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The Cephalozygoptera, a new, extinct suborder of Odonata with new taxa from the early Eocene Okanagan Highlands, western North America

S. BRUCE ARCHIBALD[1,2,3*], ROBERT A. CANNINGS[3,5], ROBERT J. ERICKSON[4,6], SETH M. BYBEE[4,7] & ROLF W. MATHEWES[1,8]

[1]*Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada.*
[2]*Museum of Comparative Zoology, 26 Oxford Street, Cambridge, Massachusetts, 02138, United States of America.*
[3]*Royal British Columbia Museum, 675 Belleville Street, Victoria, British Columbia, V8W 9W2, Canada.*
[4]*Biology Department & Monte L. Bean Museum, Brigham Young University, Provo, Utah 84606, United States of America.*
[5] *RCannings@royalbcmuseum.bc.ca; https://orcid.org/0000-0001-9491-8186*
[6] *1990platypus@gmail.com; https://orcid.org/0000-0003-1162-0355*
[7] *seth.bybee@gmail.com; https://orcid.org/0000-0001-6224-6303*
[8] *r_mathewes@sfu.ca; https://orcid.org/0000-0001-7637-199X*
[*]*Corresponding author.* *sba48@sfu.ca; https://orcid.org/0000-0002-4397-2497*

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Abstract

We describe the Cephalozygoptera, a new, extinct suborder of Odonata, composed of the families Dysagrionidae and Sieblosiidae, previously assigned to the Zygoptera, and possibly the Whetwhetaksidae n. fam. The Cephalozygoptera is close to the Zygoptera, but differs most notably by distinctive head morphology. It includes 59 to 64 species in at least 19 genera and one genus-level parataxon. One species is known from the Early Cretaceous (*Congqingia rhora* Zhang), possibly three from the Paleocene, and the rest from the early Eocene through late Miocene. We describe new taxa from the Ypresian Okanagan Highlands of British Columbia, Canada and Washington, United States of America: 16 new species of Dysagrionidae of the existing genus *Dysagrion* (*D. pruettae*); the new genera *Okanagrion* (*O. threadgillae*, *O. hobani*, *O. beardi*, *O. lochmum*, *O. angustum*, *O. dorrellae*, *O. liquetoalatum*, *O. worleyae,* all new species); *Okanopteryx* (*O. jeppesenorum*, *O. fraseri*, *O. macabeensis,* all new species); *Stenodiafanus* (*S. westersidei,* new species); the new genus-level parataxon *Dysagrionites* (*D. delinei* new species, *D.* sp. A, *D.* sp. B, both new); and one new genus and species of the new family Whetwhetaksidae (*Whetwhetaksa millerae*).

Key words: Ypresian, Republic, McAbee, Driftwood Canyon, Sieblosiidae, Zygoptera

Introduction

Odonata is a mid-sized order of about 6000 extant species, almost equally divided between dragonflies, suborder Anisoptera, and damselflies, suborder Zygoptera. The Asian genus *Epiophlebia* Calvert constitutes a third extant suborder, Anisozygoptera, the "damsel-dragonflies".

Adults are day-flying visual predators, capturing arthropod prey on the wing or sometimes on the substrate. All odonates are agile fliers, as their wings can be controlled separately, giving them great maneuverability. Their larvae are aquatic, inhabiting ponds, lakes, marshes, peatlands, flowing water, and other wetlands, although some live in wet leaf litter, water-filled treeholes and other microhabitats. They are major aquatic predators, feeding on small invertebrates and vertebrates.

Dragonflies tend to be more robust, mostly larger and stronger fliers than the usually smaller, gracile damselflies. The forewings of dragonflies narrow proximally, while their hind wings are expanded and differ from the forewings in the proximal region. Damselfly fore- and hind wings, however, are similar in shape and venation, and are usually petiolate. The heads of damselflies are distinctively "hammerhead" or "dumbbell" shaped, shortened front to back and transversely extended, bearing spherical compound eyes that bulge outward laterally. Dragonfly heads are more compact, normally semispherical to almost spherical, with the compound eyes closer together, usually meeting dorsally. Adult damselflies usually stay near the water that they occupied as larvae, whereas dragonflies may range far from it, especially during the prereproductive period. In fact, some species migrate long distances in groups, even between continents (Hobson *et al*. 2012).

As their name suggests, the damsel-dragonflies exhibit a combination of dragonfly and damselfly traits (review of *Epiophlebia*: Carle 2012). Their fore- and hind wings have similar shapes and venation to those of damselflies, but their heads and abdomens are more robust and dragonfly-like. While *Epiophlebia* is recovered as separate from the monophyletic suborders Zygoptera and Anisoptera in phylogenetic analyses of extant odonates, Anisoptera are nested within a paraphyletic Anisozygoptera when fossil taxa are included (Nel *et al*. 1993; Fleck *et al*. 2003; Bybee *et al.* 2008). By this, and the unsettled status of fossil taxa that have been historically considered members of Anisozygoptera, to avoid confusion we follow Dijkstra *et al*. (2013) in treating the Anisozygoptera as including Epiophlebiidae (*Epiophlebia*), and Bechly & Poinar (2013) in considering the mid-Cretaceous (earliest Cenomanian) Burmaphlebiidae from Burmese amber (*Burmophlebia* Bechly & Poinar) as closely related to it and so also included.

The Odonata is part of a related group of orders often called the Odonatoptera, but also referred to by other names, with varying compositions and relationships recognised by different authors (*e.g*., Grimaldi & Engel 2005; Bechly 1996; Bechly *et al*. 2001; Rasnitsyn & Pritykina 2002). The oldest Odonatoptera are from the late Carboniferous of Argentina (*e.g*., Petrulevičius & Gutiérrez 2016). The giant dragonfly-like insects of the Carboniferous and Permian, well-known to the public, belong to the odonatopteran order Meganisoptera (extensively treated by Nel *et al*. 2009). Most of these groups did not survive into the Mesozoic.

In the Mesozoic, crown Odonata appear in the Late Triassic Madygen Formation of Kyrgyzstan (see discussion in references cited by Kohli *et al*. 2016). Anisoptera first appear in the Early Jurassic (*e.g*., see the Henrotayiidae: Fleck *et al*. 2003). The oldest published Zygoptera are from the Late Jurassic or Early Cretaceous of Siberia, Russia (Kohli *et al*. 2016); however, unpublished fossils have been recovered as old as the Late Jurassic limestone of the Painten Formation (uppermost Kimmeridgian, 153 Ma) and Solnhofen Formation (150 Ma), both of Germany (Bechly, unpublished data reported by Kohli *et al*. 2016). Odonata are well represented to the mid-Cretaceous, *e.g*., see Bechly 1996; knowledge of them in mid-Cretaceous Burmese amber has recently been rapidly expanding (summary: Zheng & Jarzembowski 2020). They are less well known known in the Late Cretaceous (Rasnitsyn & Pritykina 2002), which is depauperate in insect compression fossil localities.

Anisoptera and Zygoptera fossils are plentiful in the Cenozoic, damselflies especially in the Oligocene and Miocene (Nel & Paicheler 1992, 1994). There is no Cenozoic fossil record of the Anisozygoptera (the larva *Gasophlebia taianensis* Lin from the Paleogene of China described by Lin (1982) as an anisozygopteran was considered by Nel *et al*. (1993) more likely a zygopteran). *Pseudostenolestes bechlyi Garrouste* & Nel from the Lutetian of Messel, Germany was assigned to the Anisozygoptera+Anisoptera stem group Isophlebioptera (Garrouste & Nel 2015) and the Eocene Frenguelliidae of Argentina (four species of three genera: Petrulevičius & Nel 2003, 2007, 2013; Petrulevičius 2017, 2019) was considered (stem) Anisozygoptera+Anisoptera, suborder indet. The Oligocene and Miocene Sieblosiidae, with numerous species from Eurasia, have been discussed by various authors (references in discussion below) as odonates belonging to either the Zygoptera or in an undetermined position outside of it. The

Dysagrionidae are generally considered to be damselflies, but there has been speculation that they might not belong to the suborder (*e.g*., Cockerell 1927; Zhang 1992; Garrouste & Nel 2015, see below).

Paleogene Odonata are known from localities world-wide. The Ypresian (early Eocene) rich insect-bearing deposits of the Okanagan Highlands of far-western North America have become well known only since the late twentieth century. No dragonfly had been described from there until recently, when eight species (six named) in seven genera (five named) of the extant families Aeshnidae and Gomphidae were based on nine fossils (Archibald & Cannings 2019). Much larger numbers of non-dragonfly odonate fossils have been recovered in the Okanagan Highlands and have been briefly mentioned, but none described; all have been thought to be damselflies (see below). Large numbers of leaves bearing oviposition scars have been also been found in these deposits, initially presumed to be produced by flea beetles (Coleoptera, Chrysomelidae, *Altica* Geoffroy: Lewis 1992) and later by Zygoptera.

The Okanagan Highlands was an Ypresian temperate upland spread across about a thousand kilometers of southern British Columbia, Canada from near the town of Smithers in the north, south into northern Washington, United States of America at the town of Republic (Archibald *et al*. 2011a) (Fig. 1). A series of lake basins across its length preserved plant and animal fossils from the surrounding forest communities (Moss *et al*. 2005). These existed during the Early Eocene Climatic Optimum, a time spanning about 2–3 million years of the late Ypresian. This interval saw increased atmospheric carbon and the hottest sustained global temperatures of the Cenozoic near the end of the "greenhouse world" global climate regime, before the onset of our current colder and more seasonal (outside of low latitudes) "icehouse world" climates following the Eocene (*e.g.*, Zachos *et al*. 2001, 2008). Warmer regional coastal lowlands to the west supported forests with a subtropical character (Rouse *et al*. 1971; Breedlove-strout *et al.* 2013), while at the elevations of the Okanagan Highlands, mean annual temperatures would have been upper microthermal, *i.e.*, temperate, much like those of Vancouver, British Columbia, and Seattle, Washington, today (microthermal = mean annual temperature ≤13°C). Only the locality at Quilchena, British Columbia was a few degrees warmer, with mean annual temperature estimates as high as 16.2 ± 2.0 degrees, based on leaf margin analysis (Mathewes *et al.* 2016), but odonate body fossils have not yet been found there. The Ypresian Okanagan Highlands experienced mild winters with few, if any, frost days (Wolfe & Wehr 1987; Archibald & Farrell 2003; Greenwood *et al*. 2005; Archibald *et al*. 2014).

Fossil insects have been collected and described in the Okanagan Highlands for over 140 years (*e.g*., Scudder 1877), but few were published until the 1970s (*e.g*., Wilson 1977). There was no mention of Okanagan Highlands Odonata until Lewis (1992) reported specimen UWBM 72290 from Republic (which we have not examined but confidently identify from the photograph, his Fig. 1D, as an indeterminate species of the new dysagrionid genus *Okanagrion*) and SCSU7B-16 (here with the accession number SR 93-11-01), called Zacallitidae, *Zacallites* Cockerell (?) sp., which we describe below as a species of the new genus *Whetwhetaksa* in the new family Whetwhetaksidae. All odonates in Wehr & Barksdale's (1996) list of fossil insect families from Republic were assigned to the Zygoptera: Euphaeidae, Megapodagrionidae, Platycnemididae or Megapodagrionidae, and Lestidae. Unfortunately, they did not associate specimen accession numbers with their identifications. However, we have examined all specimens available to them (except UWBM 72290, noted above), and so have revised their list here. Archibald (2007) and Archibald *et al*. (2010) reported and illustrated two specimens from the Okanagan Highlands locality McAbee, British Columbia, treated as Megapodagrionidae indet. (GSC 141100, there as SBA-2801, which we here assign to a new genus and species of the Dysagrionidae) and Zygoptera *incertae sedis* (GSC 141099, there as SBA-423, which we treat here as Cephalozygoptera *incertae sedis*). No non-anisopteran odonate from the Okanagan Highlands has been previously published with an identification below the family level.

