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

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ABSTRACT

Mesomegaloprepus magnificus gen. et sp. nov. (Odonata: Zygoptera) is described from more than 14 specimens in eight pieces of mid-Cretaceous (earliest Cenomanian, ca. 99 Ma) Burmite amber from Myanmar. Possible phylogenetic affinities with the Neotropical Latibasaliidae, Thaumatoneuridae, and Pseudostigmatinae are discussed, and a relationship with Pseudostigmatinae considered as possible, but because of conflicting evidence separate family status as Mesomegaloprepidae fam. nov. is tentatively preferred. The remarkable degree of homoplastic conflict in the wing venational similarities indicates that these represent relatively weak evidence for phylogenetic relationships. The palaeoecology, including sexual dimorphism in wing coloration, of the new taxon is discussed, and the large number of inclusions explained with possible breeding behaviour in association with water-filled tree holes (phytotelmata) of the amber tree, similar to extant Pseudostigmatinae. The position of all alleged fossil Thaumatoneuridae are discussed and revised: *Eothaumatoneura ptychoptera* Pongracz, 1935 from the Eocene Geiseltal locality is restored in Thaumatoneuridae. Cretaceous *Euarchistigma* and Paleogene *Eodysagrion* are tentatively retained as subfamilies Euarchistigmatinae and Eodysagrioninae in Thaumatoneuridae. Paleogene Dysagrioninae and Petrolestinae are removed from Thaumatoneuridae and attributed to a restored family Dysagrionidae, and Paleocene Latibasaliidae is transferred from Amphipterygoidea to Epallagoidea.

Keywords:
Pseudostigmatinae
Thaumatoneuridae
Latibasaliidae
Cenomanian
Myanmar
Phylogeny

1. Introduction

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

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

2. Materials and methods

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

We follow the wing venation nomenclature of Riek and Kukalová-Peck (1984), emended by Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera, as well as characters for family diagnoses, are largely based on the phylogenetic system proposed by Bechly (1996, 2003). Several recent works that have addressed the higher phylogeny of Zygoptera (Dumont et al., 2010; Davis et al., 2011; Dijkstra et al., 2013, 2014) have been taken into account.

2.1. Burmese amber

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

Fossil-bearing has mostly been collected from the Hukawng Valley in northern Myanmar (formerly known as Burma). For an overview of the amber deposit and its geological setting see, e.g., Zherikhin and Ross (2000), Grimaldi et al. (2002), Cruickshank and Ko (2003), and Ross et al. (2010). Radiometric U–Pb zircon dating (Shi et al., 2012) recently constrained this amber to a minimum age of 98.79±0.62 Ma, which is equivalent to the mid-Cretaceous (earliest Cenomanian). The original habitat of the amber forest is still controversial, in fact it has originally been assumed to be a tropical araucarian forest (Grimaldi et al., 2002; Poinar et al., 2007), possibly with Dipterocarpaceae as another source for the fossil resin. However, the first detailed report on the macromolecular nature and palaeobotanical affinity of Burmite (Dutta et al., 2011), based on gas chromatography - mass spectrometry, rejected Araucariaceae and Dipterocarpaceae in favour of Pinaceae as the Burmese amber tree. Grimaldi (2016), after Grimaldi and Ross (in press), considered ‘based on the abundant inclusions of leafy shoots’ that it was formed by a conifer, and ‘amber produced possibly by *Metasequoia* (Taxodiaceae) or a close relative’. Even though fossil and extant Pinaceae are generally absent from south of the equator and from tropical rainforests in particular, a notable exception is *Pinus krempfii* from the rainforests of Vietnam (Brodribb and Feild, 2008).

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

3. Systematic palaeontology

Order Odonata Fabricius, 1793
Suborder Zygoptera Selys, 1854
Family Mesomegaloprepidae fam. nov.

Type-genus. *Mesomegaloprepus* gen. nov.

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

Genus *Mesomegaloprepus* gen. nov.

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

Etymology. Named after the Mesozoic period and the extant pseudostigmatine genus *Megaloprepus* Rambur, 1842, with which it shares several wing venational similarities including a unique triadic branching of vein MP. The gender of the name is masculine.

Diagnosis. Male ligula with distal segment modified to form a very long single flagellum; wings with extensive brown colour (as preserved) pattern and very dense wing venation with a several hundreds of cells; secondary antenodal crossveins absent, except for three accessory crossveins between C and ScP distal of Ax2; series of five to seven crossveins in antesubnodal space; nodus in a very basal position, at about 20% of wing length; more than sixty postnodal crossveins; postnodal and postsubnodal crossveins not aligned; discoidal cell rectangular and crossed by a single crossvein; distal side MAb of discoidal cell not oblique or with reversed obliquity; subdiscoidal cell traversed by two crossveins; base of RP2 far distal of subnodus; vein CuP between M+Cu and AA instead of being between M+Cu and A; bases of RP3/4 and IR2 (midfork) basally recessed midway between arculus and nodus (instead of aligned with subnodus); longitudinal wing veins distally distinctly curved to posterior wing margin; CuA long, extending well beyond mid wing level, with numerous curved posterior branches and characteristical triadic branching pattern of CuA and apical part of MP (but not MA, which is unbranched); no intercalary veins between MP and CuA; pterostigma in apical position, short and rectangular (parallel-sided); pterostigmal brace reduced; no lestine oblique vein ‘O’; absence of several rows of cells between costal margin, RA, and RP1 near wing apex.

Mesomegaloprepus magnificus sp. nov.
Figs. 2–8

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

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

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

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

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

Descriptions.

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

Allotype NIGP161753. The amber piece is 3.5 cm long and 0.5 cm wide. This specimen (Figs. 2-3) features head, thorax, and the four basal abdominal segments, two fore legs, one mid leg, one hind leg, two-third of left forewing and bases of the two hind wings attached. Head transverse, 5.0 mm wide, with eyes well separated, distance between eyes ca. 4.0 mm; ocelli disposed in triangle on a low protuberance between eyes. Legs with long spines on femora and tibiae. Abdomen ca. 2.0 mm wide (it is not visible if there is a secondary copulatory apparatus on the second segment or not). Forewing uniformly dark brown owing oxidation; forewing ca. 29.0 mm long (preserved part 26.0 mm long), 8.7 mm wide, 3.7 mm wide at nodus level; distance from base to arculus 2.4 mm, from arculus to nodus 3.2 mm; nodus in a basal position, more than 19% of wing length; petiole very short, 0.8 mm long, 1.0 mm wide; distance from base to Ax1 1.8 mm, from Ax1 to Ax2 0.8 mm; arculus distinctly basal of Ax2; 3 accessory secondary antenodal crossveins between C and ScP distal of Ax2, but none between ScP and RA; antesubnodal space with a regular series of crossveins; numerous postnodal crossveins not well aligned with postsubnodal crossveins; pterostigma present but not colored, no pterostigmal brace; bases of RP3/4 and IR2 (midfork) basally recessed midway between arculus and nodus; IR2 apparently arising on RP3/4; basal space between RP3/4 and IR2 not greatly narrowed; area between RP and MA between arculus and base of RP3/4 with a crossvein; base of RP2 far distal from subnodus; no oblique crossvein; two secondary longitudinal veins between MA and MP in distal part, both apparently emerging from MP; discoidal cell crossed, rectangular, with MAb of inverted obliquity; subdiscoidal cell traversed by two crossveins; CuP between M+Cu and AA; anal area rather wide with a series of small transverse cells between AA and AP; cubital area broad, CuA elongate with numerous curved posterior branches and characteristically triadic branching pattern of CuA; area between MP and CuA broader than postdiscoidal area in their basal parts; no intercalary vein between MP and CuA.

Paratype NIGP 161754. The amber piece with this paratype is 2.6 cm long and 0.5 cm wide. This specimen (Fig. 2e-f) features fragments of thorax with part of head and first basal abdominal segments still attached, plus bases of the two right wings and the basal half of left forewing. The preserved parts of wing are nearly identical in proportions and venation to those of the holotype, documenting the conspecific status. Head transverse with eyes well separated. Thorax ca. 2.8 mm wide and ca. 4.0 mm high. Abdomen 2.0 mm wide; no secondary copulatory apparatus on segments 2-3 (thus a female specimen). Forewing dark brown with a narrow lighter transverse band distal of nodus, near base of RP2, forewing with preserved part ca. 18.0 mm long, 3.3 mm wide at nodus level; distance from base to nodus 4.4 mm, nodus in a very basal position; petiole very short, 1.2 mm long; Ax2 about opposite arculus; area between RP and MA between arculus and base of RP3/4 without any crossvein.

