A new Burmese amber hawker dragonfly helps to redefine the position of the aeshnopteran family Burmaeshnidae (Odonata: Anisoptera: Aeshnoidea)

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ABSTRACT

The new genus and species *Angustaeshna magnifica* of Burmaeshnidae is described on the basis of a new fossil from Burmese amber. The genus *Cretaeshna* from the same amber is transferred from the Telephlebiidae into the Burmaeshnidae. We redefine this last family, no longer considered as the sister group of the Late Cretaceous Enigmaeshnidae, but as putative sister group of the Telephlebiidae in the Aeshnoidea. No known fossil belongs to the Telephlebiidae.

Keywords: Insecta; Aeshnoptera; gen. et sp. nov.; Myanmar; phylogeny

1. Introduction

Mesozoic Aeshnoptera are very diverse but they mainly belong to the stem group of the extant clade Aeshnodea Bechly, 1996. Only two Allopetaliidae Cockerell, 1913, one Telephlebiidae Cockerell, 1913, and no Aeshnidae Leach, 1815 are recorded in the Cretaceous (Bechly et al., 2001; Zheng et al., 2017). Huang et al. (2017) recently described the new family Burmaeshnidae from the Burmese amber, on the basis of the basal parts of a fore- and a hindwing, and tentatively considered it as the sister group of the Late Cretaceous family Enigmaeshnidae Nel et al., 2008. It was not possible to compare *Burmaeshna azari* Huang et al., 2017 to the alleged telephlebiid *Cretaeshna* Zheng et al., 2017 because the latter is based on distal parts of wings. Here we describe a third hawker dragonfly from the Burmese amber, showing nearly complete fore- and hindwings. This fossil allows to compare *Burmaeschna azari* with *Cretaeshna* and to put all these in the same family Burmaeshnidae, as sister group of the extant Telephlebiidae.

2. Materials and methods

The fossil was 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}.

The nomenclature of the odonatan wing venation used in this paper is based on the interpretations of Riek & Kukalová-Peck (1984), as modified by Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant Aeshnoptera follows Bechly et al. (2001). Wing abbreviations are as follows: CuA, cubitus anterior; IR1, intercalary radial veins; MA, median anterior; MP, median posterior; N, nodus; Pt, pterostigma; RA, radius anterior; RP, radius posterior; Sn, subnodal crossvein. All measurements are given in mm.

The specimen is preserved in a piece of relatively clear, yellow Burmese amber. The amber piece was polished before being examined and photographed. 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’.

The family, genus, and species are registered in Zoobank under the urn: xxxx

3. Systematic palaeontology

Odonata Fabricius, 1793

Anisoptera Selys in Selys and Hagen, 1854

Aeshnoptera Bechly, 1996

Burmaeshnidae Huang et al., 2017

Type species. *Burmaeshna azari* Huang et al., 2017

Other taxa. *Cretaeshna lini* Zheng et al., 2017 nov. sit., transferred from Telephlebiidae into Burmaeshnidae; *Angustaeshna magnifica* gen. et sp. nov.

Emended diagnosis. Two characters have to be added to the diagnosis of the Burmaeshnidae: IR2 with a distal fork; accessory anal loop between the two main branches of CuA in hindwing present.

Angustaeshna gen. nov.

Type species: *Angustaeshna magnifica* sp. nov.

Etymology. Named after *angustus*, narrow in Latin for the very narrow wings, and *Aeshna*.

Diagnosis. Wing venation characters only. One oblique veins 'O'; accessory anal loop between the two main branches of CuA in hindwing very well-defined; only one antesubnodal crossvein distal of base of IR2; discoidal triangles divided into two smaller cells; base of IR1 1-2 cells basal of pterostigma.

Angustaeshna magnifica sp. nov.

Figs. 1-5

Holotype. NIGP166238 (two incomplete forewings and a complete hindwing), stored at the Nanjing institute of Geology and Palaeontology.

Locality and Horizon. Hukawng Valley, Kachin Province, Myanmar; late Upper Albian to lowermost Cenomanian, Upper Cretaceous.

Etymology. Named after the wonderful state of preservation of the wings.

Diagnosis. As for genus. Hindwing discoidal triangle divided into two cells.

