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Alaskan Palaeogene insects: a challenge for a better knowledge of the Beringian 'route' (Odonata: Aeshnidae, Dysagrionidae)

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The four 'routes', Beringian, De Geer, Thulean, and Turgai Strait, are currently considered to explain the Cenozoic continental interchanges between Eurasia and North America. These 'routes' had a crucial importance for the vertebrates but also for the insects. While fossil vertebrates are not infrequent in these zones, there are very few direct fossil evidences of insects to date the migrations and justify particular 'routes'. A 'route' is generally chosen after indirect evidences as molecular dating of clades. Alaska, along the Beringian 'route', is especially poor in fossil insects. Here we describe the first two Paleocene-Eocene insects from the Chickaloon Formation in Alaska, viz. *Basiaeschna alaskaensis* sp. nov., the first accurate fossil of this extant Nearctic aeshnid genus, and a representative of the extinct damselfly family Dysagrionidae, distributed during the Palaeogene in Eurasia and North America. These fossils are the direct evidences of the role of Beringia as a land bridge for insects during the Palaeogene. They are also new evidences for a warm temperate climate in Alaska during this global warming period.

Keywords: Insecta; Paleocene-Eocene; Beringia; Alaska; paleoclimate

Introduction

The Alaska is a crucial area for the understanding of the insect paleobiogeography in relation to the successive Beringian land bridges (among others, Mantilleri 2005, Espeland *et al.* 2015 Brunke *et al.* 2017, Kim *et al.* 2018, Dorchin *et al.* 2018), and the climatic changes at high latitudes, especially during the hot-house episode of the Paleocene-Eocene. But the Alaskan insect fossil record remains very poor, except for recent progresses in the knowledge of the Pleistocene to Holocene entomofaunas. Grimaldi & Triplehorn (2008) summarized the knowledge on pre-Pleistocene insects from Alaska. Only two Miocene (compression fossils) and a Late Cretaceous (amber) outcrops with insects are currently known. Paleocene and Eocene insects are only recorded through a few undescribed amber inclusions and traces of activities on plant remains, all from the Chickaloon Formation (Sunderlin *et al.* 2011).

Here we describe the first two Paleocene-Eocene insects from the Chickaloon Formation. One is a wing of an Aeshnidae sensu stricto, representing the oldest fossil record of this family. The second is a wing fragment of a damselfly.

Despite the recent descriptions of numerous Mesozoic dragonfly families of the clade Aeshnoptera Bechly, 1996, the modern dragonfly family Aeshnidae remains unknown in the Mesozoic (see Bechly *et al.* 2001, Huang *et al.* 2017). In the Palaeogene, the important Mesozoic diversity and morphological disparity of the Aeshnoptera is drastically reduced to the Gomphaeschnidae Tillyard & Fraser, 1940 (also Mesozoic) and the Aeshnidae sensu lato.

Among the Aeshnidae sensu lato, the most 'basal groups' Allopetaliidae Cockerell, 1913, Brachytronidae Cockerell, 1913, and Telephlebiidae Cockerell, 1913 are still unknown in the fossil record. Piton (1940) described an isolated abdomen attributable to the Aeshnoidea from the Paleocene of Menat (France) but it is impossible to accurately attribute it to the Aeshnidae (even sensu lato) and no wing has been found in this outcrop. The oldest Aeshnidae sensu stricto is *Huncoaeshna* Petrulevičius *et al.*, 2010 from the lower Eocene of Argentina. Some nymphs attributable to the Aeshnidae are also known from the Eocene Baltic amber (Bechly & Wichard 2008). The Latest Eocene of the Isle of Wight and several Oligocene outcrops have lead numerous Aeshnidae belonging to extinct or extant genera (Nel *et al.*, 1994, Nel & Fleck 2014).

