nevertheless, the following plesiomorphies of
457 *Mesomegaloprepus* contradict a placement in the crown group of Thaumtoneuridae: small
458 size; several antesubnodal crossveins; only a single row of cells between RA and RP1 distal
459 of pterostigma; absence of intercalary veins between MP and CuA. *Mesomegaloprepus*
460 strongly differs from Thaumtoneuridae in the divided discoidal cell, as well as the very short

461 and rectangular pterostigma, while the discoidal cell of *Paraphlebia* and *Thaumatoneura* is
 462 always undivided and their pterostigmata are very long with a extremely oblique basal side
 463 (but also unbraced, which seems to be a symplesiomorphy of Thaumatonneuridae, as the
 464 pterostigma of closely related genera like *Burmargiolestes* is also unbraced). Also the fact that
 465 the midfork is not basally recessed between arculus and subnodus in extant Thaumatonneuridae
 466 contradicts a relationship with *Mesomegaloprepus* Further important differences are the
 467 position of arculus that is more or less aligned with Ax2 in Thaumatonneuridae but distinctly
 468 basal of Ax2 in *Mesomegaloprepus*, as well as the position of the CuP-vestige (“anal
 469 crossing”) that is located in the petiolus in Thaumatonneuridae, while it ends on free vein AA
 470 distal of petiolus in *Mesomegaloprepus*, but the polarity of these two characters is uncertain.
 471 An antesubnodal space without any crossveins was proposed by Bechly (2007, 2003) as an
 472 autapomorphy of Thaumatonneuridae, but of course this character is highly homoplastic and
 473 also present in all Lestoidea and Coenagrionoidea (incl. Pseudostigmatinae), but it is absent in
 474 *Mesomegaloprepus*.

475 Putative synapomorphies with only the extant genus *Thaumatoneura*: broad wings
 476 with very dense wing venation (large number of cells) (as in Pseudostigmatinae:
 477 Megaloprepini); petiolus very short (still long in *Paraphlebia*); nodus even in more basal
 478 position, correlated with large number of postnodal crossveins; presence of a few accessory
 479 secondary antenodal crossveins between C and ScP distal of Ax2 (3 in *Mesomegaloprepus*, 1-
 480 2 in *Thaumatoneura*, none in *Paraphlebia*); discoidal cell rectangular with distal side MAb
 481 with reversed obliquity (still acute in *Paraphlebia*); subdiscoidal cell traversed by 1-2
 482 crossveins (however the subdiscoidal cell of *Thaumatoneura* is of very different shape and
 483 much longer); postnodal and postsubnodal crossveins secondarily non-aligned (still aligned in
 484 *Paraphlebia*); greatly expanded cubital area; CuA with numerous curved posterior branches
 485 and characteristic triadic branching pattern of CuA (similar to *Megaloprepus*, but CuA
 486 much shorter); longitudinal veins distally distinctly curved towards hind margin of wing; base

487 of RP2 very far distal of subnodus as in Pseudostigmatinae: Megaloprepini). In the anal area
488 of *Mesomegaloprepus*, there is a series of small transverse cells between AA and AP below
489 the subdiscoidal space, which is a character state also present in *Thaumatoneura*, but the
490 Pseudostigmatinae also have small crossveins in the anal area between AA and AP below the
491 subdiscoidal space. However, the anal area is distinctly narrower in Pseudostigmatinae than in
492 *Mesomegaloprepus* and *Thaumatoneura*, but it is even narrower in *Paraphlebia* (second
493 modern genus of Thaumatoneuridae). Even though all these character states seem to be
494 derived in *Thaumatoneura*, as suggested by the more “megapodagrionid”-like sister genus
495 *Paraphlebia* and the closely related genera *Bornargiolestes* and *Burmargiolestes* as
496 sistergroups, the character polarity is unclear in *Mesomegaloprepus*, mainly because of the
497 homoplastic distribution of these character states in other damselfly taxa (e.g., multiple
498 secondary antenodal crossveins is generally rather a plesiomorphy in odonates). The fact that
499 other characters (*see above*) contradict an ingroup position of *Mesomegaloprepus* within
500 Thaumatoneuridae as sister group of *Thaumatoneura*, rather suggests that the similarities
501 between these two genera are not synapomorphies.

502 *Mesomegaloprepus* strongly differs from the other extant thaumatoneurid genus
503 *Paraphlebia* in the rectangular and divided discoidal cell, very short petiolus, broad cubital
504 area, and nodus even more strongly basally recessed.

505

506 *4.1.4 Ambiguous relationship of Mesomegaloprepidae and justification for this new*
507 *family*

508

509 *Mesomegaloprepus* shows a confusing mosaic of characters shared by either the
510 thaumatoneurid genus *Thaumatoneura* or the pseudostigmatine genus *Megaloprepus*, or
511 present in both (sub)families. *Mesomegaloprepus* differs from the modern representatives of
512 the Thaumatoneuridae and Pseudostigmatinae in the much smaller size, the vestige of vein

513 CuP (“anal crossing”) between M+Cu and AA instead of being between M+Cu and A, the
514 presence of antesubnodal crossveins, and bases of RP3/4 and IR2 (midfork) basally recessed
515 midway between arculus and nodus instead of being aligned with the subnodus. These
516 differences, as well as the conflicting and thus probably convergent similarities with
517 Latibasaliidae, Thaumatonneuridae, and Pseudostigmatinae, allow us to erect a new family
518 Mesomegaloprepidae, with unresolved relationship within Zygoptera. If Mesomegaloprepidae
519 should turn out to belong to one of the discussed extant family group taxa after all, it could be
520 reclassified as distinct subfamily or tribe within them.

521 Anyway, the high degree of character conflicts in the wing venational similarities with
522 *Thaumatoneura* on the one hand and broad-winged Pseudostigmatinae-Megaloprepini on the
523 other hand, while lacking more superordinate ground-plan characters of the family group taxa
524 Thaumatonneuridae and Pseudostigmatinae, is a strong indication that wing venational
525 characters generally are of poor value for the reconstruction of phylogenetic relationships
526 within Odonata. This is also indicated by the strong difference between phylogenetic
527 classifications of damselflies based on wing venational characters (Bechly 1996, 2003) with
528 those based on modern phylogenomic studies (Bybee et al., 2008; Carle et al., 2008; Dumont
529 et al., 2010; Dijkstra et al. 2013, 2014). Because of the notorious incongruence between
530 morphological and molecular evidence in phylogenetic reconstructions it was even suggested
531 to refrain from using morphological data at all (e.g., Scotland et al., 2003), which is of course
532 impossible with fossil taxa (Wiens, 2004).