Description. Mid part of a forewing and distal half of the other one, hyaline, wing ca 31.7 mm long, 6.1 mm wide; distance from base to arculus ca. 3.5 mm; from arculus to base of RP3/4

6.0 mm; from arculus to nodus 6.4 mm; nodal crossvein and subnodus strongly oblique, ScP making a right angle in nodus; six preserved antenodal crossveins distal of Ax2, the first one being completed while the others are not aligned with those of second row between ScP and RA, Ax2 between arculus and discoidal triangle, a secondary antenodal crossvein between Ax2 and Ax1, Ax1 not preserved; anterior part of arculus slightly curved, RP and MA separated in angle of arculus where posterior part of arculus touches anterior part; hypertriangle 3.5 mm long, free; discoidal triangle 1.0 mm distal of arculus, divided into two smaller cells, not very elongate and narrow, with anterior side 2.5 mm long, and MAb 2.2 mm long, with a strong angle from which emerges distinct convex trigonal planate, short and zigzagged; postdiscoidal area with two rows of cells just after discoidal triangle and three more distally; Mspl well-defined with one row of cells between it and MAa; base of Mspl four cells distal of discoidal triangle; basal part of area between RA and RP with four crossveins basal of RP3/4, and two distal of base of RP3/4 and basal of subnodus; area between RP and MA with three crossveins basal of RP3/4; Bq space long, but two Bq crossveins; median area free; submedian area crossed by curved CuP; subdiscoidal space free; one row of cells between MP and CuA; two rows of cells in a narrow anal area; two rows of cells in area below CuA; CuA without well-defined posterior branches; base of RP2 aligned with subnodus; RP2 straight; one row of cell between RP2 and RP1; IR2 with a clear distal fork, and two rows of cells between its branches; Rspl well-defined straight, with one row of cell between it and IR2; one oblique vein ‘O’ one cell distal of subnodus; six preserved posnodal crossveins, not aligned with the eight postsubnodal crossveins; pterostigma and wing apex not preserved in one forewing, present on the second one, covering one cell and a half; a short pseudo-IR1 with its base below middle of pterostigma but aligned with a zigzagged vein that begins two cells basal of pterostigma.

Hind wing complete, hyaline, 30.0 mm long, 7.3 mm wide; with a rather long petiole, with stem of anal vein 2.2 mm long; distance from base to arculus 5.5 mm; from arculus to nodus 7.7 mm; from arculus to base of RP3/4 5.3 mm; four antenodal crossveins of primary type, viz. with a triangular membrane between C, ScP and radius, Ax0 at extreme base of wing, Ax1 3.2 mm distally, 'Ax2' 3.5 mm distally and a supplementary one 'Ax3' 1.7 mm distally, weaker than others and with a weaker membrane between C, ScP and RA; a secondary antenodal crossvein between Ax1 and Ax2 and three secondary antenodal crossveins of first row not well aligned with the three crossveins of second row, distal of most distal primary antenodal; 11 postnodal crossveins not well aligned with postsubnodal crossveins; one row of cells between RP1 and RP2; nodal veins with the same pattern as in forewing; arculus 1.1 mm basal of Ax2; Ax2 aligned with basal side of discoidal triangle; RP and MA separated in angle of arculus where posterior part of arculus touches curved anterior part; hypertriangle 3.9 mm long, free; discoidal triangle 1.1 mm distal of arculus, divided into two smaller cells, more elongate and narrower than in forewing, with basal side 1.2 mm long, anterior side 2.8 mm long, and MAb 2.2 mm long, sigmoidal; postdiscoidal area with two rows of cells just after discoidal triangle, distally broadened with 10 rows of cells along posterior wing margin; a distinct convex trigonal planate, short and zigzagged; Mspl well-defined, straight, with one row of cells between it and MAa; base of Mspl three cells distal of discoidal triangle; basal part of area between RA and RP with two crossveins basal of RP3/4, and two distal of base of RP3/4 and basal of subnodus; area between RP and MA with two crossveins basal of RP3/4; one oblique vein "O", one cell distal of base of RP2; one row of cells between IR2 and RP3/4 at least till two cells distal of subnodus; base of RP2 aligned with subnodus; Rspl straight with one row of cells between it and IR2; IR2 forked well basal of pterostigma, two rows of cells between its branches; pterostigma short, 1.5 mm long, 0.8 mm wide, covering one cell and a half; pterostigmal brace aligned with basal side of pterostigma and oblique; a short pseudo-IR1 with its base below middle of pterostigma but aligned with a zigzagged vein that begins one cell basal of pterostigma; one row of cells between MP and CuAa; median area free; submedian area crossed by curved CuP, situated between Ax1 and Ax2; subdiscoidal space free; no anal triangle; no clear anal angle (female specimen?); postero-basal wing margin (AP) nearly straight; anal area very long but not very broad, 5.5 mm long, 2.8 mm wide, with three rows of large cells between AA and AP basal of anal loop and no clear posterior branches of AA; anal loop two cells broad, much more elongate than broad, 3.9 mm long, 1.5 mm wide, hexagonal, posteriorly closed, divided into five cells; CuAb well-defined; cubito-anal area narrow, with three rows of cells between CuAa and posterior wing margin; CuAa with only one strong posterior branch that delimitates a clear subanal loop.

