



The damselfly genus *Furagrion* Petrulevičius *et al.* (Odonata, Zygoptera) from the early Eocene Fur Formation of Denmark and the dysagrionoid grade

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Abstract

The earliest Eocene odonate genus *Furagrion* Petrulevičius *et al.* from the Danish Fur Formation is revised based on eighteen specimens, two of which apparently have been lost since their publication. The holotype of *Phenacolestes jutlandicus* Henriksen, type species of *Furagrion*, is incomplete and lacks the characters currently used to differentiate species, genera and higher taxa in Odonata. We, therefore, propose that the holotype is set aside and a recently discovered nearly complete Fur Formation fossil is designated as neotype. *Furagrion* possesses all of the nine wing character states currently used along with head shape for diagnosing the Dysagrionidae; however, *Furagrion* has a characteristically zygopteran head, not the distinctive head shape of the suborder Cephalozygoptera. We, therefore, treat it as a zygopteran unassigned to family. These nine wing character states appear in different combinations not only in various Zygoptera and Cephalozygoptera, but also in the Frenguelliidae, an Eocene family of Argentina that may represent an unnamed suborder. We recognise these taxa as constituting a dysagrionoid grade, in which these character states appear either convergently or as symplesiomorphies. *Furagrion morsi* Zessin is synonymized with *Phenacolestes jutlandicus* Henriksen, **syn. nov.** and *Morsagrion* Zessin with *Furagrion* Petrulevičius, Wappler, Wedmann, Rust, and Nel, **syn. nov.**

Key words: Odonata, Zygoptera, Cephalozygoptera, *Furagrion jutlandicus*, *Furagrion morsi*

Introduction

There is a rich record of earliest Ypresian fossil insects in the diatomaceous mo-clay of the Fur Formation and underlying siliciclastic Stolleklint clay of the Ølst Formation in the western Limfjord region of northern Jutland, Denmark (*e.g.*, Henriksen 1922; Rust 1999; Madsen & Rasmussen 2021; Simonsen *et al.* 2022). This assemblage includes a diverse suite of Odonata fossils, which has received periodic attention over the last hundred years (*e.g.*, above and Nel & Paicheler 1994, Madsen & Nel 1997, Petrulevičius *et al.* 2008, Rust *et al.* 2008, Zessin 2011).

Henriksen (1922) described the odonate *Phenacolestes jutlandica* Henriksen based on a single, incomplete specimen and stated that “From a comparison with the literature, especially with the paper of Calvert [1913] it becomes evident that the wing impression must be due to a representative of the genus *Phenacolestes* Cock.” (Henriksen 1922, p. 11). Petrulevičius *et al.* (2008) recognized that Henriksen’s incomplete type fossil lacks important characters (Fig. 1) and redescribed the species based on a nearly complete wing (Fig. 2). Realizing that

the species did not belong in *Phenacolestes* Cockerell, they erected the genus *Furagrion*, which they placed in the Dysagrioninae, then a subfamily of Thaumatonneuridae. Zessin (2011) described a second species of the genus, *F. morsi* Zessin, based on the basal portion of a wing, and established a new genus and species *Morsagrion ansorgei* Zessin based on a single, nearly complete wing.

Our survey of Odonata fossils in mo-clay collections and the literature finds 24 specimens of *Furagrion*, some rather complete, some in the literature that are apparently lost, and some illustrated (see below). We take this opportunity to evaluate the genus and its relationship to *Morsagrion* Zessin. As Henriksen's holotype is too poorly preserved to adequately describe and diagnose *Furagrion* or support a higher-level assessment of the phylogenetic affinities of the genus, we propose the holotype is set aside and that a nearly complete fossil is designated as the neotype of *Furagrion jutlandicus*.

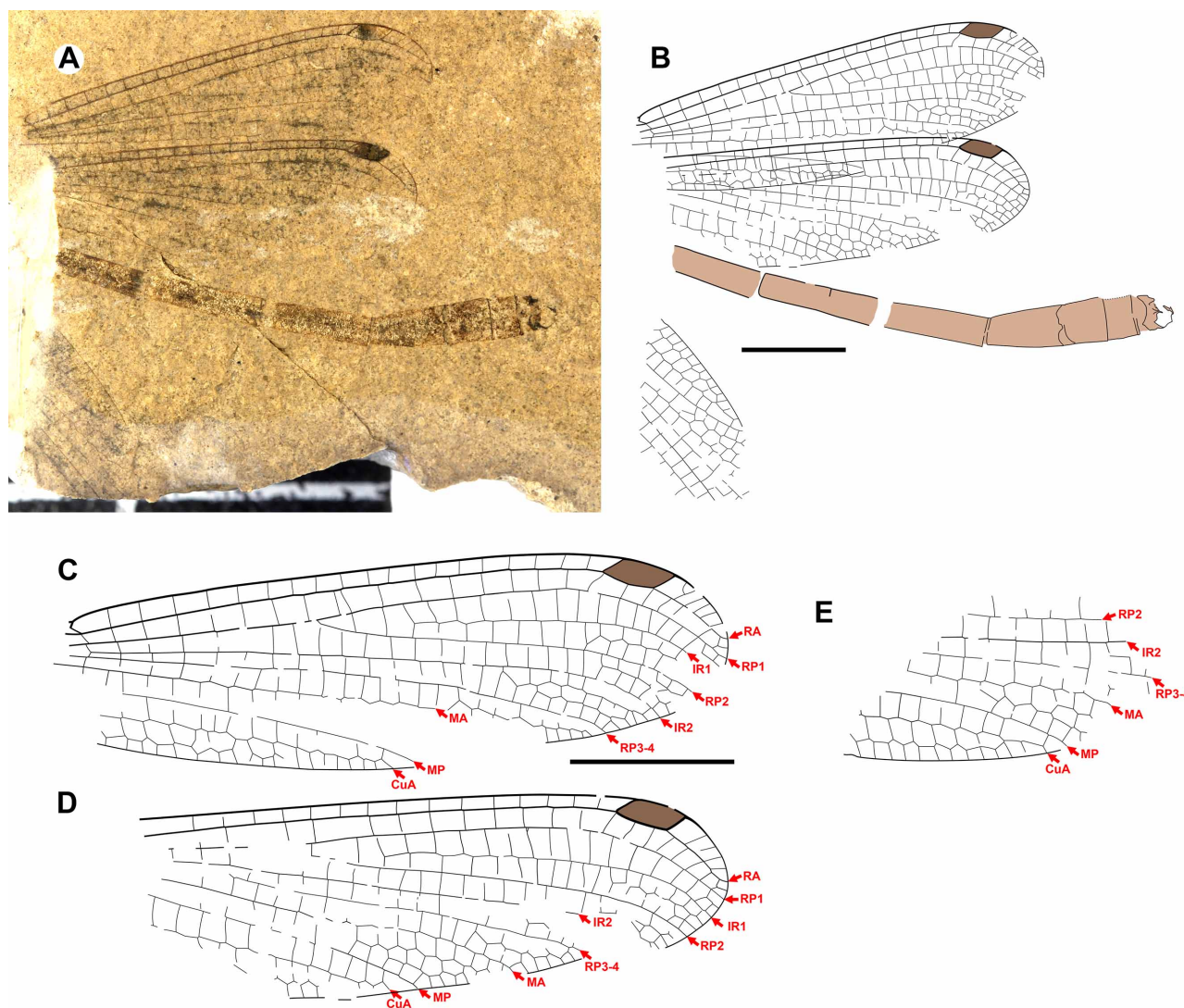


FIGURE 1. MGUH 1819, Henriksen's type specimen of *Phenacolestes jutlandica*: A, photograph; B, drawing; C–E, labelled wings. A, B to scale, C–E to scale, both scales 5 mm.

Material and methods

We examined 16 *Furagrion* or possible *Furagrion* fossils in the collections of Museum Mors (Nykøbing Mors, Denmark, main and Madsen collections), Museum Salling (Skive, Denmark), and the Natural History Museum of Denmark (University of Copenhagen, Denmark), formerly known as the Geological Museum, University of Copenhagen. We evaluated two more that we could not locate and might be lost by the published descriptions, photographs, and drawings of Zessin (2011). Nine fossils were examined by Rust (1999): MM 16-B3618, MM

14M-A2163, MM 14M-3801, MM14M-C2557, MM I2601, ERK KL94 F8, ERK GU E7, ERK KL T1, and FM 1106. We examined FM 1106 (now FUM-N 14704), MM 14M-A2163 (now 14M-A2163), MM 14M-3801 (now 14M-3801), ERK KL T1 (now FUM-N 13856), and ERK GU E7 (now FUM-N 11146). The remaining specimens examined but not illustrated by Rust were not located by us.

Specimens were photographed with a Canon EOS 1300D camera with a Tamron SP Di2 60 mm macro lens at the Natural History Museum Aarhus. Those in concretions were photographed with a droplet of deionized water on them to enhance contrast and reveal more morphology. Those preserved in soft diatomite were photographed dry, as wetting may damage them. Line drawings were made with Adobe Illustrator and assembled as figures in Adobe Photoshop. Specimens were generally examined under a Wild Heerbrugg M5A stereo microscope and measurements were taken using a 20x micro scale eyepiece (Tables 1–3). Morphological diagnostic characters for the genus are discussed below; we evaluated the usefulness of these descriptive diagnostic characters for phylogenetics but found them to be unable to provide sufficient resolution among taxa in preliminary parsimony and maximum likelihood analyses (not shown).

To visualise similarity of wing shape and to clarify potential morphological groupings, we conducted principal component analyses (PCAs), which may reveal patterns in large datasets with several variables (Davis 1986, Hammer & Harper 2006). PCA plots were constructed using the free PAST (Paleontological Statistics) software (Hammer *et al.* 2001), to visualise results in two dimensions with the two most significant axes plotted. In cases where the measurements compared are ratios only, we used a variance-covariance matrix, while the correlation coefficient matrix was used when both distances and ratios are included. The PCA is visualized in biplots where objects (individual wings) and variables (ratios) are presented simultaneously. We coded for six morphometric distance measurements and eight ratio values. The distance measurements were (see Fig. 2) arculus–apex (arc-apx), nodus–apex (nod-apx), RP2–apex (RP2-apx), arculus–pterostigma (arc-pt), nodus–pterostigma (nod-pt) and maximum width of wing (w). Five ratios were of wing length and width: arc-apx/w, nod-apx/w, RP2-apx/w, arc-pt/w and nod-pt/w; and three were of variations of wing length: arc-apx/nod-apx, arc-apx/RP2-apx, and arc-pt/nod-pt (Table 4). Because of the relatively low number of specimens for which all characters were preserved, the PCA analyses were used solely for visual comparison of the specimens.

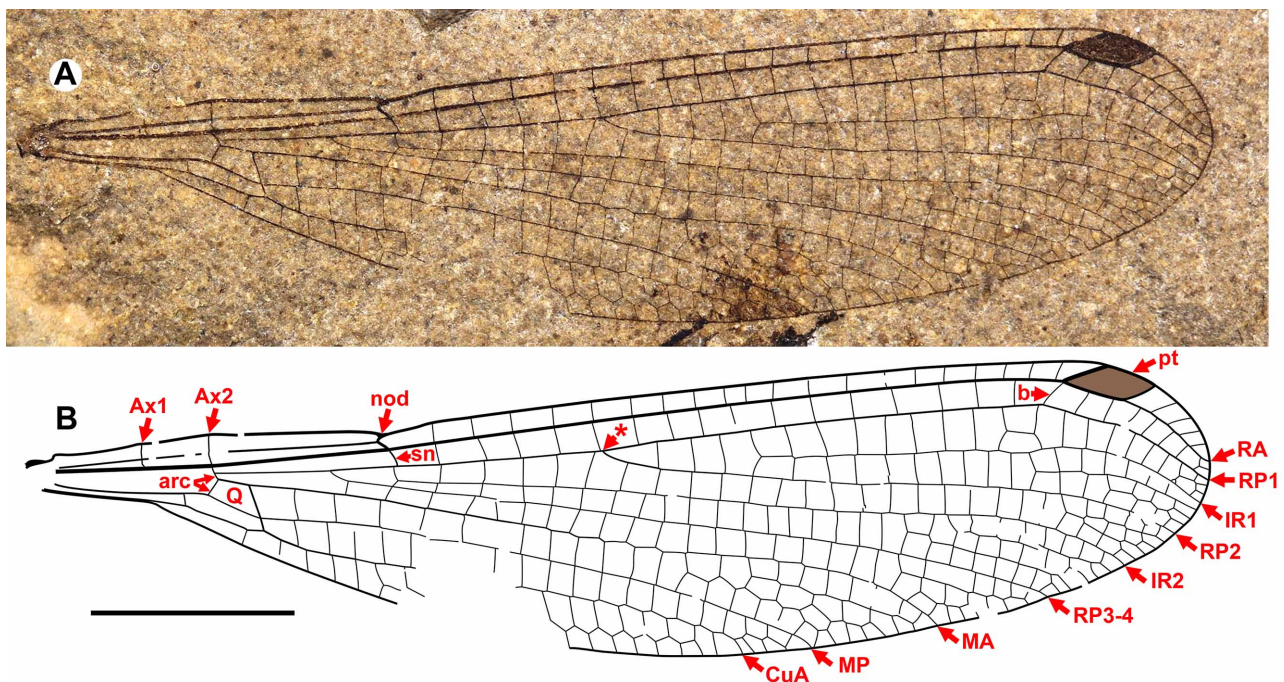


FIGURE 2. FUM-N 13856, with which Petrulevičius *et al.* (2008) defined *Furagrion* (as ERK-KL-T1): A, photograph; B, drawing. Both to scale, 5 mm. A forewing. Ax1, Ax2 = antenodal cross veins 1 and 2; arc = arculus; b = brace vein; CuA = anterior branch of the cubitus; IR1, IR2 = intercalar vein 1 and 2; MA, MP = the anterior and posterior branches of the media; nod = nodus; pt = pterostigma; Q = quadrangle; RA = radius anterior; RP1, RP2, RP3-4 = branches of the radius posterior; sn = subnodus; * = origin of RP2.

Figures show wings with the apex to the right for ease of comparison.

We use the venational terminology employed by Garrison *et al.* (2010). Contrary character states of compared taxa are provided in brackets.

Systematic paleontology

Order Odonata Fabricius, 1793

Suborder Zygoptera Selys, 1854

Family indet.

Genus *Furagrion* Petrulevičius, Wappler, Wedmann, Rust, and Nel, 2008: 176. Type species: *Phenacolestes jutlandica* Henriksen, 1922, by original designation

***Morsagrion* Zessin, 2011: 65. Type species: *Morsagrion ansorgei* Zessin, 2011, by original designation. Syn. nov.**

Figs. 1–4, 6–8, 1124.

Included species. *Furagrion jutlandica* (Henriksen, 1922), *Furagrion ansorgei* (Zessin, 2011) **comb. nov.**

Range and age. Earliest Ypresian Fur Formation, Jutland, Denmark. Specimens of this genus are known to range from just below ash layer -13 within the Knudeklint Member to the lower part of the Silstrup Member (the ash layer +25 – +30 interval) of the Fur Formation, which has an absolute age of approximately 55.5 Ma (Storey 2007, Stokke *et al.* 2020). Six of the sixteen examined fossils, however, are from unknown levels within the Fur Formation.

Emended diagnosis. The wings of *Furagrion* differ from those of similar extant and extinct Zygoptera by possession of all nine wing character states of the Dysagrionidae Cockrerell (Cephalozygoptera) diagnosis listed below, but the genus is excluded from that family and suborder by their zygopteran bulging, hemispherical compound eyes set far apart on a short head (see Archibald *et al.* 2021). Wings most easily distinguished from those of other Zygoptera and from taxa that possess many of the nine wing character states listed below and might be Zygoptera or Cephalozygoptera as follows: from *Viridiflumineagrion* Nel by pterostigma *ca.* 2.5 times longer than wide [*ca.* 4.7 times], from *Miopodagrion* Kennedy by C-RA space distad pterostigma with one row of cells [apparently two full rows]. Wings distinguished from genera with similar wings without an associated head by one or more of the following: 10, C-RA space distad pterostigma almost always with a single row of cells, rarely a few rows two cells wide immediately distad pterostigma; 11, CuA-A space usually two, sometimes maximum three cells wide; 12, possession of a brace vein; 13, no accessory (“secondary”) antenodal crossveins:

Allenbya Archibald and Cannings: [10: 2 and 3 cells wide throughout];

Valerea Garrouste *et al.*: [10: many, up to five cells wide];

Thanetophilosina Nel *et al.*: [12: no brace vein];

Electrophenacolestes Nel and Arillo: [11: up to five wide, 13];

Menatagrion Nel and Jouault, 2022 [12, 13];

Chickaloon specimen of Garrouste & Nel (2019): [11: up to four wide];

Specimen MeI6572 (Megapodagrionidae genus and species A of Petrulevičius *et al.* 2008, *cf.* Megapodagrionidae genus and species A of Archibald *et al.* 2021): [10: most of C-RA space two cells wide].