533

534 4.2 Status of alleged fossil *Thaumatonneuridae*

535

536 Pongrácz (1935) described *Eothaumatoneura* from the Eocene of Germany and
537 attributed it to Thaumatonneuridae, but Nel and Paicheler (1994) transferred it to Zygoptera
538 *incertae sedis*. Bechly (1996, 2003) attributed the mostly Paleogene Dysagrioninae Cockerell,

539 1908 (*Petrolestes*, *Congqingia*, *Dysagrion* Scudder, 1878, and *Phenacolestes* Cockerell,
540 1908) and Early Cretaceous Euarchistigmatinae (*Euarchistigma* Carle and Wighton 1990) to
541 Thaumtoneuridae within Amphipterygoidea. Petrulevičius and Nel (2004) considered the
542 Paleogene *Latibasalia* as possibly related to Dysagrioninae within Amphipterygoidea, but we
543 here transferred this taxon to Epallagoidea (*see above*). Nel et al. (2005) described
544 *Primorilestes* from the Eocene of Russia. Nel and Arillo (2006) added *Electrophenacolestes*
545 from Eocene Baltic amber to Dysagrioninae, and Rust et al. (2008) added *Eodysagrion* in a
546 separate subfamily Eodysagrioninae (and synonymized Thaumtoneuridae with
547 Dysagrionidae). Nel and Fleck (2014) described an unnamed dysagrionine from the Eocene-
548 Oligocene of the Isle of Wight. Finally, Zheng et al. (2016c, 2016d) described
549 *Palaeodysagrion* and *Burmadysagrion*, both from Burmite. These fossil taxa are discussed
550 below and their phylogenetic position is revised.

551 *Eothaumatoneura ptychoptera* Pongrácz, 1935 is a fossil damselfly that is only known
552 from wing fragments of a single specimen from the Middle Eocene (Middle Lutetian, MP13,
553 44.3 Ma) Geiseltal locality in eastern Germany. Nel and Paicheler (1994) considered that this
554 material as too incompletely preserved to be accurately placed, and therefore transferred this
555 taxon from Thaumtoneuridae to Zygoptera *incertae sedis*. Nevertheless, the preserved parts
556 of the wing venation of *Eothaumatoneura* are very similar to the corresponding structures in
557 the extant Neotropical damselfly genus *Thaumatoneura*, especially in the very long postnodal
558 area, base of RP2 far removed from subnodus, absence of lestine oblique vein 'O', main veins
559 strongly curved posteriorly, presence of 2-3 secondary longitudinal veins in distal part of
560 postdiscoidal area between MA and MP, presence of 4-5 secondary longitudinal veins in
561 distal part of area between MP and CuA, cubital area certainly broad, even if poorly preserved
562 (see Pongrácz, 1935: figs. 11-14). This pattern of venation is not shared by any of the known
563 Paleogene damselfly-like Odonata with large wings (e.g., Sieblosiidae, Dysagrionidae, or
564 even the damsel-dragonfly family Pseudostenolestidae from the Eocene of Messel, Garrouste

565 and Nel, 2015). Consequently, there are no arguments against an attribution of
566 *Eothaumatoneura ptychoptera* to Thaumatonneuridae, which is suggested by the above
567 mentioned wing venational similarities. Therefore, we here propose to restore this fossil taxon
568 in Thaumatonneuridae. *Eothaumatoneura* seems to be more closely related to the extant genus
569 *Thaumatoneura* than to the other extant thaumatoneurid genus *Paraphlebia*, because the wing
570 venation is much more similar to the former genus in several derived character states.

571 Bechly (2003, 2007, 2010) attributed *Euarchistigma* from the Lower Cretaceous Crato
572 Formation of Brazil to the Thaumatonneuridae (Euarchistigmatini) rather than to the
573 Pseudostigmatinae (as originally proposed by Carle and Wighton, 1990), on the basis of the
574 following putative synapomorphies: antesubnodal space without any crossveins; nodus and
575 bases of IR2 and RP3/4 shifted to an extremely basal position, correlated with a large number
576 of postnodal crossveins; IR2 apparently arising on RP3/4; very dense wing venation with a
577 high number of cells; dark colour pattern of wings; longitudinal wing veins distally distinctly
578 curved to the posterior wing margin. All these characters are also present in at least some
579 modern Pseudostigmatinae, but do mostly not belong to the ground plan of this family. Even
580 though the position of *Euarchistigma* remains somewhat unclear, we here tentatively retain it
581 in Thaumatonneuridae as Euarchistigmatinae stat rest. *Mesomegaloprepus* differs from
582 *Euarchistigma* in the presence of three secondary antenodal crossveins, presence of several
583 rows of cells in cubital area, intercalary veins present between main longitudinal veins, triadic
584 branching pattern of CuA and MP (Bechly, 2007, 2010).

585 The Dysagrioninae are an extinct Cenozoic damselfly group, with the sole exception
586 of *Congqingia* from the Cretaceous of China. The placement of the Dysagrioninae
587 (Dysagrionini Cockerell, 1908 and Petrolestini Cockerell, 1927) within the
588 Thaumatonneuridae, as proposed by Bechly (1996, 2003) and Rust et al. (2008) is only
589 supported by two very weak alleged synapomorphies: basal costal margin between wing base
590 and nodus is distinctly convex curved; antesubnodal space without any crossveins. The first

591 character is probably correlated to the shortening the antenodal space and could have been
592 convergently acquired. The second character is present in several unrelated clades, and thus
593 very homoplastic, as already indicated above. Since the affinities of the Dysagrioninae are
594 uncertain, we prefer to exclude these damselflies from the Thaumtoneuridae and suggest to
595 restate the Dysagrionini and Petrolestini as subfamilies to a separate family Dysagrionidae
596 stat. rest., as already suggested by Garrouste and Nel (2015) and Zheng et al. (2016d). Our
597 rejection of the synonymy of Thaumtoneuridae with Dysagrionidae (*contra* Rust et al., 2008)
598 implies that Thaumtoneuridae is restored as valid family as well. The Dysagrioninae are
599 characterized by a potential synapomorphy, viz a rather unique shape of the discoidal cell
600 with a distal side distinctly longer than its basal side and anterior and posterior sides not
601 parallel, even if it is also present in the Cenozoic Sieblosiidae. *Mesomegaloprepus* does not
602 share the above mentioned two potential synapomorphies of Dysagrioninae and
603 Thaumtoneuridae, and also lacks the typical dysagrionine shape of the discoidal cell.