Discussion. *Angustaeshna* gen. nov. can be attributed to the Neoaeshnida Bechly, 1996 (= Gomphaeschnidae Tillyard & Fraser, 1940 + Aeshnodea Bechly, 1996) because of the very elongate discoidal triangles; presence of only one row of cells between RP1 and RP2; well-defined Mspl and Rspl, parallel to MA and IR2; both pairs of wings with a strong convex secondary longitudinal vein (trigonal planate) in postdiscoidal area; in both pairs of wings MP and CuA closely parallel with only one row of cells between them up to wing margin; only one oblique vein ‘O’ (Bechly, 1996; 2016).

Angustaeshna has several characters currently considered as synapomorphies of the Gomphaeschnidae, viz. the most distal part of antesubnodal area between RA and RP free of antesubnodal crossveins (such a ‘cordulegastrid gap’ is not present in the fossil gomphaeschnid *Alloaeschna quadrata* Wighton and Wilson, 1986); no accessory cubito-anal crossveins in submedian space between CuP and PsA; discoidal triangles only divided into two cells by a single crossvein; hypertriangles secondarily unicellular. Nevertheless, *Angustaeshna* has also a crucial apomorphy of the Eueshnodea Bechly et al., 2001, viz. IR2 with a distal dichotomic furcation, absent in all Gomphaeschnidae, recent and fossil. It cannot be attributed to the Brachytronidae Cockerell, 1913 because its pterostigmal brace is not reduced and MP and CuAa are distally not divergent. *Angustaeshna* has also a crucial synapomorphy of the Aeshnoidea

Leach, 1815, viz. a very well-defined accessory anal loop between the two main branches of CuA in hindwing, also absent in all Gomphaeschnidae. *Angustaeshna* also has a synapomorphy (proposed by Bechly, 1996, 2016) of the extant Telephlebiidae, viz. Ax2 recessed to basal angle of discoidal triangle (close to, at, or even basal).

Nevertheless, *Angustaeshna* strongly differs from all the recent representatives of the Telephlebiidae in the shape of the anal loop, clearly longer than wide, while it is wider than long in the extant Telephlebiidae, as in the Aeshnidae. Also, its anal stem is distinctly longer than in the modern Aeshnoidea. These structures are synapomorphies of the Burmese amber family Burmaeshnidae Huang et al., 2017, together with the presence of three primary antenodal crossveins Ax1, 'Ax2' and 'Ax3' in hindwing. Peters & Theischinger (2007) proposed a series of synapomorphies for the Telephlebiidae, all based on body structures, unknown in these fossils.

The genus *Burmaeshna* Huang et al., 2017 differs from *Angustaeshna* in several characters, the most important being the presence of two oblique veins 'O' instead of one (a character of the Neoaeshnida). This character is subject to homoplasies in the whole clade Aeshnoptera, so it is possibly also the case here. The accessory anal loop between the two main branches of CuA in hindwing is less well-defined in *Burmaeshna* than in *Angustaeshna*. *Burmaeshna* has also more antesubnodal crossveins distal of the base of IR2 than in *Angustaeshna*; and discoidal triangles divided into three smaller cells instead of two in *Angustaeshna*.