Here, we describe the Odonata of the Okanagan Highlands that are neither Anisoptera nor, we find, Zygoptera, and place them in context with other odonates. These include all but one of the Okanagan Highlands specimens discussed above as damselflies. The sole zygopteran will be described in a future work.

Material and methods

We examined 77 fossils; most are isolated wings, but a few are more complete. All are preserved in lacustrine shales of Okanagan Highlands deposits from (Fig. 1): Republic, Washington, United States of America (52 specimens); McAbee, British Columbia, Canada (24 specimens); and Driftwood Canyon Provincial Park near Smithers, British Columbia, Canada (one specimen). These localities are described, below. The sole specimen known to us that we did not examine is the dysagrionid illustrated by Lewis (1992) mentioned above. We are aware of no other Cephalozygoptera fossils from the Okanagan Highlands.

Fossils were examined and photographed using a Leica M205C stereomicroscope and an attached Leica DFC495 digital camera at the Vancouver laboratory of Parks Canada. Head measurements (Table 1) are taken from these photographs.

Head measurements of extant Zygoptera species (Table 2) are taken from specimens in the Royal British Columbia Museum insect collection using a Leica MS5 dissecting microscope and an ocular micrometer.

We follow the terminology for wing morphology of Riek & Kukalová-Peck (1984) as used by Garrison *et al*. (2010), *e.g*., the discoidal cell of many authors is here called the quadrangle. Some details of venation in the base of the wing follow the terminology of Bechly (1996), which are illustrated by him there. Abbreviations used in the text and figures are: A, anal vein; a, arculus; aa, accessory antenodal crossveins; Ax0, Ax1, Ax2, antenodal crossveins; CuA, cubitus anterior; IR2, intercalar vein 2; MA, media anterior; MP, media posterior; n, nodus; Q, quadrangle; RA, radius anterior; RP1 radius posterior 1; IR1, intercalar vein 1; RP1-2, radius posterior 1+2; RP2, radius posterior 2; RP3-4, radius posterior 3+4; ScP, subcosta posterior; sn, subnodus; sq, subquadrangle. Forewing and hind wing are abbreviated FW and HW in some figures. Also see terminology illustrated in Fig. 1 of Bechly *et al*. (2001). Antefurcal crossveins are those between RP and MA distal to the arculus and proximal to the midfork (branching of RP to RP1-2 and RP3-4). By a vein being "linear", we mean not zigzagged. By "normal obliquity" of the subnodus, we mean angled such that the anterior end of this crossvein is more proximal than the posterior, *e.g.*, in all Dysagrionidae except species of *Dysagrion* Scudder; "reverse obliquity", the opposite, *e.g.*, in all *Dysagrion* species, see below. Hyperstigmal crossveins are those that are between the oblique proximal margin of pterostigma and the Costa.

We follow the systematics of Dijkstra *et al*. (2013, 2014). Like them, we avoid as informal the term Epiproctophora (or Epiprocta) used by some authors to group the Anisoptera and Anisozygoptera.

We use the following institution abbreviations: TRU for Thompson Rivers University in Kamloops, British Columbia; RBCM for the Royal British Columbia Museum in Victoria, British Columbia; and in the United States of America: SCSU for the Saint Cloud State University, Saint Cloud, Minnesota; SR and SRUI for the Stonerose Interpretive Center in Republic, Washington; UWBM for the Burke Museum of Natural History and Culture, Seattle; MCZ for the Museum of Comparative Zoology, Cambridge, Massachusetts; YPM for the Yale Peabody Museum, New Haven, Connecticut; and UCM for the University of Colorado (Boulder) paleontology collections.

Republic Klondike Mountain Formation locality codes A0307, A0307B, B4131 and B9201 are designations of the Burke Museum that are also employed by the Stonerose Interpretive Center. We also refer to locality codes of the Geological Survey of Canada as described below.

Contrary character states of compared taxa in diagnoses are provided in brackets.

Cladistic analyses

Character selection. We scored 102 phylogenetically informative morphological character states of the head, body, abdomen and wing venation from extant and fossil specimens and from published drawings and descriptions. Both continuous and discrete characters were scored. All 23 continuous characters were wing venation characters, while the remaining discrete characters included eight head, two thoracic, two abdominal and 69 additional wing characters (see character list, Appendix A).

We used continuous characters for phylogenetic resolution of closely related species (de Bivort *et al*. 2010; Mongiardino Koch *et al*. 2015; Parins-Fukuchi 2018; Gutiérrez *et al*. 2020). Whenever possible, we scored the states of these as ranges, accounting for intraspecific variation. We standardized these to provide optimal topologies with TNT ("Tree analysis using New Technology" phylogenetic software: Goloboff *et al*. 2003) by transforming the full range of each continuous character into a single step (Goloboff *et al*. 2006; Goloboff *et al*. 2008; Mongiardino Koch *et al*. 2015). All discrete characters were treated as unordered. The matrix contained 2754 coded characters with 1121 instances of missing (40.7%) and 114 of inapplicable data (4.1%) (Appendix B). We were unable to score 1229 characters (44.6%) in fossils due to incomplete preservation.

Taxon sampling. We assessed the following relationships: Analysis 1, Cephalozygoptera to the remaining suborders of Odonata; Analysis 2, the relationship of Whetwhetaksidae to the Cephalozygoptera and its families; and, Analysis 3, the genus-level phylogeny of Dysagrionidae. The outgroup was comprised of Tarsophlebiidae (*Tarsophlebia eximia* Hagen), Anisoptera (48 families, 11 extant and 37 extinct), Anisozygoptera (*Burmaphlebia reifi*

Bechly and *Epiophlebia superstes* Selys), and Zygoptera (35 families, 29 extant and 6 extinct, as well as *Burmadysagrion zhangi* Zheng *et al*., and the combined species of *Electrodysagrion* Zheng *et al*., and of *Palaeodysagrion* Zheng *et al*.).

The ingroup was comprised of the Dysagrionidae and likely Dysagrionidae species: *cf*. Dysagrioninae genus and species A (Megapodagrionidae genus and species A of Petrulevičius *et al*. 2008, revised here), *Congqingia rhora* Zhang, *Dysagrionites delinei* new collective genus and species, *Electrophenacolestes serafini* Nel & Arillo, *Furagrion jutlandicus* Henriksen, *Stenodiafanus westersidei* new genus and species, *Thanetophilosina menatensis* Nel *et al*., and *Valerea multicellulata* Garrouste *et al*., and the combined species (listed in Appendix B) of *Dysagrion*, *Okanagrion* new genus, *Okanopteryx* new genus, *Petrolestes* Cockerell, *Phenacolestes* Cockerell, *Primorilestes* Nel *et al*.; the Sieblosiidae genera *Paraoligolestes* Nel & Escuillé and *Stenolestes* Scudder; the Sieblosiidae species *Germanostenolestes lutzi* Nel & Fleck, *Miostenolestes zherikhini* Nel *et al*., *Parastenolestes oligocenicus* Nel & Paicheler, *Sieblosia jucunda* (Hagen); and the sole species of Whetwhetaksidae, *Whetwhetaksa millerae* new species.

Analyses. Analyses were done using TNT version 1.5 (Goloboff *et al*. 2008, Goloboff & Catalano 2016) using maximum parsimony. Implied weighting (Goloboff 1993) under default settings were used for Analysis 3. Bayesian and likelihood methods were not used for phylogenetic reconstruction as not compatible with TNT using continuous characters (see above). In all analyses, we used a heuristic search based on 100 random addition sequences of taxa (RAS), followed by tree-bisection-reconnection (TBR) branch swapping, holding 10 trees per replication. The most parsimonious trees were used for a final round of TBR branch swapping. Branch support in the most parsimonious trees was evaluated with symmetric resampling, permitting characters to be up- or downweighted with equal probability (Goloboff *et al*. 2003), with 1000 replicates. Trees were rooted in Analysis 1 to Tarsophlebiidae and in Analyses 2 and 3 to Zygoptera.

Localities

The fossils are from McAbee, Republic, and Driftwood Canyon Provincial Park (Fig. 1), lacustrine shale deposits with radiometric dates ranging through the second half of the Ypresian. These shales are thought to have been deposited in lakes formed in grabens resulting from regional Ypresian tectonic uplift and/or associated volcanism damming drainage systems across the mountainous landscape (Ewing 1980; Tribe 2005).

Driftwood Canyon: The northernmost locality of the Okanagan Highlands. The fossiliferous Ootsa Group shale exposed at Driftwood Canyon Provincial Park near Smithers in west-central British Columbia has been dated as mid-Ypresian, 51.77 ± 0.34 Ma (Mortensen and Archibald cited as personal communication by Moss *et al*. 2005).

McAbee: The McAbee locality is an exposure of Kamloops Group shale near Cache Creek and Ashcroft, British Columbia. It is dated at 52.90 ± 0.83 Ma (Mortensen and Archibald cited by Archibald *et al*. 2010), the oldest of the series. Its insects are among the best known of the Okanagan Highlands (*e.g*., Archibald *et al*. 2010, 2018) despite a relatively small amount of scientific collecting; the great majority of collecting has been for a commercial fossil operation with limited access for research. All McAbee fossils reported here are from the Hoodoo Face beds, *i.e*., the exposure 13 kilometers east of Cache Creek facing Highway 1 beneath prominent hoodoos, including and immediately adjoining the beds previously mined for fossils by the commercial fossil claim. The Hoodoo Face beds are designated Geological Survey of Canada locality codes V-016800 (for specimens GSC 141099 Cephalozygoptera *incertae sedis*, GSC 141100 *Okanopteryx macabeensis* new species, GSC 141102 *Okanopteryx macabeensis*, GSC 141103 *Okanopteryx incertae sedis*, and GSC 141104 *Okanopteryx fraseri* new species) and V-016801 (for specimen GSC 141101 *O. macabeensis*). Other exposures include the Eastern beds, *i.e*., in and surrounding another mineral claim, a now-defunct zeolite mine (fossil-bearing shale was ground and sold as kitty litter) approximately half a kilometer east of the Hoodoo Face beds, and the Western beds exposed in the hillside above the highway and a cattle ranch about five kilometers west of the Hoodoo Face beds.

Republic: The southernmost locality of the Okanagan Highlands. The Republic exposures of the fossiliferous Tom Thumb Tuff Member of the Klondike Mountain Formation are within and immediately surrounding the village of Republic, Washington. Along with McAbee, the Republic locality has the best-known insect record of the Okanagan Highlands, as there has been an intensive, organised collecting effort by the Stonerose Interpretive Center since the 1970s. The site has been dated at 49.42 ± 0.54 Ma (Wolfe *et al*. 2003), the youngest of the series.