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

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

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

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

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

4. Discussion

4.1 Phylogenetic relationships

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

4.1.1 Comparison with Latibasaliidae Petrulevičius and Nel, 2004

Latibasaliidae (Zygoptera: Amphipterygoidea) are an enigmatic fossil family from the Paleogene (Upper Palaeocene) of Argentina (Petrulevičius and Nel 2004, 2007). A potential relationships with the fossil genera *Petrolestes* Cockerell, 1927 and *Congqingia* Zhang, 1992 (Amphipterygoidea: Thaumatoneuridae) was discussed in the original description, because they share the absence of secondary antenodal crossveins and the absence of antesubnodal crossveins. However, these characters are very homoplastic and weak. We transfer here Latibasaliidae from Amphipterygoidea to Epallagoidea as sister group of Zacallitidae, because of the shared convex longitudinal intercalary vein in the cubital field as unique putative synapomorphy.

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

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

The mentioned differences in *Mesomegaloprepus* are all derived states that could be autapomorphies; so they would not contradict a relationship with Latibasaliidae. However, many of the similarities are either of uncertain polarity, or symplesiomorphies, or homoplastic, so that the evidence for a relationship is weak and inconclusive. We therefore can neither exclude nor establish a sister group relationship of Mesomegaloprepidae with Latibasaliidae. Nevertheless, the densely reticulated wings with short petiolus, and especially the rectangular shape of the discoidal cell with a distal side MAb with reversed obliquity would support a position in Epallagoidea (new position for Latibasaliidae), and the expanded cubital field would agree with Zacallitidae (here recognized as sister group of Latibasaliidae). Furthermore, the recession of the midfork, the reduced pterostigmal brace and lestine oblique vein ‘O’, as well as the coloured wings would support a position in Caloptera (Calopterygoidea sensu Dijkstra et al., 2013), if this group is monophyletic at all, which is rather doubtful (Dijkstra et al., 2014).

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

Pseudostigmatinae (formerly classified as distinct family Pseudostigmatidae) is a group of mainly Neotropical giant damselflies (also known as helicopter damselflies) that oviposit in phytotelmata, where the dendrolimnetic larvae develop. Adults pluck orb-weaver spiders and their prey from spider webs (Fincke, 1984; Clausnitzer, 2002). The extremely long abdomen is apparently not developed for oviposition in phytotelmata but used as balance while hovering in front of spider webs (Clausnitzer, 2002). The only Pseudostigmatinae outside of the Neotropical realm is the Eastern African *Coryphagrion grandis* Morton, 1924, which was formerly classified in a monotypic separate family Coryphagrionidae Pinhey, 1962, but recognized as most closely related to or belonging to Pseudostigmatinae by Bechly (1996, 2003), Clausnitzer and Lindeboom (2002), Rehn (2003), Groeneveld et al. (2007), Yu and Bu (2011), and Ingley et al. (2012). *Coryphagrion* Morton, 1924 is very similar to *Mecistogaster* Rambur, 1842. Like all Neotropical Pseudostigmatinae, it oviposits in phytotelmata and exclusively feeds on spiders and insects picked out of spider webs (Lounibos, 1980; Clausnitzer, 2002; Clausnitzer and Lindeboom, 2002). All Neotropical genera have a more or less reduced pterostigma and males have characteristical hamuli anteriores and a terminal single flagellum on the ligula (Schmidt, 1915; Dijkstra et al., 2014), while *Coryphagrion* has retained a normal pterostigma and lacks the terminal ligula flagellum (Kimmins, 1931; Dijkstra et al., 2014). Morphological and genomic data have shown that the Pseudostigmatinae (incl. *Coryphagrion*) nest deeply within Coenagrionidae and thus should be classified within this family (Ramírez, 1997; Bybee et al., 2008; Carle et al., 2008; Yu and Bu, 2011; Ingley et al, 2012; Dijkstra et al., 2014). Dijkstra et al. (2013) therefore formally sunk the family Pseudostigmatidae in Coenagrionidae, where it forms a subfamily Pseudostigmatinae with three tribes (Bechly, 1996, 2003; Ingley, 2012): Coryphagrionini (only including *Coryphagrion* as sister group to Neotropical pseudostigmatines), Pseudostigmatini (including the two narrow-winged genera *Mecistogaster* and *Pseudostigma* Selys, 1860 with simple longitudinal veins), and Megaloprepini (broad-winged genera *Microstigma* Rambur, 1842, *Anomisma* McLachlan, 1877, and *Megaloprepus* , with characteristic triadic branchings of longitudinal veins MA and CuA). The phylogeny and character distribution shows that narrow wings without triadic branchings represent the plesiomorphic ground plan condition, from which derived broad winged forms evolved (Bechly, 1996, 2003; Ingley, 2012). The extant genus *Megaloprepus* represents the largest known damselfly of all times with a wingspan of up to 19 cm and an abdomen length of 10 cm (Groeneveld et al., 2007).

Putative synapomorphies of *Mesomegaloprepus* with Pseudostigmatinae (incl. Coryphagrionini) are as follows: similar shape of wing with very dense venation and a large number of cells (also present in *Thaumatoneura*); very basal position of nodus at about 20% of wing length (also present in *Thaumatoneura*), correlated with a basal recession of the midfork at about 25% of wing length, and a high number of postnodal veins and an origin of RP2 far distal of subnodus; discoidal cell elongated (also present in Thaumatoneuridae); IR2 apparently arising from RP3/4 (as in Thaumatoneuridae); more than two rows of cells between RP1 and RP2 (also present in *Thaumatoneura*), with very long IR1 and a shorter negative intercalary between IR1 and RP1 (very much like Pseudostigmatinae, and unlike *Thaumatoneura*); pterostigma very short, rectangular, and in apical position. Finally the possible association with phytotelmata (*see below*) might represent evidence for a relationship with Pseudostigmatinae (incl. *Coryphagrion*), but also occurs by convergence in some unrelated tropical damselfly and dragonfly taxa. However, the following plesiomorphies of *Mesomegaloprepus* contradict a placement within the crown group of Pseudostigmatinae or even in Coenagrionoidea: much smaller size (all Pseudostigmatinae show gigantism); presence of three accessory secondary antenodal crossveins between C and ScP distal of Ax2 (unknown in Coenagrionoidea, but 1-2 present in *Thaumatoneura*); multiple antesubnodal crossveins (unknown in Coenagrionoidea); postnodal and postsubnodal crossveins not aligned (unknown in Coenagrionoidea, but present in *Thaumatoneura*); RA and RP1 not sigmoidally curved at apex, and RP1 and RP2 not converging apically; basal part of space between IR2 and RP3/4 not strongly narrowed; only a single row of cells between C and RA at apex (two or more rows in Pseudostigmatinae, except for some but not all specimens of *Coryphagrion* and *Mecistogaster*, but also Thaumatoneuridae). *Mesomegaloprepus* differs from nearly all known Coenagrionidae (including all Pseudostigmatinae), with the sole exception of Protoneurinae *s.str.* (subfamily of Coenagrionidae according to Dijkstra et al., 2014), in the rectangular shape of the discoidal cell (as in *Thaumatoneura*, and less developed in *Megaloprepus*). Also *Mesomegaloprepus* differs from all known Coenagrionoidea (including all Pseudostigmatinae) in the position of the arculus distinctly basal of Ax2 (but the polarity of this character is unclear), the recession of the midfork (origins of IR2 and RP3/4) distinctly basal of subnodus (a derived state that never occurs in Coenagrionoidea and Thaumatoneuridae, but is typical for Lestoidea and “Calopterygoidea”), and the presence of several secondary (intercalary) longitudinal veins in the median and radial areas (as in Thaumatoneuridae).

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

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

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

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

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

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

4.1.3 Comparison with Thaumatoneuridae Tillyard and Fraser, 1938 (sensu Dijkstra, 2014)

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

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

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

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

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

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

Putative synapomorphies of *Mesomegaloprepus* with extant Thaumatoneuridae (*Paraphlebia* + *Thaumatoneura*) (see Bechly, 1996, 2003) are as follows: dark banded colour pattern of wings with sexual dimorphism (as in *Megaloprepus*); dense wing venation with several hundreds of cells; nodus in very basal position, correlated with large number of postnodal crossveins (as in Pseudostigmatinae); triadic branching of CuA; subdiscoidal cell traversed by a crossvein; discoidal cell elongated (as in Pseudostigmatinae); IR2 apparently arising from RP3/4 (as in Pseudostigmatinae); presence of several secondary (intercalary) longitudinal veins in median and radial area. Nevertheless, the following plesiomorphies of *Mesomegaloprepus* contradict a placement in the crown group of Thaumatoneuridae: small size; several antesubnodal crossveins; only a single row of cells between RA and RP1 distal of pterostigma; absence of intercalary veins between MP and CuA. *Mesomegaloprepus* strongly differs from Thaumatoneuridae in the divided discoidal cell, as well as the very short and rectangular pterostigma, while the discoidal cell of *Paraphlebia* and *Thaumatoneura* is always undivided and their pterostigmata are very long with a extremely oblique basal side (but also unbraced, which seems to be a symplesiomorphy of Thaumatoneuridae, as the pterostigma of closely related genera like *Burmargiolestes* is also unbraced). Also the fact that the midfork is not basally recessed between arculus and subnodus in extant Thaumatoneuridae contradicts a relationship with *Mesomegaloprepus* Further important differences are the position of arculus that is more or less aligned with Ax2 in Thaumatoneuridae but distinctly basal of Ax2 in *Mesomegaloprepus*, as well as the position of the CuP-vestige ("anal crossing") that is located in the petiolus in Thaumatoneuridae, while it ends on free vein AA distal of petiolus in *Mesomegaloprepus*, but the polarity of these two characters is uncertain. An antesubnodal space without any crossveins was proposed by Bechly (2007, 2003) as an autapomorphy of Thaumatoneuridae, but of course this character is highly homoplastic and also present in all Lestoidea and Coenagrionoidea (incl. Pseudostigmatinae), but it is absent in *Mesomegaloprepus*.