Emended description. Head short. Compound eyes bulging, hemispherical, set apart twice their width in dorsal aspect. Thorax, legs generalised as known by preservation. Forewing. Membrane darkly infusate, but some might be hyaline as preserved (see below). Measurements, ratios of these see Tables 1 and 2. Antenodal crossvein Ax0 absent, Ax1 and Ax2 somewhat lengthened to moderately expand antenodal space. No accessory antenodal crossveins. Pterostigma *ca.* 2–3 times longer than wide; anterior, posterior margins oblique; subtends 2–3 cells; distinctly oblique brace vein at basal-posterior corner in RA-RP1 space. Crossveins in postnodal, postsubnodal

spaces mostly aligned basally, usually not distally. C-RA space distad pterostigma almost always with a single row of cells, rarely briefly two cells wide (see *F. jutlandicus* proposed neotype, Figs. 3–4); RA meets margin at or very near apex; slightly upturned near margin. Wing dense with cells throughout. RP2: origin 6.5–9 cells distal to origin of IR2. IR2: origin at or very near, basal to subnodus. RP3-4: origin about 3/5 from arculus to subnodus. Arculus at or very close basad Ax2. All major veins linear except MA zigzagged distad *ca.* mid-way between arculus, termination; CuA zigzagged, slightly near quadrangle, increasingly toward terminus. No crossvein O. CuA terminates on posterior margin *ca.* mid-way between nodus, apex; CuA–A space 2–3 cells wide at widest. Hind wing. Like forewing except shorter relative to width; measurements, ratios of these see Tables 1 and 2. Abdomen generalised as known by preservation.

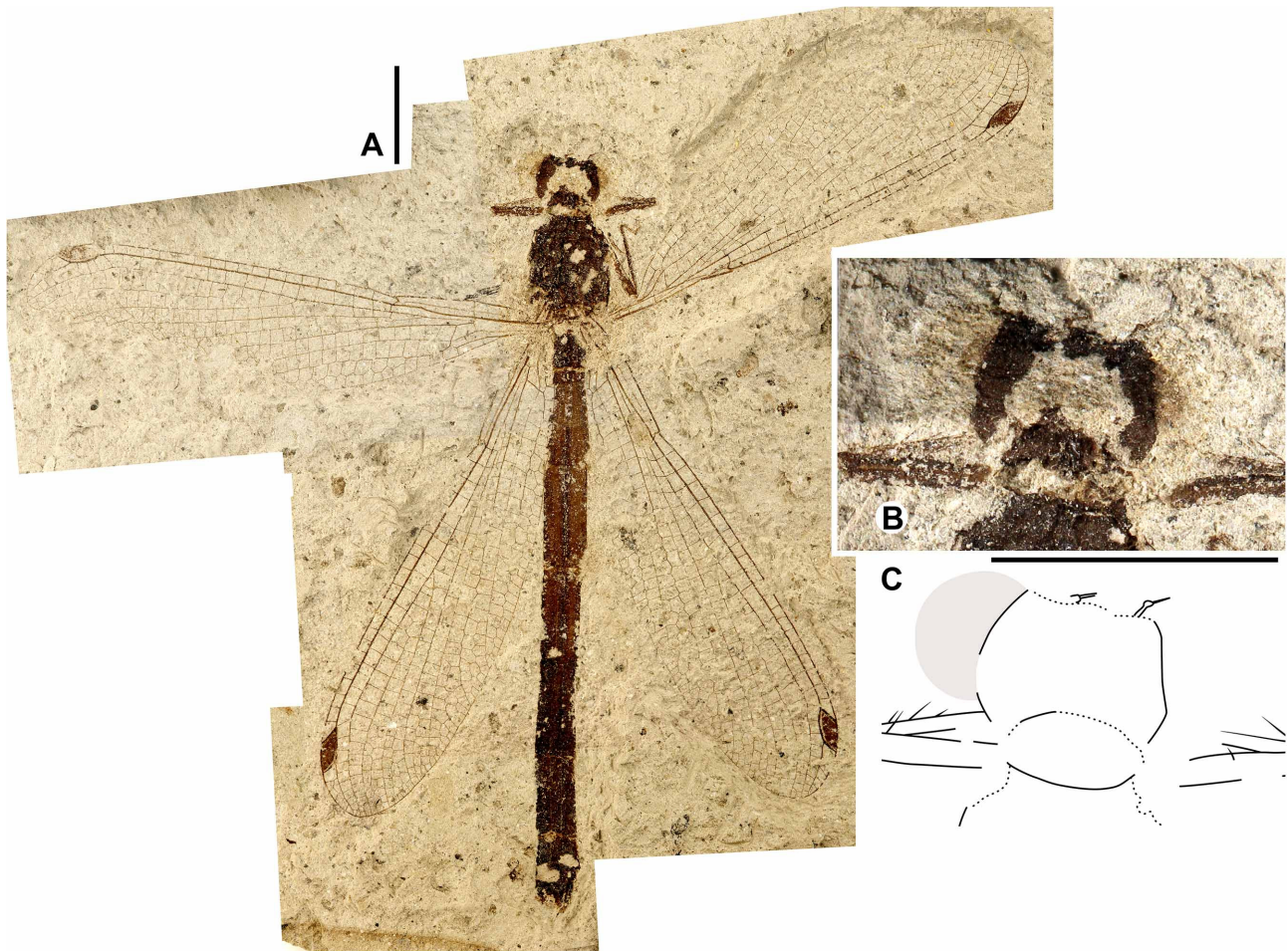


FIGURE 3. *Furagrimon jutlandicus* proposed neotype MM-10752: A, photograph of the whole insect; B, photograph of the head; C, drawing of the head, showing bulging left compound eye. A to scale, 5 mm; B, C to scale, 5 mm.

TABLE 1. Measured distances from known *Furagrimon* fore- and hind wings in millimeters: pt = pterostigma, apx = apex, arc = arculus, nod = nodus, RP2 = the origin of RP2, w = maximum width.

Specimen	Forewing						Hind wing					
	arc-apex	nod-apx	RP2-apex	arc-pt	nod-pt	w	arc-apx	nod-apex	RP2-apx	arc-pt	nod-pt	w
MM-10752	24.6	19.9	13.7	21.0	17.0	6.7	23.0	19.4	14.3	20.0	15.7	6.6
MM-10750	25.4	21.1	14.6	21.8	17.2	6.8	23.7	19.7	15.0	20.0	16.2	6.9
MM-4785AB	23.4	19.8	13.6	19.6	15.8	6.0	21.6	-	13.6	18.4	-	6.1
14M-3801	22.9	19.2	-	19.4	15.6	-	20.7	17.2	12.2	17.8	14.3	5.5
MGUH 1819	-	20.8	13.5	-	15.6	6.4	-	-	-	-	-	-

TABLE 2. Ratios of measurements in Table 1. Abbreviations as in Table 1.

Specimen	Forewing					Hind wing				
	arc-apx/w	nod-apx/w	RP2-apex/w	arc-pt/w	nod-pt/w	arc-apx/w	nod-apx/w	RP2-apex/w	arc-pt/w	nod-pt/w
MM-10752	3.67	2.97	2.04	3.13	2.54	3.48	2.94	2.17	3.03	2.38
MM-10750	3.74	3.10	2.15	3.21	2.53	3.43	2.86	2.17	2.90	2.35
MM-4785	3.90	3.30	2.27	3.27	2.63	3.54	-	2.23	3.02	-
14M-3801	3.62	2.99	-	3.15	2.41	-	-	2.22	-	-
MGUH 1819	-	3.25	2.11	-	2.44	-	-	-	-	-

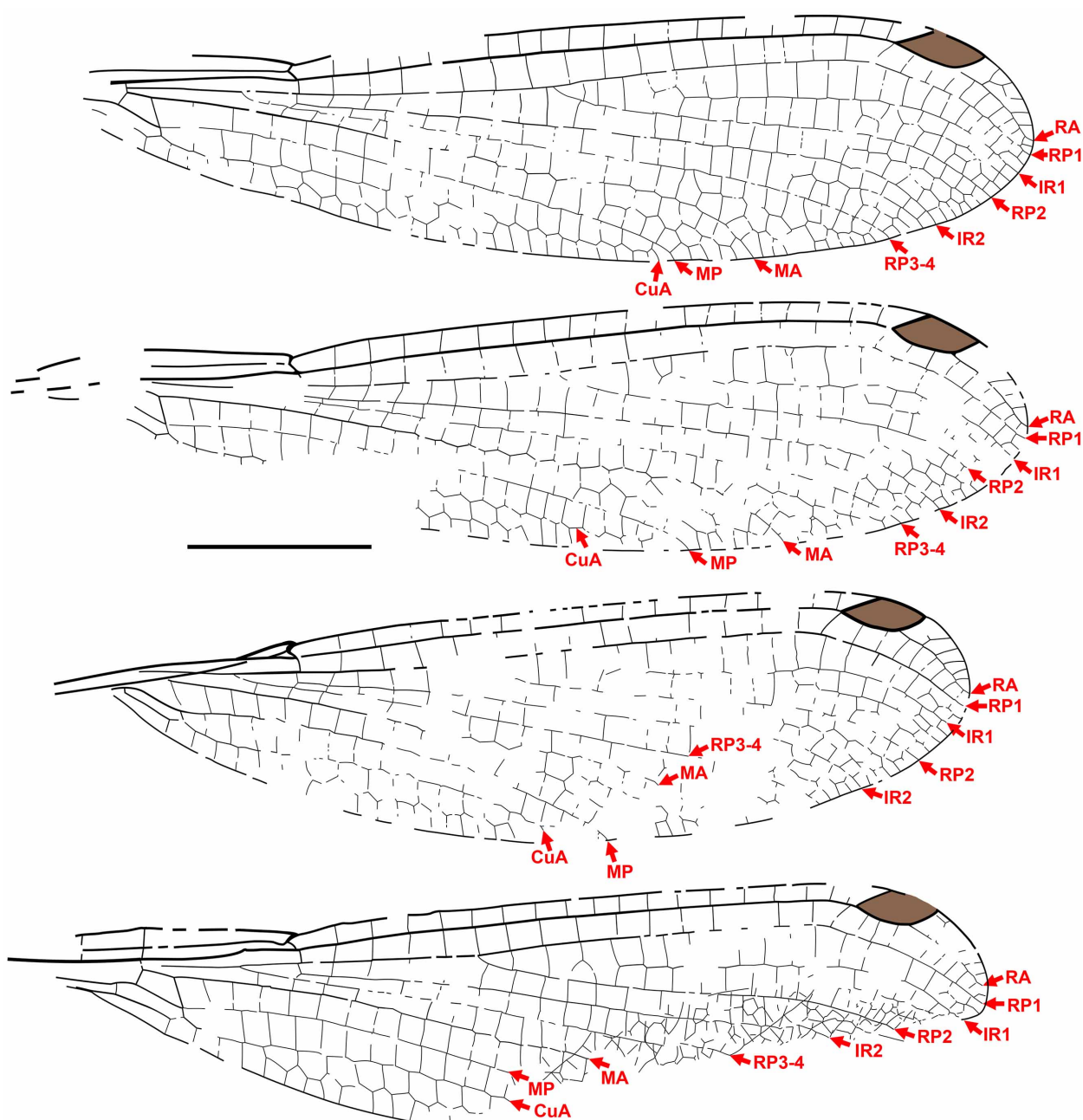


FIGURE 4. Wings of *Furagrion jutlandicus* proposed neotype MM-10752. The top two are hind wings and the bottom two are forewings. All to scale, 5 mm.

Remarks. Proposed neotype designation. Henriksen's (1922) holotype and only specimen then known (Fig. 1) is incomplete, consisting of two wings that are partially complete distal to the nodus, the mid-posterior fragment of a third, and an abdomen that is complete except for a portion of its base (MGUH 1819, Natural History Museum of Denmark, University of Copenhagen, Denmark). Lacking information from the diagnostically important antenodal region of the wings, he assigned the species to *Phenacolestes*, an extinct genus of the extinct suborder Cephalozygoptera known from the Eocene and possibly Miocene (see table 3 of Archibald *et al.* 2021) with similar venation in its preserved portions. Cockerell (1908) had assigned the genus to the Dysagrioninae, then a zygopteran subfamily of Agrionidae Leach (now Calopterygidae Sélys). Recognising the limitations of the incomplete type specimen, Nel & Paicheler (1994) considered the species '*Phenacolestes*' *jutlandica* as family indet. Rust (1999) expressed even less confidence in the generic assignment, treating the species as 'Dysagrioninae gen. indet. *jutlandica*', illustrating it (his fig. 4 and plate 1, fig. a) with the non-type specimen FUM-N 13856 (then ERK KL T1), an almost complete isolated wing and 14M-A2163 (his plate 1, fig. b).

Petrulevičius *et al.* (2008) assigned the species to their new, monotypic genus *Furagrion* based on ERK-KL-T1 (FUM-N 13856) (Fig. 2). Zessin (2011) subsequently described *Furagrion morsi* and *Morsagrion ansorgei*, erroneously citing FUM-N 13856 (as ERK-KL-T1) of Petrulevičius *et al.* as the holotype of *Furagrion jutlandicus*. Archibald *et al.* (2021) considered *Furagrion* a dysagrionid in the Cephalozygoptera.

We agree that FUM-N 13856 is conspecific with Henriksen's holotype by the extensive similarity of all preserved parts. Despite subsequently being treated as the specimen of reference, this fossil was not designated a neotype, however, and lacks the head, necessary for assessing family and suborder affinities (see below). Therefore, to bring clarity and nomenclatural stability to the *Furagrion* concept, we will be requesting in a forthcoming Case to the International Commission on Zoological Nomenclature that they designate as neotype of *Phenacolestes jutlandicus* specimen MM-10752, which is a well-preserved specimen in dorsal aspect, with all four wings and body almost complete, including the faint but distinct left compound eye (the right is indistinct), and parts of three legs (Figs. 3–4).

TABLE 3. Measurements in millimeters and ratios of these for wings not known to be fore- or hind wings. Abbreviations as in Table 1.

Specimen	Measurements (distances)						ratios				
	arc-apx	nod-apx	RP2-apx	arc-pt	nod-pt	w	arc-apx/w	nod-apx/w	RP2-apx/w	arc-pt/w	nod-pt/w
MM-2805	24.6	20.3	14.2	21.4	16.4	6.8	3.62	2.99	2.09	3.15	2.41
FUM-N 13856	24.9	20.9	15.4	21.4	17.2	6.8	3.66	3.07	2.26	3.15	2.53
FUM-N 11146	-	20.6	14.2	-	17.8	6.4	-	3.22	2.22	-	2.78
FUM-N 16192	-	18.9	13.9	-	15.4	6.6	-	2.86	2.11	-	2.33
FUM-N 11616	22.8	18.9	14.1	19.4	15.6	6.6	3.45	2.86	2.14	2.94	2.36
FUM-N 14704	26.5	21.3	14.1	21.8	16.9	6.6	4.02	3.23	2.14	3.30	2.56
MGUH 34113	23.4	19.6	12.7	20.2	16.3	5.9	3.97	3.32	2.15	3.42	2.76
MOA 770	25.5	21.0	13.8	22.1	17.8	6.3	4.05	3.33	2.19	3.50	2.83

*not included in PCA, lacking too many characters.