Material and method

The Chickaloon Formation near Anchorage is well-known for its macroflora together with numerous traces of insect feeding activities on leaves, together with amber with some arthropod inclusions (Sunderlin *et al.* 2011). It is currently considered as straddling the Paleocene-Eocene boundary (Triplehorn *et al.* 1984, Neff *et al.* 2011). The old Baxter mine from where the insects come, is a well-known locality for fossil leaves, situated at 61 °42.6' N., 149°05' W (Wolfe 1966). The palaeoenvironment corresponds to fluvio-lacustrine system surrounded by a forest under warm temperate conditions. The specimens were studied using a Nikon SMZ 1500 and a Nikon SMZ 25. Photographs were taken using a Nikon D800, dry and under alcohol. The nomenclature of the dragonfly wing venation is based on the interpretations of Riek & Kukalová-Peck (1984), amended by Nel *et al.* (1993) and Bechly (1996). For the basal classification of the Aeshnoptera, we follow Bechly *et al.* (2001) and Ellenrieder (2002) for the classification of the extant Aeshnidae. Vein abbreviations are ScP subcostal posterior; RA radius anterior; RP radius posterior; IRxx intercalary radial veins;

Rpsl and Mspl supplementary radial and median veins; Bqs crossveins between RP1/2, IR2 and 'O'; 'O' oblique vein between RP2 and IR2.

Systematic palaeontology

Order **Odonata** Fabricius, 1793

Suborder **Anisoptera** Sélys, 1854

Family **Aeshnidae** Rambur, 1842

Genus ***Basiaeschna*** Sélys, 1883

Included species. *Basiaeschna janata* (Say, 1839); *Basiaeschna alaskaensis* sp. nov.

Basiaeschna alaskaensis sp. nov.

(Figs 1-2)

Diagnosis. Wing characters only. Pterostigma covering only three cells (four in *B. janata*); wing ca. 40 mm long, instead of ca. 34 mm in *B. janata*.

Material. Holotype USGS Paleobotany Loc 9870a, collection 'J. Wolfe & Hopkins 1962', stored at the National Museum of Natural History, Washington, USA.

Etymology. Named after Alaska, state from which the fossil comes.

Age and outcrop. Paleocene-Eocene, Chickaloon Formation, Premier Coal Group, new strip pit near Baxter Mine, Anchorage C-6 quad, Alaska.

Description. An incomplete wing, with postero-basal half missing, probably hyaline (no trace of coloration under alcohol); length of fragment 35.0 mm, estimate wing length ca. 40.0 mm, wing 10.1 mm wide in part distal of nodus, distance between arculus and nodus ca. 13.0 mm, between nodus and pterostigma 15.3 mm, between pterostigma and apex 4.2 mm; pterostigma 4.8 mm long, 1.06 mm wide, covering three cells; pterostigmal brace present, distinctly oblique, and aligned with basal margin of pterostigma; Ax2 visible, ca. 10 secondary crossvein distal of Ax2 not well aligned with nine antenodal crossveins between ScP and RA; 14 postnodal crossveins not aligned with 14 postsubnodals; four antesubnodal crossveins above the Bq space; five Bqs crossveins; Mspl without strong concave bend, and with two rows of cells between it and MA; two rows of cells between Mpsl and MP; MA and RP3/4 parallel and MA with a weak concave bend before wing margin, two rows of cells between MA and RP3/4 in distal part; base of RP3/4 5.7 mm basal of nodus, that of IR2 3.8 mm; base of RP2 aligned with subnodus; oblique vein 'O' one cell distal of base of RP2; distal fork of IR2 nearly absent; three rows of cells in area between RP2 and IR2; RP2 parallel with anterior branch of IR2, making a distinct curve; one row of cells between RP1 and RP2 basal of pterostigma; base of IR1 at level of pterostigmal brace; Rspl nearly straight, with two rows of cells between it and IR2.

Discussion. The presence of a RP2 modified to a characteristic curvature beneath the pterostigma is a synapomorphy of the Aeshnodea Bechly, 1996. Affinities with the Allopetaliidae Cockerell, 1913 are excluded because there is only one row of cells between RP1 and RP2 basal of the pterostigma. The presence of an anterior fork of IR2, even if it is rudimentary, supports an attribution to the Euaeshnodea Bechly *et al.*, 2001. The presence of the characteristic (but weakly indicated) bulge in the distal part of the MA ('aeshnid bulla') supports an attribution to the Aeshnidae Leach, 1815. *Telephlebia* is excluded because of the well-developed pterostigmal brace and the rudimentary fork of IR2 in *Basiaeschna alaskaensis* sp. nov. Affinities with *Brachytron* and *Aeschnophlebia* are excluded because of the well-developed pterostigmal brace in *Basiaeschna alaskaensis*. The rudimentary fork of IR2 could indicate affinities with the *Oplonaeschna* Selys, 1883 and the Cenozoic *Oligaeschna* Piton and Théobald, 1939 but the narrow area between IR2 and Rspl due to the nearly straight Rspl does not fit with these genera (Nel *et al.* 1994).