Putative synapomorphies with only the extant genus *Thaumatoneura*: broad wings with very dense wing venation (large number of cells) (as in Pseudostigmatinae: Megaloprepini); petiolus very short (still long in *Paraphlebia*); nodus even in more basal position, correlated with large number of postnodal crossveins; presence of a few accessory secondary antenodal crossveins between C and ScP distal of Ax2 (3 in *Mesomegaloprepus*, 1-2 in *Thaumatoneura*, none in *Paraphlebia*); discoidal cell rectangular with distal side MAb with reversed obliquity (still acute in *Paraphlebia*); subdiscoidal cell traversed by 1-2 crossveins (however the subdiscoidal cell of *Thaumatoneura* is of very different shape and much longer); postnodal and postsubnodal crossveins secondarily non-aligned (still aligned in *Paraphlebia*); greatly expanded cubital area; CuA with numerous curved posterior branches and characteristical triadic branching pattern of CuA (similar to *Megaloprepus*, but CuA much shorter); longitudinal veins distally distinctly curved towards hind margin of wing; base of RP2 very far distal of subnodus as in Pseudostigmatinae: Megaloprepini). In the anal area of *Mesomegaloprepus*, there is a series of small transverse cells between AA and AP below the subdiscoidal space, which is a character state also present in *Thaumatoneura*, but the Pseudostigmatinae also have small crossveins in the anal area between AA and AP below the subdiscoidal space. However, the anal area is distinctly narrower in Pseudostigmatinae than in *Mesomegaloprepus* and *Thaumatoneura*, but it is even narrower in *Paraphlebia* (second modern genus of Thaumatoneuridae). Even though all these character states seem to be derived in *Thaumatoneura*, as suggested by the more "megapodagrionid"-like sister genus *Paraphlebia* and the closely related genera *Bornargiolestes* and *Burmargiolestes* as sistergroups, the character polarity is unclear in *Mesomegaloprepus*, mainly because of the homoplastic distribution of these character states in other damselfly taxa (e.g., multiple secondary antenodal crossveins is generally rather a plesiomorphy in odonates). The fact that other characters (*see above*) contradict an ingroup position of *Mesomegaloprepus* within Thaumatoneuridae as sister group of *Thaumatoneura*, rather suggests that the similarities between these two genera are not synapomorphies.

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

4.1.4 Ambiguous relationship of Mesomegaloprepidae and justification for this new family

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

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

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

4.2 Status of alleged fossil Thaumatoneuridae

Pongrácz (1935) described *Eothaumatoneura* from the Eocene of Germany and attributed it to Thaumatoneuridae, but Nel and Paicheler (1994) transferred it to Zygoptera *incertae sedi*s. Bechly (1996, 2003) attributed the mostly Paleogene Dysagrioninae Cockerell, 1908 (*Petrolestes, Congqingia, Dysagrion* Scudder, 1878, and *Phenacolestes* Cockerell, 1908) and Early Cretaceous Euarchistigmatinae (*Euarchistigma* Carle and Wighton 1990) to Thaumatoneuridae within Amphipterygoidea. Petrulevičius and Nel (2004) considered the Paleogene *Latibasalia* as possibly related to Dysagrioninae within Amphipterygoidea, but we here transferred this taxon to Epallagoidea (*see above*). Nel et al. (2005) described *Primorilestes* from the Eocene of Russia. Nel and Arillo (2006) added *Electrophenacolestes* from Eocene Baltic amber to Dysagrioninae, and Rust et al. (2008) added *Eodysagrion* in a separate subfamily Eodysagrioninae (and synonymized Thaumatoneuridae with Dysagrionidae). Nel and Fleck (2014) described an unnamed dysagrionine from the Eocene-Oligocene of the Isle of Wight. Finally, Zheng et al. (2016c, 2016d) described *Palaeodysagrion* and *Burmadysagrion*, both from Burmite. These fossil taxa are discussed below and their phylogenetic position is revised.

Eothaumatoneura ptychoptera Pongrácz, 1935 is a fossil damselfly that is only known from wing fragments of a single specimen from the Middle Eocene (Middle Lutetian, MP13, 44.3 Ma) Geiseltal locality in eastern Germany. Nel and Paicheler (1994) considered that this material as too incompletely preserved to be accurately placed, and therefore transferred this taxon from Thaumatoneuridae to Zygoptera *incertae sedis*. Nevertheless, the preserved parts of the wing venation of *Eothaumatoneura* are very similar to the corresponding structures in the extant Neotropical damselfly genus *Thaumatoneura*, especially in the very long postnodal area, base of RP2 far removed from subnodus, absence of lestine oblique vein ‘O’, main veins strongly curved posteriorly, presence of 2-3 secondary longitudinal veins in distal part of postdiscoidal area between MA and MP, presence of 4-5 secondary longitudinal veins in distal part of area between MP and CuA, cubital area certainly broad, even if poorly preserved (see Pongrácz, 1935: figs. 11-14). This pattern of venation is not shared by any of the known Paleogene damselfly-like Odonata with large wings (e.g., Sieblosiidae, Dysagrionidae, or even the damsel-dragonfly family Pseudostenolestidae from the Eocene of Messel, Garrouste and Nel, 2015). Consequently, there are no arguments against an attribution of *Eothaumatoneura ptychoptera* to Thaumatoneuridae, which is suggested by the above mentioned wing venational similarities. Therefore, we here propose to restore this fossil taxon in Thaumatoneuridae. *Eothaumatoneura* seems to be more closely related to the extant genus *Thaumatoneura* than to the other extant thaumatoneurid genus *Paraphlebia*, because the wing venation is much more similar to the former genus in several derived character states.

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

The Dysagrioninae are an extinct Cenozoic damselfly group, with the sole exception of *Congqingia* from the Cretaceous of China. The placement of the Dysagrioninae (Dysagrionini Cockerell, 1908 and Petrolestini Cockerell, 1927) within the Thaumatoneuridae, as proposed by Bechly (1996, 2003) and Rust et al. (2008) is only supported by two very weak alleged synapomorphies: basal costal margin between wing base and nodus is distinctly convex curved; antesubnodal space without any crossveins. The first character is probably correlated to the shortening the antenodal space and could have been convergently acquired. The second character is present in several unrelated clades, and thus very homoplastic, as already indicated above. Since the affinities of the Dysagrioninae are uncertain, we prefer to exclude these damselflies from the Thaumatoneuridae and suggest to restate the Dysagrionini and Petrolestini as subfamilies to a separate family Dysagrionidae stat. rest., as already suggested by Garrouste and Nel (2015) and Zheng et al. (2016d). Our rejection of the synonymy of Thaumatoneuridae with Dysagrionidae (*contra* Rust et al., 2008) implies that Thaumatoneuridae is restored as valid family as well. The Dysagrioninae are characterized by a potential synapomorphy, viz a rather unique shape of the discoidal cell with a distal side distinctly longer than its basal side and anterior and posterior sides not parallel, even if it is also present in the Cenozoic Sieblosiidae. *Mesomegaloprepus* does not share the above mentioned two potential synapomorphies of Dysagrioninae and Thaumatoneuridae, and also lacks the typical dysagrionine shape of the discoidal cell.

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

4.3 Palaeobiogeography and Palaeoecology

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

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

Concluding remarks

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

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References

Bechly, G., 1996. Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. Petalura, Böblingen, Special Volume 2, 402 pp.

Bechly, G., 2003. Phylogenetic Systematics of Odonata. In: Schorr, M., Lindeboom, M. (Eds.), Dragonfly Research 1.2003 (CD-ROM) (also online at: https://dl.dropboxusercontent.com/u/13756162/Website/odonata/phylosys.htm).

Bechly, G., 2007. Odonata: damselflies and dragonflies. In: Martill, D., Bechly, G., Loveridge, R. (Eds.), The Crato fossil beds of Brazil: Window into an ancient world. Cambridge University Press, Cambridge, 624 pp., 184–222.

Bechly, G., 2010. Additions to the fossil dragonfly fauna from the Lower Cretaceous Crato Formation of Brazil (Insecta: Odonata). Palaeodiversity 3 (Supplement), 11–77.