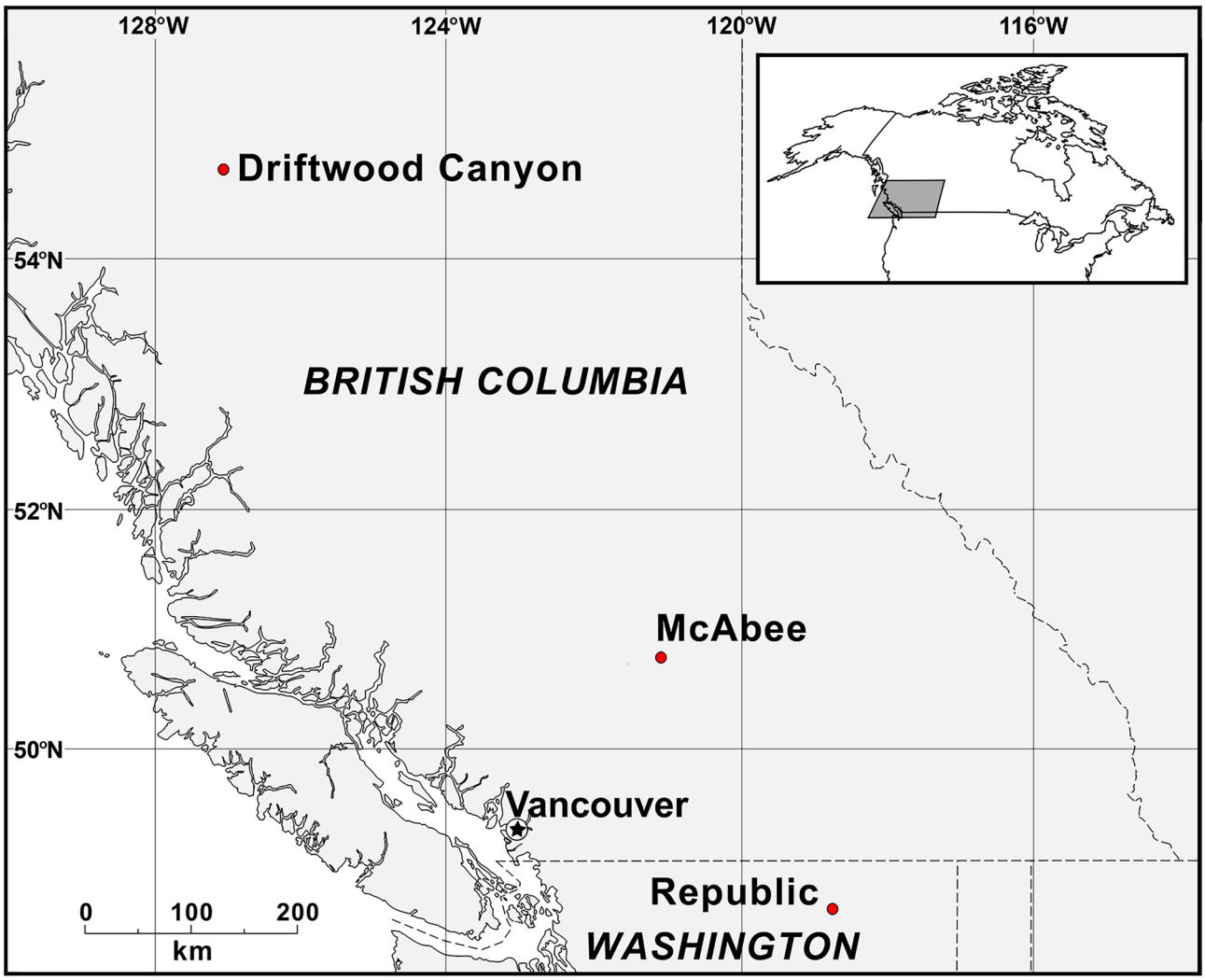

FIGURE 1. Map of Okanagan Highlands localities with Cephalozygoptera fossils: Driftwood Canyon Provincial Park, McAbee, and Republic.

Systematic paleontology

Reassessment of the Dysagrionidae

Taxon concepts based on the presence of accessory antenodal crossveins. The Dysagrioninae was originally proposed by Cockerell (1908a) as a subfamily of Agrionidae (Zygoptera), comprised of the two extinct genera *Dysagrion* and *Phenacolestes*. He distinguished it from other agrionids solely by the presence of accessory antenodal crossveins, *i.e*., in the costal space between Ax2 and the nodus: two in *Dysagrion* and three in *Phenacolestes* (*P. mirandus* Cockerell from the Priabonian shale of Florissant, Colorado was then its only confirmed species, Fig. 2).

Calvert (1913) examined six specimens of *P. mirandus*, five of which had the antenodal region preserved, and found that three of these had three accessory antenodal crossveins, and the other two had two. He agreed with Campion (1913) that this variability made Cockerell's Dysagrioninae untenable. Campion thought that *P. mirandus* most closely resembles the extant Neotropical *Thaumatoneura* McLachlan, which also has a variable number of accessory antenodal crossveins. Tillyard & Fraser (1939), Fraser (1957) and Nel & Paicheler (1994) did not recognise Cockerell's Dysagrioninae, placing *Phenacolestes* in the Amphipterygidae (Tillyard & Fraser 1939) and Pseudolestidae (Thaumatoneurinae) (Fraser 1957; Nel & Paicheler 1994). Modern photographs clearly confirm the presence of three accessory antenodal crossveins in the holotype of *P. mirandus* (US National Parks Service website, see our drawing from this photograph, Fig. 2).

Cockerell (1908a) also described a new species from Florissant as *Phenacolestes*? *parallelus* Cockerell, a tentative member of the genus as the region of the diagnostic accessory antenodal crossveins is not preserved (University of Colorado: UCM 4503, part and counterpart). Subsequently discovered specimens confirmed that the species is a *Phenacolestes*: a proximal half of a wing (Yale Peabody Museum: YPM IP 220974) has four accessory antenodal crossveins (Cockerell 1908b) and a third, almost complete specimen (University of Colorado: UCM 4545), also from Florissant (Cockerell 1908c), has three in both forewings and three in both hind wings. Here, we figure these (Figs. 2, 3) as, to our knowledge, no specimen of the species has been previously illustrated other than by a poor-quality photograph of UCM 4545 (Cockerell 1908c, his Fig. 4).

The third species attributed to the genus, *P.*? *coloratus* (Hagen) (mid-Miocene, Radoboj, Croatia) is poorly known, inadequately described, and we know of no published drawing or photograph (Hagen 1848; and see Nel & Paicheler 1994; Nel *et al*. 2005b). We treat it as a possible member of the genus (adding the question mark), family, and suborder pending examination of the specimen.

The discussions of the above authors concerned the appropriateness of basing the taxon on a variable character state, *i.e*., two or three accessory antenodals in *P. mirandus* (the variability in *P. parallelus* described above was not known to them); the presence of two such crossveins in *Dysagrion*, however, was not doubted. Although Scudder's original drawings should have established that this is not always the case, it remained unquestioned from the time of Cockerell's works cited above to the present day. Scudder's drawing of *Dysagrion fredericii* Scudder (Ypresian, Green River Formation, Wyoming) (1890: plate 6*,* Fig. 9) type specimen 4167/4168 (now MCZ numbers 381A, B) shows two accessory antenodal crossveins; however, there are none in his drawing (1890: plate 6*,* Fig. 3) of the type of *D. packardii* Scudder (Green River Formation, Wyoming) (Scudder cites the specimen as Packard number 146), a copy of which had already appeared in a work by Zittel (1885: Fig. 979) which Scudder edited. Tillyard & Fraser (1939: Fig. 3.1) provided a drawing of the wing (re-drawn from Scudder?), *adding* two accessory antenodal crossveins, which Fraser subsequently reproduced (1957: Fig. 34.1) (the specific epithet spelled "*packardi*" in both). Although Carpenter had the Museum of Comparative Zoology (MCZ) specimens available to him, his drawing of *D. packardii* (1992, his Fig. 52.1) included these presumptive accessory antenodal crossveins, by which he in part distinguished the genus. Bechly (1996) based his tribe Congqingiini (*Congqingia* Zhang and *Petrolestes* Cockerell) on its members lacking accessory antenodal crossveins, in contrast to his Dysagrionini (*Dysagrion* and *Phenacolestes*), reported to possess them as above.

To resolve confusion as to the presence, and so the diagnostic usefulness, of accessory antenodal crossveins in *Dysagrion* species, considering the prominent role they have played in understanding their relationships at various taxonomic levels, we examined new, high resolution photographs of Scudder's original *Dysagrion* specimens housed in the collections of the MCZ. The location of the holotype of *D. packardii* (Fig. 4C, re-drawn here from Scudder 1890, plate 6 Fig. 3) is unknown, but we were able to examine new photographs of cotype MCZ 4656 (Packard number 252) (Fig. 4A, B). In this specimen, the proximal portion of the antenodal region is missing, but the region where these crossveins should occur, if present, is reasonably well preserved. We did not detect any (either dry or wetted with ethanol), consistent with Scudder's original description and *contra* subsequent authors. We also examined new photographs of the *D. lakesii* Scudder (Green River Formation, Wyoming) type specimen MCZ 4101 (Packard number 259, not previously illustrated) (Fig. 5); these also show no evidence of such accessory crossveins, which should be readily detectible if present.

In the type of *D. fredericii* (Scudder's number 4167/4168, now MCZ numbers 381A, B), we see one weakly preserved accessory crossvein, which we indicate by a dotted line in Fig. 6, but we doubt there are two, differing from Scudder's drawing (1890) as discussed by Cockerell (1908a). Tillyard & Fraser (1939) and Fraser (1957: Fig. 34.2, spelled "*frederici*") subsequently reproduced Scudder's drawing of this specimen with two accessory crossveins. We also examined photographs of MCZ 382, 1497, and 4147, but these fossils are fragmentary and do not possess this region. Cockerell and subsequent authors (as above) were then incorrect in asserting that the presence of accessory antenodal crossveins characterises *Dysagrion* and justifies its association with *Phenacolestes*.

Seven genera have been subsequently associated with *Dysagrion* and *Phenacolestes* as forming the current Dysagrionidae: *Primorilestes*, *Petrolestes, Congqingia*, *Electrophenacolestes* Nel & Arillo, *Burmadysagrion* Zheng *et al*., *Electrodysagrion*, and *Palaeodysagrion* (we exclude the latter three, see below) (Figs. 7–9). None of these except *Electrophenacolestes* possess an accessory antenodal crossvein. None of the new species that we associate here with the family (below) possess them. A presence of accessory crossveins is not, therefore, a useful character state on which to base this family concept, define constituent subfamilies, nor characterise the genus *Dysagrion*.