Basiaeschna alaskaensis has a narrow area with two rows of cells between IR2 and Rspl, and 'aeshnid bulla', and a nearly straight Rspl. This combination of structures can be found only in *Epiaeschna* and *Basiaeschna*. *Epiaeschna* differs from *Basiaeschna alaskaensis* in the distinctly forked IR2 and base of IR1 well distal to the pterostigmal brace, while it is below it in *Basiaeschna alaskaensis* (Garrison *et al.* 2006). All the visible characters of *Basiaeschna alaskaensis* fit well with those of *Basiaeschna*, viz. a very rudimentary fork of IR2 (or even no fork at all), Rspl and Mspl nearly straight, 2-3 rows of cells between Rspl and IR2 and between Mspl and MA, a weak 'aeshnid bulla', one row of cells between RP1 and RP2, and same pattern of IR1.

Two fossil taxa have been attributed to the genus *Basiaeschna*, viz. *Basiaeschna separata* Scudder, 1890 and *Basiaeschna ashutasica* Martynov, 1929, but later transferred into the genus *Oligaeschna* by Nel *et al.* (1994). Thus *Basiaeschna alaskaensis* is the first fossil species of the genus *Basiaeschna*.

The Eocene South American genus *Huncoaeshna* Petrulevičius *et al.*, 2010 has also a two-celled area between a nearly straight Rspl and IR2 and an unforked IR2 (Petrulevičius *et al.* 2010), but it differs from *Basiaeschna alaskaensis* in the presence of four rows of cells between IR2 and RP2, and it differs from *Basiaeschna janata* in the postdiscoidal area with 3–4 rows of cells just distal of discoidal triangle, instead of two in *Basiaeschna janata*.

Suborder Zygoptera Sélys, 1854

Family Dysagrionidae Cockerell, 1908

Genus and species undetermined

(Fig. 3)

Material. Specimen USGS Paleobotany Loc 9870b, collection 'J. Wolfe & Hopkins 1962', stored at the National Museum of Natural History, Washington, USA.

Age and outcrop. Paleocene-Eocene, Chickaloon Formation, Premier Coal Group, new strip pit near Baxter Mine, Anchorage C-6 quad, Alaska.

Description. Wing apparently hyaline, except for a darker area at level of base of IR1; length of preserved part of wing 14.7 mm, width 7.4 mm; base of RP3/4 ca. 2.0 mm basal of subnodus; base of IR2 2.0 mm distal of that of RP3/4, opposite subnodus; 10 postnodal crossveins preserved, not really aligned with the 11 corresponding postsubnodal crossveins; base of RP2 four cells and 3.7 mm distal of that of IR2; no oblique vein 'O'; areas between IR2 and RP3/4 and between RP3/4 and MA not distally broadened in preserved part of wing; postdiscoidal area with one row of cells between discoidal cell and level of base of IR1, then greatly broadened, with two rows of cells; area between MP and CuA not distally broadened, with only one row of cells; cubito-anal area very broad, with four rows of cells between CuA and posterior wing margin.

Discussion. This wing is clearly that of Zygoptera or an Epiproctophora of the isophlebiopteran lineage for the gracile venation and pattern of organization of the bases of the branches of RP relatively to the position of the nodus. The very broad cubito-anal area is encountered in few families of this kind. Affinities with the Epiproctophora are unlikely because the base of IR2 is opposite subnodus while it is generally basal to it in this clade, especially in the Eocene family Pseudostenolestidae (Garrouste & Nel 2015). The same character plus the absence of the oblique vein 'O' excludes affinities with the Sieblosiidae and the Latibasaliidae (Nel *et al.* 2005a, Petrulevičius & Nel 2007). Affinities with the Caloptera Belyshev and Haritonov, 1983 are excluded because of the relatively distal position of the midfork (Bechly 1996). The Thaumatoneuridae Tillyard & Fraser, 1938 have a very different cubito-anal area with several posterior branches of CuA. The Frenguelliidae have also an oblique vein 'O' (Petrulevičius & Nel 2003). The Eocene Austroperilestidae have the base of IR2 aligned with the subnodus but an oblique vein 'O' (Petrulevičius & Nel 2005).