Family assignment and the dysagrionoid grade. The wings of MM-10752 and the FUM-N 13856 wing are consistent with all nine wing character states used in part for the Dysagrionidae diagnosis (Archibald *et al.* 2021), and Henriksen's MGUH 1819 possesses those character states for the characters that are observable. These are (see Fig. 5, shown on the *Dysagrion lakesii* Scudder wing):

- 1- crossvein O absent;
- 2- arculus at or closely proximad Ax2;
- 3- quadrangle broad, distal side longer than proximal, posterior side longer than anterior, distal-posterior angle oblique, proximal-anterior angle usually about 90°;

- 4- nodus at least a quarter wing length, usually more;
- 5- AA, AP branch before joining CuP, AA briefly free distad petiole;
- 6- RP3-4 originates *ca.* one to usually two thirds the length from arculus to subnodus;
- 7- antesubnodal space without crossveins (note: Nel & Jouault (2022) mistakenly read this as *antenodal space*);
- 8- CuA–A space expanded in middle, at least two cells wide;
- 9- CuA long, ends on posterior margin at mid-wing or further

These character states define the Dysagrionidae in combination with head character states of the suborder Cephalozygoptera (diagnosis of Archibald *et al.* 2021): width across eyes about twice the length from the anterior margin of antefrons to the posterior of the occiput; compound eyes more or less adpressed to head capsule, convex laterally but not hemispherical, their posterolateral corners extended posteriorly to varying degrees, sometimes even acutely; the distance between compound eyes at the level of the centre of the ocelli is about the width of one eye or less, *i.e.*, the head is not shortened and distinctly extended laterally with bulging, hemispherical compound eyes as in Zygoptera.

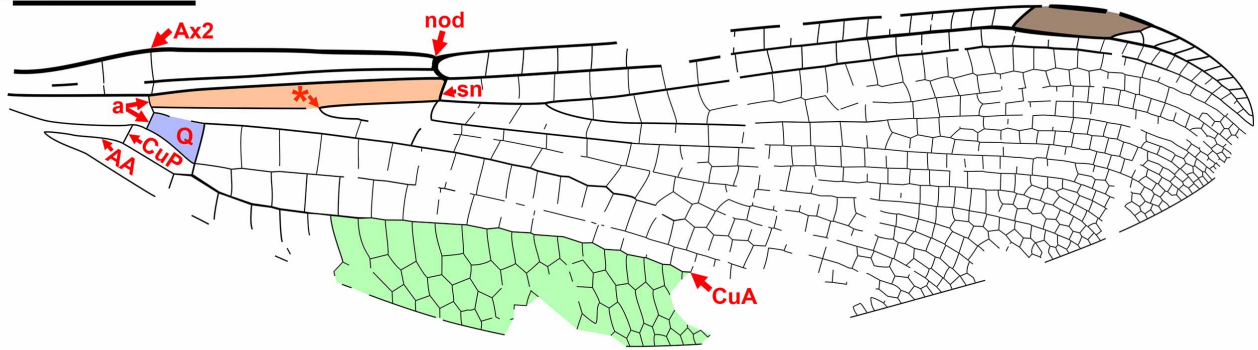
Archibald *et al.* missed that Rust (1999) had found that although the compound eyes are indistinctly preserved in *Furagrion* specimen 16-B3618, they are present and widely separated as in Zygoptera (“Von den großen Komplexaugen sind nur undeutliche Reste überliefert. Sie liegen, wie für Zygoteren charakteristisch, weit voneinander getrennt an den Außenseiten des Kopfes”, p. 19). He did not illustrate this specimen, and its whereabouts is not known to us.

We examined several specimens that conform to Rust’s observation and, therefore, treat the genus as a zygoteran. The compound eyes are clearly preserved in 14M-A2163 (Fig. 6) and are faintly but confidently preserved in the proposed neotype MM-10752 (Fig. 3). These have the typical zygoteran shape, hemispherical, widely set and bulging outward, and the head is short. The compound eyes are not preserved in MM-10750 (Figs. 7–8), but the remaining head capsule is short and wide as in Zygoptera. Such a loss of eyes in fossils may happen, especially in Zygoptera, as they protrude and are more fragile, apparently more easily degraded than the robust head capsule, or they might simply break away from the head in death. Such missing compound eyes can also be clearly seen in multiple specimens of *Lestes ceresti* Nel & Papazian from the Oligocene of Céreste, France, *cf.* the holotype MNHN. F.R07445 (Archibald & Cannings 2021 fig. 1B and 1C) and PNRL 2019 and PNRL 2021 (Nel & Jouault 2022, figs 11A and 12; the head of *L. ceresti* PNRL 2020 in their fig. 11B appears too poorly preserved to confidently evaluate) and see *Chalcolestes tibetensis* Xia *et al.* (Xia *et al.* 2022, figs. 3A and 4) and Nel & Zheng (2021 fig. 2B).

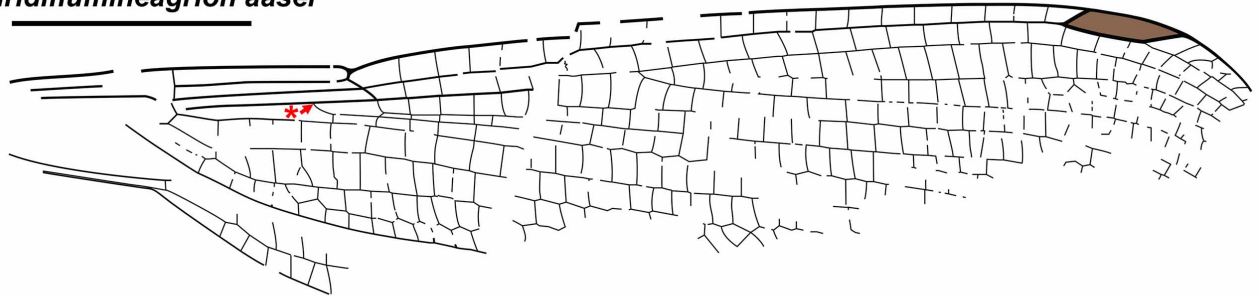
Some other Zygoptera possess wing venation with many of the nine diagnostic character states of Dysagrionidae. For example, the extant *Argia funcki* Sélys (Coenagrionidae, Coenagrionoidea) only differs by character state 6, and species of *Austroargiolestes* Kennedy (Argiolestidae Fraser, ‘Calopterygoidea’) by 5 and 6 (both Fig. 5). The wing of the Eocene *Viridiflumineagrion aasei* Nel (Fig. 5) differs by character state 6 (assigned to “Megapodagrionidae” *sensu lato*), which is highly polyphyletic, see Dijkstra *et al.* (2014), and so we treat it as family indet.). The extinct zygoteran *Oligolestes* Nel & Escuillé (family indet., see below) bears all character states but 1, 6, and 9 and *Eodysagrion* Rust *et al.* (Rust *et al.* 2008, Fig. 9) (provisionally in the Thaumtoneuridae: Huang *et al.* 2017) differs only by character state 3. *Miopodagrion* possesses a zygoteran head, but much of its overlapping and variably preserved wings are difficult to separate and interpret with confidence (Fig. 9). These wings can be established to possess character states 2, 3, 4, 8 and 9, but 1, 5, 6, and 7 appear uncertain or unknowable in its single fossil. We also consider it to be of unknown family. *Treintamilun* Petrulevičius (Frenguelliidae) (Fig. 5) shares all nine character states except character state 1 (absence of crossvein O), which cannot be assessed by preservation; however, Petrulevičius & Nel (2003) report this crossvein in the other described frenguelliid genus, *Frenguella* Petrulevičius & Nel. Frenguelliids bear a distinctive CuP, indicating that that family might not belong to either the Zygoptera or Cephalozygoptera, but could belong to an undescribed suborder (Petrulevičius & Nel 2003, Petrulevičius 2017). Combinations of dysagrionid wing character states are then found widely across even distantly related odonates.

Genera belonging to the Dysagrionidae *sensu* Archibald *et al.* (2021) or possibly so were previously assigned to a variety of extant zygoteran families by wing venation, highlighting the generalisation of these character states. These include the “calopterygoid” families Thaumtoneuridae, Pseudolestidae, Megapodagrionidae (as then defined), Amphipterygidae, and “Agrionidae” (= Calopterygidae) (*e.g.*, Scudder 1878, Campion 1913, Tillyard & Fraser 1939, Fraser 1957, Carpenter 1992, Nel & Paicheler 1994, Bechly 1996, Rust 1999, Nel *et al.* 2005a, 2005b; Nel & Arillo 2006, Rust *et al.* 2008, Garrouste & Nel 2015, Nel *et al.* 2016; Zheng *et al.* 2016a, 2016b, 2017, Huang *et al.* 2017).

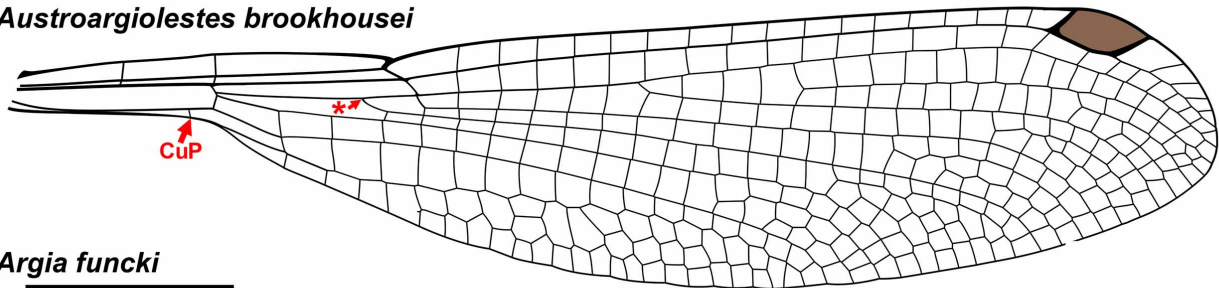
Dysagrion lakesii



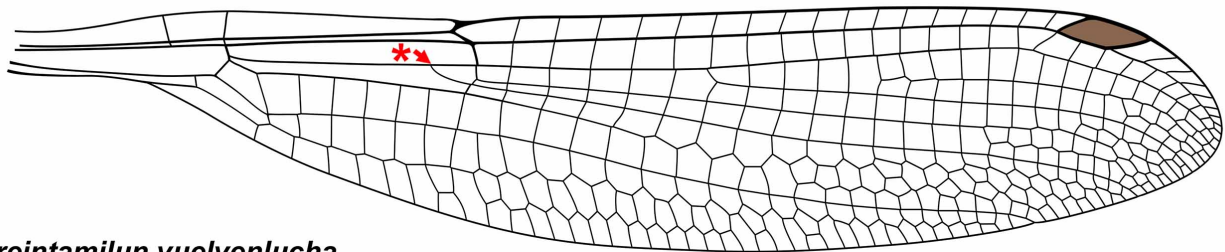
Viridiflumineagrion aasei



Austroargiolestes brookhousei



Argia funcki



Treintamilun vuelvenlucha

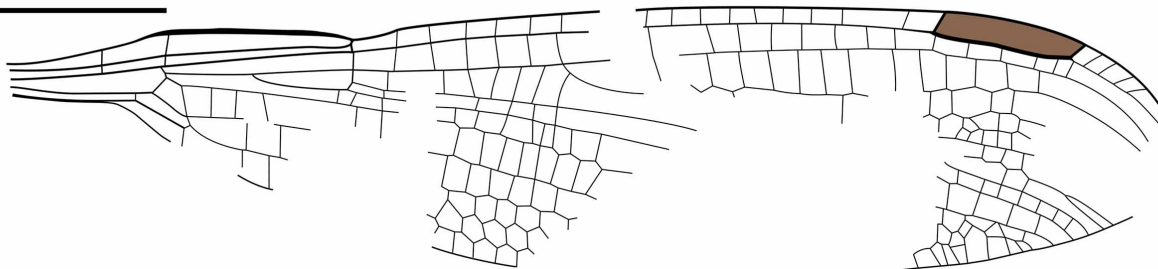


FIGURE 5. The wing of the Eocene *Dysagrion lakesii* showing the nine character states of Dysagrionidae (see text) and wings of other odonates bearing many of these. Orange indicates the antesubnodal space, blue the quadrangle, and green the CuA-A space. Asterisk indicates the origin of RP3-4. All scale bars 5 mm, *Argia funcki* (Selys) and *Austroargiolestes brookhousei* Theischinger & O'Farrell to same scale. *D. lakesii* redrawn from Scudder (1890), *Viridiflumineagrion aasei* from Nel (2022), *Austroargiolestes brookhousei* from Tann (2021), *Argia funcki* from Garrison *et al.* (2010), and *Treintamilun vuelvenlucha* redrawn from Petrulevičius (2017). Abbreviations as in Fig. 2 except: AA = anterior anal vein; CuP = posterior cubitus; * = origin of RP3-4.

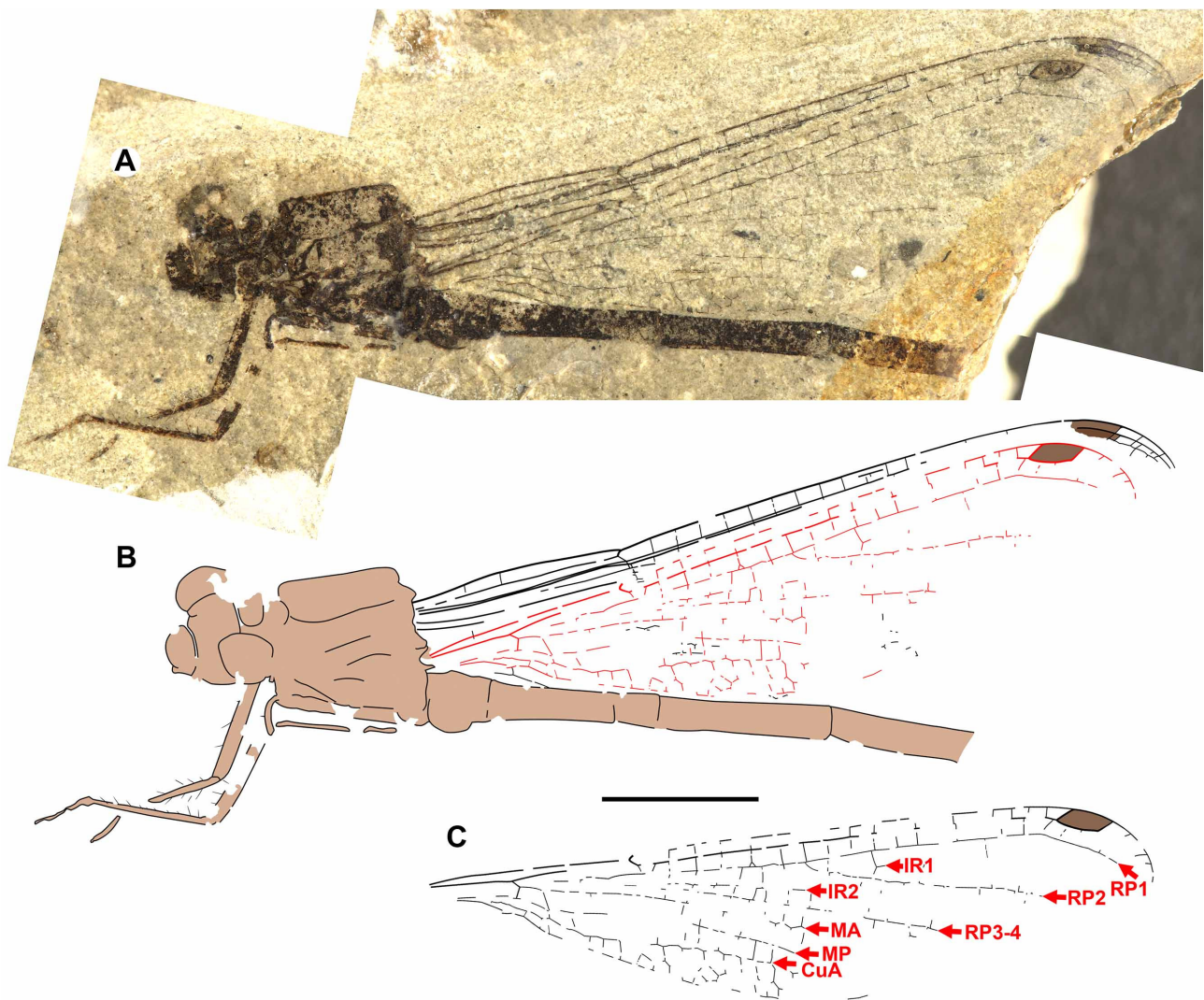


FIGURE 6. 14M-A2163: A, photograph; B, drawing; C. drawing of the hind wing (red in Fig. 6B). All to scale, 5 mm.

There is thus a “dysagrionoid grade” of wing venation found among Zygoptera and Cephalozygoptera, and following Petrulevičius & Nel (2003) and Petrulevičius (2017) on the status of Frenguelliidae, then even outside of these suborders. These dysagrionoid wing character states might be symplesiomorphies shared by common ancestors which date back at least to the early Jurassic (Kohli *et al.* 2021, Suvorov *et al.* 2022) with their stem taxa possessing wings that might look very much like those of *e.g.*, the Frenguelliidae Petrulevičius & Nel (or *Congqingia* Zhang?).