604 *Eodysagrion* Rust et al., 2008 from the Paleogene of Denmark was placed in a
605 separate subfamily Eodysagrioninae within Dysagrionidae (Rust et al., 2008). *Eodysagrion*
606 shares two apomorphies with the Thaumtoneurinae: discoidal cell perfectly rectangular; and
607 IR2 apparently arising on RP3/4. Also, in *Eodysagrion*, the broadening of the antenodal area,
608 typical of *Thaumtoneura*, is weakly indicated, and the dark banded colour pattern of the
609 wings may correspond as well. However, *Eodysagrion* differs markedly from *Thaumtoneura*
610 in its clearly less numerous secondary longitudinal veins, its nodus not in a very basal
611 position, less numerous postdiscoidal crossveins, and its longitudinal wing veins not distinctly
612 curved distal to the posterior wing margin. Note that the *Eodysagrion* and *Euarchistigma* do
613 not have the discoidal cell of 'sieblosiid' type as in Dysagrioninae. Nevertheless, we
614 provisionally maintain *Eodysagrion* in the Thaumtoneuridae. *Mesomegaloprepus* differs
615 from *Eodysagrion* in the presence of three secondary antenodal crossveins, and a different
616 pattern of veins in the cubital area (Rust et al., 2008).

617

618 *4.3 Palaeobiogeography and Palaeoecology*

619

620 Even though the evidence for phylogenetic relationships of Mesomegaloprepidae still
621 is ambiguous, the three most likely candidates for sister group are all Neotropical taxa.
622 Together with an unequivocal fossil Thaumtoneuridae from the Eocene of Europe, our new
623 discovery may suggest a great antiquity and wide past distribution for at least some of these
624 Neotropical damselfly groups.

625 The fact that we have the surprising number of six pieces of Burmite amber with
626 totally 11 conspecific specimens (three pieces contain both sexes) of this new damselfly taxon
627 strongly suggests that it was a rather abundant element of the Myanmar amber forest. Most
628 probably these insects oviposited like modern Pseudostigmatinae in phytotelmata on the
629 amber tree, and also mated there, because this would have greatly increased the likelihood of
630 getting trapped in tree resin, and therefore could explain the relatively large number of
631 inclusions. This could even be a further hint towards a pseudostigmatine relationship of
632 Mesomegaloprepidae, because recent males of Pseudostigmatinae defend large water-filled
633 tree holes as breeding territories, where they mate with multiple females that oviposit in the
634 tree hole, where the cannibalistic larvae develop (Fincke, 1984, 1992a, 1992b, 1996, 2006).

635

636 **Concluding remarks**

637

638 This fossil damselfly represents a new family, genus, and species from mid-
639 Cretaceous amber from Myanmar, with ambiguous phylogenetic relationships to modern
640 Neotropical taxa. It adds to our knowledge of the diverse entomofauna of Burmese amber,
641 and to our knowledge of Mesozoic damselflies and their palaeobiogeographic distribution.

642

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644

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654

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850 Figures legends

851 Figure 1: *Mesomegaloprepus magnificus* gen. et sp. nov., habitus. a- Holotype, female, NIGP
852 164902. b- Paratype male NIGP 164903. c- Paratype male NIGP 164904. D- Paratypes,
853 several males and females, NIGP 164950. Scale bars = 1 cm.

854 Figure 2: *Mesomegaloprepus magnificus* gen. et sp. nov., habitus. a- Paratypes, several males
855 and females, NIGP 164951. b- Paratype, female, NIGP 161754. c- Allotype, male, NIGP
856 161753. d- Two photographs of paratype SMNS Bu-231. Scale bars = 1 cm.

857 Figure 3: *Mesomegaloprepus magnificus* gen. et sp. nov., head. a- Photograph of head of
858 paratype, male, specimen number NIGP 164904. b- Drawing of head of holotype, female,
859 specimen number NIGP 164902. Scale bar = 1 cm.

860 Figure 4: *Mesomegaloprepus magnificus* gen. et sp. nov., photograph of wings of holotype,
861 female, NIGP 164902. a- Forewing. b- Hindwing.

862 Figure 5: *Mesomegaloprepus magnificus* gen. et sp. nov., drawing of wings of holotype,
863 female, NIGP 164902. a- Forewing. b- Hindwing. Scale bar = 1 cm.

864 Figure 6: *Mesomegaloprepus magnificus* gen. et sp. nov., drawing of wings. a- Forewing of
865 male paratype NIGP 164951. b- Forewing of paratype NIGP 161753, male. c- Forewing of
866 male paratype NIGP 164903. d- Hindwing of male paratype NIGP 164903. Scale bar = 1 cm.

867 Figure 7: *Mesomegaloprepus magnificus* gen. et sp. nov., male terminalia; paratype NIGP
868 164903, ventral side. a- Photograph. b- Drawing. Scale bar = 1 cm.

869 Figure 8: *Mesomegaloprepus magnificus* gen. et sp. nov., male genitalia on second abdominal
870 segment; paratype NIGP 164903. a- Photograph of lateral view. b- Photograph of ventro-
871 lateral view. c- Drawing of ventro-lateral view. Scale bar = 1 cm.