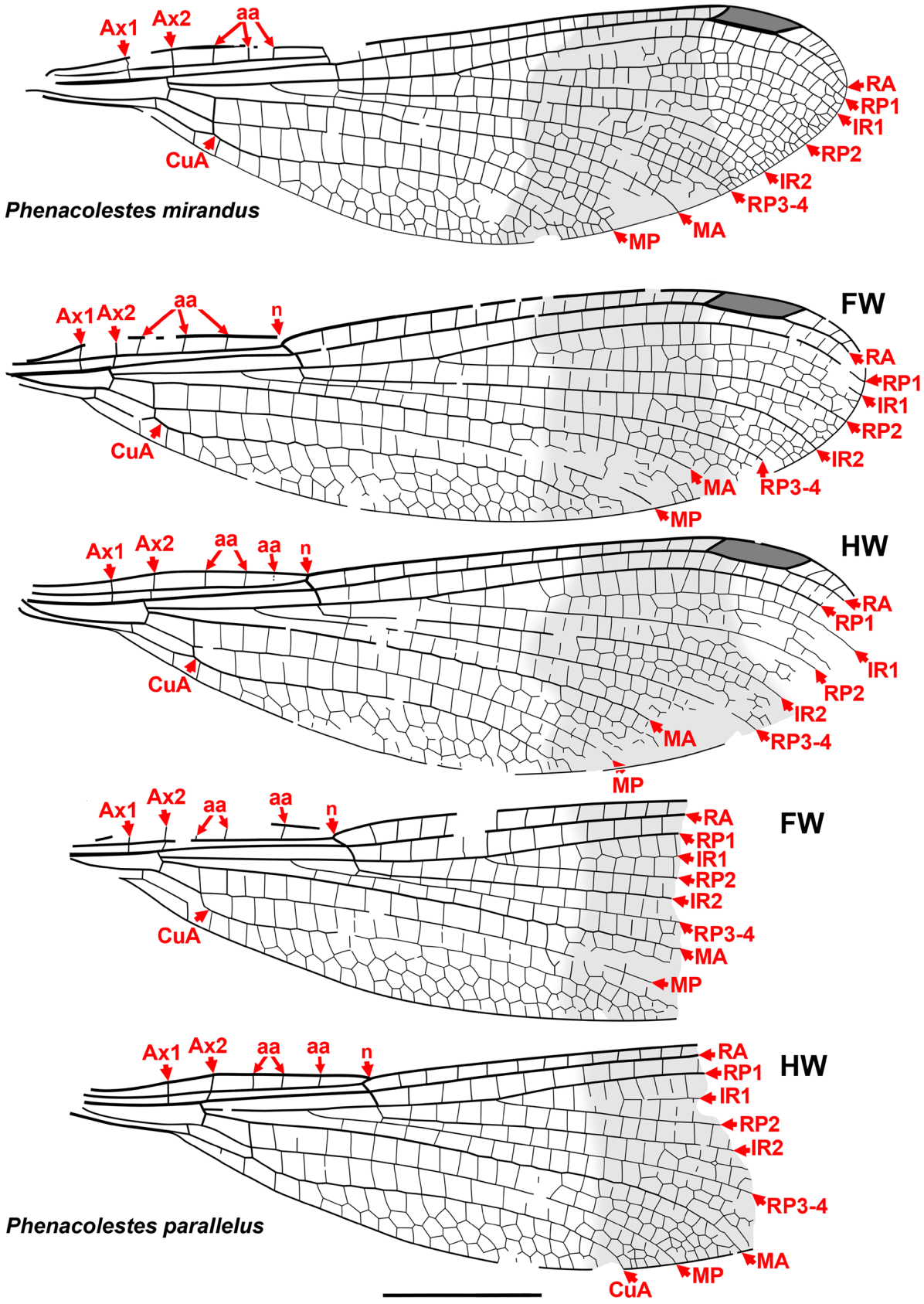

FIGURE 2. Drawings of wings of *Phenacolestes*. Top wing, *P. mirandus*, likely a hind wing, drawn from a photograph on the Florissant National Monument website (US National Parks Service website). Bottom four wings, *P. parallelus*: UCM-4545 drawn from photograph supplied by the University of Colorado (Boulder) (Paleontology, Colorado Museum of Natural History), see Fig. 3E. All to scale, 5 mm. FW, forewing; HW, hind wing.

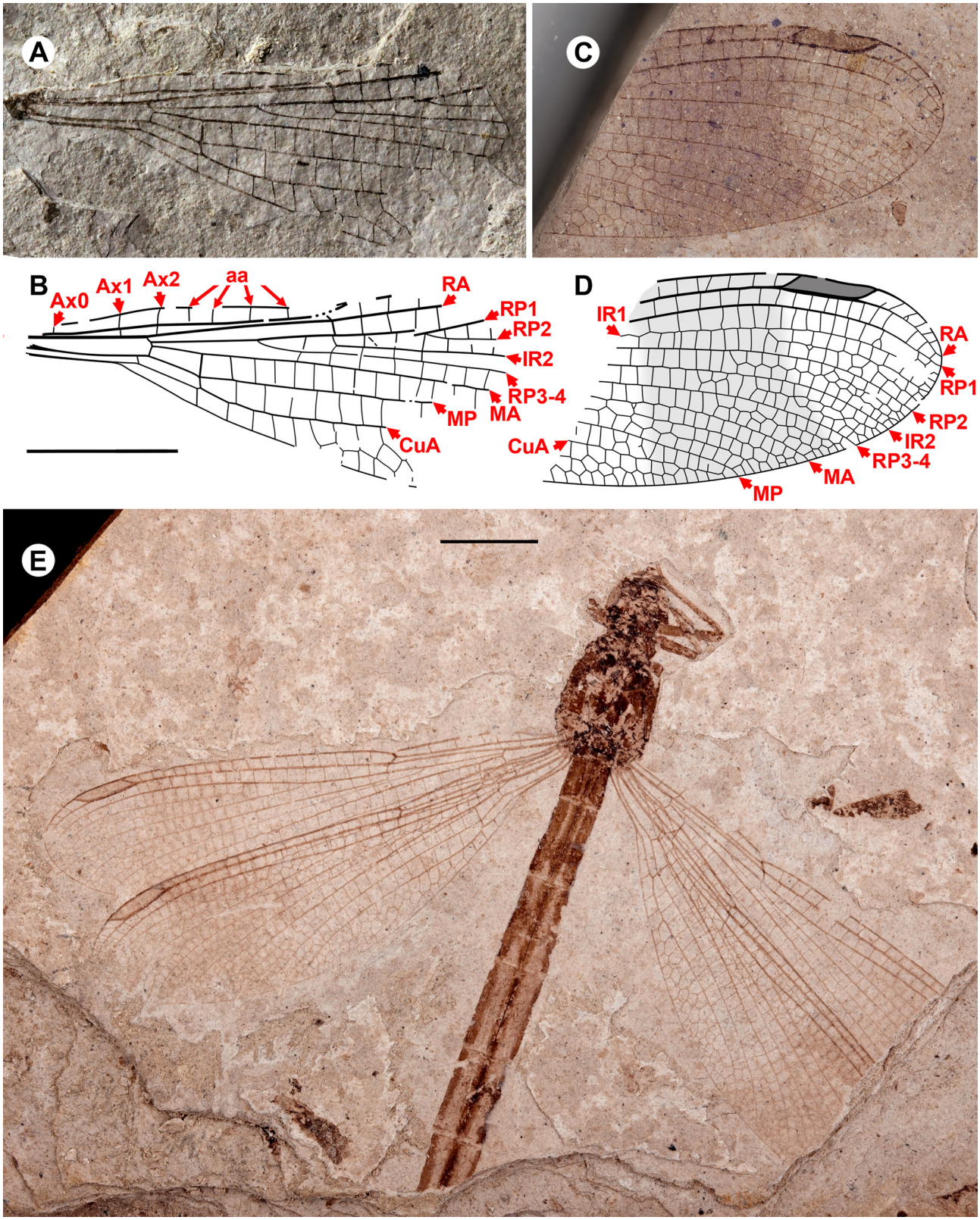

FIGURE 3. *Phenacolestes parallelus*. A, specimen YPMIP-220974 of the Yale Peabody Museum; B, drawing from A, photograph provided by Peabody Museum personnel; C, holotype, UCM-4503 of the University of Colorado (Boulder) paleontology collections; D, drawing of C, photograph provided by University of Colorado personnel; E, UCM-4545, University of Colorado (Boulder). A–D to scale, E to scale, both scale bars 5 mm.

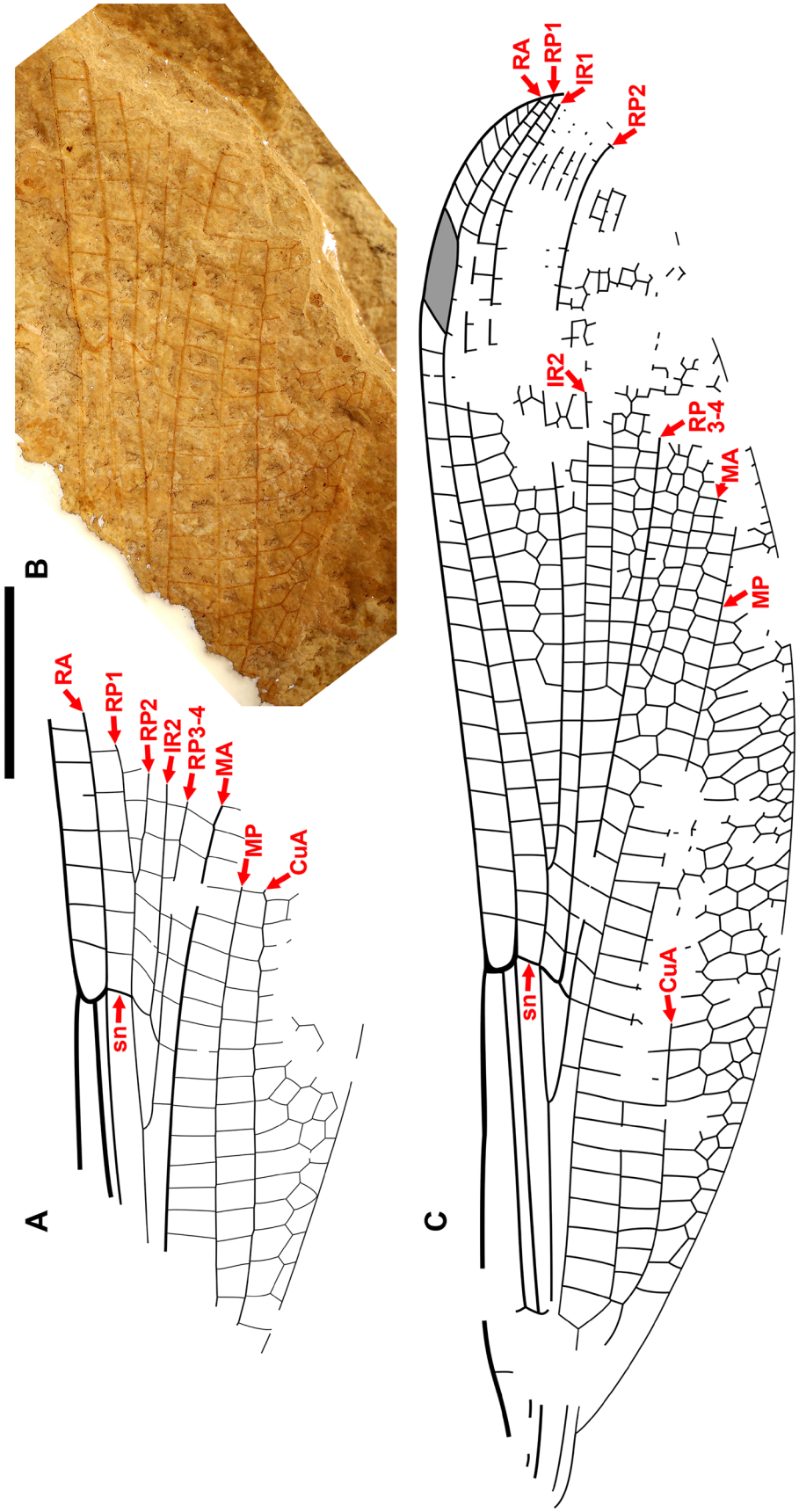

FIGURE 4. *Dysagrion packardii* cotype MCZ 4656 (Packard number 252): A, drawing; B, photograph; C, holotype (Packard number 146) redrawn from Zittel (1885: his Fig. 979), also redrawn by Scudder (1890: his plate 6, Fig. 3). A, B drawn from a photograph supplied by MCZ personnel. All to scale, 5 mm.