Brodribb, T.J., Feild, T.S., 2008. Evolutionary significance of a flat-leaved *Pinus* in Vietnamese rainforest. New Phytologist 178, 201–209.

Bybee, S.M., Ogden, T.H., Branham, M.A., Whiting, M.F., 2008. Molecules, morphology and fossils: a comprehensive approach to odonate phylogeny and the evolution of the odonate wing. Cladistics 24, 477–514.

Calvert, P.P., 1914. Studies on Costa Rica Odonata. V. The waterfall-dwellers: *Thaumatoneura* imagos and possible male dimorphism. Entomological News 25, 337–348.

Calvert, P.P., 1915a. Studies on Costa Rica Odonata. VI. The waterfall-dwellers: the transformation, external features and attached diatoms of *Thaumatoneura* larva. Entomological News 26, 295–305.

Calvert, P.P., 1915b. Studies on Costa Rica Odonata. VII. The waterfall-dwellers: The internal organs of *Thaumatoneura* larva and the respiration and rectal tracheation of zygopterous larvae in general. Entomological News 26(9), 385–393.

Carle, F.L., Wighton, D.C., 1990. Odonata. Bulletin of the American Museum of Natural History 195, 51–68.

Carle, F.L., Kjer, K.M., May, M.L., 2008. Evolution of Odonata, with special reference to Coenagrionoidea (Zygoptera). Arthropod Systematics & Phylogeny 66, 37–44.

Clausnitzer, V., 2002. IDF-Report 4(1), 11–17.

Clausnitzer, V., Lindeboom, M., 2002. Natural history and description of the dendrolimnetic larvae of *Coryphagrion grandis* (Odonata). International Journal of Odonatology 5, 29–44.

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukaung Valley, northern Myanmar. Journal of Asian Earth Sciences 21, 441–455.

Davis, R.B., Nicholson, D.B., Saunders, E.L.R., Mayhew, P.J., 2011. Fossil gaps inferred from phylogenies alter the apparent nature of diversification in dragonflies and their relatives. BMC Evolutionary Biology 11(252), 1–10.

Dijkstra, K.-D.B., Bechly, G. Bybee, S.N., Dow, R.A., Dumont, H.J., Fleck, G., Garrison, R.W., Hämäläinen, M., Kalkman, V.J., Karube, H., May, M.L., Orr, A.G., Paulson, D., Rehn, A.C., Theischinger, G., Trueman, J.W.H., Tol, J.v., von Ellenrieder, N., Ware, J., 2013. The classification of dragonflies and damselflies (Odonata). Zootaxa 3703(1), 036–045.

Dijkstra, K.-D.B., Kalkman, V.J., Dow, R.A., Stokvis, F.R., Van Tol, J., 2014. Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). Systematic Entomology 39(1), 68–96.

Dow, R.A., 2014. A review of the genus *Bornargiolestes* Kimmins, 1936 (Odonata: Zygoptera) with a description of two new species from Sarawak, Malaysia. Journal of Threatened Taxa 6(5), 5700–5711.

Dumont, H.J., Vierstraete, A., Vanfleteren, J.R., 2010. A molecular phylogeny of the Odonata (Insecta). Systematic Entomology 35, 6–18.

Dutta, S., Mallick, M., Kumar, K., Mann, U., Greewood, P.F., 2011. Terpenoid composition and botanical affinity of Cretaceous resins from India and Myanmar. International Journal of Coal Geology 85, 49–55.

Fincke, O.M., 1984. Giant damselflies in a tropical forest: reproductive biology of *Megaloprepus coerulatus* with notes on *Mecistogaster* (Zygoptera: Pseudostigmatidae). Advances in Odonatology 2, 13-27.

Fincke, O.M., 1992a. Consequences of larval ecology for territoriality and reproductive success of a Neotropical damselfly. Ecology 73, 49–462.

Fincke, O.M., 1992b. Interspecific competition for tree holes: consequences for mating systems and coexistence in Neotropical damselflies. The American Naturalist 139(1), 80–101.

Fincke, O.M., 1996. Larval behaviour of a giant damselfly: territoriality or size-dependent dominance? Animal Behaviour 51, 77–87.

Fincke, O.M., 2006. Use of forest and tree species, and dispersal by giant damselflies (Pseudostigmatidae): their prospects in fragmented forests. In Cordero Rivera, A. (Ed.), Forests and dragonflies (4th WDA Symposium of Odonatology, Pontevedra, Spain, July 2005), Sofia-Moscow. Pensoft, 103–125.

Fogarty, F.A., Bybee, S.M., Ingley, S.J., Branham, M.A., 2008. Phylogenetic relationships of Central and South American flatwing damselflies (Odonata: Zygoptera: Megapodagrionidae): An examination of monophyly in a convoluted group. Poster Presentation at the Annual Meeting of the Entomological Society of America, November 16-19, 2008. (https://esa.confex.com/esa/2008/webprogram/Paper37035.html).

Garrison, R.W., von Ellenrieder, N. and Louton, J.A., 2010. Damselfly genera of the New World, an illustrated and annotated key to the Zygoptera. The Johns Hopkins University Press, Baltimore.

Garrouste, R., Nel, A., 2015. New Eocene damselflies and first Cenozoic damsel-dragonfly of the isophlebiopteran lineage (Insecta: Odonata). Zootaxa 4028, 354–366.

González-Soriano, E., Córdoba-Aguilar, A., 2003. Sexual behaviour in *Paraphlebia quinta* Calvert: male dimorphism and a possible example of odonate female control (Zygoptera: Megapodagrionidae). Odonatologica 32, 345–353.

Grimaldi, D., 2016. Diverse orthorrhaphan flies (Insecta: Diptera: Brachycera) in amber from the Cretaceous of Myanmar: Brachycera in Cretaceous amber, Part VII. Bulletin of the American Museum of Natural History 408, 1–131.

Grimaldi, D., Engel, M.S., Nascimbene, P., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361, 1–72.

Grimaldi, D., Ross, A.S., (in press). Extraordinary Lagerstaetten in amber, with particular reference to the Cretaceous of Burma. In: Fraser, N.C., Sues, H.-D. (eds). Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land. Dunedin Press, Edinburgh, UK.

Groeneveld, L.F., Clausnitzer, V., Hadrys, H., 2007. Convergent evolution of gigantism in damselflies of Africa and South America? Evidence from nuclear and mitochondrial sequence data. Molecular Phylogenetics and Evolution 42, 339–346.

Huang, D., Azar, D., Cai, C., Nel, A., 2015. New damselfly genera in the Cretaceous Burmese amber attributable to the Platystictidae and Platycnemididae Disparoneurinae (Odonata: Zygoptera). Cretaceous Research 56, 237–243.

Ingley, S.J., Bybee, S.M., Tennessen, K.J., Whiting, M.F., Branham, M.A., 2012. Life on the fly: phylogenetics and evolution of the helicopter damselflies (Odonata, Pseudostigmatidae). Zoologica Scripta 41(6), 637–650.

Kalkman, V.J., Choong, C.Y., Orr, A.G., Schütte, K., 2010. Remarks on the taxonomy of Megapodagrionidae with emphasis on the larval gills (Odonata). International Journal of Odonatology 13(1), 119–135.

Kalkman, V.J., Theischinger, G., 2013. Generic revision of the Argiolestidae (Odonata), with four new genera. International Journal of Odonatology 16(1), 1–52.

Kimmins, D.E., 1931. Description of the male of *Coryphagrion grandis* Morton (Odonata). Annals and Magazine of Natural History (10)7, 215–217.

Lounibos, L.P., 1980. Larval Odonata in water-containing treeholes at the Kenya coast. Notulae odonatologicae 1: 99-100.

Metcalfe, I., 2011. Palaeozoic–Mesozoic history of SE Asia. In: Hall, R., Cottam, M.A., Wilson, M.E.J. (Eds.), The SE Asian gateway: history and tectonics of the Australia-Asia collision. Geological Society of London, Special Publications 355, 7–35.

Möstel, C., Schorr, M., Bechly, G., in press. A new stem-coenagrionoid genus of damselflies (Odonata: Zygoptera) from mid-Cretaceous Burmese amber. Zootaxa.

Morton, K.J., 1924. A new genus and new species of dragonfly from East Africa belonging to the legion Podagrion (Odonata). The Entomologist 57(737), 217–220.

Nel, A., Arillo, A., 2006. The first Baltic amber dysagrionine damselfly (Odonata: Zygoptera: Thaumatoneuridae: Dysagrioninae). Annales de la Société Entomologique de France (N.S.) 42, 179–182.

Nel, A., Fleck, G., 2014. Dragonflies and damselflies (Insecta: Odonata) from the Late Eocene of the Isle of Wight. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 104, 283–306.

Nel, A., Martinez-Delclos, X., Paicheler, J.-C., Henrotay, M., 1993. Les ‘Anisozygoptera’ fossiles. Phylogénie et classification (Odonata). Martinia, Numéro Hors Série 3, 1–311.