Huang et al. (2017) indicated that *Burmaeshna* shares with the Late Cretaceous family Enigmaeshnidae the very elongate anal area with an anal loop distinctly longer than wide, as putative synapomorphies. But *Enigmaeshna* Nel et al., 2008 strongly differs from *Burmaeshna* and *Angustaeshna* in the complete absence of the accessory anal loop between the two main branches of CuA; absence of a stem of anal vein; presence of numerous crossveins in the hindwing subdiscoidal space; presence of numerous secondary antenodal crossveins between Ax1 and Ax2; Ax2 well distal of base of discoidal triangle; and absence supplementary primary antenodal crossvein in hindwing. Thus the similar shapes of the anal loops of *Enigmaeshna* with those of *Angustaeshna* and *Burmaeshna* is a parallelism.

In conclusion, we consider that *Angustaeshna* belongs to the family Burmaeshnidae, but to a genus different from *Burmaeshna*. Also the family Burmaeshnidae belongs to the clade Aeshnoidea (Telephlebiidae + Aeshnidae), and is probably the sister group of the modern family Telephlebiidae for the Ax2 recessed close to the basal angle of discoidal triangle.

Zheng et al. (2017) described the Burmese amber genus *Cretaeshna* on the basis of weak arguments, viz. a distal half of a wing. They attributed it to the family Telephlebiidae on the basis of the shape of the nearly straight vein Rspl; absence of the bulge in the distal part of MAa (plesiomorphies); and presence of a forked IR2 (a synapomorphy of the Eueshnodea). Nevertheless the preserved structures of *Cretaeshna* are very similar to those of *Angustaeshna*, the unique clear difference being the shorter vein IR1 that begins below the pterostigma in *Cretaeshna* while it begins 1-2 cells basal of pterostigma in *Angustaeshna*. *Cretaeshna* differs from *Burmaeshna* in the presence of only one oblique vein 'O'. The lack of information on all the structures of the basal halves of the wings in *Cretaeshna* forbids us to better compare it to *Burmaeshna* and *Angustaeshna*. Nevertheless the quasi identity in venation strongly indicates that *Cretaeshna* also belongs to the Burmaeshnidae. Therefore the family Telephlebiidae sensu stricto is still unknown in the fossil record.

4. Conclusions

The Burmese amber family Burmaeshnidae is not related to the Enigmaeshnidae, but belongs to the Aeshnoidea, as putative sister group of the extant family Telephlebiidae, suggesting that the modern aeshnoids began to diversify during the mid-Cretaceous, if the most diverse extant Aeshnidae are still only known from the Paleogene.

Acknowledgments

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Figures

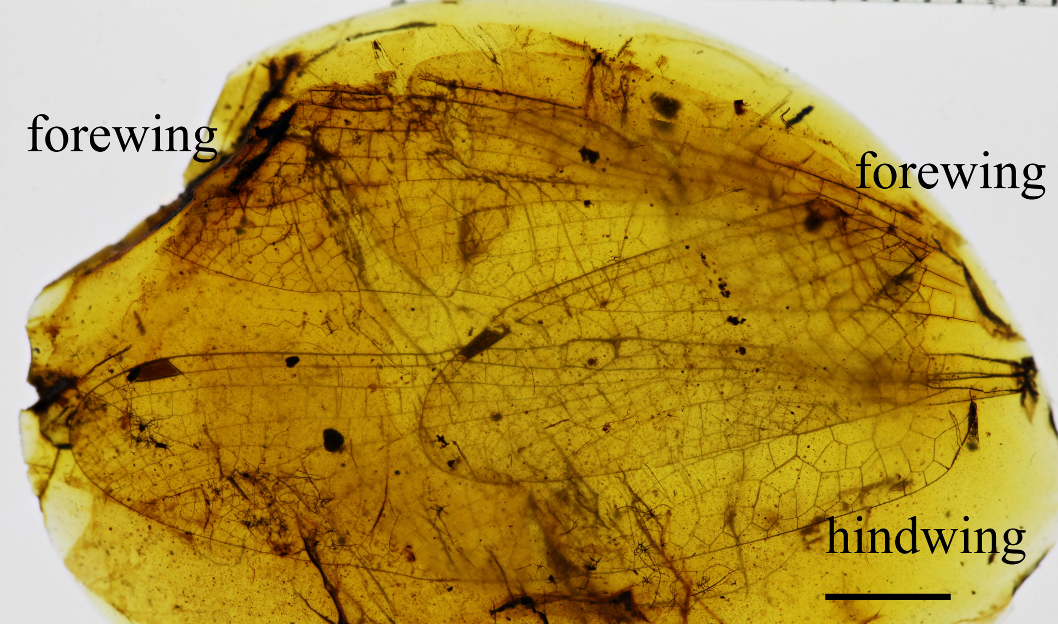
Fig. 1. *Angustaeshna magnifica* gen. et sp. nov., holotype NIGP166238, photograph of two fore- and one hindwing. Scale bar = 2 mm.