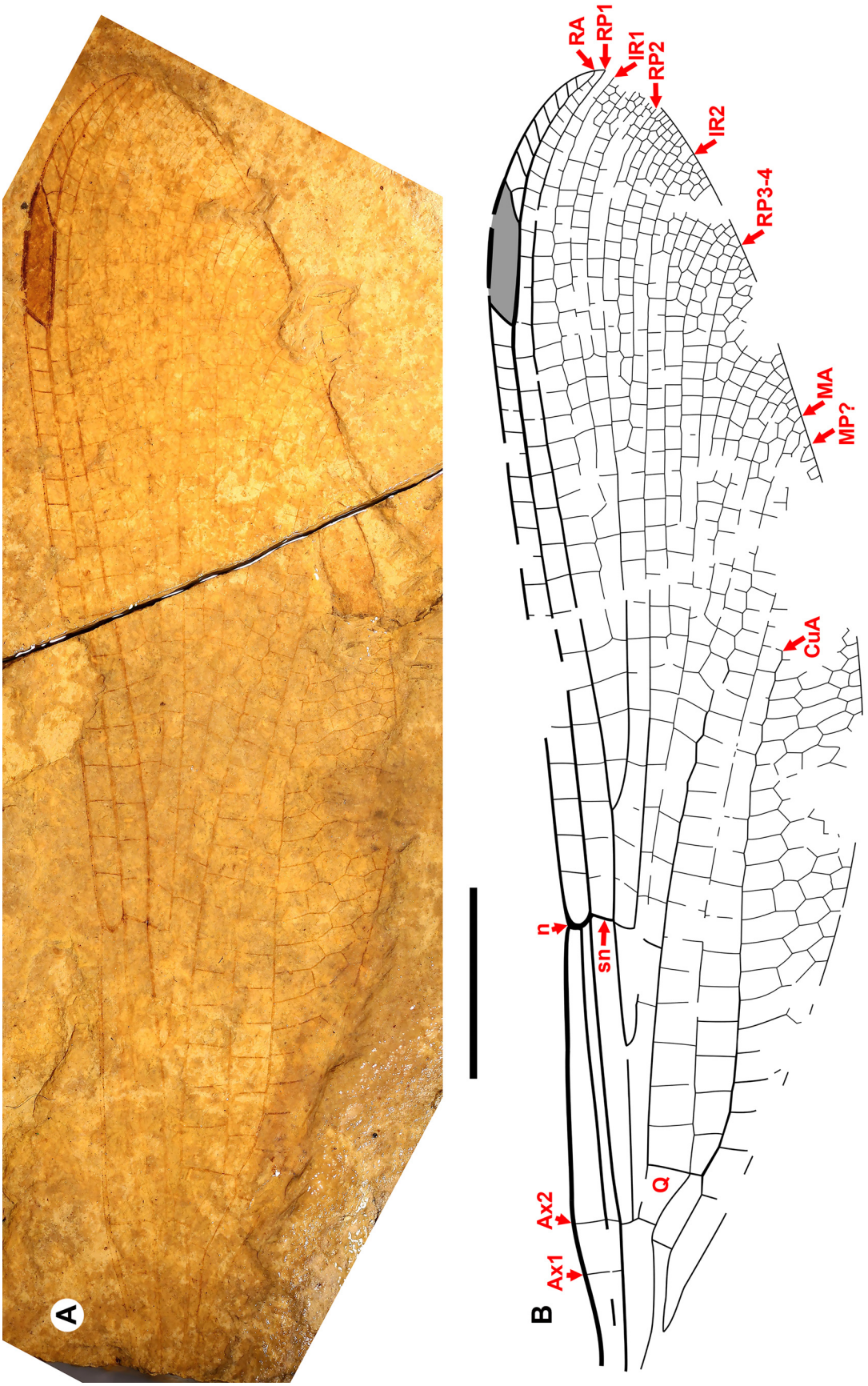

FIGURE 5. *Dysagrion lakesii* Scudder type specimen MCZ 4101 (Packard number 259, not previously illustrated): A, photograph; B, drawing from a photograph supplied by MCZ personnel. Both to scale, 5 mm.

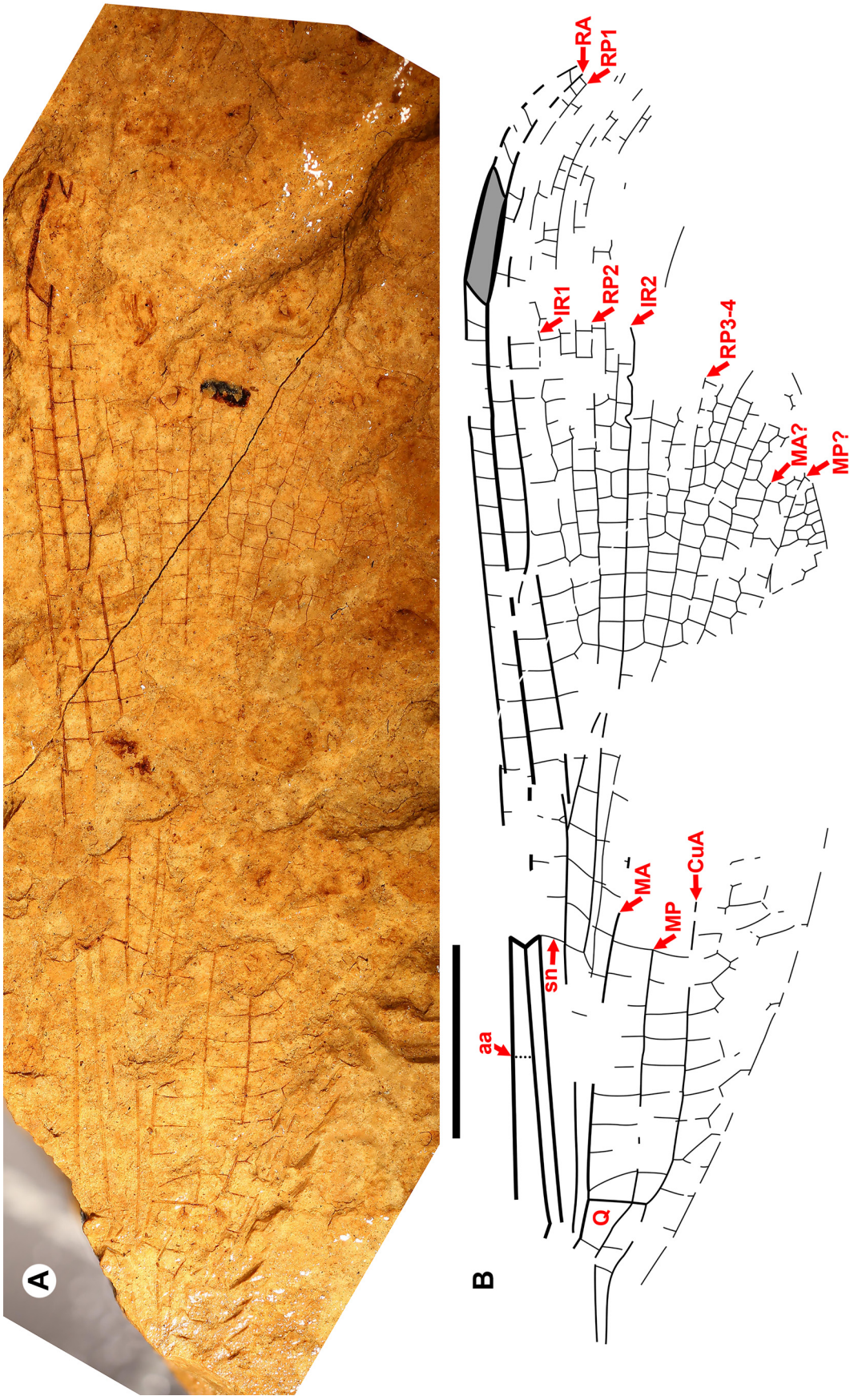

FIGURE 6. *Dysagrion fredericii* Scudder's number 4167/4168 (now MCZ numbers 381A, B "type"): A, photograph; B, drawing from a photograph supplied by MCZ personnel. Both to scale, 5 mm.