The family-level phylogeny of extant Zygoptera has undergone considerable development since the largely unresolved cladogram of Dijkstra *et al.* (2014) (see Bybee *et al.* 2021, Kohli *et al.* 2021, and Suvorov *et al.* 2022) and the superfamily Lestioidea Calvert appears to be well supported as sister group to the remaining extant Zygoptera. Within the latter, Platystictidae Kennedy are sister to the remaining non-lestoid Zygoptera (Bybee *et al.* 2021, Kohli *et al.* 2021, Suvorov *et al.* 2022). Neither Lestioidea nor Platystictidae include taxa that possess the dysagrionoid wing venation (*e.g.*, Garrison *et al.* 2010). The presence of dysagrionoid character states in zygopteran taxa might also represent homoplastic reversals as adaptations to similar selection pressures. A thorough study of the deep-time evolution of these wing characters based on basal zygopteran-cephalozygopteran phylogeny falls well outside the scope of this paper, but should be the focus of a future study.

The family and suborder designations of dysagrionoid grade taxa. The heads of *Dysagrion* Scudder, *Phenacolestes*, *Petrolestes* Cockerell, *Congqingia*, *Okanagrion* Archibald & Cannings, and *Okanopteryx* Archibald & Cannings, are known and consistent with the Dysagrionidae and Cephalozygoptera concepts (Archibald *et al.* 2021; Archibald & Cannings 2021) and so are confidently established in that family and suborder.

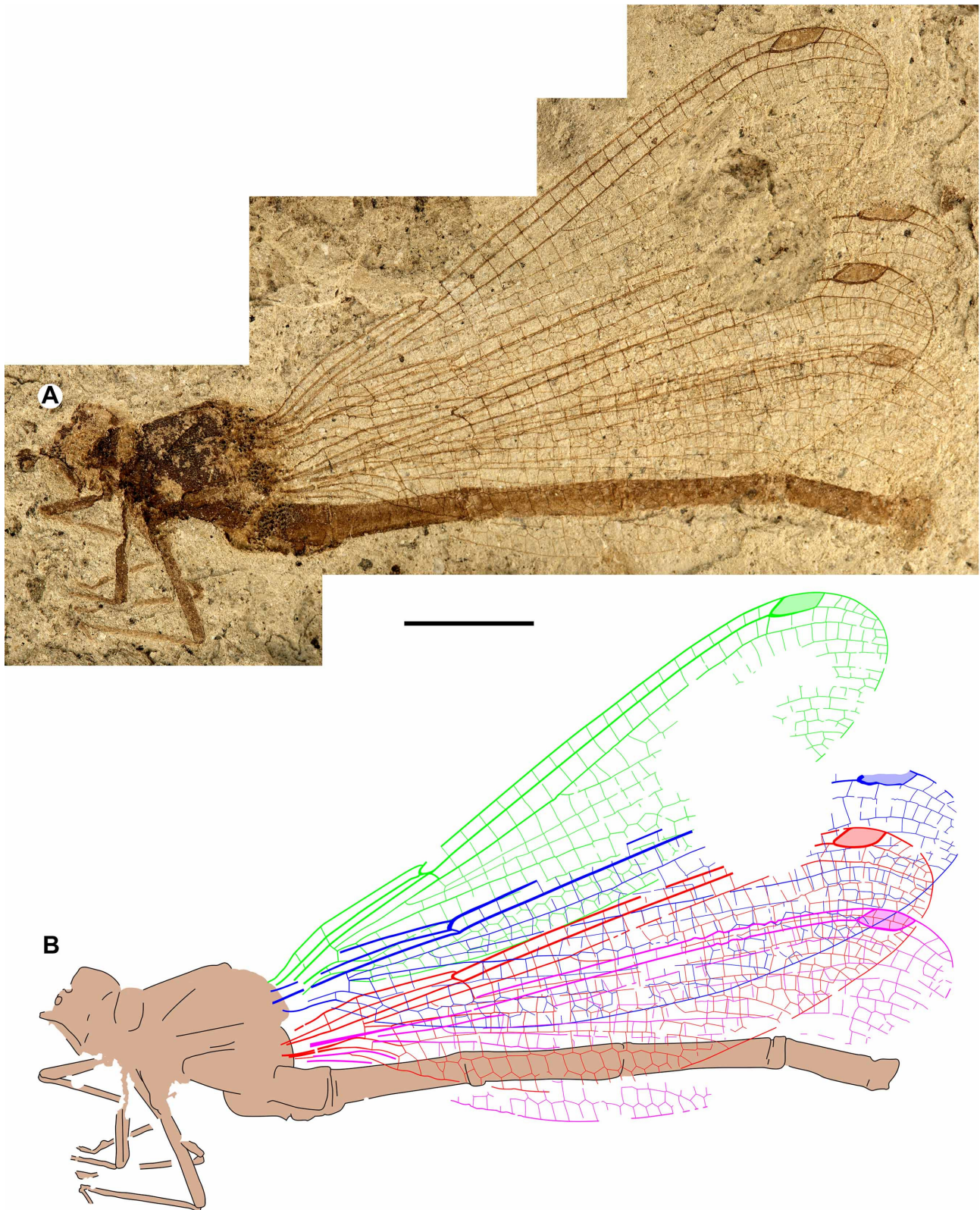


FIGURE 7. MM-10750: A, photograph; B, drawing, wing colours as in Fig. 8. Both to scale, 5 mm.

Archibald *et al.* (2021) further mention the presence of antenodal crossvein Ax0 as a potentially important character for identifying possible Cephalozygoptera fossils where the head is unknown. Although the wing base where Ax0 is found is often poorly preserved or absent in fossils, the vein is found in Dysagrionidae and Sieblosiidae where this region is well-preserved, and also found in the Whetwhetaksidae Archibald & Cannings, strengthening the notion that they are closely related (Archibald *et al.* 2021, Simonsen *et al.* 2022). Ax0 is absent or covered by

sclerotization in Zygoptera (Bechly 1996, Rehn 2003), except found in two Eocene species of Euphaeidae Jacobson & Bianchi (Archibald *et al.* 2012) and *Burmadysagrion zhangii* Zheng *et al.* (Zheng *et al.* 2016a). The wing base is well preserved in several of the fossils studied here (*e.g.*, Figs 2, 16-18, 21), and although we find sclerotization in the region (*e.g.*, Fig. 21), we do not find evidence for the presence of Ax0.

The family affinities of *Furagrion* and *Viridiflumineagrion* are unknown, as their dysagrionoid wing venation (poorly known in *Miopodagrion*) alone is insufficient to establish this, and other relevant characters are little known beyond aspects of their heads that establish them as zygopterans.

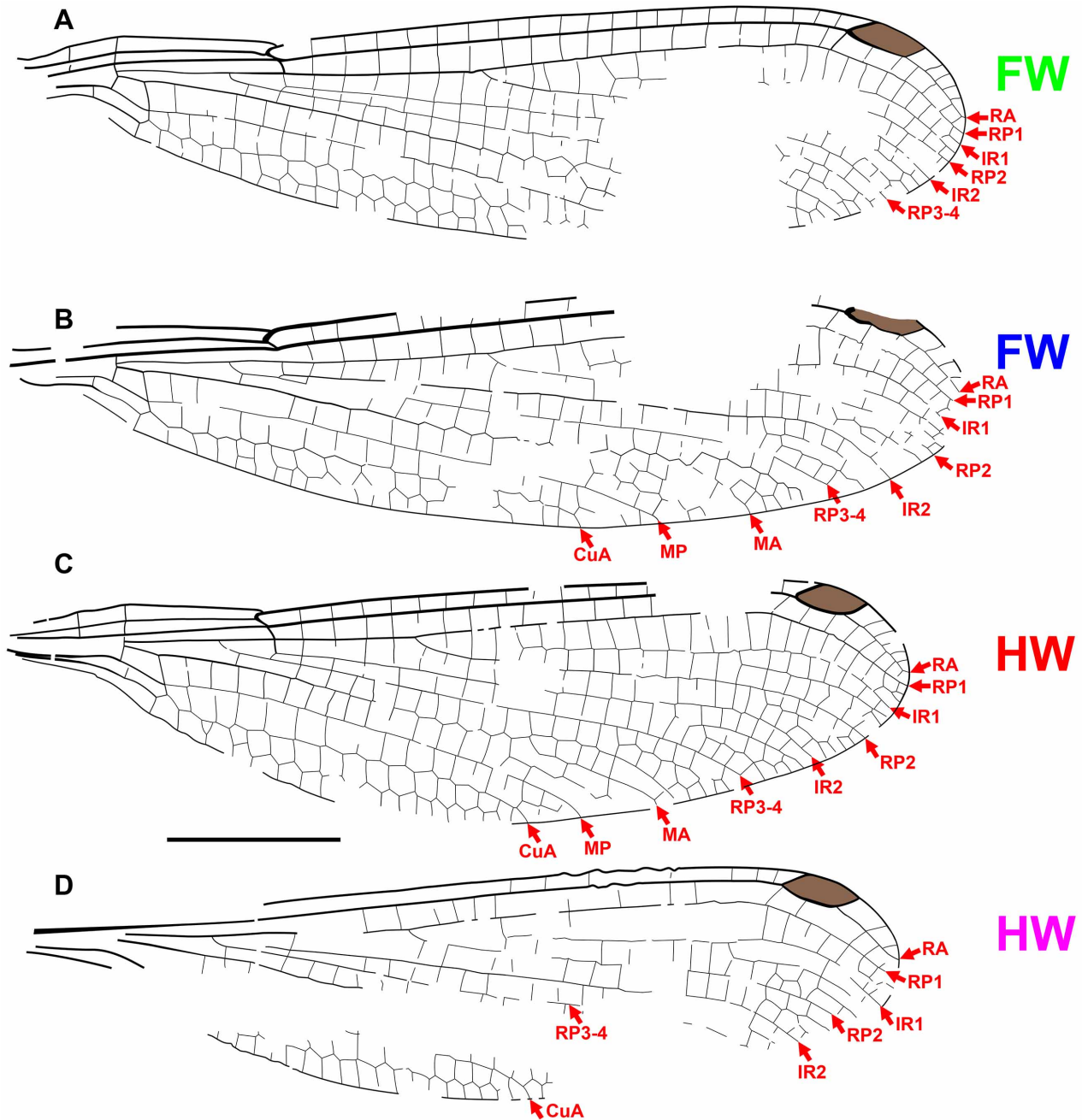


FIGURE 8. Wings of MM-10750, colour-coded forewings (FW) and hind wings (HW) to match colours in Fig. 7. All to scale, 5 mm.

The family affinity of *Oligolestes* Schmidt is also unknown (Nel *et al.* 2005a; Nel *et al.* 2020; Nel & Zheng 2021; Nel & Jouault 2022). These authors compared it to the Sieblosiidae Handlirsch, but excluded that family as its diagnosis (Nel *et al.* 2005a, p. 223) consists of a single character state that *Oligolestes* lacks: “highly specialised nodus apparently traversed by ScP, as the terminal kink of CP is shifted basally together with the nodal and subnodal veinlets and the nodal membrane sclerotisation is reduced”. Nel *et al.* (2005a, p. 223) concluded that “*Oligolestes*

could be closely related to the Sieblosiidae *sensu stricto*, but there is no proof supporting this hypothesis because all these characters are individually present in other damselfly lineages.” We agree with Nel & Jouault (2022) that *Oligolestes stoeffelensis* Nel *et al.* is a zygopteran by its distinctly zygopteran head and with all of the above authors that the genus cannot be assigned to a family given current knowledge. Further, the Cephalozygopteran head is clearly seen in the Sieblosiidae (see *Stenolestes* Scudder: *Stenolestes cf. fischeri* Nel MNHNF-B.47288 and less clearly in *Stenolestes falloti* (Théobald) holotype MNHN.F.B24507, Archibald & Cannings 2021, fig. 2a, b).



FIGURE 9. *Miopodagrion optimum* (Cockerell), Priabonian of Florissant Formation, Florissant, Colorado, United States of America. A, full fossil; B, closeup of basal portion of the wings showing difficulty in confidently discerning, *e.g.*, character states 5–7 of the dysagrionoid grade. Scale bars are 5 mm. Photo Talia Karim (University of Colorado, Boulder).

Odonates with dysagrionoid wings where the head is unknown are also then family and suborder indet., and at most might be considered *cf.* Cephalozygoptera, Dysagrionidae. These include *Primorilestes* Nel *et al.*; *Electrophenacolestes* Nel & Arillo; *Stenodiafanus* Archibald & Cannings; *Menatagrion* Nel & Jouault; *Allenbya* Archibald & Cannings; *Thanetophilosina* Nel *et al.*; *Valerea* Garrouste *et al.*; the unnamed Alaskan Chickaloon specimen of Garrouste & Nel (2019); specimen Me16572 of the Senckenberg Museum, Frankfurt, Germany, treated as Megapodagrionidae genus and species A by Petrulevičius *et al.* (2008) and as *cf.* Dysagrionidae gen and sp. A by Archibald *et al.* (2021); specimen NHMUK I.9866/I.9718 of Nel & Fleck (2014). The Whetwhetaksidae is *cf.* Cephalozygoptera with more confidence by the presence of Ax0 (see above).

Principle component analysis and variation within the genus. PCA results are shown in Fig. 10. The “ratios” plot (Fig. 10A) is based on the eight calculated ratios only, *i.e.*, is based on wing shape. Twelve specimens are included. Because ratios are the only characters used in this case, the plot was based on the variance-covariance matrix. The variables are shown here as straight, green vectors spreading from the centre of the plot. Greater length of a vector (*e.g.*, the RP2-apx/w ratio) shows more significant impact on the location of each specimen in the plot and the location of each specimen in relation the vectors show which ratios are most important in individual specimens. For example, FUM-N 14704 is in the lower right quadrant, indicating that the Arc-apx/RP2-apx and Arc-apx/w ratios are high (see also Table 4).

The “combined” plot (Fig. 10B) includes six size related data (measured distances of wing elements) and eight wing shape related data (ratios of these). The PCA calculations were based on the correlation coefficient matrix. Twelve measured wings were included, all with a full data set (Table 4). The variance is almost equally distributed along the two shown axes with 40 % of the variance between the points occurring along the horizontal PCA-1 axis, and 38 % along the vertical PCA-2 axis. The results show that:

- 1- In the “ratios” plot almost all of the total variation (91%) is explained by the PCA-1, horizontal axis, while 6% is explained by the PC-2, vertical axis. In the plot comprising both ratios and direct measurements the values are 41% and 36% respectively.
- 2- MOA 770, the type of *F. ansorgei*, is located to the far right in both plots, supporting its separation from *F. jutlandicus* by its relatively narrower wing.

- 3- The more slender MOA 770 wing is probably a forewing, assuming the same forewing/hind wing differences as in *F. jutlandicus*.
- 4- MGUH 34113 is located very close to MOA 770 in the “ratios” plot (Fig. 10A), but not in the “combined” plot (Fig. 10B), showing that while the shapes of the two wings are very similar, their sizes are not.
- 5- The far-right position of MGUH 34113 and MOA 770 in Fig. 10A results from higher values of the ratios arc-pt/w and nod-pt/w than in *F. jutlandicus* (Table 3).
- 6- The arc-apx/RP2-apx ratio (Table 4) is larger in MGUH 34113 and FUM-N 14704 than in the remaining *F. jutlandicus* specimens.
- 7- FUM-N 11616 and FUM-N 13856 plot closer to known *F. jutlandicus* hindwings than forewings when only ratios are considered (Fig. 10A) and are characterised by arc-apx/w and arc-apc/RP2-apx values similar to known hindwings of *F. jutlandicus*.
- 8- Known hind wings of *F. jutlandicus* are placed in the upper left of the “ratios” plot and far to the left in the “combined” plot by their generally smaller values than forewings of the ratios that are divided by width, *i.e.*, they are generally relatively wider than forewings.