Nel, A., Paicheler, J.-C., 1994. Les Lestoidea (Odonata, Zygoptera) fossiles: un inventaire critique. Annales de Paléontologie 80(1), 1–59.

Nel, A., Petrulevicius, J.F., Jarzembowski, E.A., 2005. New fossil Odonata from the European Cenozoic (Insecta: Odonata: Thaumatoneuridae, Aeshnidae, Idionychidae, Libellulidae). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 235(3), 343–380.

Novelo-Gutiérrez, R., 2008. Description of the larva of *Paraphlebia zoe* Selys in Hagen, 1861 (Odonata: Megapodagrionidae). Zootaxa 1876, 29–34.

Petrulevičius, J.F., Nel, A., 2004. A new damselfly family from the Upper Palaeocene of Argentina. Palaeontology 47(1), 109–116.

Petrulevičius, J.F., Nel, A., 2007. Enigmatic and little known Odonata (Insecta) from the Paleogene of Patagonia and Northwest Argentina. Annales de la Société Entomologique de France (N.S.) 43(3), 341–347.

Poinar, G., Jr., Bechly, G., Buckley, R., 2010. First record of Odonata and a new subfamily of damselflies from early Cretaceous Burmese amber. Paleodiversity 3, 15–22.

Poinar, G.O., Jr., Lambert, J.B., Wu, Y., 2007. Araucarian source of fossiliferous Burmese amber: spectroscopic and anatomical evidence. Journal of the Botanical Research Institute of Texas 1, 449–455.

Pongrácz, A., 1935. Die eozäne Insektenfauna des Geiseltales. Nova Acta Leopoldina (N.F.) 2, 485–572.

Ramírez, A., 1997. Description and natural history of the Costa Rican Odonata larvae. 5. *Megaloprepus caerulatus* (Drury, 1782) (Zygoptera, Pseudostigmatidae). Odonatologica 26(1), 75–81.

Rehn, A.C., 2003. Phylogenetic analysis of higher-level relationships of Odonata. Systematic Entomology 28, 181–239.

Riek, E.F., Kukalová-Peck, J., 1984. A new interpretation of dragonfly wing venation based upon Early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. Canadian Journal of Zoology 62, 1150–1166.

Romo-Beltrán, A., Macías-Ordóñez, R., Córdoba-Aguilar, A., 2009. Male dimorphism, territoriality and mating success in the tropical damselfly, *Paraphlebia zoe* Selys (Odonata: Megapodagrionidae). Evolutionary Ecology 23: 699–709.

Ross, A., Mellish, C., York, P., Crighton, B., 2010. Burmese amber. In: Penney, D. (Ed.), Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester, 208–235.

Rust, J., Petrulevičius, J., Nel, A. 2008. The first damselflies from the Lowermost Eocene of Denmark, with a description of a new subfamily (Odonata, Zygoptera: Dysagrionidae). Palaeontology 51(3), 709–713.

Schmidt, E., 1915. Vergleichende Morphologie des 2. und 3. Abdominalsegments bei männlichen Libellen. Zoologische Jahrbücher, Anat. 39(1), 87–200, pls 9–11.

Scotland, R.W., Olmstead, R.G., Bennett, J.R., 2003. Phylogeny reconstruction: the role of morphology. Systematic Biology 52(4), 539–548.

Shi, G.-H., Grimaldi, D.A., Harlow, G.E., Wang, J., Yang, M.-C., Lei, W.-Y., Li, Q., Li, X.-H., 2012. Age constraints on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163.

Wiens, J.J., 2004. The role of morphological data in phylogeny reconstruction. Systematic Biology 53(4), 653–661.

Yu, X., Bu, W., 2011. A preliminary phylogenetic study of Megapodagrionidae with focus on the Chinese genera *Sinocnemis* Wilson & Zhou and Priscagrion Zhou & Wilson (Odonata: Zygoptera). Hydrobiologia 665, 195–203.

Zahirovic, S., Seton, M., Müller, R.D., 2014. The Cretaceous and Cenozoic tectonic evolution of Southeast Asia. Solid Earth 5, 227–273.

Zheng, D., Zhang, Q., Chang, S.-C., Wang, B., 2016a. A new damselfly (Odonata: Zygoptera: Platystictidae) from mid-Cretaceous Burmese amber. Cretaceous Research 63, 142–147.

Zheng, D. Wang, B., Jarzembowski, E.A., Chang, S.-C, Nel, A., 2016b. The first fossil Perilestidae (Odonata: Zygoptera) from mid-Cretaceous Burmese amber. Cretaceous Research 65, 199–205.

Zheng, D., Wang, B., Chang, S.-C., Nel, A., 2016c. Burmadysagrioninae, a new subfamily (Odonata: Zygoptera: Dysagrionidae) from mid-Cretaceous Burmese amber. Cretaceous Research 67(1), 126–132.

Zheng, D., Zhang, Q., Nel, A., Jarzembowski, E.A., Zhou, Z., Chang, S.-C., Wang, B., (in press). New damselflies (Odonata: Zygoptera: Hemiphlebiidae, Dysagrionidae) from mid-Cretaceous Burmese amber. Alcheringa, doi:10.1080/03115518.2016.1164402.

Zherikhin, V.V., Ross, A.J., 2000. A review of the history, geology and age of Burmese amber (Burmite). Bulletin of the Natural History Museum, Geological Series 56, 3–10.

Figures legends

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

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

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

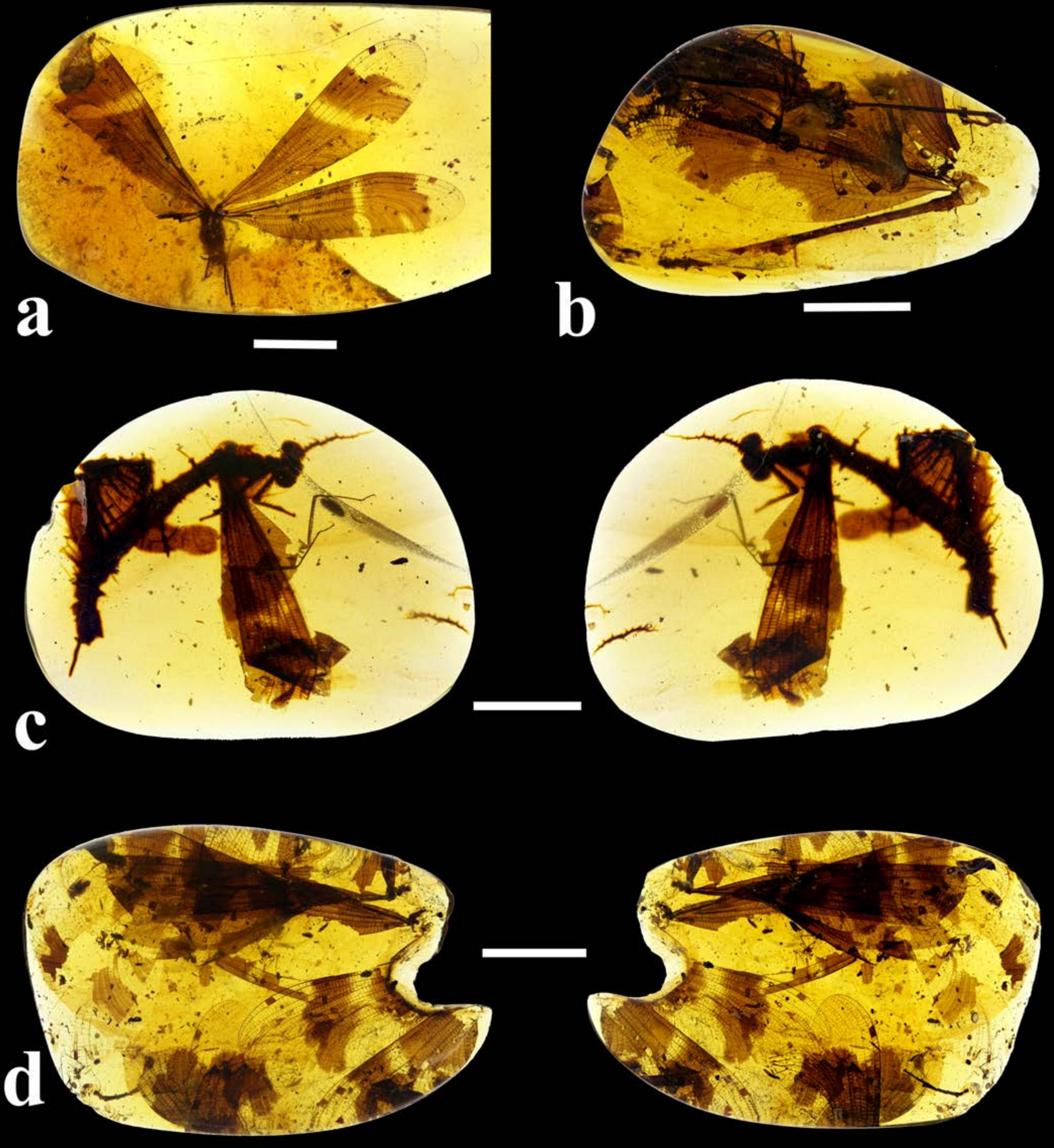
Figure 4: *Mesomegaloprepus magnificus* gen. et sp. nov., photograph of wings of holotype, female, NIGP 164902. a- Forewing. b- Hindwing.