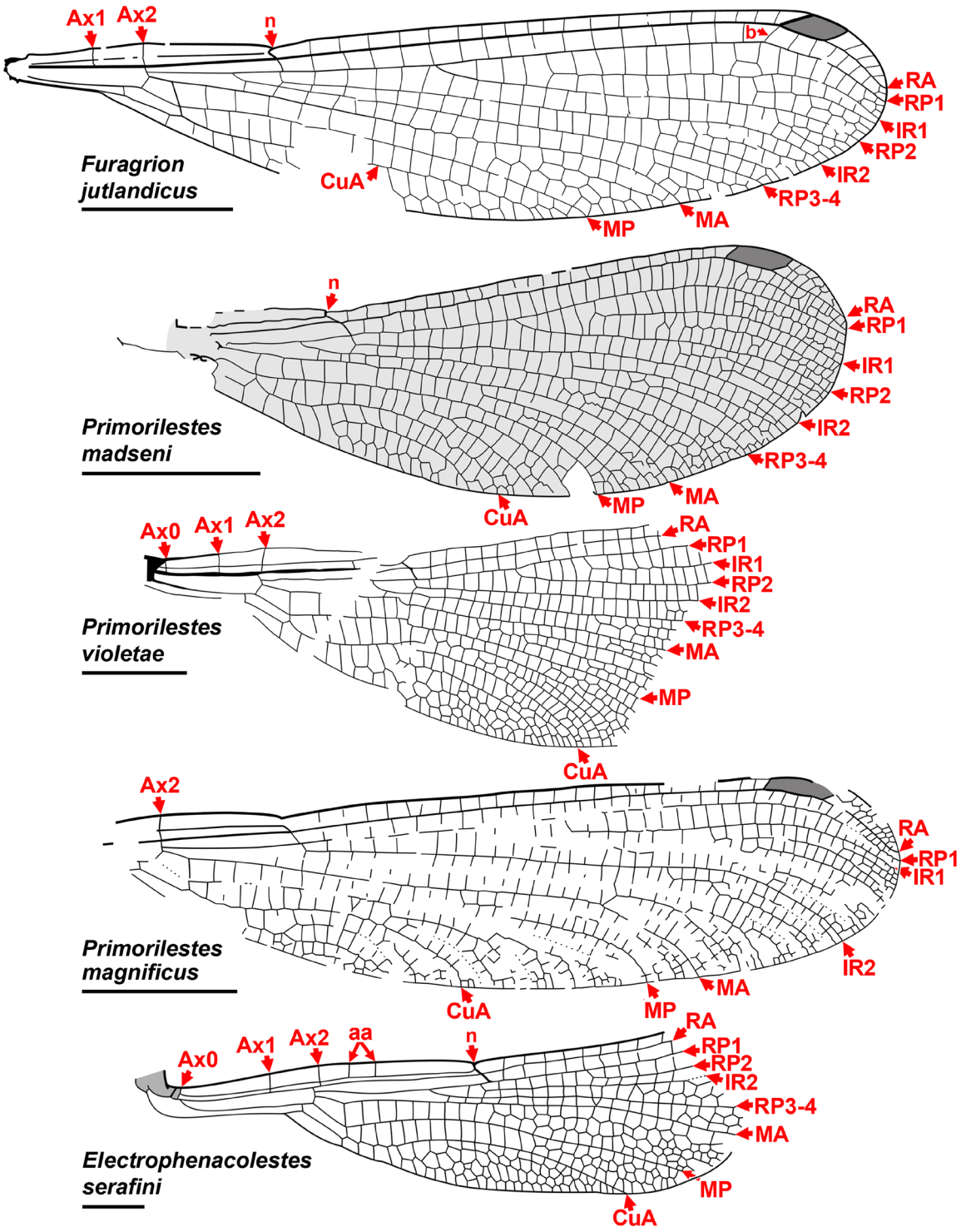

FIGURE 7. Drawings of the wings of Dysagrionidae, Dysagrioninae (in part). *Furagrion jutlandicus*, new drawing from new, large file photographs of the part and counterpart, FUM-N-11289 and FUM-N-13856 of the Fur Museum, Museum Salling, Denmark. This is the fossil previously numbered ERK KL T1 (Geological Museum, Copenhagen) and illustrated by Petrulevičius *et al*. (2008) as their figure 3, which includes a photograph of this specimen. We find the crossvein shown in their drawing between CuP+AA' and AA''+AP proximal to AA2 (*i.e*., crossing the cell posterior to the quadrangle that borders the wing margin, directly posterior to the arculus) to be imperfections in the rock. We further examined photographs of specimens were this region is well-preserved (FUM-N-14704, FUM-N-11616, FUM-N-11574, FUM-N-10781) and saw no crossvein in this position. *Primorilestes madseni* is redrawn from Rust *et al*. (2008, their Fig. 2), *Primorilestes violetae* from Nel *et al*. (2005b, their Fig. 1), *Primorilestes magnificus* was drawn from Nel *et al*. (2016) Fig. 4, and *Electrophenacolestes serafini* from (Nel & Arillo 2006, their Fig. 2). All scale bars 5 mm.

Subsequent definitions of Dysagrionidae. Some or all of the above genera and sometimes *Thaumatoneura*, *Eodysagrion* Rust *et al*., and others have been grouped in various family configurations, including in the Agrionidae, Amphipterygidae, Pseudolestidae, Megapodagrionidae, as subfamilies of Thaumatoneuridae (Dysagrioninae and Thaumatoneurinae: *e.g*., Bechly 1996; Nel *et al*. 2005a, 2005b; Nel & Arillo 2006), or of the Dysagrionidae (Dysagrioninae, Thaumatoneurinae and Eodysagrioninae: Rust *et al*. 2008; Dysagrioninae, Burmadysagrioninae and Eodysagrioninae: Zheng *et al*. 2016a, 2016b, 2017; and independent of *Thaumatoneura* and *Eodysagrion*: Garrouste & Nel 2015; Nel *et al*. 2016; Huang *et al*. 2017).

Bechly (1996) distinguished the taxon as Dysagrioninae (within Thaumatoneuridae: *Dysagrion*, *Petrolestes*, *Phenacolestes* and *Congqingia*) by quadrangle shape as its single defining trait, although he did not describe this, and noted that it is also present in Sieblosiidae. Nel & Arillo (2006) agreed, further distinguishing it by the combination of: antesubnodal space without crossveins; absence of the oblique vein O; CuA–A space very broad; the base of IR2 positioned proximal to the nodus; RP3-4 arising between the arculus and nodus closer to nodus; and the base of RP2 being in a very distal position. Nel & Fleck (2014) closely followed this definition.

Rust *et al*. (2008) erected the Eodysagrioninae for *Eodysagrion* as an equal rank taxon with Dysagrioninae and Thaumatoneurinae within the Dysagrionidae.

The Dysagrionidae is currently not considered to be close to the Thaumatoneuridae. Garrouste & Nel (2015) questioned a close relationship between them because of inconsistencies in positions of the nodus and bases of branches of RP and IR2, the difference in shape of their quadrangles and of their leg spines and thoracic skewedness, and as an incomplete interpleural suture is present in *Petrolestes*, but it is complete in *Thaumatoneura*. They further suggested that Dysagrionidae might not even belong in the Zygoptera. Huang *et al*. (2017) explicitly separated them, elevating Dysagrioninae and Thaumatoneurinae to family level. They rejected their putative synapomorphies of costal margin curvature and lack of crossveins in the antesubnodal space as weakly supported and most likely convergent, also discussing their difference in quadrangle shape. They further considered *Eodysagrion* as a provisional member of the Thaumatoneuridae, among their reasons further stressing the importance of quadrangle shape, which is rectangular in *Eodysagrion* like that of *Thaumatoneura*, not Dysagrionidae.

Subfamilies of Dysagrionidae. Huang *et al*. (2017), in elevating the Dysagrioninae to family status, also elevated the former tribes Petrolestini and Dysagrionini to subfamilies: Petrolestinae, comprised of *Petrolestes* (*P. hendersoni* Cockerell: Ypresian Green River Formation, Colorado, United States of America; *P. messelensis* Garrouste & Nel: Lutetian, Grube Messel, Germany) and *Congqingia* (*C. rhora*, Aptian, *i.e*., Early Cretaceous, Laiyang Formation, Shandong, China; recent age estimate: Zhou *et al*. 2020) (Fig. 8); and their revised concept of Dysagrioninae, comprised of *Dysagrion*, *Phenacolestes*, *Primorilestes* (*P. violetae* Nel *et al*.: Priabonian, Bolshaya Svetlovodnaya (Biamo), Primorye, Russia; *P. madseni* Rust *et al*.: earliest Ypresian Fur Formation, Denmark; *P. magnificus* Nel *et al*.: Miocene, Satovcha Graben, Sivik Formation, Bulgaria), and *Electrophenacolestes* (*E. serafini*: Priabonian, Baltic amber, Poland) (Fig. 7).

Bechly (1996) separated these (as tribes) by Petrolestinae having: 1, no accessory antenodal crossveins; 2, IR1 shortened and strongly zigzagged; and 3, the bases of RP3-4 and IR2 situated midway between nodus and arculus [Dysagrioninae: origin of RP3-4 in middle third between arculus and nodus, usually at about two-thirds the distance; IR2 originates at or very near subnodus]. However, character state 1 is, as above, variable and not informative. Nel *et al*. (2005b) rejected character state 2, as this region is not preserved in the type species *Petrolestes hendersoni* and is not consistent in other specimens. Character state 3 is the sole trait separating these taxa. In the Dysagrioninae the origin of RP3-4 is in the middle third between the arculus and nodus, usually at about two-thirds of the distance, and IR2 originates at or very near the subnodus. In the Petrolestinae, the origin of RP3-4 is more proximally positioned, closer to or at the point midway between the arculus and subnodus, and IR2 originates close to or on RP3-4. There are no currently recognised taxa of tribe-level rank of the Dysagrionidae.

Emended diagnosis of the Dysagrionidae. The wings of Dysagrionidae are easily separated from those of other Cephalozygoptera and tentative Cephalozygoptera (new suborder, see below) by a combination of:

1- oblique crossvein O absent [Sieblosiidae: present];
2- arculus at or immediately proximal to Ax2 [Whetwhetaksidae: nearer to Ax1].

They are distinguished from similar appearing Zygoptera by a combination of the above and the following character states 3–9 of the wings, slightly amended from the diagnoses of Nel & Arillo (2006) and Nel & Fleck (2014), and 10, of the head:

3- quadrangle broad, distal side longer than proximal side, posterior side longer than anterior, distal-posterior angle oblique, proximal-anterior angle usually about 90°;
4- nodus positioned at least a quarter wing length, usually more;
5- anterior anal vein separates from posterior anal vein briefly before joining CuP (*i.e*., is briefly free distal to petiole);
6- RP3-4 originating roughly between one third to two thirds length from arculus to subnodus, usually about two thirds (*Primorilestes violetae* furthest, just distal to middle third, but *P. madseni* within middle third);
7- antesubnodal space without crossveins;
8- CuA–A space expanded in middle to at least two cells wide, often more;
9- CuA long, terminating on posterior margin at mid-wing or longer (termination most proximal in *Primorilestes* species, but there mid-wing);
10- head width across eyes about twice the length from anterior margin of antefrons to posterior of occiput; compound eyes more or less adpressed to the head capsule, convex laterally but not spherical, posterolateral corners extended posteriorly to varying degrees, sometimes even acutely; distance between compound eyes at level of centre of ocelli about one eye's width or less; head not distinctly extended laterally with bulging, spherical compound eyes as in Zygoptera (*i.e*., not "hammerhead" or "dumbbell" shaped).

We agree with Nel & Arillo (2006), Nel & Fleck (2014), and Garrouste & Nel (2019) that an expanded CuA–A space is characteristic of the Dysagrionidae (character state 8).

These character states associate *Dysagrion*, *Phenacolestes*, *Primorilestes*, *Petrolestes*, *Electrophenacolestes,* and *Congqingia* in agreement with previous authors, as well as *Furagrion* Petrulevičius *et al*. (restored, below); the new genera described here, *Okanagrion*, *Okanopteryx* and *Stenodiafanus*; and species of the new collective genus *Dysagrioninites*. They exclude *Electrodysagrion, Palaeodysagrion* and *Burmadysagrion* (see below). We tentatively include the Thanetian (late Paleocene: see age discussed by Wedmann *et al*. 2018) *Valerea* Garrouste *et al*. (one species: *V*. *multicellulata*, Menat Formation, France) for reasons discussed below.