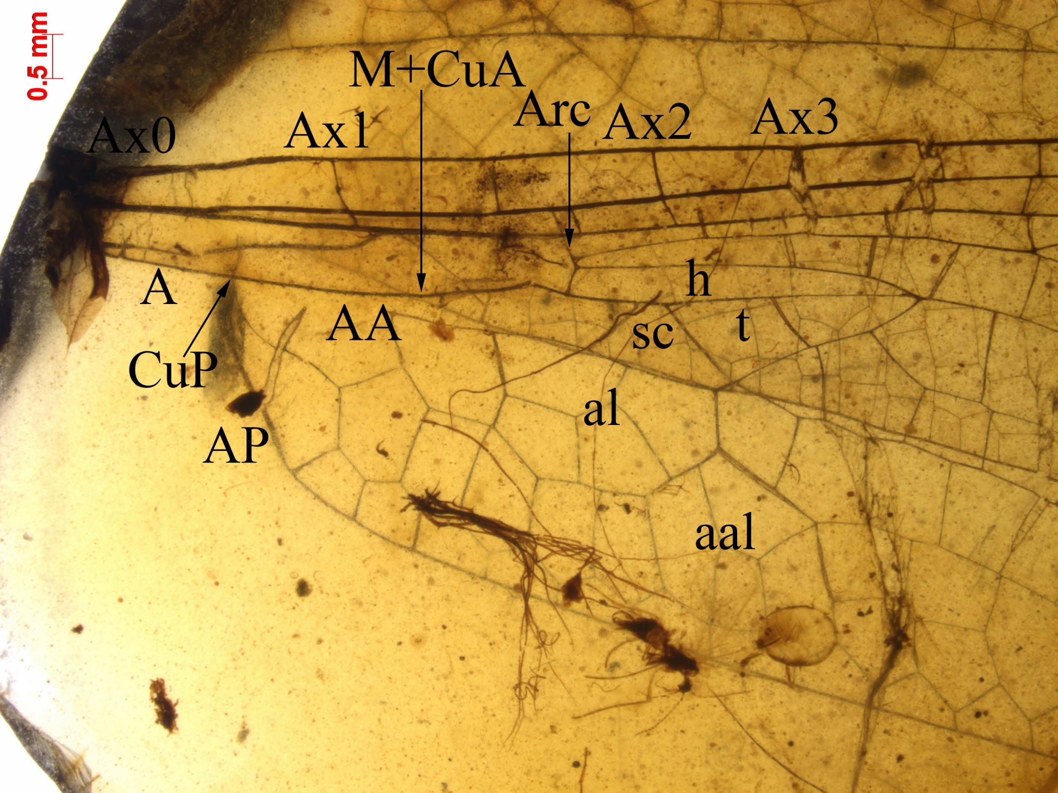
Fig. 2. *Angustaeshna magnifica* gen. et sp. nov., holotype NIGP166238, photograph of hindwing base. Scale bar = 0.5 mm.

Fig. 3. *Angustaeshna magnifica* gen. et sp. nov., holotype NIGP166238, photograph of mid part of hindwing. Scale bar = 1 mm.

Fig. 4. *Angustaeshna magnifica* gen. et sp. nov., holotype NIGP166238, photograph of hindwing pterostigma. Scale bar = 0.2 mm.