This fossil better fits with the Dysagrionidae in the positions of the main veins, the broad cubito-anal area, and the absence of oblique vein 'O'. This family currently comprises the genera *Congqingia* Zhang, 1992 (early Cretaceous of China); *Palaeodysagrion* Zheng *et al.*, 2017, *Burmadysagrion* Zheng *et al.*, 2016, *Electrodysagrion* Zheng *et al.*, 2017 ('mid' Cretaceous of Myanmar); *Dysagrion* Scudder, 1878 (Eocene of Wyoming), *Phenacolestes* Cockerell, 1908 (Eocene of Colorado), *Petrolestes* Cockerell, 1927 (Eocene of Colorado and Germany), *Eodysagrion* Rust *et al.*, 2008 (Eocene of Denmark), *Electrophenacolestes* Nel & Arillo, 2006 (Eocene Baltic amber), and *Primorilestes* Nel *et al.*, 2005 (Eocene of Denmark, Russia and Miocene of Bulgaria).

Burmadysagrion has much narrower wings with narrow cubito-anal area (Zheng *et al.* 2016). Our fossil differs from *Petrolestes* in the base of IR2 opposite the subnodus instead of being much more basal (Garrouste & Nel 2015). It differs from *Congqingia* in the broader postdiscoidal area, the narrower area between MP and CuA and the position of the base of IR2 (Zhang 1992). *Electrodysagrion* has the base of RP3/4 just basal of nodus, which is not the case in our fossil (Zheng *et al.* 2017a). *Eodysagrion* differs from our fossil in the broad area between MP and CuA four cells distal of nodus level (Rust *et al.* 2008). *Electrophenacolestes* and *Primorilestes* have a base of RP3/4 well basal of nodus, a postdiscoidal area distally broad, but it differs from our fossil in the area between MP and CuA becoming broader three cells distal of nodus (Nel *et al.* 2005b, 2016, Nel & Arillo 2006, Rust *et al.* 2008). *Phenacolestes* shares with our fossil the same position for the base of RP3/4, but its postdiscoidal area becomes broader more distally than in our fossil, while the area between MP and CuA remains narrow as in our fossil (Calvert 1913). *Dysagrion* has a narrow area between MP and CuA, but differs from our fossil in the narrow postdiscoidal area and the area between RP3/4 and IR2 becoming distally very broad (Nel & Paicheler 1994). *Palaeodysagrion* is based on a wing base, with nearly no comparable structure with our fossil.

Nevertheless its cubito-anal area has only one row of cells opposite the nodus, instead of two in our fossil (Zheng *et al.* 2017b).

This fossil differs from all the dysagrionid genera, thus it probably corresponds to a new genus. Nevertheless we avoid naming it because of the lack of information on the basal structures of the wing, especially the discoidal cell.

Conclusion

Basiaeschna is clearly not a 'basal' taxon in the phylogeny of the Aeshnidae (Ellenrieder 2002: fig. 20). Thus its discovery in the Paleocene-Eocene strongly supports the hypothesis that the Aeshnidae sensu stricto diversified much earlier, probably during the Campanian-Maastrichian, more or less in accordance with the dating obtained by Letsch *et al.* (2016). Unfortunately, no fossil Odonata is recorded from the Latest Cretaceous.

After Garrison *et al.* (2006), the habitat of *Basiaeschna janata* is the 'forested rivers, streams and lakes with little shore vegetation, and oxygenated ponds'. It corresponds to the paleobiota of the Chickaloon Formation during the Paleocene – Eocene hothouse phase. Also, 57 M.a. ago the area was ca. 200 to 500 km southward (Sunderlin *et al.* 2007, 2011, 2014). The discovery of a *Basiaeschna* supports temperate, warmer conditions than today in the area, favorable for Beringian interchanges.