We include Furagrion *in the Dysagrionidae and treat* Valerea *as a tentative member.* Henriksen (1922) originally described *Furagrion jutlandicus* (Henriksen) from the early Ypresian Fur Formation of Denmark ("Mo-Clay") as a species of *Phenacolestes*, and therefore a member of Cockerell's Dysagrioninae. He based it on a specimen with three partial wings and part of the abdomen. None of these wings are preserved proximal to the nodus, and although they then lack the quadrangle and antenodal space, he associated the species with *Phenacolestes* by shared character states of the preserved portion. Owing to the lack of the proximal wing characters, Nel & Paicheler (1994) treated the species as "*Phenacolestes*" *jutlandicus* of indeterminate family. Rust (1999) reported a new, almost complete wing which he called "Dysagrioninae gen. indet. *jutlandicus*". Petrulevičius *et al*. (2008) revised the species based on this fossil, erecting the monotypic genus *Furagrion* for it. They assigned it to the Megapodagrionidae, finding an association with the Dysagrionidae unlikely by the lack of a distinct broadening of the antenodal area at the level of Ax1 and Ax2, and the distal side of the quadrangle not distinctly longer than the proximal. However, the amount of broadening of the antenodal area is variable in the family, and is in some species quite slight, and so this character state does not have clear diagnostic value in distinguishing it; in *Furagrion* it is comparable with that of *Electrophenacolestes*. While the distal side of the quadrangle of *Furagrion* is not much longer than the proximal side as it is in many dysagrionids, it is still longer, like that of *Congqingia* (Fig. 8). *Furagrion* then satisfies all wing character states of the diagnosis provided above, and so we restore it to the Dysagrionidae. Zessin (2011) described a second species of the genus, *F*. *morsi* Zessin, based on the proximal half of a wing.

Although the enigmatic Thanetian *Valerea multicellulata* (Fig. 9) is known from a single, fragmentary wing in which only character state 1 of our family definition is determinable, we tentatively associate it with the Dysagrionidae by its otherwise notable similarity with the new genus *Okanagrion* with which it shares distinctive character states, some not otherwise known in the Odonata (see below, in the discussion of *Okanagrion* and support by our cladistic analysis).

The Alaskan Chickaloon specimen and "Megapodagrionidae" genus and species A are probably dysagrionids; Thanetophilosina *Nel et al. and NHMUK I.9866/I.9718 could be dysagrionids*. We agree with Garrouste & Nel (2019) that the fragmentary specimen from the Thanetian or Ypresian Chickaloon Formation of Alaska (unnamed) is likely a dysagrionid by its density of veins and long CuA with an expanded CuA–A space up to four cells deep (Fig. 9). Its preserved portion only possesses character states 1, 8 and 9 of the Dysagrionidae diagnosis, and so we treat it here as a probable member of the family.

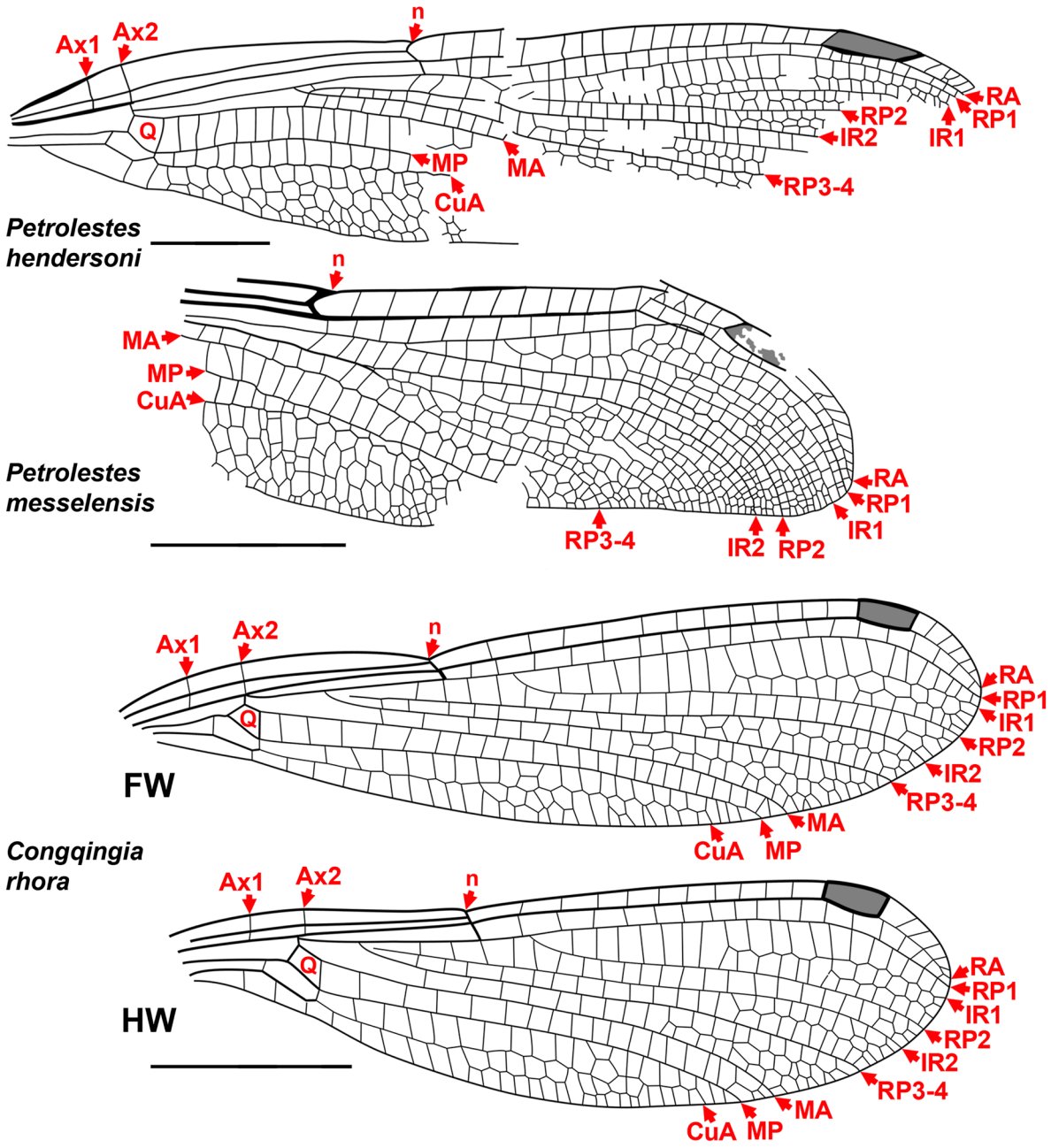

FIGURE 8. Drawings of wings of Dysagrionidae, Petrolestinae. *Petrolestes hendersoni*, redrawn from Fig. 2 of Garrouste & Nel (2015) the most complete specimen, see their Fig. 3 for Cockerell's less complete holotype; *P. messelensis* from Fig. 7 of Garrouste & Nel (2015); *Congqingia rhora* wings redrawn from Fig. 4 of Zhang (1992). To various scales, all 5 mm.

Similarly, the partial wing "Megapodagrionidae" genus and species A of Petrulevičius *et al*. (2008) from the early Lutetian of Grube Messel, Germany, shares character states 1, 8 and 9 of the Dysagrionidae diagnosis with the Chickaloon specimen, and is more complete than it, with the apical portion present and well-preserved. Petrulevičius *et al*. (2008) discuss various possible family associations and only tentatively assign it to the Megapodagrionidae, noting that as then constituted, that family could not be defined by any known synapomorphies of wing venation. The Megapodagrionidae, long considered to be polyphyletic, has since been separated into a number of families based on a revised molecular phylogeny (Dijkstra *et al*. 2014). We treat this fossil as also probably a dysagrionid, *cf*. Dysagrionidae genus and species A (Fig. 9).

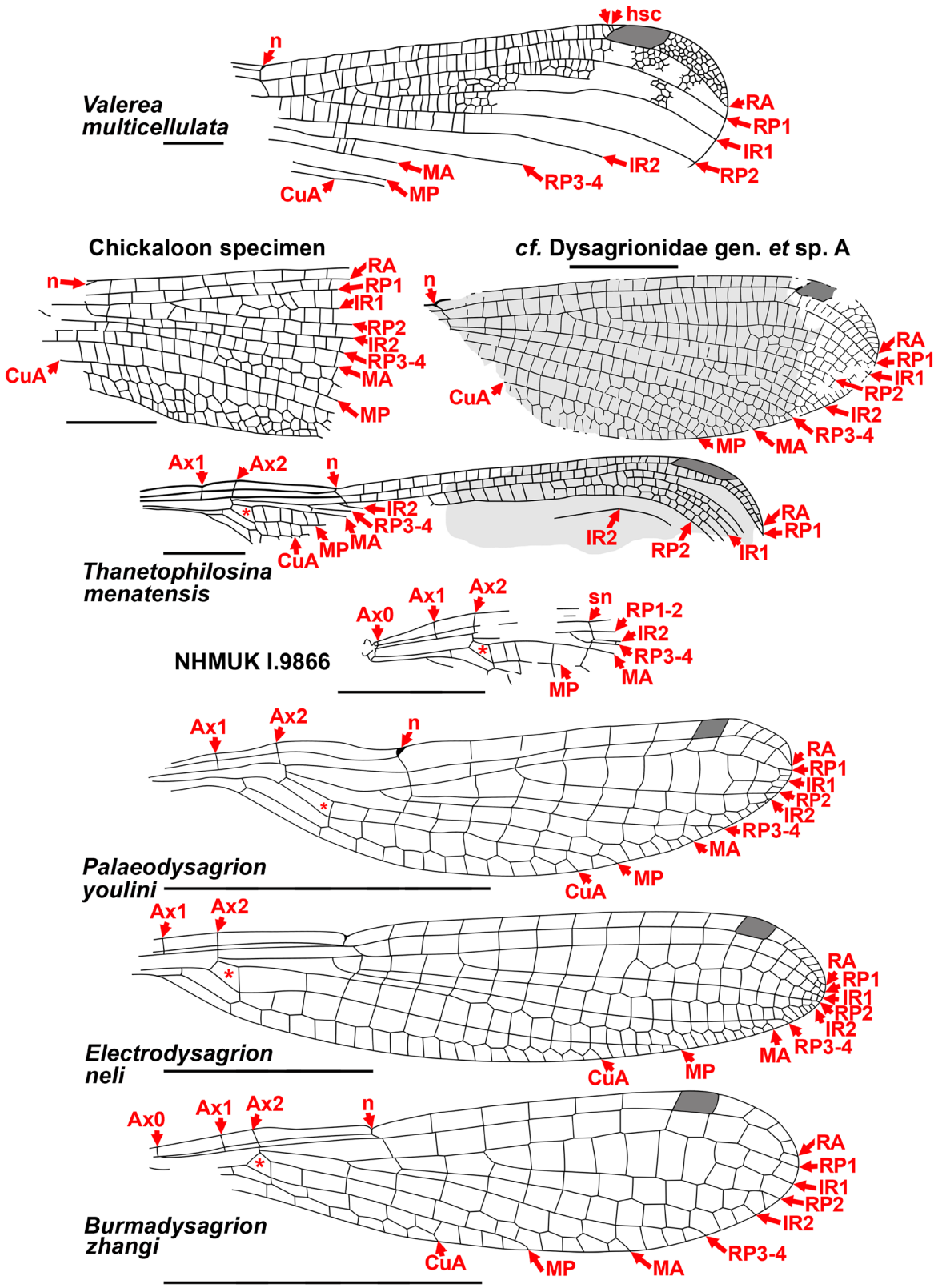

FIGURE 9. Wing drawings of: *Valerea multicellulata* redrawn from Fig. 1 of Garrouste *et al*. (2017); Chickaloon Formation (Alaska) specimen redrawn from Fig. 3 of Garrouste & Nel (2017); *cf*. Dysagrionidae gen. *et*. sp. A redrawn from Fig. 4 of Petrulevičius *et al*. (2008) (there as "Megapodagrionidae gen. *et*. sp. A"); *Thanetophilosina menatensis* redrawn from Fig. 21 of Nel *et al*. (1997); NHMUK I.9866 (Isle of Wight) redrawn from Fig. 28 of Nel & Fleck (2014); *Palaeodysagrion youlini* redrawn from Fig. 2 of Zheng *et al*. (2018); *Electrodysagrion neli* redrawn from Fig. 2 of Zheng *et al*. (2019); *Burmadysagrion zhangi* redrawn from Fig. 3 of Zheng *et al*. (2016a). To associated scales, all 5 mm. Asterisks indicate quadrangles.