Fig. 5. *Angustaeshna magnifica* gen. et sp. nov., holotype NIGP166238, photograph of hindwing apex. Scale bar = 2 mm.


forewing
forewing
hindwing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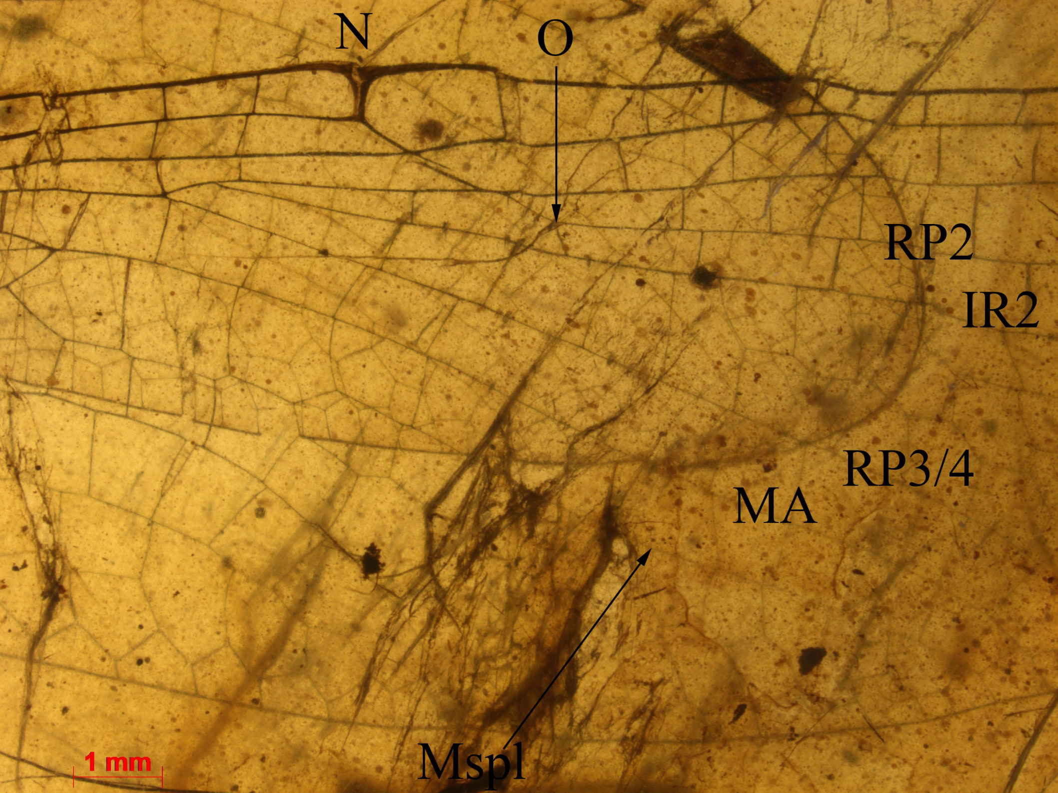