The Paleocene-Eocene was an exceptional period for the hot-house conditions and for the Asiatic-North American interchanges, relatively well-documented by fossil plants and vertebrates (Brikiatis 2014), but relatively poorly known for the terrestrial arthropods, despite recent advances in the topic (Archibald 2005; Archibald *et al.* 2005; Archibald & Rasnitsyn 2018). Generally the available information for insect Beringian interchanges is indirect, obtained through dating in molecular phylogenies (Kim *et al.* 2018, Dorchin *et al.* 2018), or through discoveries of Palaeogene Eurasiatic fossils related to modern or fossil Nearctic taxa

(Archibald *et al.* 2011). The same problem occurs with the three other 'routes' of De Geer, Thulean, and Turgai Strait (Fig. 4), even if some Paleocene insects are known from Spitzberg in De Geer 'route' (Wappler *et al.* 2013). The monospecific Eastern Nearctic genus *Epiaeschna* is a good example of such situation as it is well-represented in the fossil record by five Palaearctic species, viz. *Epiaeschna pseudoheros* Nel and Petrulevičius, 2010 (late Oligocene, France), *Epiaeschna stauropolitana* Martynov, 1927 (mid Miocene, Crimea), *Epiaeschna magnifica* (Martynov 1929) (late Oligocene, Kazakhstan), *Epiaeschna gossi* (Campion 1916) (middle-late Eocene, UK), *Epiaeschna matutina* (Zhang 1989) (Miocene, China) (Nel & Petrulevičius 2010, Li *et al.* 2011). The Dysagrionidae are known in the Palaeogene of North America, Central Asia, and Europe, but also in the 'mid' Cretaceous Burmese amber, suggesting faunal transfers between Eurasia and North America. The new Alaskan Dysagrionidae suggests that at least some of these transfers were made through the Beringian Bridge.

Basiaeschna is a widespread Eastern Nearctic monospecific genus, nowaday going west to Saskatchewan (Garrison *et al.* 2006, Hutchings 2004), thus its discovery in the North-Western part of the same region is not surprising. But it is surprising that *Basiaeschna* remains unknown in the Cenozoic of Eurasia.

Odonata are generally not the most frequent insects found as fossils. Thus these discoveries together with the presences of numerous traces of insect activities show that the Chickaloon Formation could potentially give a rich insect assemblage, important for future direct evidences of Palaeogene Beringian interchanges.

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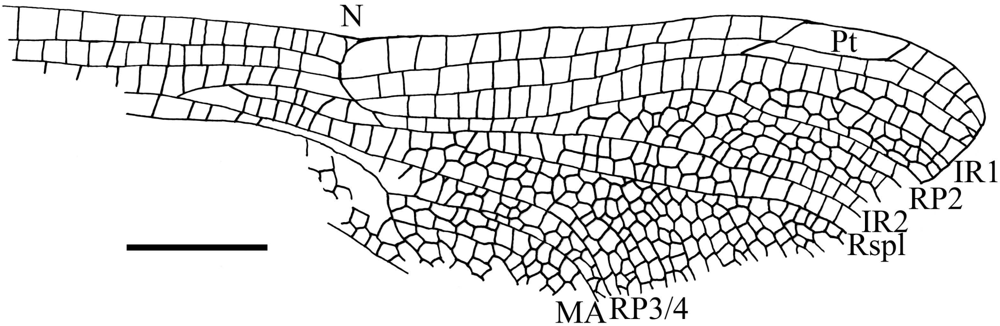
Figure 1. *Basiaeschna alaskaensis* sp. nov., holotype USGS Paleobotany Loc 9870a. **A**, photograph of wing. **B**, reconstruction. Scale bars: 5 mm.

Figure 2. *Basiaeschna alaskaensis* sp. nov., holotype USGS Paleobotany Loc 9870a. Photograph under alcohol of costo-apical part of wing. Scale bar: 4 mm.

Figure 3. Dysagrionidae genus and species undetermined, USGS Paleobotany Loc 9870b. **A**, photograph of wing. **B**, reconstruction. Scale bars: 5 mm.