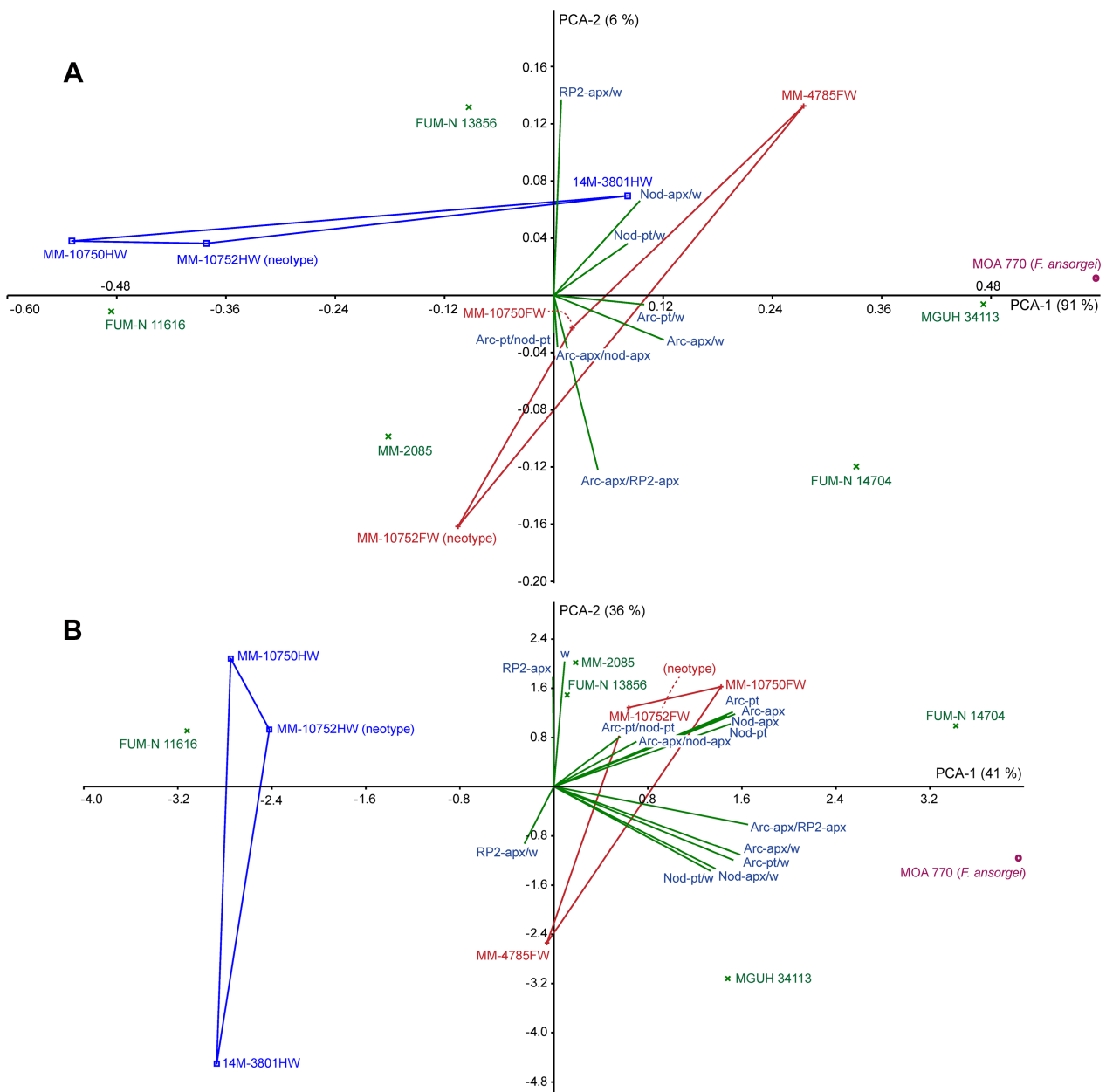


FIGURE 10. Principle component analysis of *Furagron* wings. *F. jutlandicus* forewings in red, hindwings in blue, those unknown as fore- or hind wings in green, and the *F. ansorgei* wing is in purple. A, based on ratios only; B, based on both measured distances and ratios. See Table 4 for input data.

TABLE 4. Measurements in millimeters and ratios of these used in principle component analysis. Colours correspond to those in Fig. 10: known forewings (FW) in red and hindwings (HW) in blue, those unknown as fore- or hind wings are in green, and the *F. ansorgei* wing is in purple. Abbreviations as in Table 1.

specimen	Measurements (distances)						ratios							
	arc- apx	nod- apx	RP2- apx	arc- pt	nod- pt	w	arc- apx/w	nod- apx/w	RP2- apx/w	arc- pt/w	nod- pt/w	arc- apx/ nod- apx	arc- apx/ RP2- apx	arc- pt/ nod- pt
MM-10752FW	24.6	19.9	13.7	21	17	6.7	3.67	2.97	2.04	3.13	2.54	1.24	1.80	1.24
MM-10750FW	25.4	21.1	14.6	21.8	17.2	6.8	3.74	3.10	2.15	3.21	2.53	1.20	1.74	1.27
MM-4785FW	23.4	19.8	13.6	19.6	15.8	6.0	3.90	3.30	2.27	3.27	2.63	1.18	1.72	1.24
14M-3801FW*	22.9	19.2	-	19.4	15.6	-	-	-	-	-	-	1.19	-	1.24
MGUH 1819FW*	-	20.8	13.5	-	15.6	6.4	-	3.25	2.11	-	2.44	-	-	-
MM-10752HW	23	19.4	14.3	20	15.7	6.6	3.48	2.94	2.17	3.03	2.38	1.19	1.61	1.27
MM-10750HW	23.7	19.7	15	20	16.2	6.9	3.43	2.86	2.17	2.90	2.35	1.20	1.58	1.23
MM-4785HW	21.6	-	13.6	18.4	-	6.1	3.54	-	2.23	3.02	-	-	1.59	-
14M-3801HW	20.7	17.2	12.2	17.8	14.3	5.5	3.76	3.13	2.22	3.24	2.60	1.20	1.70	1.24
MM-2085	24.6	20.3	14.2	21.4	16.4	6.8	3.62	2.99	2.09	3.15	2.41	1.21	1.73	1.30
FUM-N 13856	24.9	20.9	15.4	21.4	17.2	6.8	3.66	3.07	2.26	3.15	2.53	1.19	1.62	1.24
FUM-N 11146	-	20.6	14.2	-	17.8	6.4	-	3.22	2.22	-	2.78	-	-	-
FUM-N 16192	-	18.9	13.9	-	15.4	6.6	-	2.86	2.11	-	2.33	-	-	-
FUM-N 11616	22.8	18.9	14.1	19.4	15.6	6.6	3.45	2.86	2.14	2.94	2.36	1.21	1.62	1.24
FUM-N 14704	26.5	21.3	14.1	21.8	16.9	6.6	4.02	3.23	2.14	3.30	2.56	1.24	1.88	1.29
MGUH 34113	23.4	19.6	12.7	20.2	16.3	5.9	3.97	3.32	2.15	3.42	2.76	1.19	1.84	1.24
MOA 770	25.5	21	13.8	22.1	17.8	6.3	4.05	3.33	2.19	3.51	2.83	1.21	1.85	1.24

*not included in PCA, lacking too many characters.

***Furagrion jutlandicus* (Henriksen, 1922)**

Figs. 1–4, 6–8, 11–18.

Furagrion morsi Zessin, 2011, syn. nov.

Emended diagnosis. The wings of *Furagrion jutlandicus* may be distinguished from those of *Furagrion ansorgei* by shape: both fore- and hind wings have smaller length/width ratios in all measurements except RP2 to apex / width (Tables 2 and 3, and see PCA, above); and by the IR1-RP2 space becoming more than one cell wide at about level of basal end of pterostigma or slightly basal to that [*F. ansorgei*: distad distal end of pterostigma (tentative, see below)].

Emended description. As for genus description and diagnosis, species diagnosis, and see forewing, hind wing measurements and ratios of these for the proposed neotype and additional specimens in Tables 1 and 2.

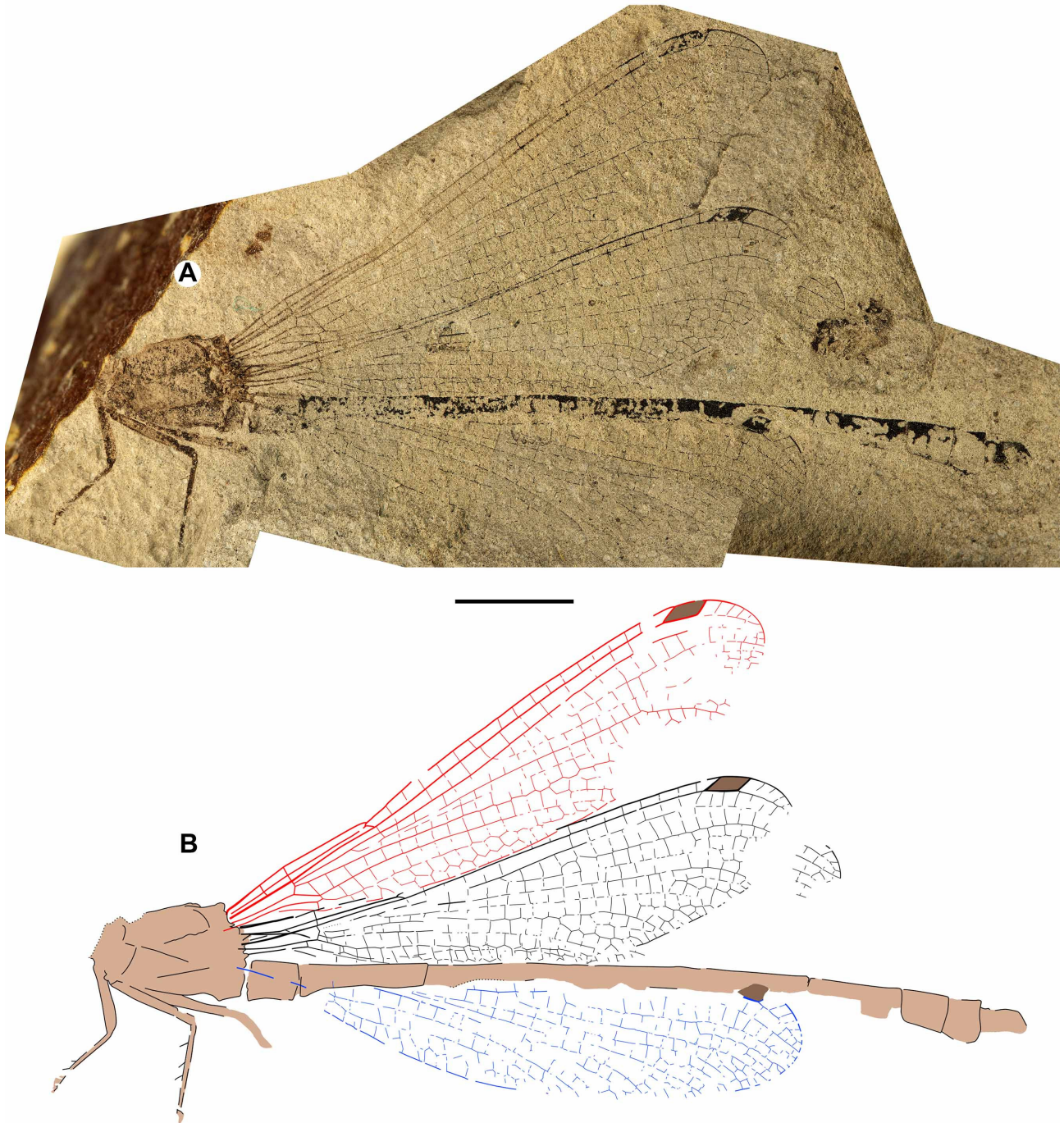


FIGURE 11. MM-4785A: A, photograph; B, drawing. Both to scale, 5 mm.

Type material. *Proposed neotype* MM-10752 (previously MHM-17-42) (Figs. 3–4): head mostly indistinct, with faintly preserved left compound eye, complete thorax and abdomen, all four wings, in soft diatomite, coll. Henrik Madsen at Skarrehege mo-clay pit, Mors, Knudeklint Member (informally the Skarrehege bed, 0.6–1.0 m below ash layer -13), Fur Formation in December 2009, in the Fossil and Mo-clay Museum, Museum Mors, Nykøbing Mors, Denmark.

Other material. MM-10750 (previously MHM-17-40) (Figs. 7–8): head missing the compound eyes, complete thorax and almost complete abdomen, most of all four wings, parts of five legs, in soft diatomite, coll. Henrik Madsen at Skarrehege mo-clay pit, Mors, Knudeklint Member (informally Skarrehege bed), Fur Formation, December 2009, in the Fossil and Mo-clay Museum.

MM-4785 (previously MHM-5242A) (Figs. 11–12): head missing, almost complete thorax and abdomen, one forewing with damaged posterior margin and two hind wings in varying states of incomplete preservation, in soft diatomite, coll. by unknown museum guest at the Ejerslev mo-clay pit, Mors, Knudeklint Member, Fur Formation, June 21, 2013, in the Fossil and Mo-clay Museum.

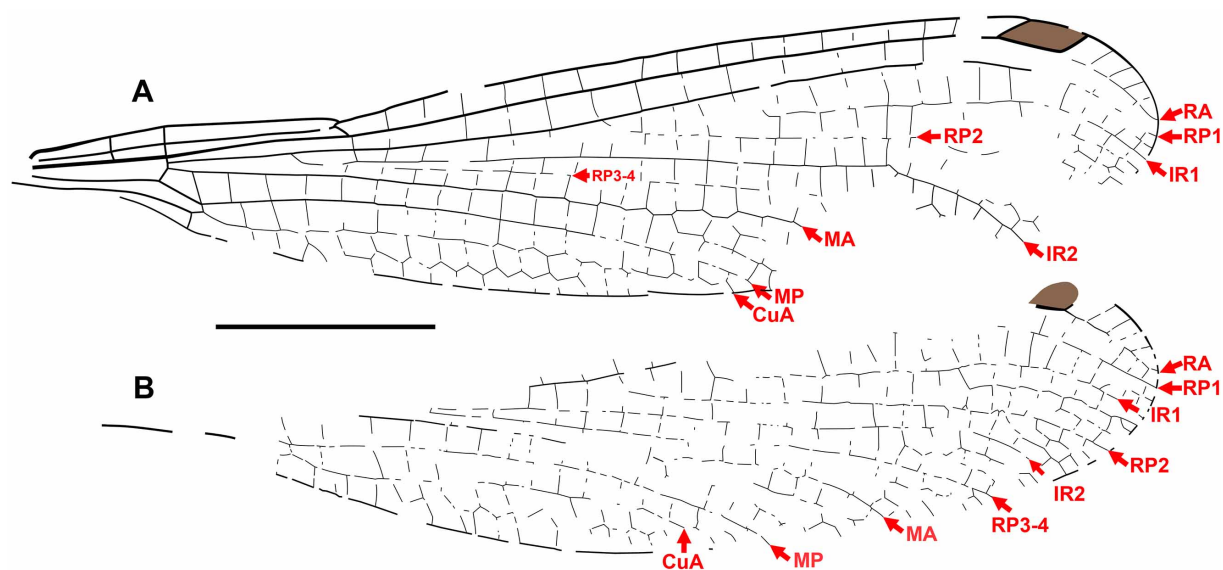


FIGURE 12. Wings of MM-4785A: A, top wing in Fig. 9 (red), a forewing; B, wing below (blue), a hind wing. Both to scale, 5 mm.

FUM-N 13856 (Fig. 2): an almost complete forewing missing a portion of the posterior at about a third length, in a concretion, coll. Erwin Rettig at Klitgaard Cliff, Mors, Fur Formation, date unknown, in the Fur Museum.

FUM-N 11146 (previously ERK GU E7) (Fig. 13): an almost complete forewing missing parts of the wing basad the nodus, coll. Erwin Rettig at Gullerup; Mors, Fur Formation, date unknown, in the Fur Museum.

FUM-N 16192 (Fig. 14): an almost complete hind wing missing parts basad about Ax2, in a concretion, coll. Jan and Elly Verkleij at the Ejerslev mo-clay pit, Mors, Knudeklint Member, Fur Formation, 2008, in the Fur Museum.

14M-2765 (Fig. 15): a partial thorax and basal fragment of abdomen with a [fore- or hind?] wing attached, the distal posterior portion of which is folded over the rest of the wing, coll. Henrik Madsen at the Ejerslev mo-clay pit, Mors, Knudeklint Member, Fur Formation, November 14, 1991, in the negative series, in the Fossil and Mo-clay Museum, Museum Mors.

FUM-N 11616 (Fig. 16): two very complete hind wings joined by a small fragment of thorax, in a concretion, coll. Jan and Elly Verkleij at Manhøj, new pit, Fur Formation, 2008, in the Fur Museum.

FUM-N 14704 (previously FM 1106) (Fig. 17): an almost complete forewing missing a small portion of the apex, coll. Erik Fjeldsø at Stolleklint Cliff, Silstrup Member, between ash layers +25 and +30, Fur Formation, date unknown, in the Fur Museum.