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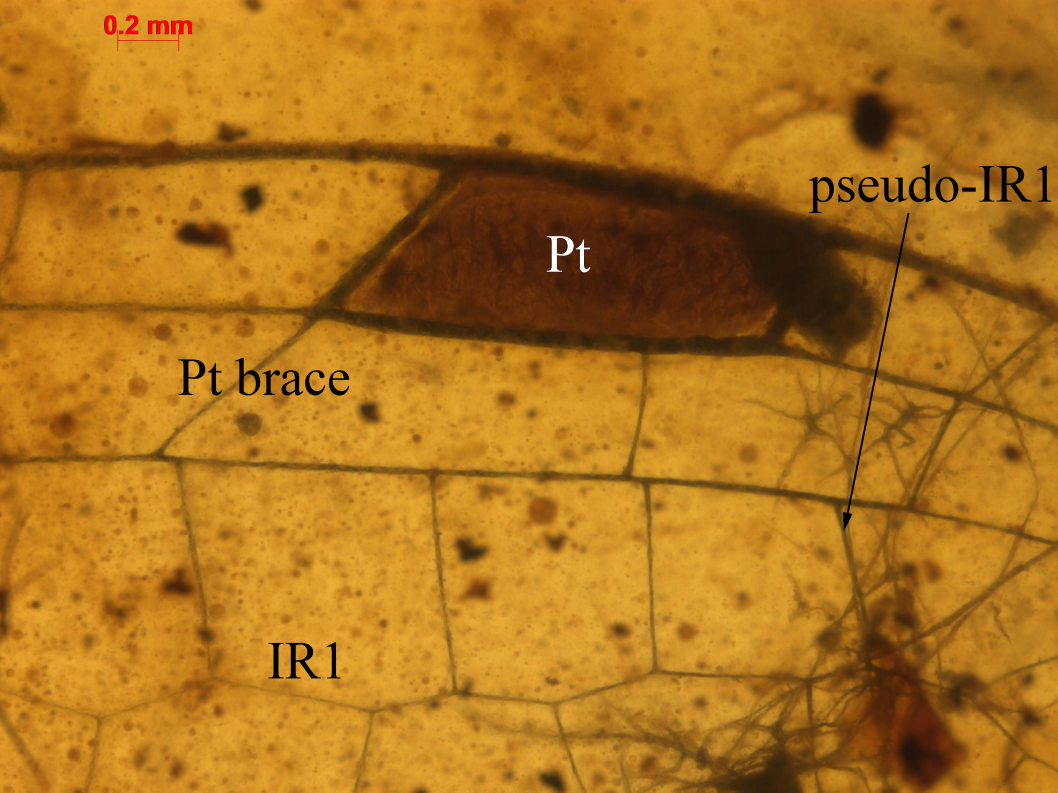
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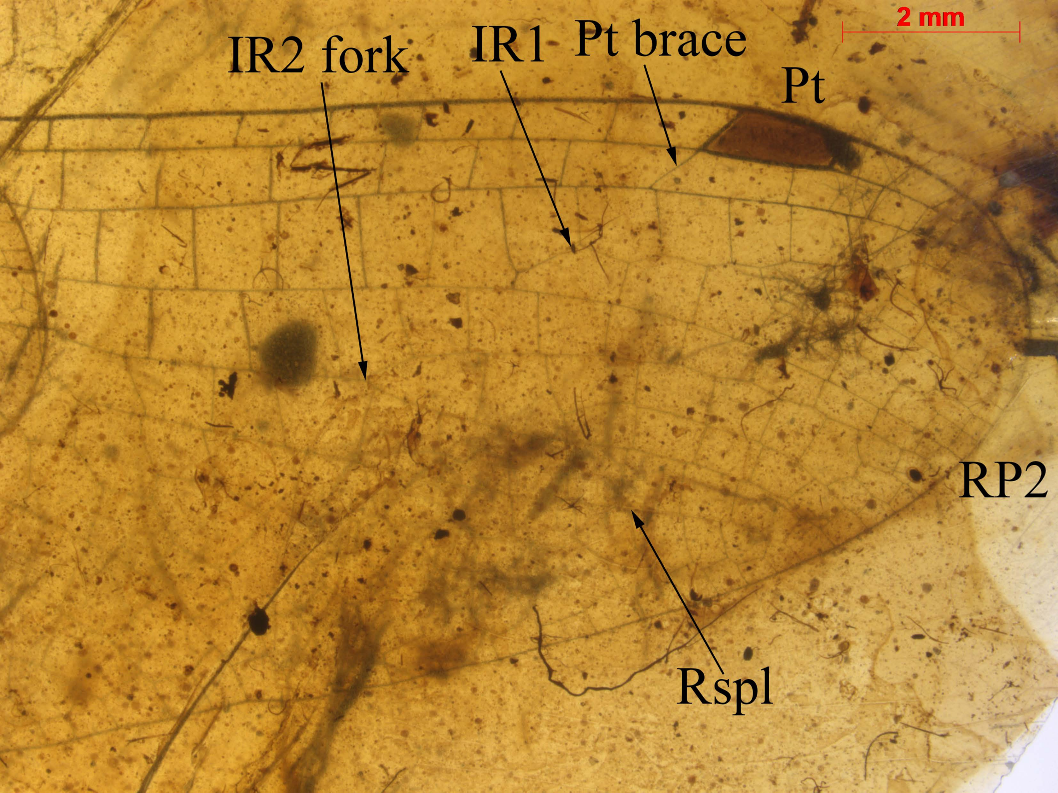
pseudo-IR1
Pt brace
IR1



2 mm
IR2 fork
IR1
Pt brace
Pt
RP2
Rspl