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

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

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

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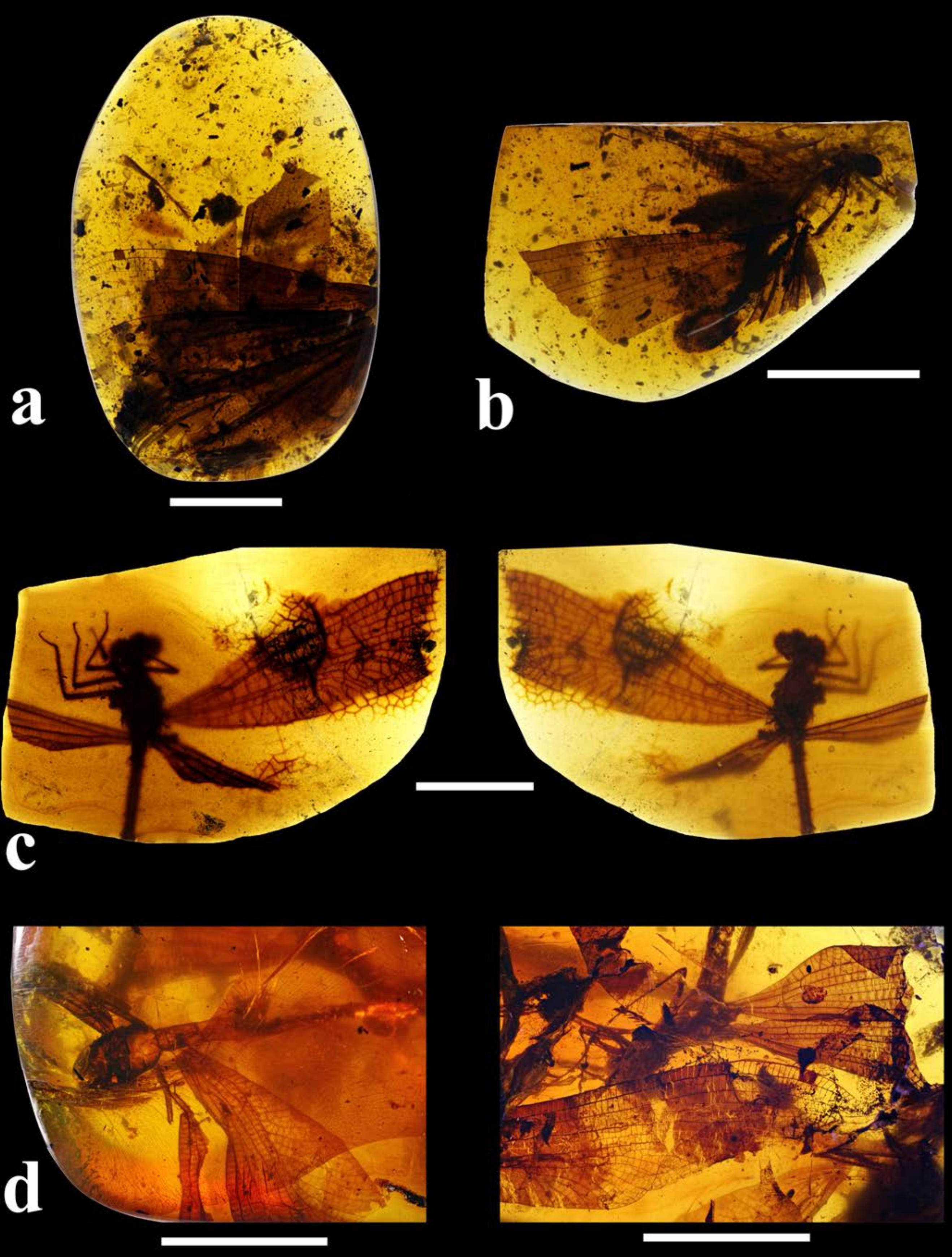
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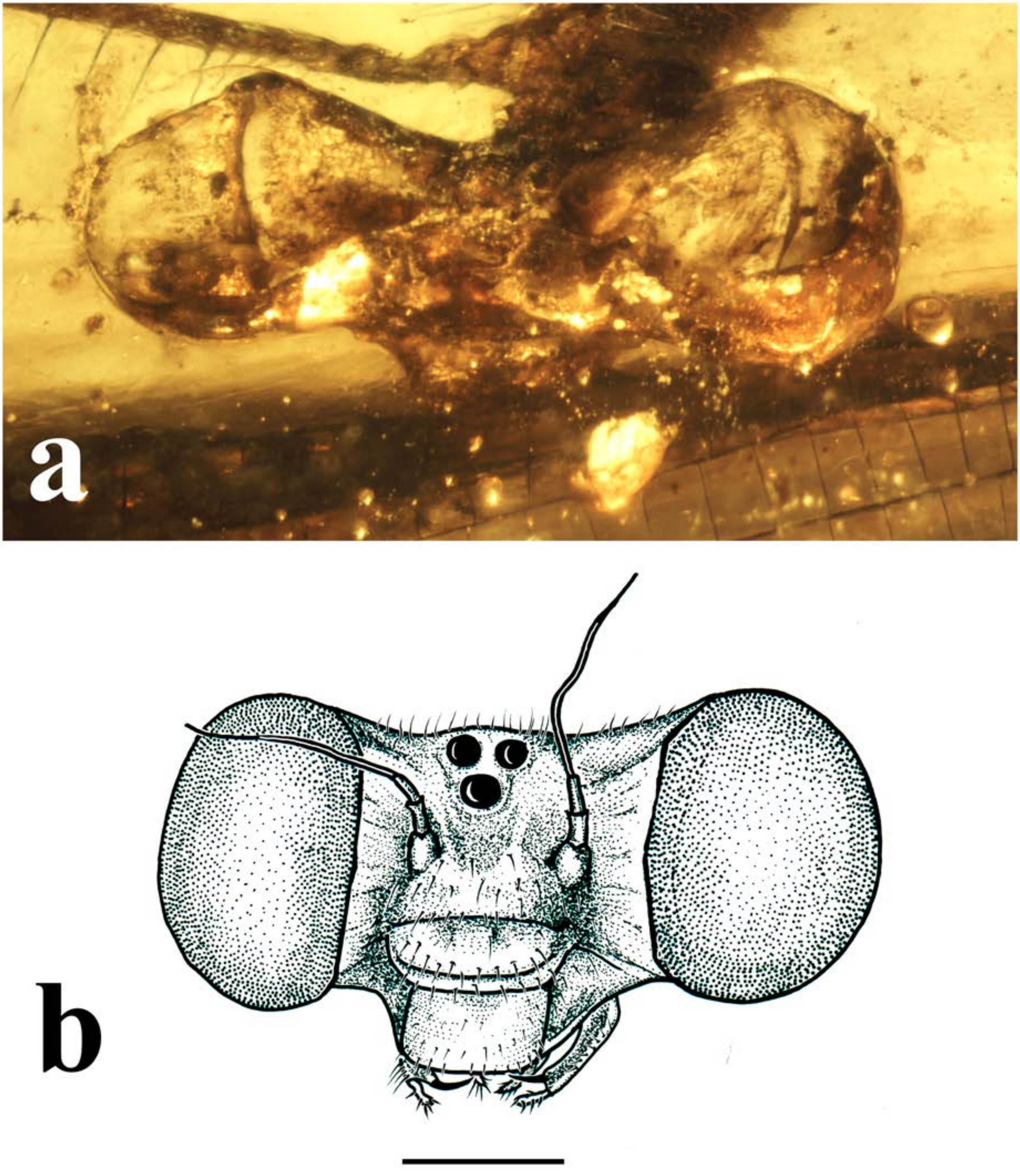
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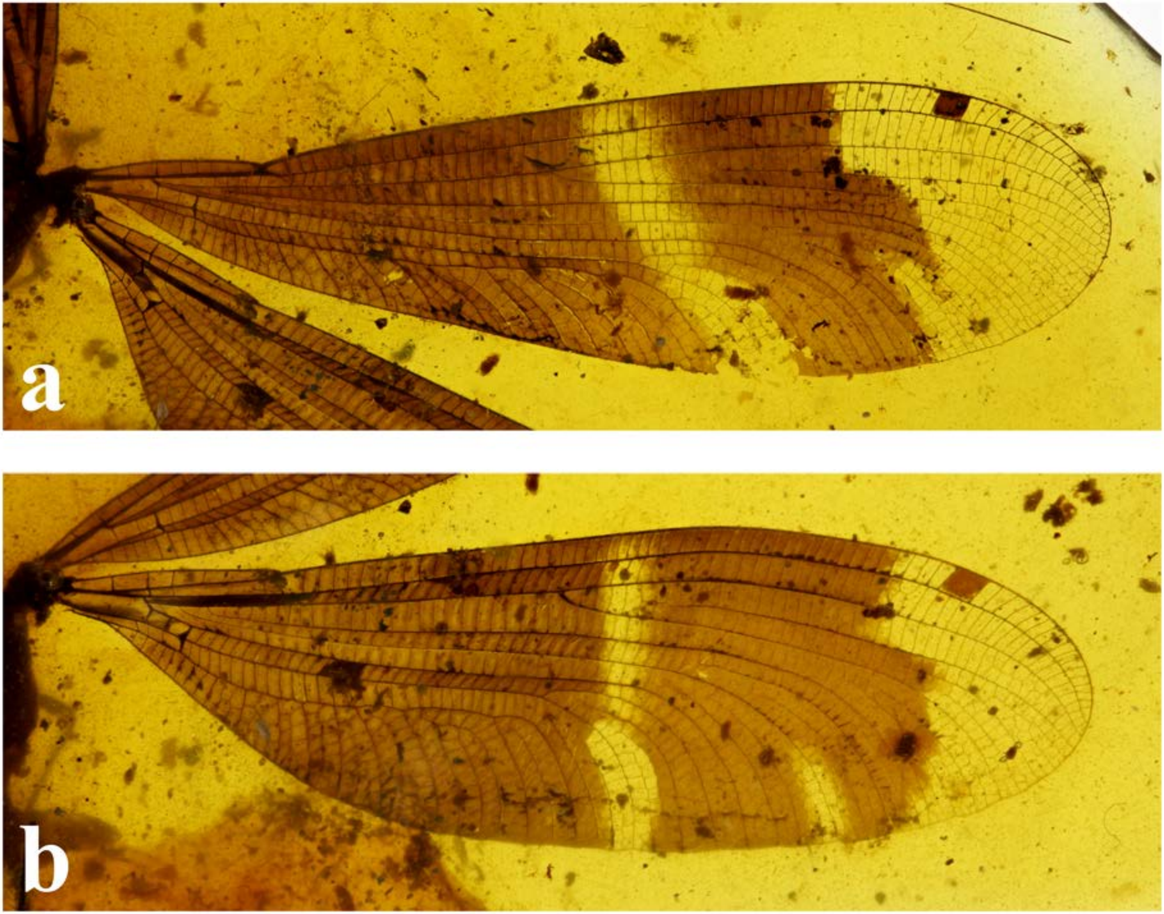