Figure 4. Palaeogeographical reconstruction of Earth during the Paleocene. The numbers point out the key geo-dispersal nodes discussed in the text: (1) Beringia, (2) Thulean route, (3) De Geer route, and (4) Turgai Strait. Map modified after **Scotese, C.R. 2001.** Atlas of Earth History, Volume 1, Paleogeography, PALEOMAP Project, Arlington, Texas, 52 pp. https://www.researchgate.net/publication/264741875_Atlas_of_Earth_History.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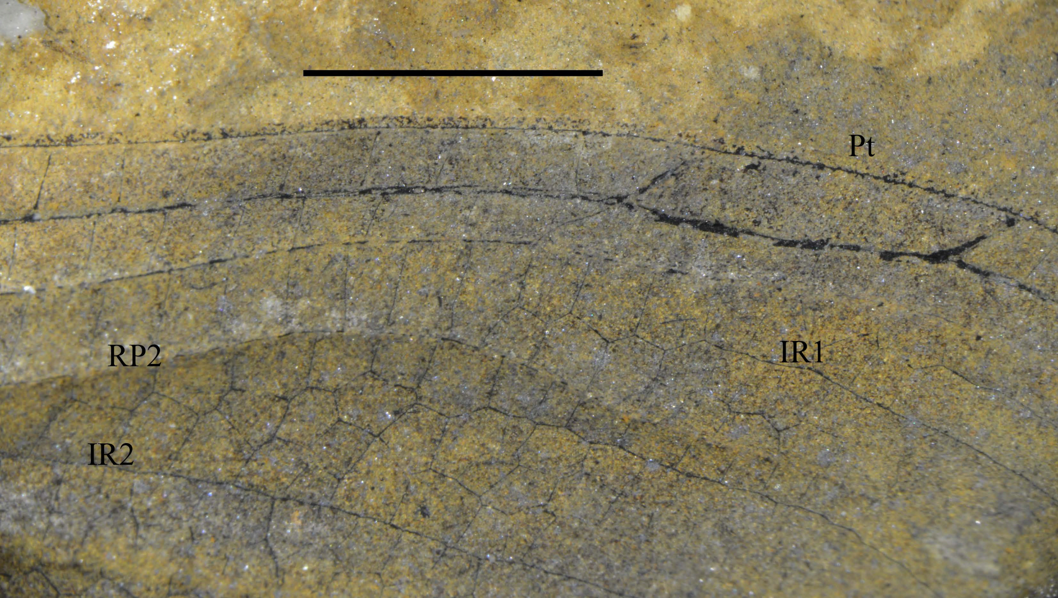
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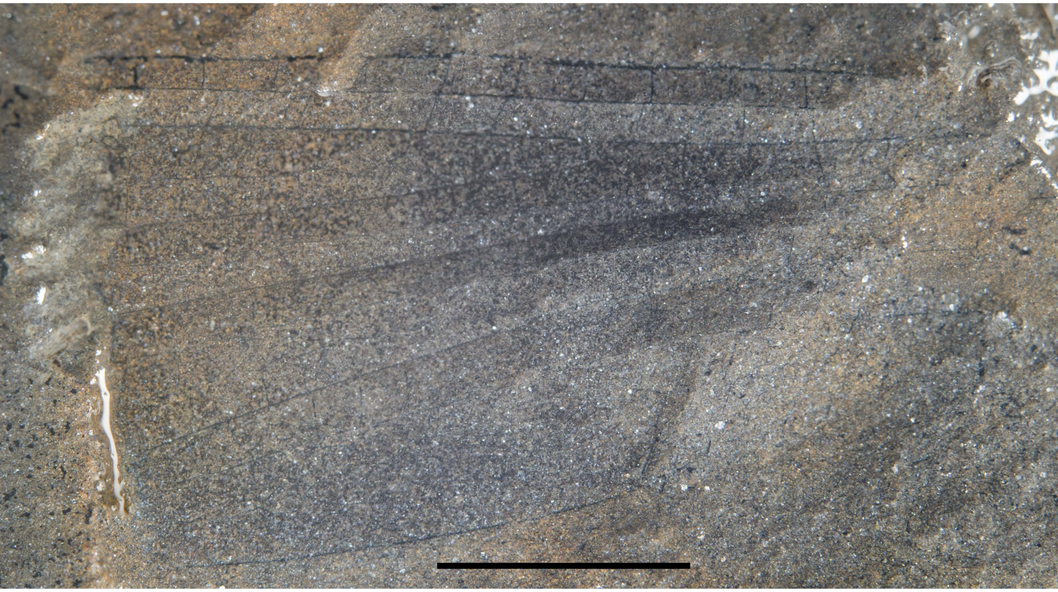