MM-2085 (previously MHM-i1583AB): (Fig. 18): an almost complete forewing in a concretion, coll. Henrik Madsen at Ejerslev mo-clay pit, Mors, Knudeklint Member, between ash layers +25 and +30, Fur Formation, 2005, in the Fossil and Mo-clay Museum, Museum Mors.

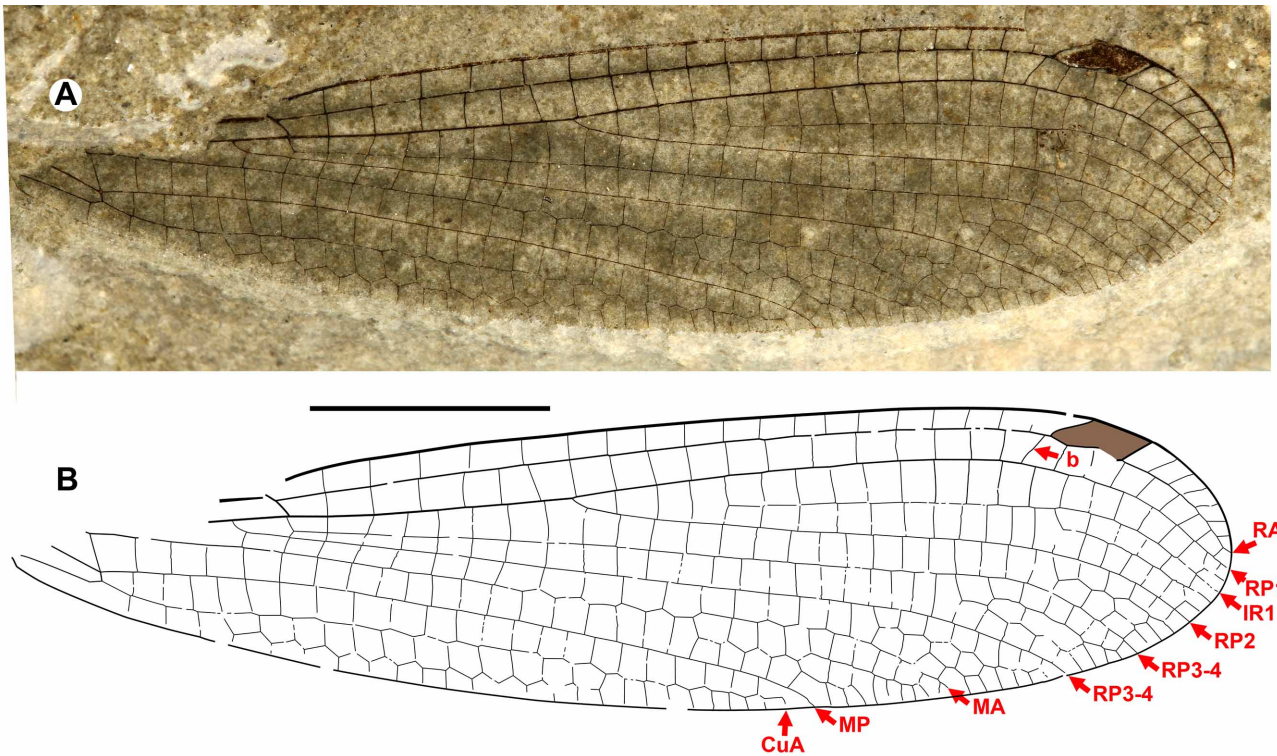


FIGURE 13. FUM-N 11146: A, photograph; B, drawing. Note infuscation (see text). Both to scale, 5 mm. A forewing.

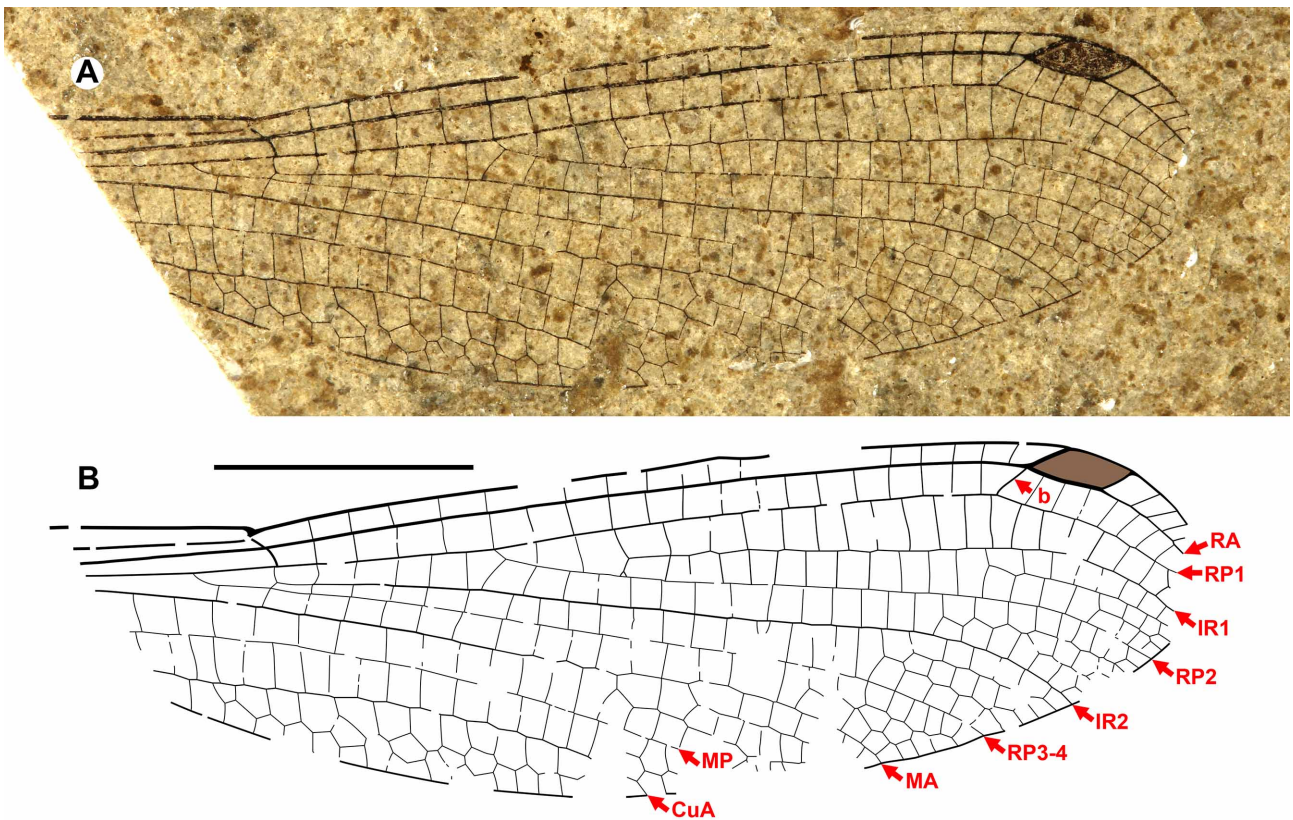


FIGURE 14. FUM-N 16192: A, photograph; B, drawing. Both to scale, 5 mm. A hind wing.

MGUH 1819 (Fig. 1): the distal portions of three wings and much of the abdomen, coll. and date unknown, Struer, loose slab from an unknown level within the Fur Formation, in the Geological Museum, University of Copenhagen, Denmark.

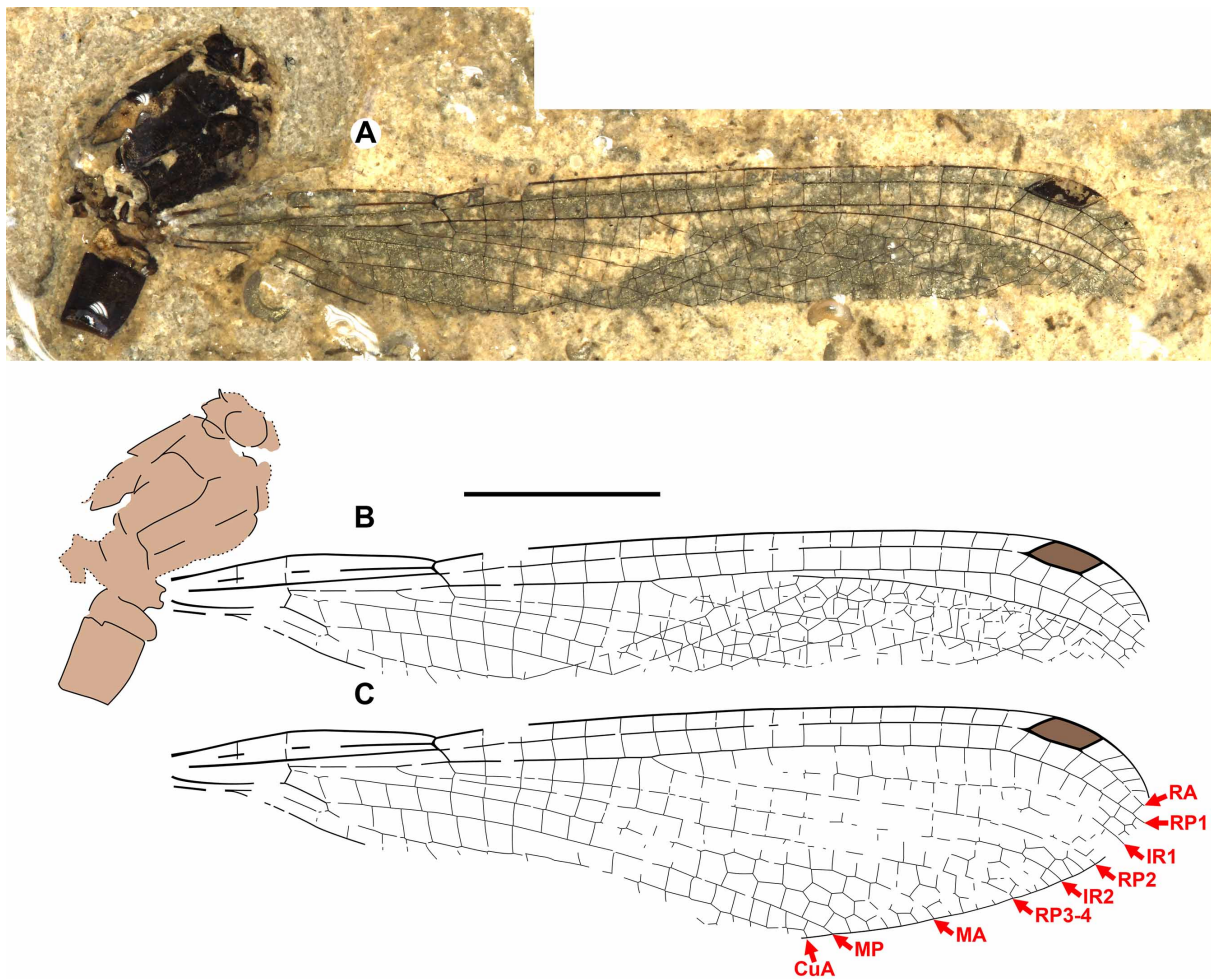


FIGURE 15. 14M-2765: A, photograph; B, drawing as preserved; C, the fore- or hind wing graphically unfolded. All to scale, 5 mm.

14M-A2163 (Fig. 6) (MM 14M-A2163 of Rust 1999, see his plate 1, fig. b): with a well-preserved head, including compound eyes, thorax, and most of the abdomen, the anterior of a forewing and much of a hind wing, parts of two legs, coll. Henrik Madsen at Ejerslev mo-clay pit, Mors, Knudeklint Member between ash layers -11 and -13, Fur Formation, August 21, 1993, in the Fossil and Mo-clay Museum. Although the distal IR1-RP2 region is missing and the maximum wing width is not known, the preserved portion of the hind wing is shaped like those of *F. jutlandicus*, clearly not as slender as the *F. ansorgei* wing.

14M-3801 (Fig. 19): missing the head, thorax, and abdomen mostly complete, one forewing and one hind partly preserved, parts of three legs, in a concretion, coll. Henrik Madsen at the Ejerslev mo-clay pit, Mors, Knudeklint Member between ash layers -13 and -14, Fur Formation, October 2, 1992, in the Fossil and Mo-clay Museum, Museum Mors. Although the distal IR1-RP2 region is missing, its wing shape is not as slender as the *F. ansorgei* wing.

MOA 769/1, 2 (part, counterpart), “*Furagrion morsī*” is known by the basal portion of a wing (Fig. 20). We could not locate the fossil and based our discussion on the description, photograph and drawing of Zessin (2011). We find its putative differences with *F. jutlandicus* and *F. ansorgei* to be within their intraspecific variations (Fig. 20B–D). The shape of its preserved portion is like *F. jutlandicus* not as slender as the *F. ansorgei* wing, and so we treat “*Furagrion morsī*” as a junior synonym of *F. jutlandicus*.

MM-11044 (Fig. 21): basal portion of a wing in a concretion, coll. Henrik Madsen, 2018, Ejerslev mo-clay pit, Mors, Knudeklint Member, between ash layers +25 - +30, Fur Formation, in the Fossil and Mo-clay Museum, Museum Mors. Incomplete and lacking the IR1-RP2 space. Although the distal portion of the wing is missing, we tentatively assign this fossil to *F. jutlandicus*, as its preserved portion appears not as slender as an equivalent portion of the *F. ansorgei* wing.

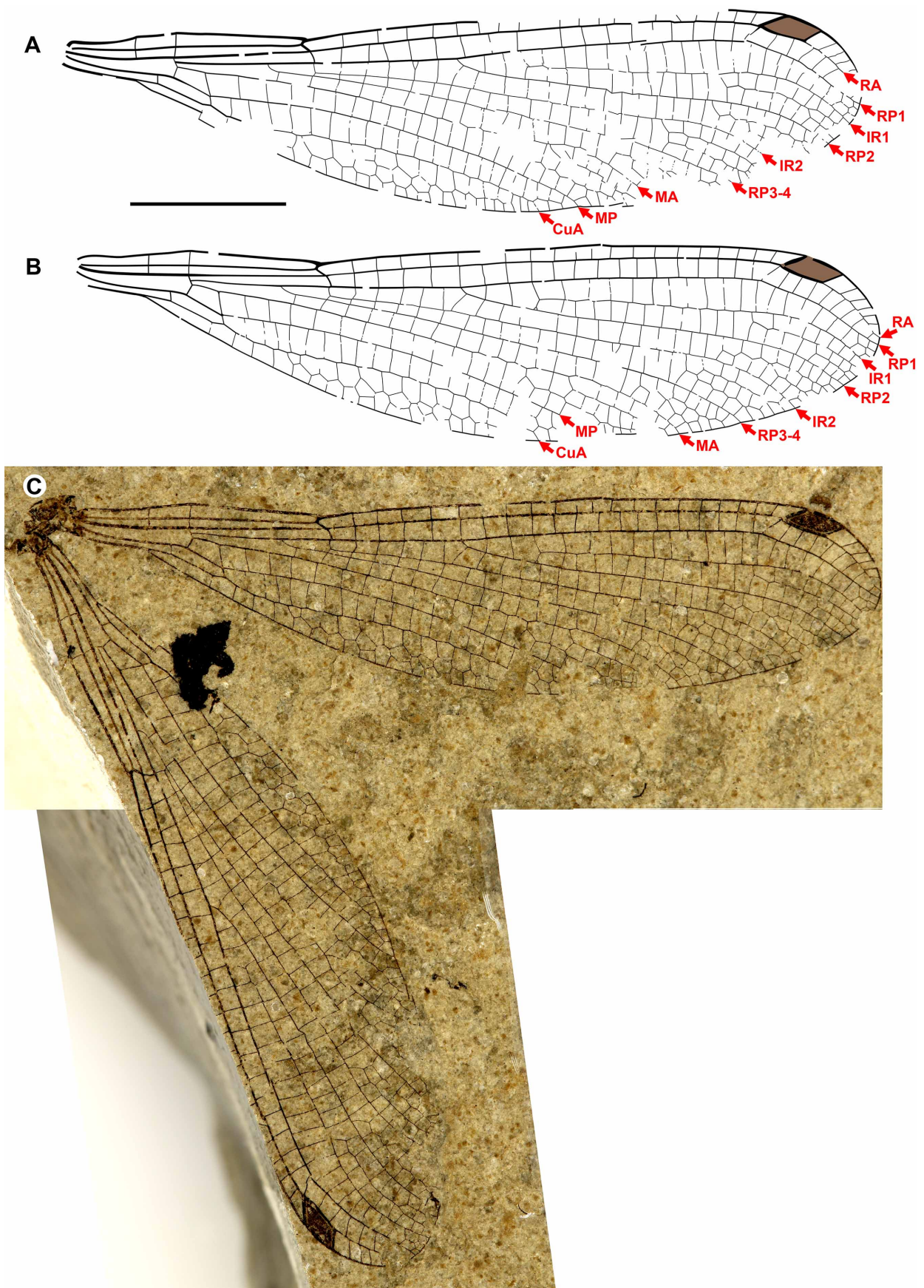


FIGURE 16. FUM-N 11696: A, drawing of bottom wing in 17C; B, drawing to top wing in 17C; C, photograph. All to scale, 5 mm.