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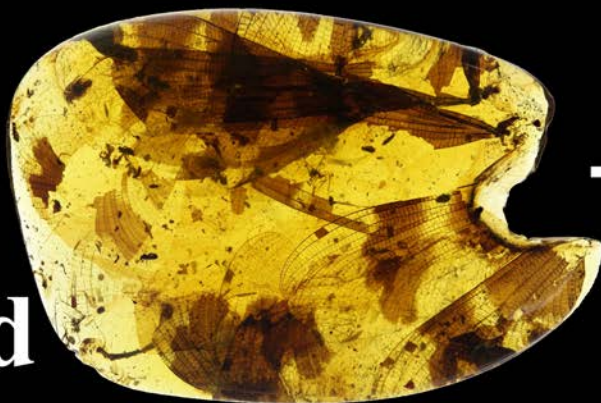
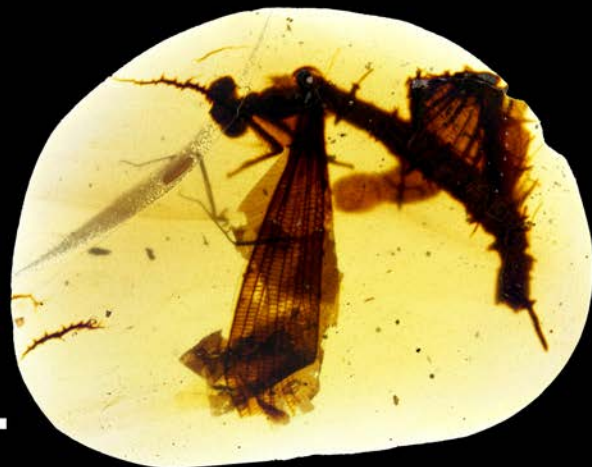
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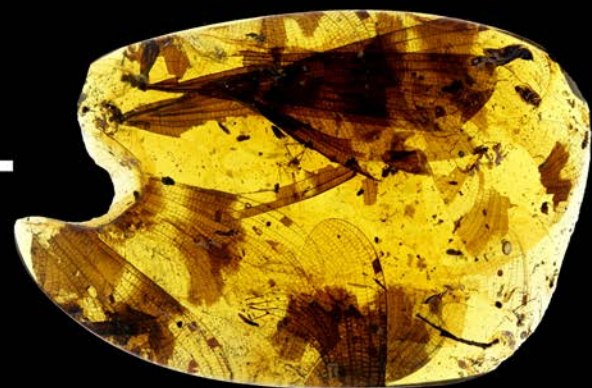
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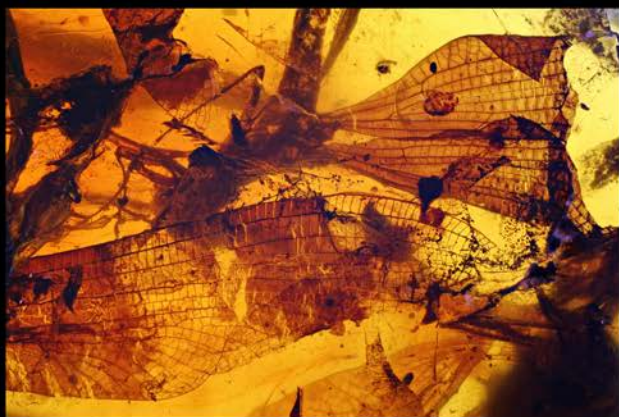
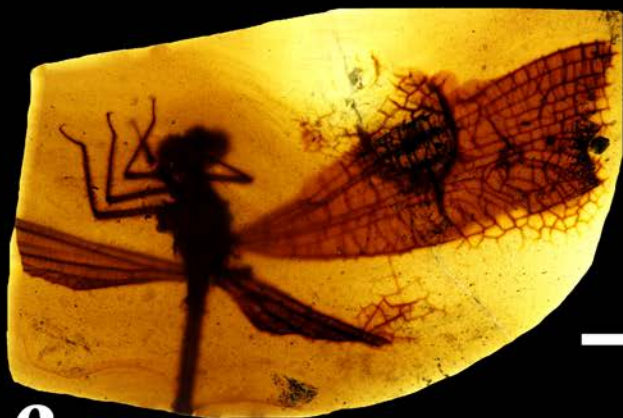