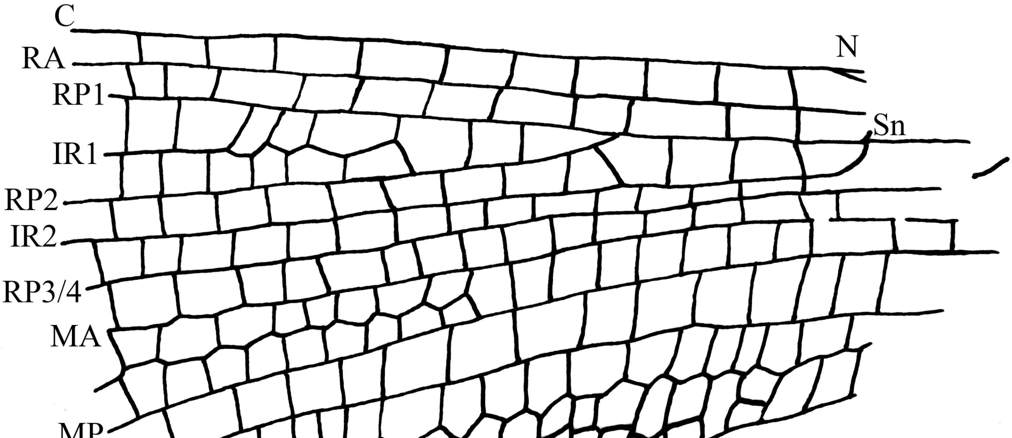

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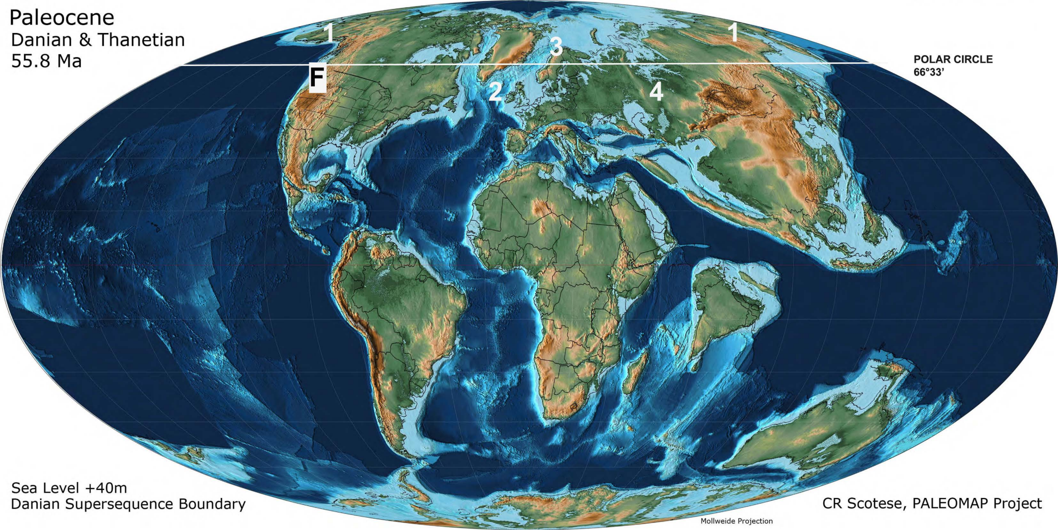
Paleocene
Danian & Thanetian
55.8 Ma
1
1
3
F
2
4
POLAR CIRCLE
66°33'
Sea Level +40m
Danian Supersequence Boundary
CR Scotese, PALEOMAP Project
Mollweide Projection