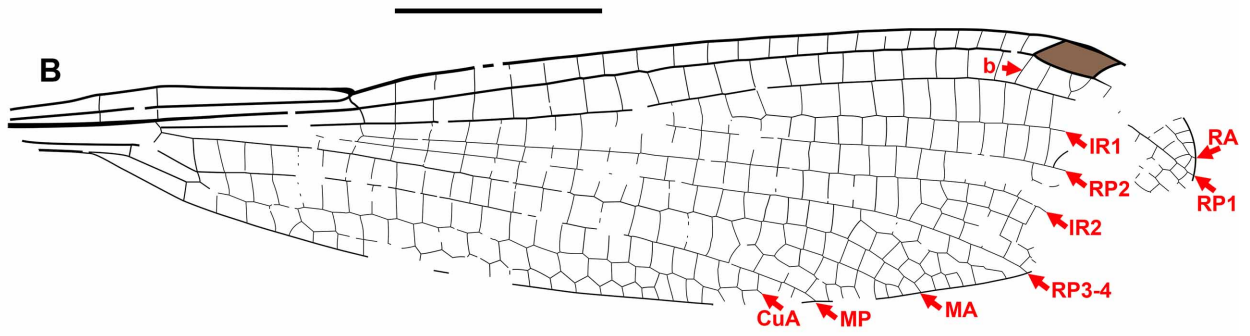
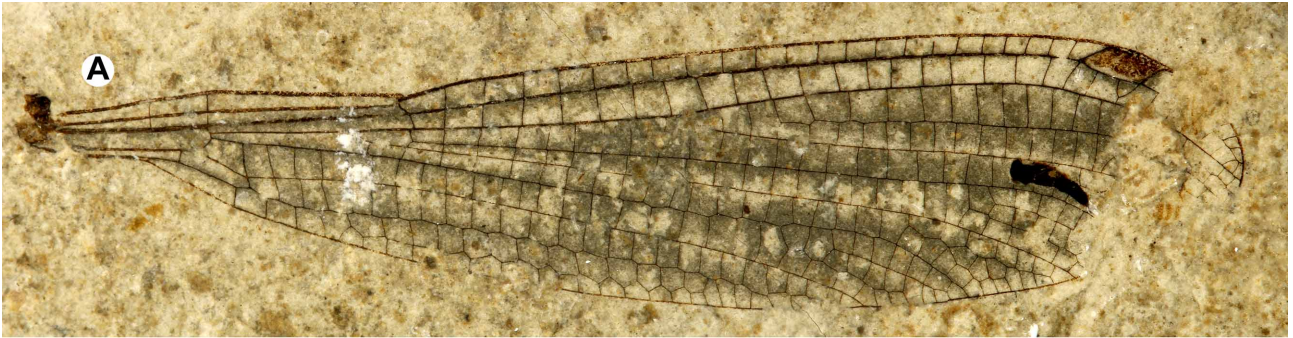


FIGURE 17. FUM-N 14704: A, photograph; B, drawing. A forewing. Both to scale, 5 mm.

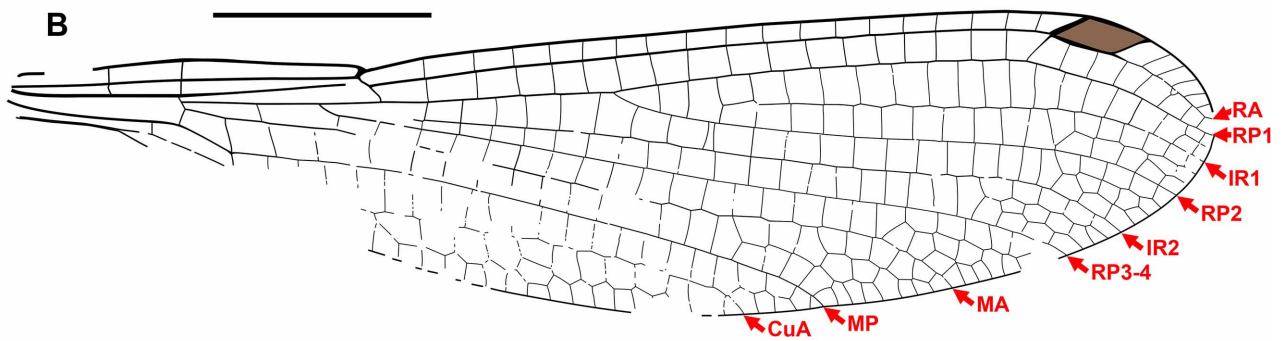
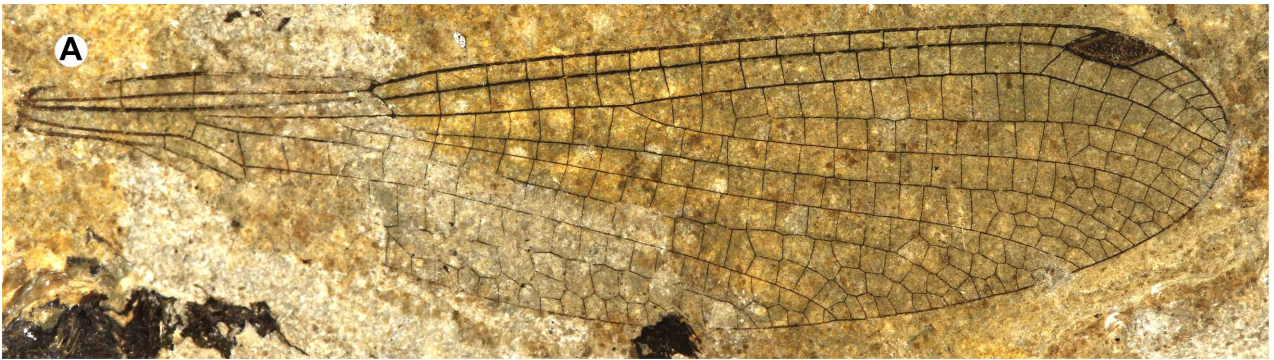


FIGURE 18. MM-2085: A, photograph; B, drawing. A forewing. Both to scale, 5 mm.

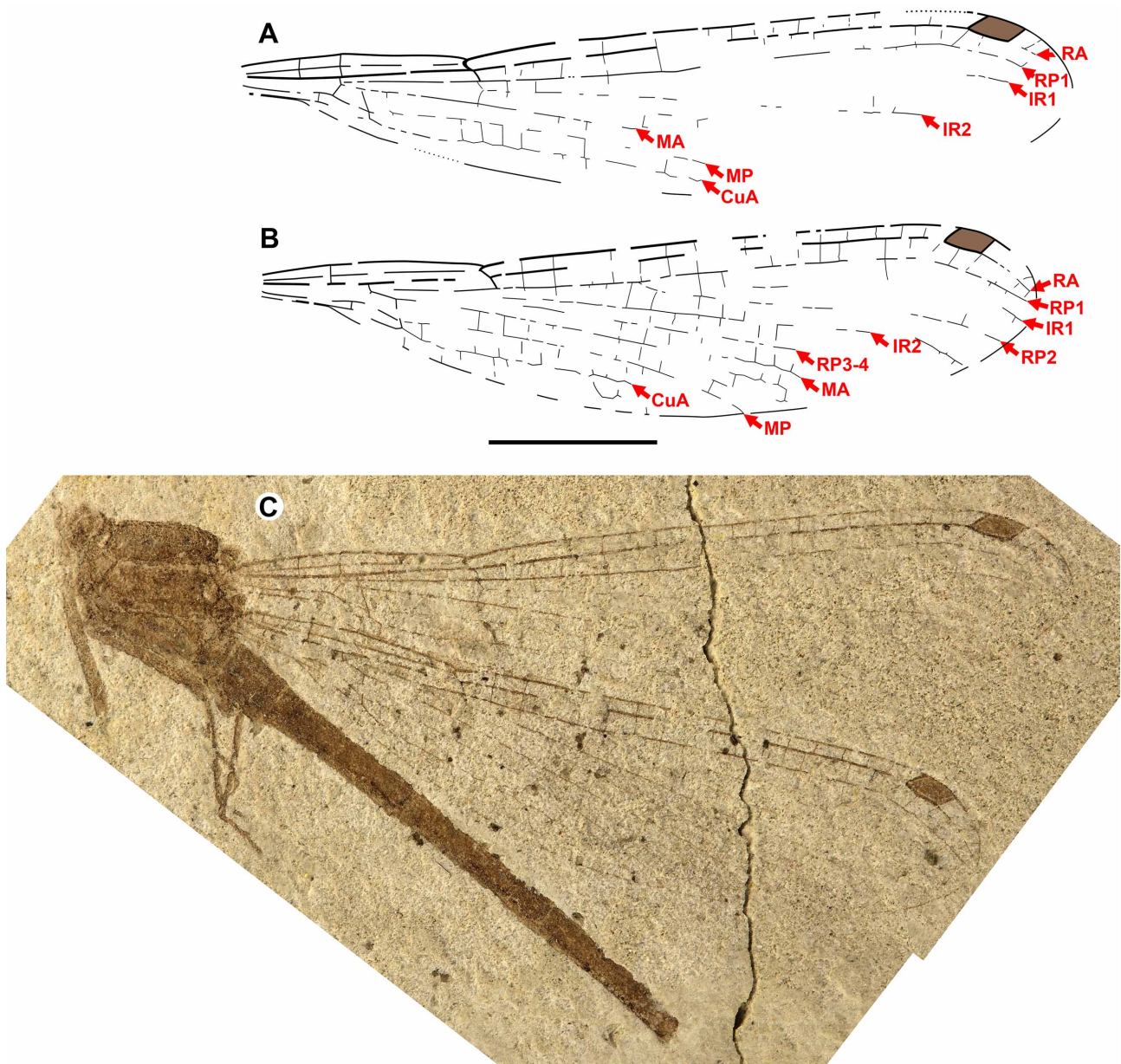


FIGURE 19. 14M-3801: A; drawing of forewing; B, drawing of the hind wing; C, photograph, complete. All to scale, 5 mm.

Remarks. The proposed neotype MM-10752 was figured by Pedersen *et al.* (2012, fig. 46D) who characterised it as a damselfly (translated from Danish: *vandnymfe*) from the level just below ash layer -13 in the Skarrebage mo-clay pit, Mors. The specimen was not named or described in further detail.

Range and age. Earliest Ypresian Fur Formation, Jutland, Denmark. The proposed neotype is from the Skarrebage mo-clay pit (N 56°56.65–, E 8°52.41–) between 61 and 100 cm below ash layer -13, informally named the Skarrebage bed of the Knudeklint Member, Fur Formation. All specimens: as for genus, above.

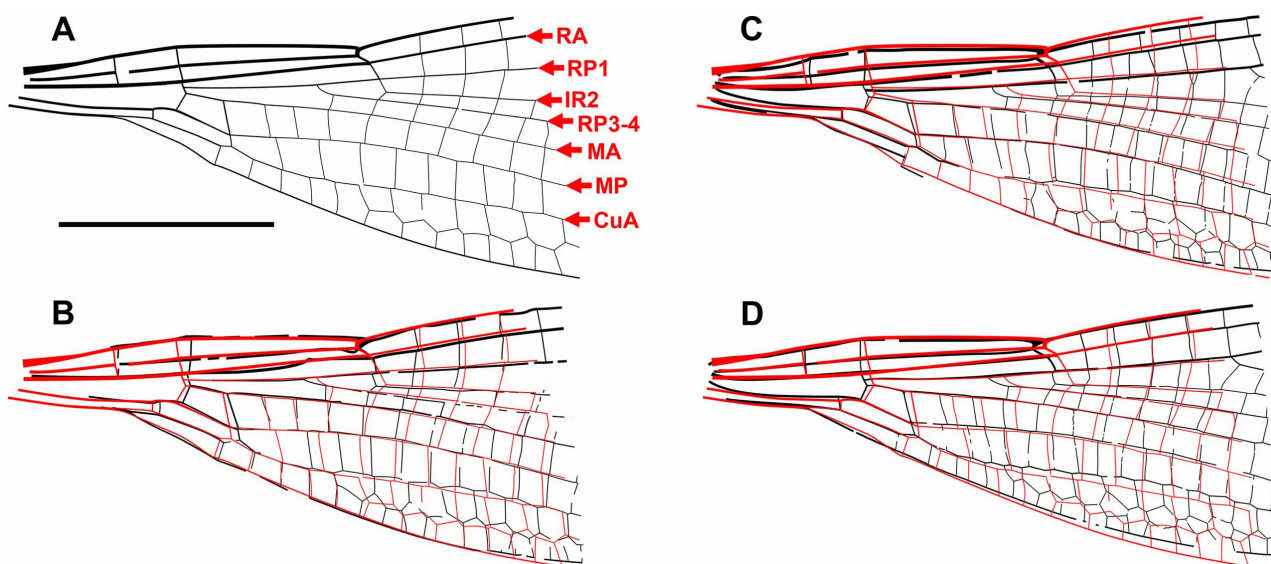


FIGURE 20. A, “*Furagrion morsi*” MOA 769 redrawn from part and counterpart photographs (Zessin 2011 Figs. 6 and 7); B–D, *F. morsi* (red) superimposed on *F. jutlandicus* wings: B, MHM 1742; C, D, FUM-N 11616. All to scale, 5 mm.

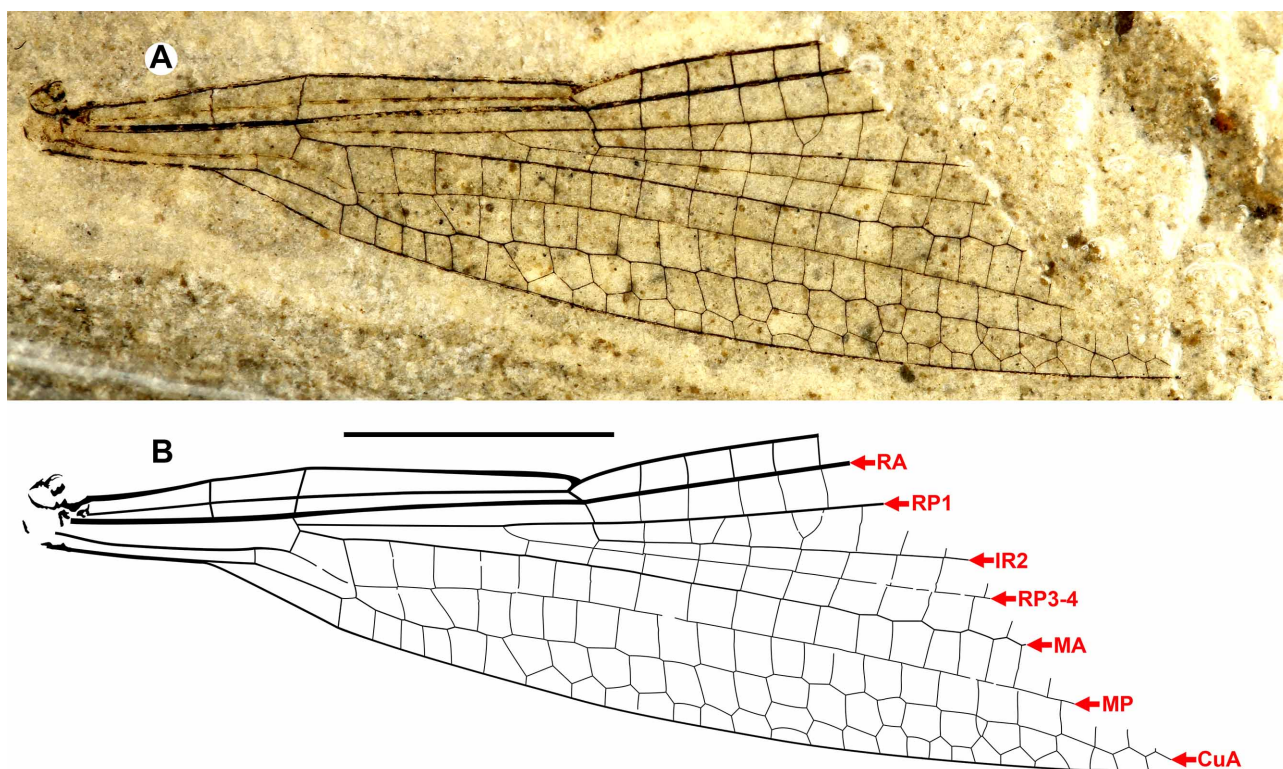


FIGURE 21. MM-11044: A, photograph; B, drawing. A fore- or hind wing. Both to scale, 5 mm.