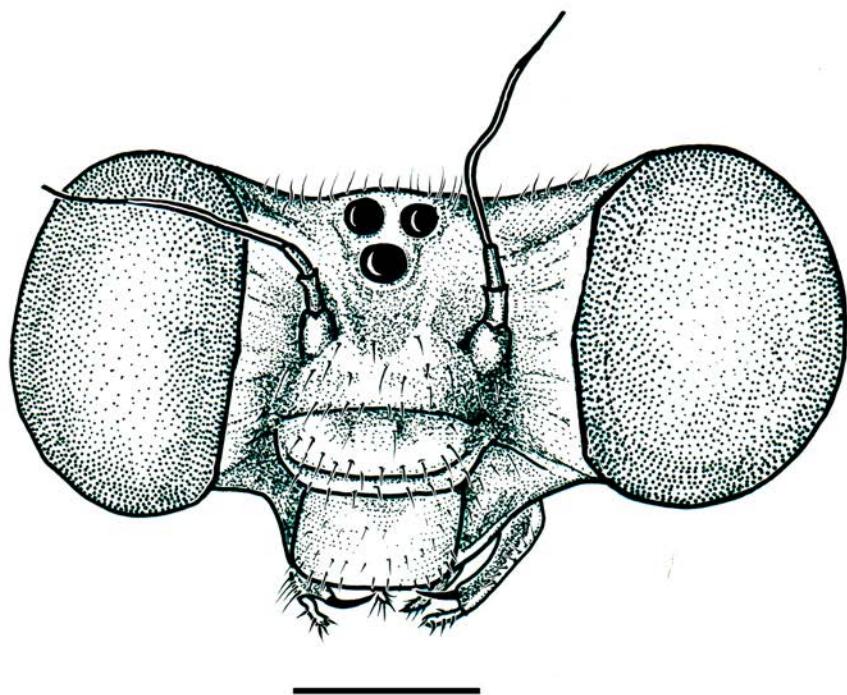
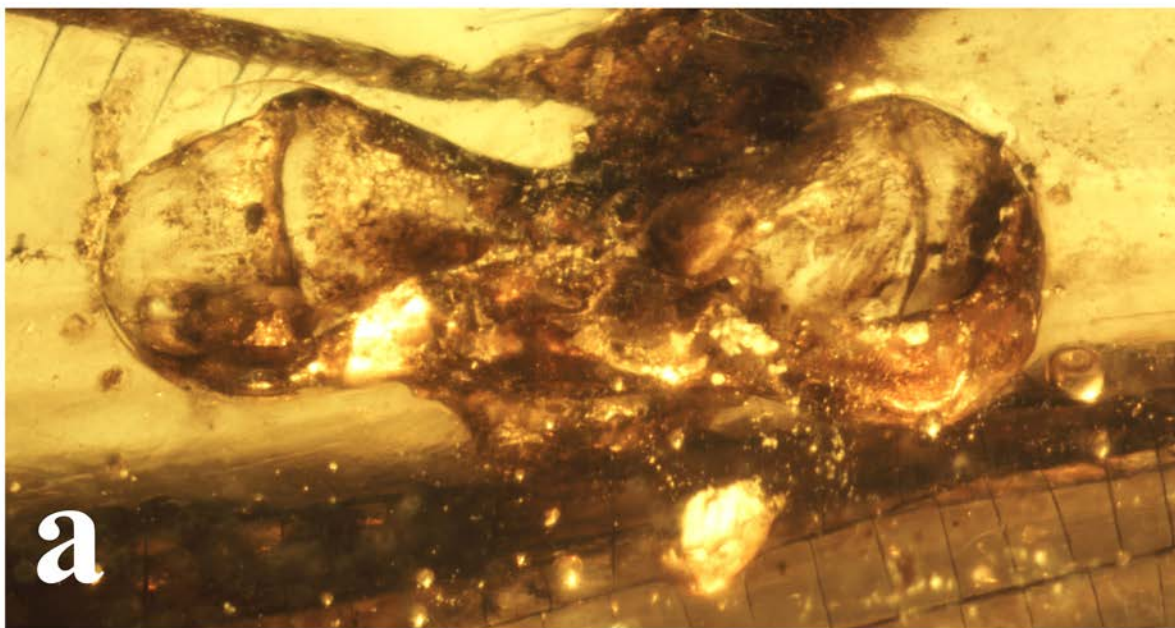
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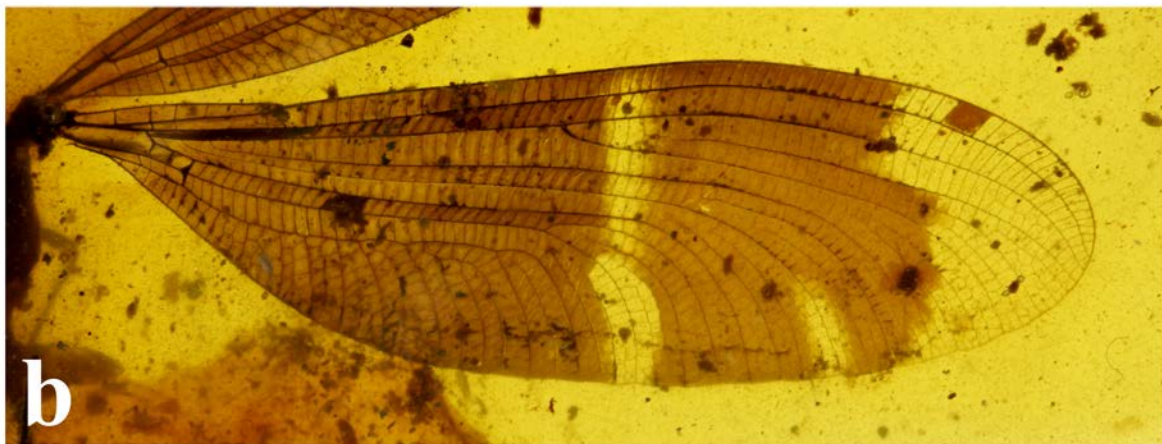
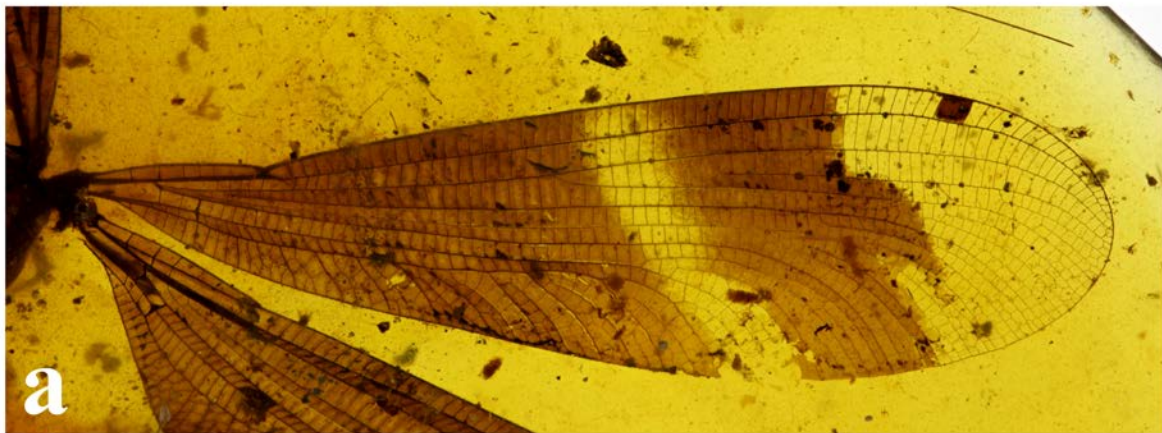