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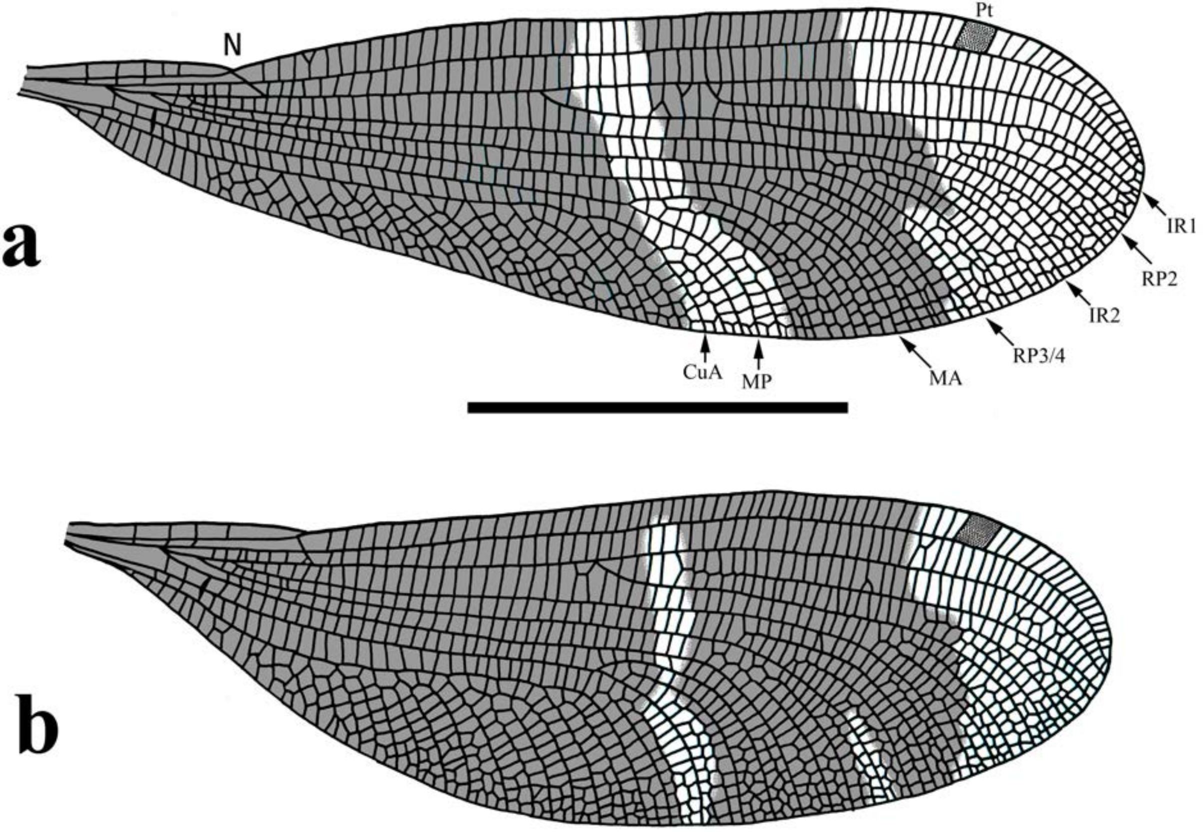
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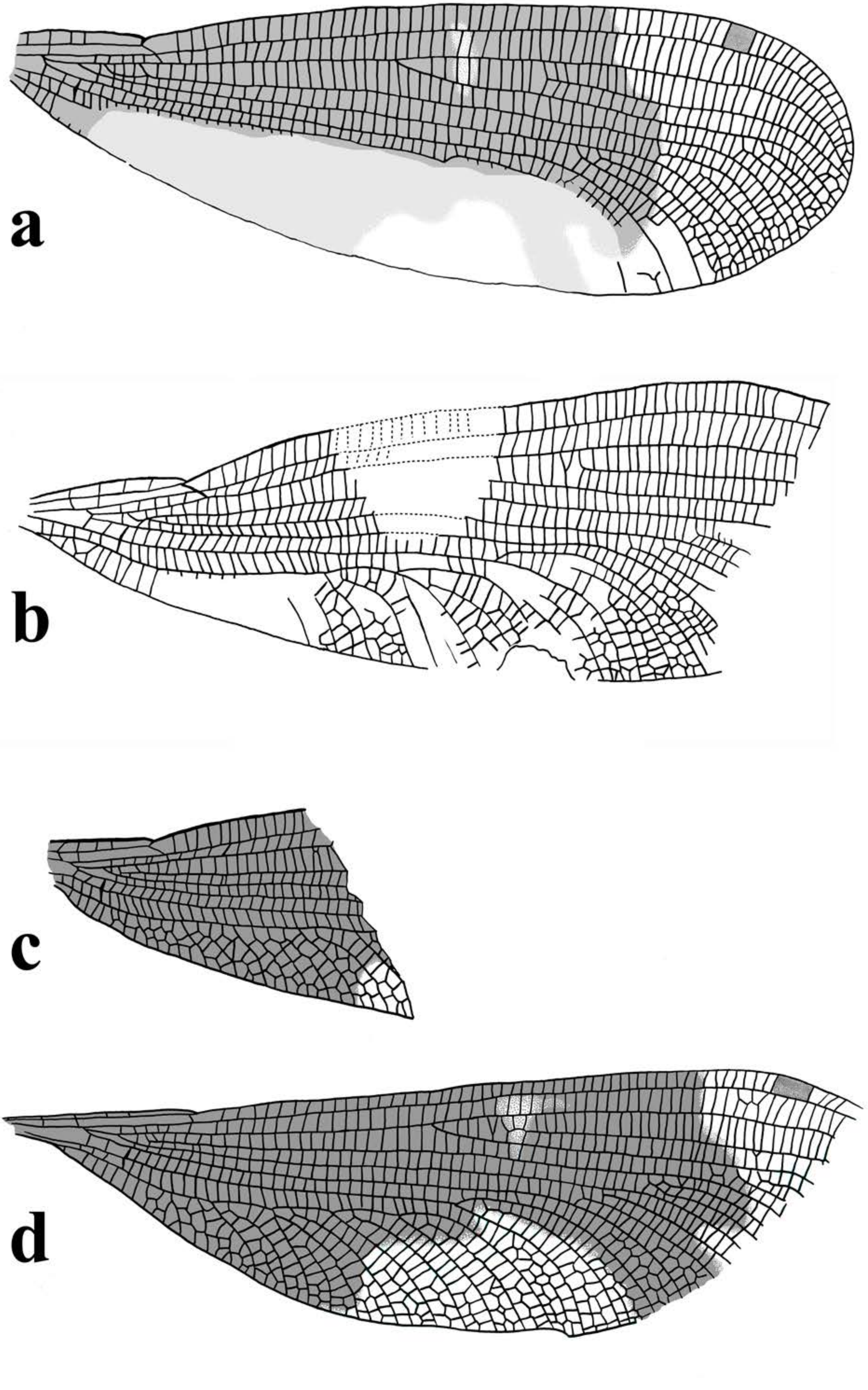
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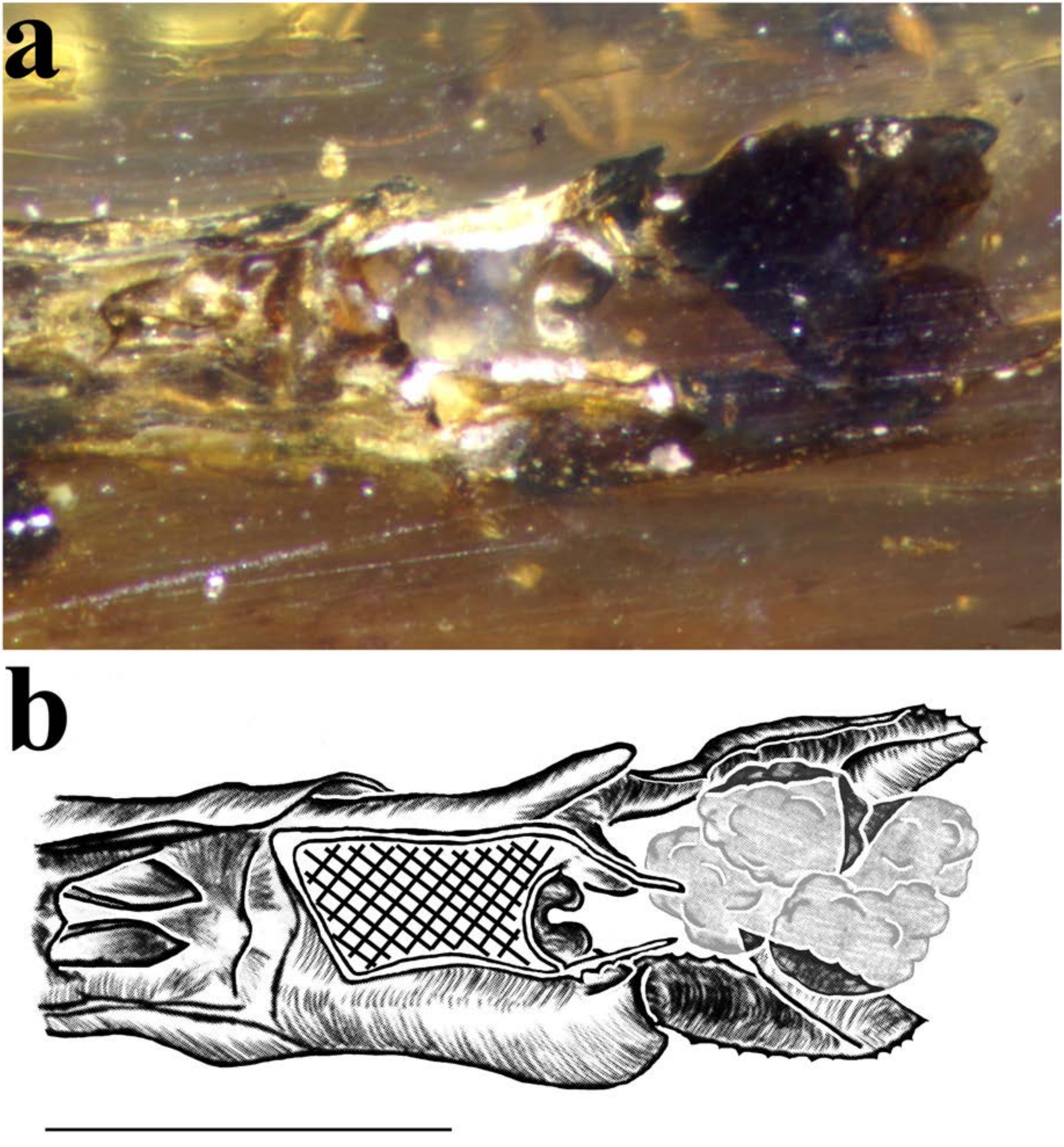
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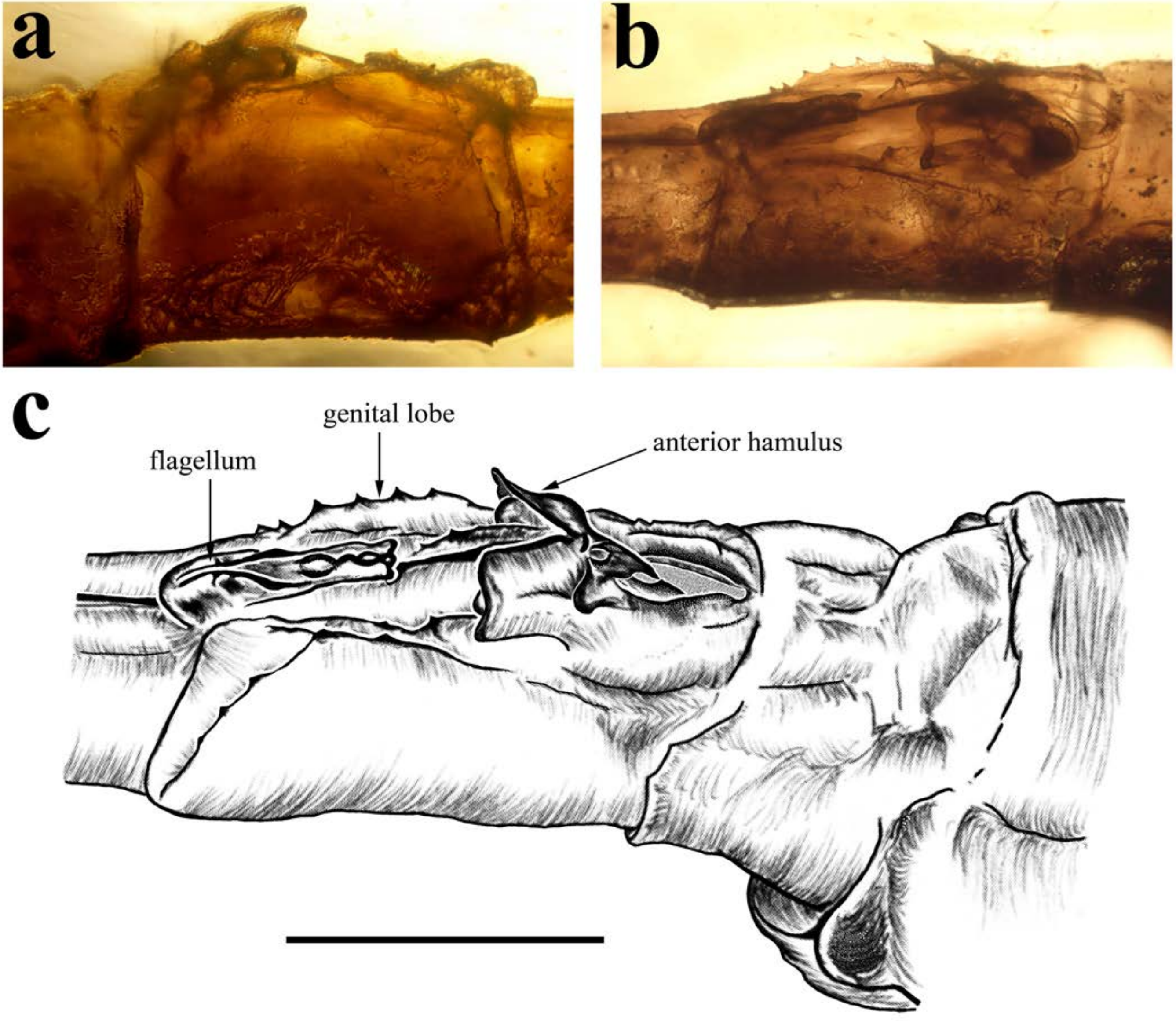
a
b
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genital lobe
anterior hamulus
flagellum

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. fredericcii* 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 (Eocence, Florissant, USA)
    - *P.* (?) *parallelus* Cockerell, 1908 (Eocene, Florrisant, 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.

Thaumatoneurinae 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)
- *Thaumatoneura* 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. mikkelseni* Rust et al., 2008 (Paleocene-Eocene, Fur, Denmark)