Discussion

Forewing/hind wing differences. In known forewings and hind wings, the ratio of wing length relative to width is greater in forewings, allowing identification of most disarticulated wings as either (Tables 2 and 3, and see Fig. 23B, 23C, and PCA, above).

Is wing colouration informative? The membrane of wings assigned to *F. jutlandicus* range from hyaline (e.g., FUM-N 13856, the proposed neotype, and FUM-N 16192, Figs. 2, 3, and 14) to dark infusate (e.g., FUM-N 11146, FUM-N 14704, 14M-2765, Figs. 12, 17, and 15). This could suggest more than one species, sexual dimorphism,

or polymorphism within a single species. However, it might also be an artefact of preservation resulting from the action of the particular geochemistry of these beds during diagenesis. The latter possibility is indicated by the part of MGUH 34113 (Fig 22A), which is preserved with little or no infuscation, while its counterpart (Fig 22B) shows distinct infuscation. Therefore, at least some and perhaps all wings that we associate with the genus were infusate in life.

Does width of the CuA-A space distinguish species? This space is more than two cells wide at its widest in FUM-N 11616, FUM-N 16192, 14M-A2163, MM-11044 and MM-2085, while in all others it is no more than two cells wide. This is not a forewing/hind wing difference, as wings that are clearly fore- and hind wings do not differ in this way.

The width of the CuA-A space is a distinctive trait separating the dysagrionid *Okanopteryx fraseri* Archibald & Cannings, where the CuA-A space is two cells wide (rarely a single column of three) from *O. jeppesenorum* Archibald & Cannings where this space is always four cells wide, and *O. macabeensis* Archibald & Cannings, where this is always three cells wide. This is supported as informative in distinguishing *O. fraseri* and *O. macabeensis*, as they are also separated by body shape and size (Archibald *et al.* 2021, fig. 55). Further, all six specimens of *O. fraseri* are from the McAbee locality (British Columbia, Canada) while all six *O. jeppesenorum* specimens are from Republic (Washington, USA), some 300 kilometers to the southeast. These localities are, however, within perhaps a million years of each other (Rubino *et al.* 2021) and with similar climates and forests (Greenwood *et al.* 2005). The CuA-A space of *O. fraseri* is three cells wide and in *O. jeppesenorum* four cells wide for an extended space, whereas in the *Furagrion* specimens listed above, it is briefly three cells wide. Therefore, while there is strong support that this is diagnostic in the Okanagan Highlands species, in *Furagrion* we consider this indistinguishable from possible intraspecific variation given current knowledge.

***Furagrion ansorgei* (Zessin, 2011) comb. nov.**

Figs. 22–23

Emended diagnosis. The wing of *Furagrion ansorgei* may be distinguished from those of *F. jutlandicus* as in its diagnosis, above.

Emended description. Holotype: see genus description and its distinctive character states in the diagnosis of *F. jutlandicus*.

Type material. Holotype (Fig. 23) MOA 770/1, 2: likely a forewing by its slender shape (Fig. 23B), coll. Jörg Ansorge, northern coast of Mors, Skærbæk, Fur Formation, in a calcareous concretion, in the Natural History Museum, Natural Research Society Mecklenburg, Natureum at Ludwigslust Castle (part) and Natural History Museum of Denmark, Copenhagen, Denmark (counterpart). We were not able to examine the fossil as the part and counterpart could not be located at the institutions listed. Our discussion is based on Zessin's (2011) description and illustrations, and a higher resolution copy of his figure 3 provided by Jörg Ansorge.

Other material. MGUH 34113 (Fig. 22) tentatively belongs to the species: a complete forewing in a concretion, coll. Thomas Klode on Fur Island, Knudeklint Member, possibly between ash layers -11 and -13, Fur Formation, 1968, in the Natural History Museum of Denmark, University of Copenhagen.

Range and age. Earliest Ypresian Fur Formation, Jutland, Denmark. Range: see type and other material, above.

Remarks. With the ability to examine a larger sample of *Furagrion* specimens than was available to Zessin (2011), we find that the character states of *Morsagrion* that he proposed would separate it from *Furagrion* do not do so. These are:

- 1- The RA-RP1 space is two cells wide from about the middle of the level of the pterostigma.
 - We find this difficult to discern from his fig. 3 photograph and we are not confident that this is established.
- 2- The form of the pterostigma.
 - We find that it does not significantly differ.
- 3- The relationship between Zessin's "premedial cell" ("prmc") and the cells below it in the MA-MP space. The premedial cell is the space between RP to slightly past the base of RP3-4 and MA without crossveins from the arculus to the first crossvein between RP-3-4 and MA. He excludes the quadrangle and counts four cells in the MA-MP space subtending this in *Morsagrion* and two cells in this space in *Furagrion*.

- By our count, this is about three and a half cells long in *M. ansorgei*, and in the larger sample of *Furagrion* available to us, two (e.g., FUM-N 13856, Fig. 2) to four (FUM-N 14704, Fig. 17) cells long and, therefore, consider this to be within intraspecific variation.
- 4- The number of cells in the precubital field (MP-CuA space) to the level of the origin of RP3-4 (three in *Morsagrion* n. gen., four at *Furagrion*).
- Like Zessin, we count three in *M. ansorgei*, but with our larger sample we find between two (hind wings of MM-10752) to five (FUM-N 11146) in *Furagrion*. We, therefore, also consider this to be intraspecific variation.
- 5- Eight cells between the beginning of IR2 and RP2 in *Morsagrion* and five in *Furagrion*. This varies from eight cells in Henriksen's type MGUH 1819 to five in FUM-N 13856, with fewer in hind wings, e.g., MM-10750 with 7.5 and 6.5 cells in the forewings and 4.5 in the hind wing.
- In all of these except MGUH 34113, which we tentatively associate with MOA 770, the IR1-RP2 space is more than one cells wide distad about the level of the pterostigma base (see below).
- 6- The shape of the discoidal and subdiscoidal cell.
- We find that this does not greatly differ.
- 7- The length of the double rows of cells in the IR1-RP2 space.
- This space is more than one cell wide for only about three cells from ending on the wing margin, whereas in *F. jutlandicus*, this space is more than one cell wide to about the level of or slightly more basal of the basal end of the pterostigma. This occurs in all *Furagrion* specimens that we examined except possibly MGUH 34113 (below) and does appear distinctive.

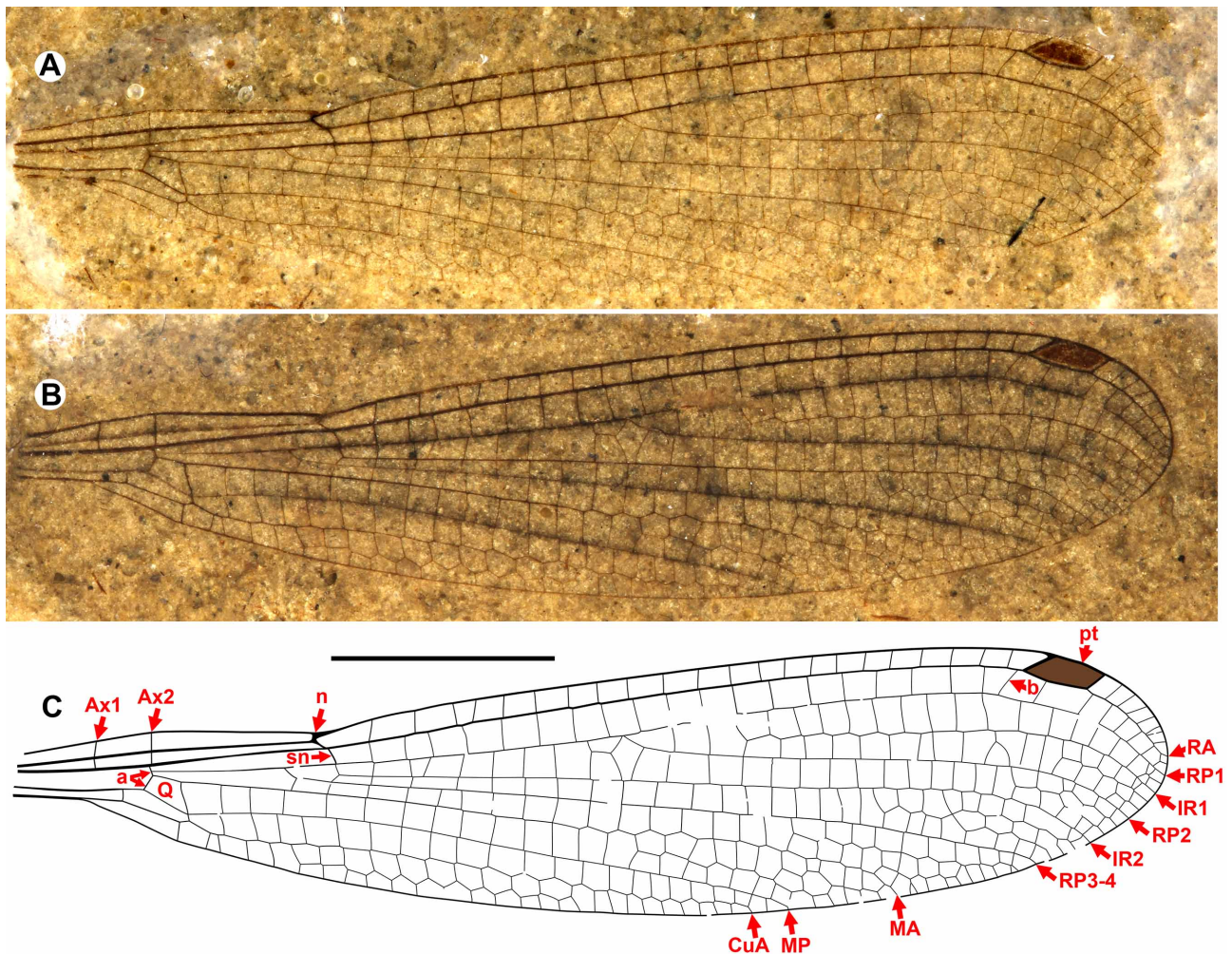


FIGURE 22. MGUH 34113, a forewing: A, photograph of the part; B, photograph of the counterpart; C, drawing from both A and B. Note infuscation very light on the part as preserved, darker on the counterpart (see text). All to scale, 5 mm.

We, therefore, find that MOA 770/1 and MGUH 34113 do not differ enough from the fossils assigned here to *F. jutlandicus* to justify placing them in a separate genus, and so treat *Morsagrion* as a junior synonym of *Furagrion*.

Character state 7 of MOA 770 does appear distinctive among the *Furagrion* specimens examined (but see MGUH 34113, below), supporting its status as a separate species. However, while it is shown in Zessin's drawing (his figs. 1 and 4), this region appears unclear in his photograph (his fig. 3) and in a slightly higher resolution version of it provided by J. Ansoerge (see our drawing made from this, Fig. 23). We consider this character state as tentative until the type specimen can be examined.

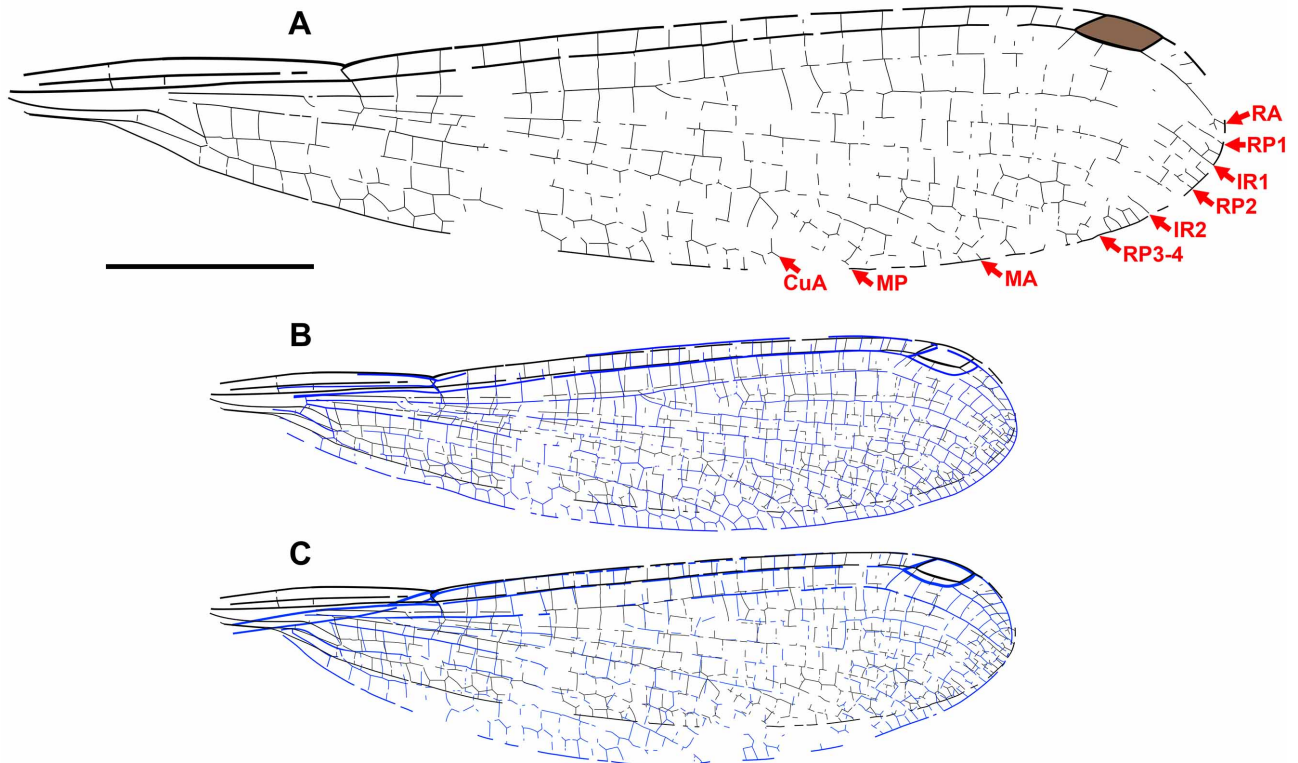


FIGURE 23. A, *Furagrion ansorgei* MOA 770 redrawn from a higher resolution copy of Zessin's (2011) figure 3 photograph provided by J. Ansoerge; shape compared with that of the proposed neotype (blue) B, forewing; C, hind wing. A to scale, 5 mm; B, C wings to no scales, the sizes of proposed neotype wings are adjusted to match arculus to apex and anterior wing margin of MOA 770 to compare shape.

The shape of wing MOA 770 provides stronger support for recognizing it as a separate species (Fig. 23B, 23C). It has a greater length / width ratio than all *Furagrion* wings, fore- or hind, by all length measurements except RP2 to apex / width (Tables 2 and 3 and see PCA, above).

By these reasons, we treat MOA 770 as *Furagrion ansorgei* (Zessin) **comb. nov.**

MGUH 34113 (Fig. 22) might be conspecific with MOA 770: Its IR1-RP2 space becomes more than one cell wide closer to the level of the distal end of pterostigma than basal, suggesting an association with *F. ansorgei* MOA 770. This is, however, not as distinct as in Zessin's drawing of the MOA 770 wing. More importantly, this wing is relatively narrow like MOA 770. Furthermore, it is smaller (see PCA and Tables 3 and 4), although this might represent intraspecific variation or sexual dimorphism. Given this uncertainty, we tentatively treat this specimen as *F. ansorgei*.

Possible *Furagrion*

FUM-N 17242 (Fig. 24): poorly preserved partial head, thorax, part of the abdomen and four legs, indistinct basal parts of all wings, coll. Jan and Elly Verkleij, 2010, Skarrehege, Mors, diatomite, near ash layer -13, in the Fur Museum. Resembles, but might not be *Furagrion*.



FIGURE 24. FUM-N 17242: A, photograph, B, drawing. A fore- or hind wing. Both to scale, 5 mm. Diagonal bands in the lower left and upper right are plant material.

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