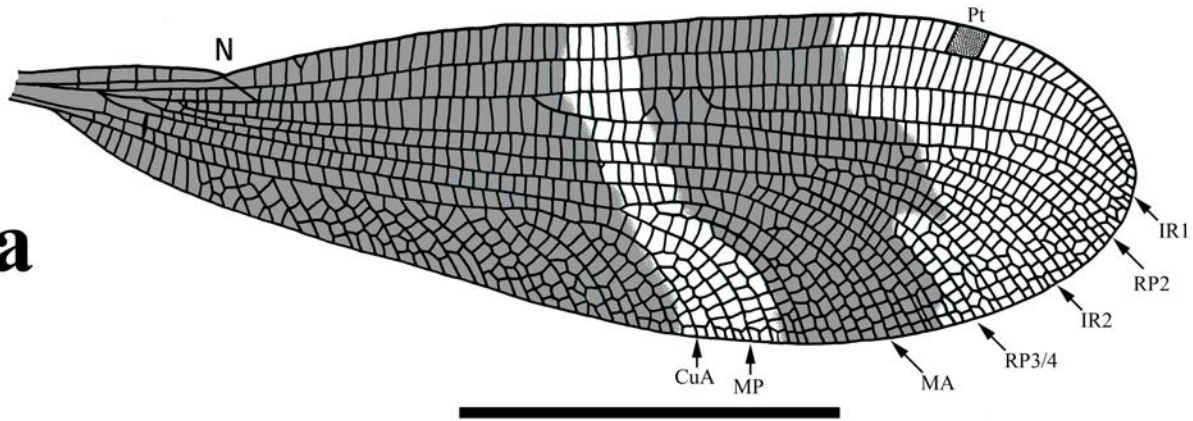
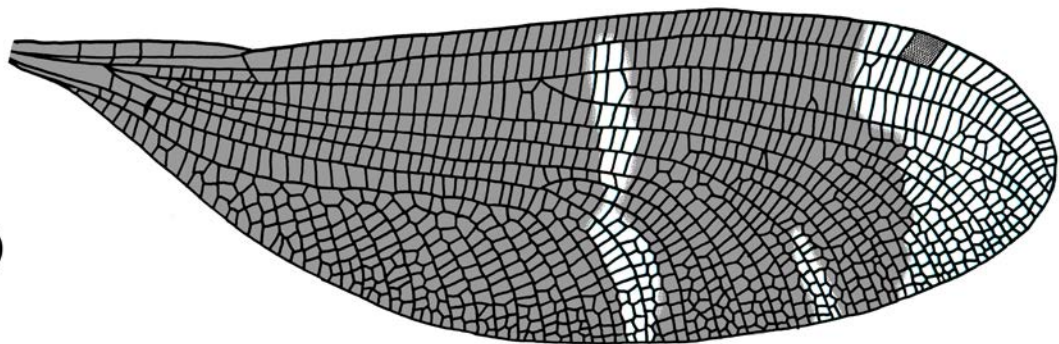
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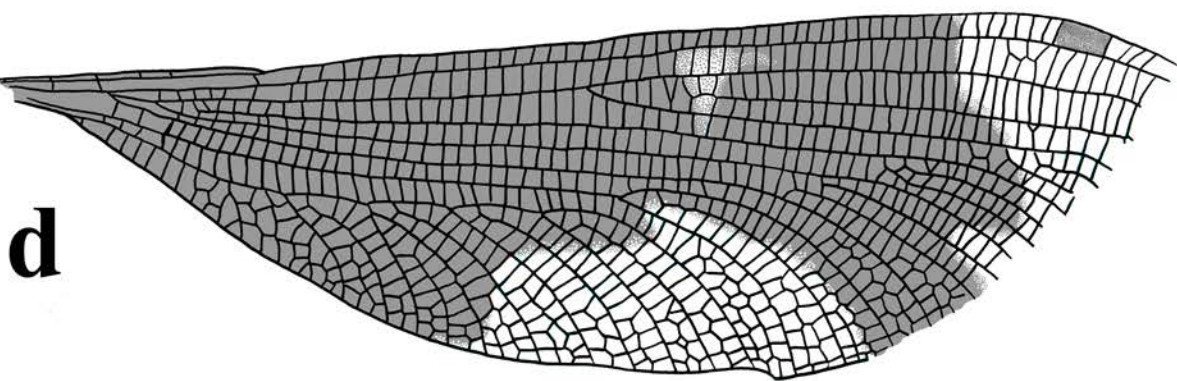
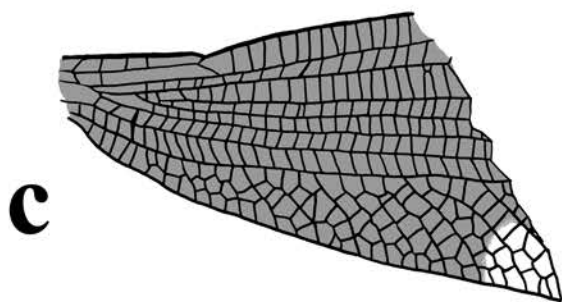
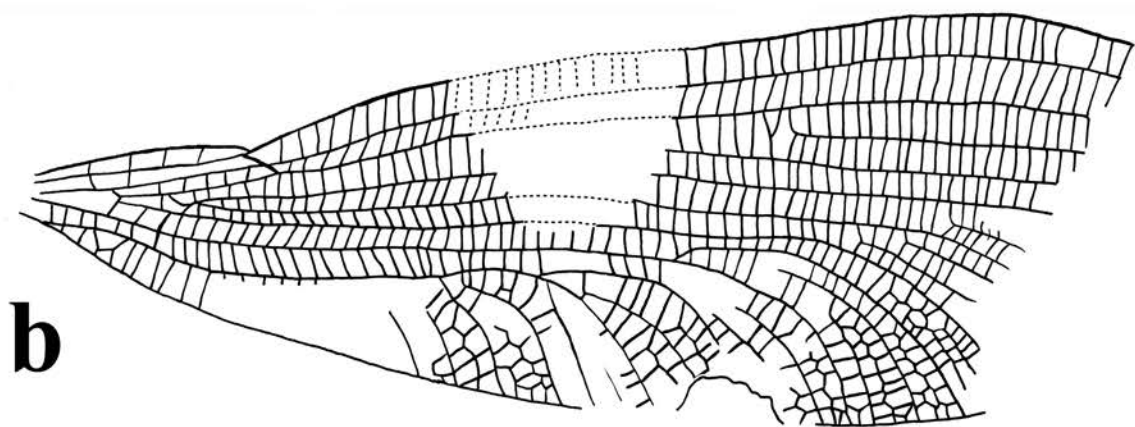
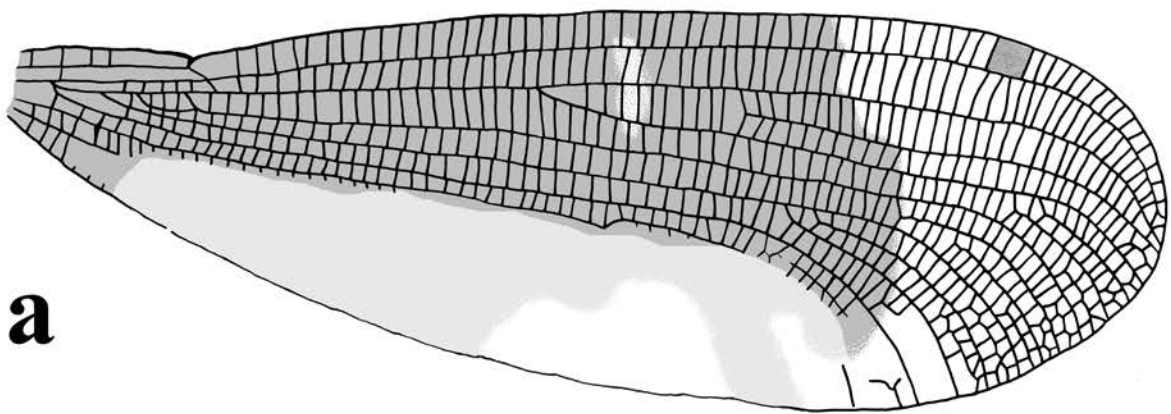


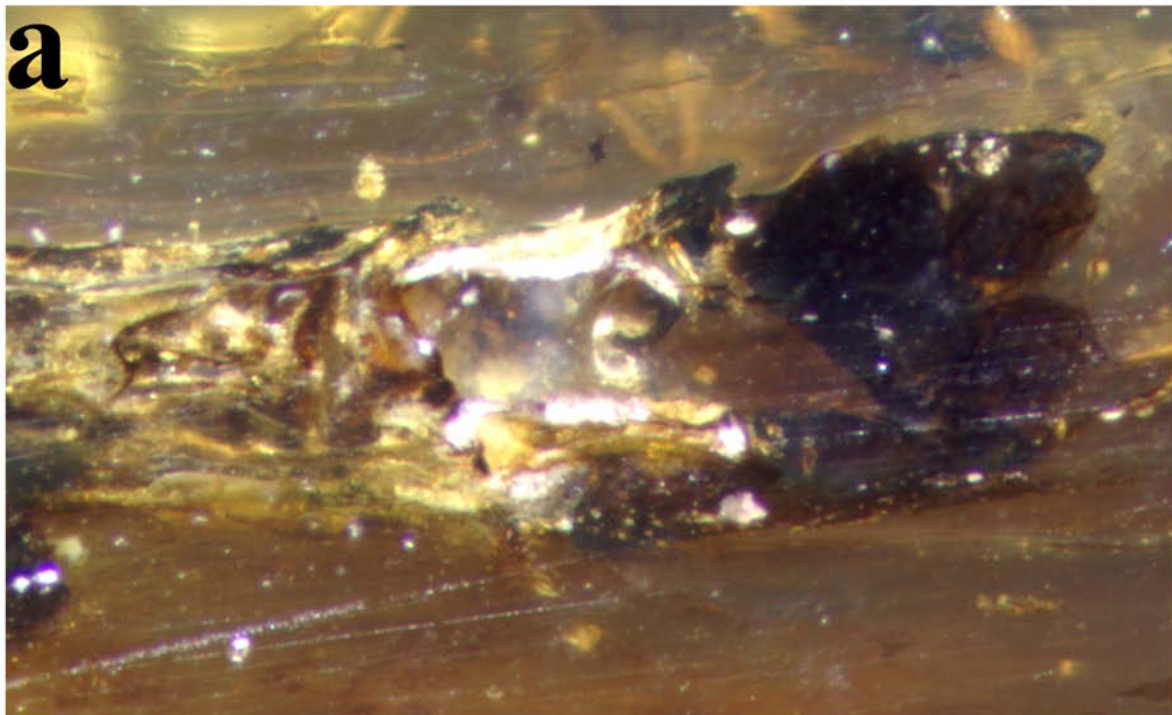
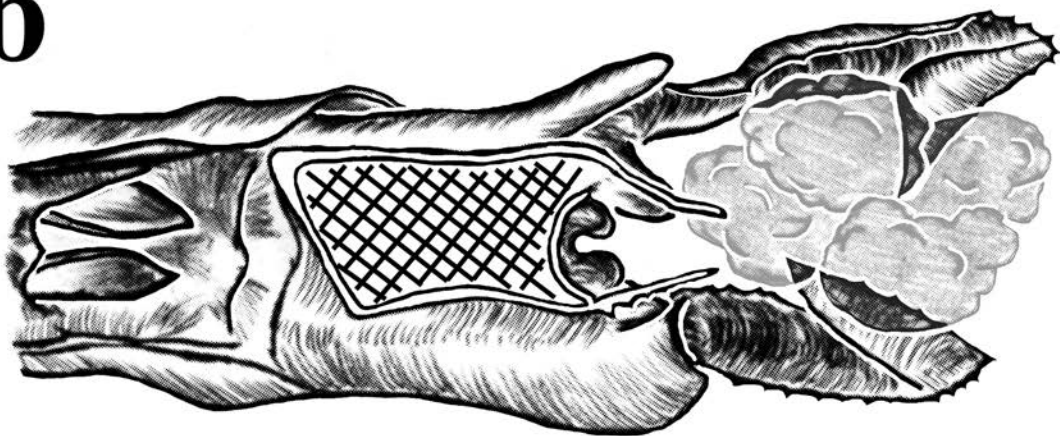


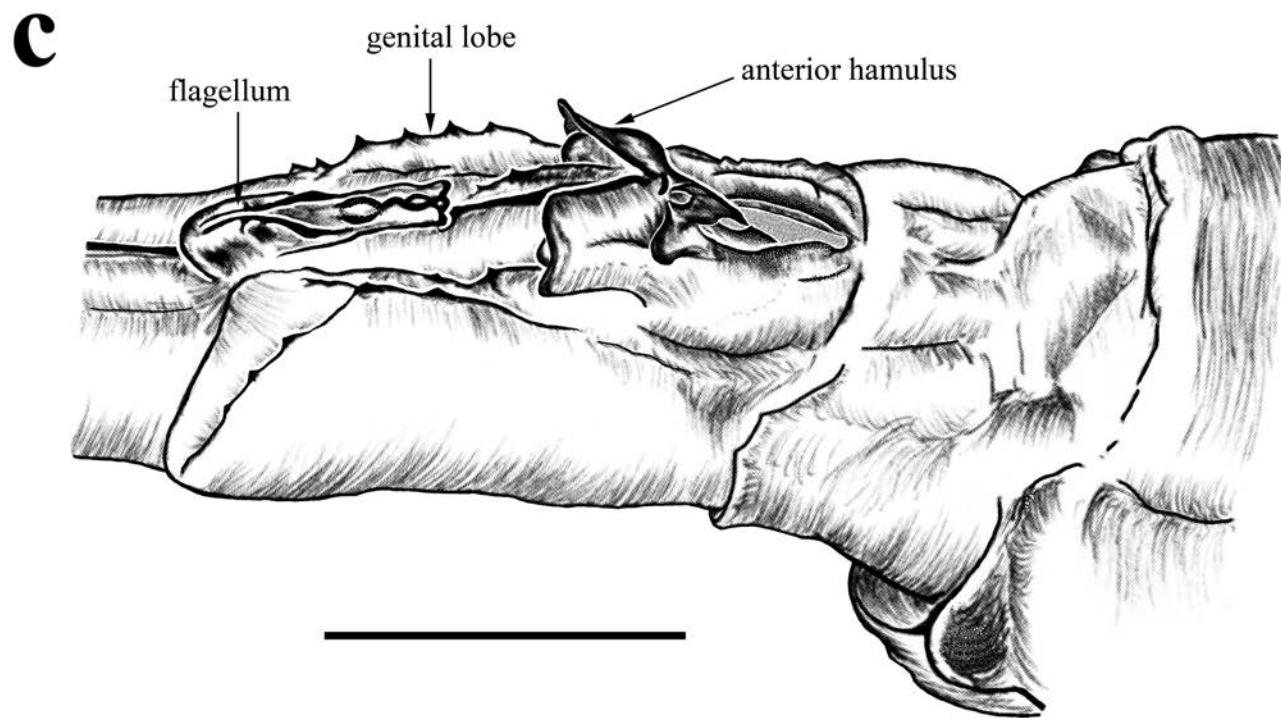
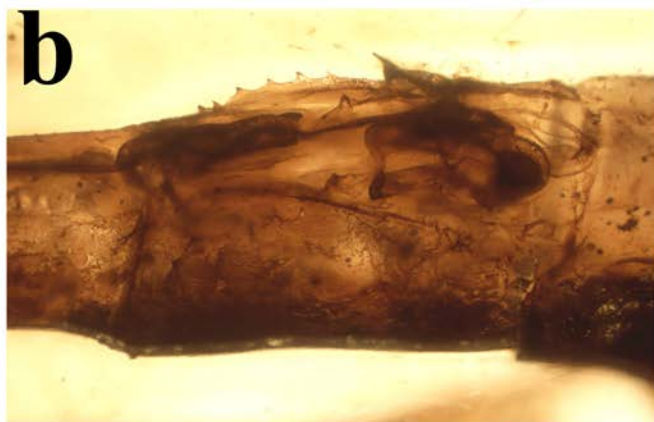
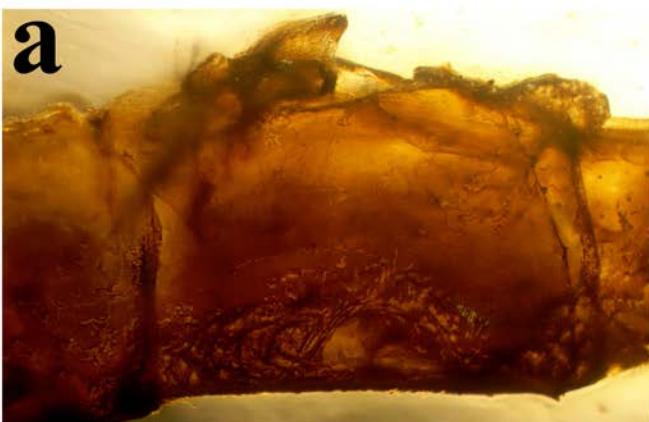




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Supplementary material

Revised classification of discussed fossil damselfly taxa:

Dysagrionidae Cockerell, 1908 (stat. nov. as family by Rust et al., 2008) (in Zygoptera *incertae sedis*)

Dysagrioninae Cockerell, 1908 stat. rest. (Dysagrionini sensu Bechly, 1996)

Dysagrion Scudder, 1878

D. fredericci Scudder, 1878 (Eocene, Green River, USA)

D. packardii Scudder, 1885 (Eocene, Green River, USA)

D. lakesii Scudder, 1890 (Eocene, Green River, USA)

Phenacolestes Cockerell, 1908

P. mirandus Cockerell, 1908 (Eocene, Florissant, USA)

P. (?) parallelus Cockerell, 1908 (Eocene, Florissant, USA)

P. coloratus (Hagen, 1848) (belongs to *Phenacolestes* according to Nel and Paicheler, 1994) (Miocene, Radoboj, Croatia)

Electrophenacolestes Nel and Arillo, 2006

E. serafini Nel and Arillo, 2006 (Eocene, Baltic amber)

unnamed genus and species Nel and Fleck, 2014 (Eocene-Oligocene, Isle of Wight)

Burmadysagrioninae Zheng et al., 2016

Burmadysagrion Zheng et al., 2016

B. zhangi Zheng et al., 2016 (mid-Cretaceous, Burmite amber, Myanmar)

Petrolestinae Cockerell, 1927 stat. rest. (Petrolestini sensu Bechly, 1996, Congqingiidae Zhang, 1992)

Primorilestes Nel et al., 2005 pos. nov. (closer to *Petrolestinae* than to *Dysagrioninae*, as already suggested by Rust et al., 2008)

P. violetae Nel et al., 2005 (Eocene, Biamo, Russia)

P. madseni Rust et al., 2008 (Paleocene-Eocene, Fur, Denmark)

Petrolestes Cockerell, 1927

P. hendersoni Cockerell, 1927 (Eocene, Green River, USA)

P. messelensis Garrouste and Nel, 2015 (Eocene, Messel, Germany)

Congqingia Zhang, 1992

C. rhora Zhang, 1992 (Early Cretaceous, Laiyang, China)

Subfamily *incertae sedis*

Palaeodysagrion Zheng et al., 2016

P. cretacicus Zheng et al., 2016 (mid-Cretaceous, Burmite amber, Myanmar)

Latibasaliidae Petrulevičius and Nel, 2004 (transferred from *Amphipterygoidea* to *Epallagoidea* as sister group of *Zacallitidae*)

Latibasalia Petrulevičius and Nel, 2004

L. elongata Petrulevičius and Nel, 2004 (Paleocene, El Fuerte, Argentina)

L. quispeae Petrulevičius and Nel, 2004 (Paleocene, El Fuerte, Argentina)

Mesomegaloprepidae (in *Zygoptera incertae sedis*)

Mesomegaloprepus gen. nov.

M. magnificus spec. nov. (mid-Cretaceous, Burmite, Myanmar)

Thaumatoneuridae Tillyard and Fraser, 1938 stat. rest.

Thaumatoneturinae Tillyard and Fraser, 1938

Paraphlebia Selys 1862 (*Paraphlebia* as used by Hagen, 1861 is a *nomen nudum* according to Garrison, 1991 unpubl.)

P. duodecima Calvert, 1901 (Recent, Neotropical)

P. hyalina Brauer, 1871 (Recent, Neotropical)

P. quinta Calvert, 1901 (Recent, Neotropical)

P. zoe Selys, 1862 (Hagen, 1861 is a *nomen nudum* according to Garrison, 1991 unpubl.) (Recent, Neotropical)

Thaumatonaura McLachlan, 1897

T. inopinata McLachlan 1897 (Recent, Neotropical)

Garrison, 1991 unpubl) (Recent)

Euarchistigmatinae Carle and Wighton, 1990 stat. rest.

Euarchistigma Carle and Wighton, 1990

E. atrophium Carle and Wighton, 1990 (Early Cretaceous, Crato, Brazil)

E. marialuiseae Bechly, 2007 (Early Cretaceous, Crato, Brazil)

E. peterknobli Bechly, 2010 (Early Cretaceous, Crato, Brazil)

Eodysagrioninae Rust et al., 2008

Eodysagrion Rust et al., 2008

E. mikkelsenii Rust et al., 2008 (Paleocene-Eocene, Fur, Denmark)