Nel *et al*. (1997) assigned *Thanetophilosina menatensis* from the Thanetian of France (Fig. 9) to the Megapodagrionidae, rejecting Dysagrionidae based on its differences with *Dysagrion*, however, knowledge of the family has increased in subsequent decades; it does conform to character states 2 through 5 and 7 of the diagnosis provided here. It is too incomplete to assess the other character states of the diagnosis and we treat it as a possible dysagrionid of indeterminate family affinity.

Specimen NHMUK I.9866/I.9718 (Fig. 9), "Dysagrionini" species A of Nel & Fleck (2014), a fragmentary proximal portion of a wing from the Priabonian of the Isle of Wight, could also belong to the Dysagrionidae. The authors assigned this species to the family and Dysagrioninae (then Dysagrionini) by an inferred broad CuA–A space, the position of the base of IR2 relative to the nodus, and the shape of the quadrangle. The quadrangle is of the Dysagrionidae type and the origin of IR2 conforms with its position in the Dysagrioninae as then defined, however, a possible broadening of the CuA–A space is not clear to us. This quadrangle shape is also found in the Sieblosiidae, the new family Whetwhetaksidae, and at least some Frenguelliidae (see below). Note the presence of Ax0, found in the Dysagrionidae, Sieblosiidae and Whetwhetaksidae. It is excluded from the Sieblosiidae and Whetwhetaksidae by the position of the origin of IR2. Although it is most like the Dysagrionidae, the origin of RP3-4 is closer to the subnodus than it is in any member of the family; only *Primorilestes violetae* approaches this condition, but even there it is not so close; if NHMUK I.9866/I.9718 is a member of the Dysagrionidae, it differs strongly by this.

Burmadysagrion, Electrodysagrion, *and* Palaeodysagrion *are not dysagrionids*. These three genera from mid-Cretaceous Burmese amber (Fig. 9) were assigned to the Dysagrionidae by their authors; however, they do not conform with its diagnosis.

In the wing of *Electrodysagrion lini* Zheng *et al*. (Cenomanian, Myanmar) (Fig. 9), the pterostigma is hyaline and rectangular with straight sides, unlike those of all known dysagrioninds. Although almost the entire CuA–A space is missing in both preserved wings, the authors inferred by its almost straight, very slightly curved CuA that it had a single row of cells with a slight broadening of the CuA–A space distally. Zheng *et al*. (2019) described *Electrodysagrion neli*, a second species of the genus, which has a single row of cells in the CuA–A spaces of its fore- and hind wings. This contradicts character state 8 of the Dysagrionidae diagnosis, that the CuA–A space is expanded in the middle, two or more cells wide.

The CuA–A space of *Burmadysagrion* (*B*. *zhangi*, Cenomanian, Myanmar) (Fig. 9) is also narrow with a single row of cells. Further, its quadrangle is wider proximally than distally, far from its distinctive shape found in the Dysagrionidae (see diagnostic character state 3) (Zheng *et al*. 2016a).

Zheng *et al*. (2016b) noted that the distinctly elongate—length over two and a half times its maximum width—and nearly rectangular quadrangle of *Palaeodysagrion cretacicus* Zheng *et al*. (Cenomanian, Myanmar) differs from that of all known Dysagrionidae, and recognized that it does not fit either of its established subfamilies. Huang *et al*. (2017) suggested that the phylogenetic positions of *Palaeodysagrion* and *Burmadysagrion* should be revised and commented that in their opinion, the only Mesozoic dysagrionid is *Congqingia* (*Electrodysagrion*, also published in 2017, was not included in their consideration). The more complete *Palaeodysagrion youlini* Zheng *et al*. (Fig. 9) was subsequently described, in which the entire CuA–A space is one cell wide, similar to the that of *Burmadysagrion* (Zheng *et al*. 2018).

For these reasons, we treat *Palaeodysagrion*, *Electrodysagrion* and *Burmadysagrion* as zygopterans of undetermined family affinity. This is further supported by our cladistic analysis, see below.

Suborder placement of the Dysagrionidae

There has been some suggestion that the Dysagrionidae might not belong to the Zygoptera (*e.g*., Cockerell 1927; Zhang 1992; Garrouste & Nel 2015). The following character states were considered diagnostic of the Zygoptera by Bechly (1996: character states 1, 2, 4–7, 12), Rehn (2003: 1–2, 8–12) and Fleck *et al*. (2004: 3):

1- head capsule anterio-posteriorly compressed and transversely elongate;
2- eyes dorsally separated by at least the width of one of them, usually by considerably more, eye width almost always less than a third of head width (we emend this, below);
3- ocelli arranged in a close equilateral triangle on the same plane;
4- fore- and hind wings petiolate;
5- fore- and hind wings with the same shape;

6- fore- and hind wings wing with the same venation;
7- crossvein Ax0 missing or obscured by sclerotization;
8- midfork (branching of RP1-2 and RP3–4) at less than a quarter wing length;
9- origin of IR2 at less than a quarter wing length;
10- arculus at or immediately proximal to Ax2;
11- males with well-developed pair of ventral paraprocts at the apex of the abdomen that, along with a pair of cerci, function to grasp the female during mating;
12- the ligula as a multisegmented copulatory organ in the secondary male genital apparatus.

Character state 12 and others of the Zygoptera provided by these authors (*e.g*., spine density on some veins or those of larvae) are not preserved in these fossils. The amount of thoracic skewedness (Rehn 2003) could not be confidently assessed on the few fossil specimens available and in any case may not be informative (Fleck *et al*. 2004; Garrouste & Nel 2015).

Bechly (1996: page 361) characterises the eyes as "very widely separated", and Rehn (2003: page 217) that the distance between them is greater than their own width. We find that they are separated by about twice the eye width or more (Table 2). Bechly (1996), Rehn (2003), and Fleck *et al*. (2004) list instances of reversals and homoplasies of all wing and many body character states proposed to characterise the suborder. Some appear plesiomorphic with regard to Odonata. Head/eye morphology and that of the ligula are then of primary importance in defining the Zygoptera concept.

Garrouste & Nel (2015, Fig. 4) noted that the head is stout, not as in Zygoptera, in the only specimen of *Petrolestes hendersoni* with the head preserved. They recognized that this has implications for its suborder affinity, and by extension for that of *Congqingia* and possibly *Dysagrion*. The compound eyes of *P. hendersoni* do not bulge out from the head as much as they do in Zygoptera, but are adpressed to it to form a more compact structure; although the inner eye margins are somewhat unclear, the distance between them is roughly 1.3 times the width of an eye (Table 1). Garrouste & Nel presumed that this morphology as preserved may be due to post-mortem distortion and not reflect true head shape; however, they maintained some doubt, referring the Dysagrionidae to "?suborder Zygoptera" based on other reasons. Cockerell (1927: page 82) said of the holotype wing of *P. hendersoni* (the head is not present on this specimen): "it is perhaps significant that in some aspects *Petrolestes* reminds one of certain Anisozygoptera" and compared it with those of *Epiophlebia*.

We are aware of four other previous specimens of Dysagrionidae that have the head preserved: the holotype of *Congqingia rhora*, two assigned to *Dysagrion fredericii*, and one to *Phenacolestes parallelus*. Zhang (1992: page 376) described the head of *Congqingia* as not transversely elongate but nearly semicircular, with large eyes, "not as lateral swellings", and separated by less than their width (see Figs. 1–3 of Zhang 1992). This is like the head of *P. hendersoni*. He suggested that by this morphology, *Congqingia* is excluded from the Zygoptera and might belong to the Anisozygoptera. He also described (page 380) an undoubted zygopteran that "clearly shows a large transverse head, obviously wider than long, with eyes strongly projecting from the sides of the head and almost stalked …" from the same locality, showing that the distinctive damselfly head shape may be clearly preserved as such in these beds. Zhang specifically mentioned that fossils in this deposit are not distorted. Nel *et al*. (1993) also considered *Congqingia* as a possible anisozygopteran. The *D. fredericii* specimens were figured by Scudder (1890, plate VI, Figs. 2 and 10, Packard numbers 4183 and 4179, reproduced here as our Fig. 6). Number 4183 is associated with the species by the proximal portion of an attached wing, and 4179 by its great similarity to 4183. These heads show this same rounded morphology with adpressed, closely set eyes. The *Phenacolestes parallelus* specimen (UCM 4545 from Florissant: University of Colorado, Boulder collection) also shares this head and eye morphology (low resolution photograph published by Cockerell 1908c, his Fig. 4; see our Figs. 3E, 10K).

We can now evaluate the heads of the new dysagrionids reported here. Both specimens of *Okanopteryx macabeensis* (Fig. 10L, 10 O) with the head preserved, and one each of *O. fraseri* (Fig. 10N), *Okanagrion beardi* new species (Fig. 10M), and Cephalozygoptera *incertae sedis* (Figs. 10J, 59E), all have heads like that of *P. hendersoni, P. parallelus* and *C. rhora*. Their maximum width is about 2.0 to 2.7 times the length from anterior edge of antefrons to the posterior of occiput; the mean is 2.3. In the extant Zygoptera that we examined, this width/length ratio ranges from 2.8 to 5.5 with a mean of 3.7. The eyes are adpressed to the head capsule, *i.e*., not bulging outward from it as in Zygoptera, convex laterally but not spherical, and the posterolateral corners are extended posteriorly to varying degrees, sometimes even acutely. They are narrower dorsally relative to head width and the space between them

is relatively narrower than in Zygoptera. The distance between the compound eyes at the level of the centre of the ocelli is about one eye's width or less (width between eyes/width eye has a range of 0.8–1.1, mean 0.9: Table 1, Dysagrionidae only), more closely set than in the Zygoptera (*i.e*., contradicts character states 1 and 2). This cannot be explained as an artefact.

Insects preserved as compression fossils in shale invariably undergo mechanical damage, and sometimes plastic distortion during and after diagenesis. Mechanical damage is that damage that is produced post-mortem but before the insect enters the substrate. It may include partial or complete disarticulation from various factors, *e.g.*, those specimens that experience high-energy environments and so buffeting and impacts from *e.g.*, wave action during floating on the surface of the lake or in transportion by running water to the depositional setting. While floating on the water surface, insects may be subject to scavenging, perhaps by other arthropods or vertebrates that might consume the body and reject the wings. At least some mechanical damage invariably happens, and all specimens reported here are at least somewhat disarticulated and are usually isolated wings, often incomplete. Such mechanical damage may at times cause mouthparts to be displaced, perhaps at times projected forward, which may give a false impression of head shape in some specimens; this is clearly not the case in these fossils. Further, mechanical damage would not plastically distend the head evenly along a single plane and change the shape and positioning of the eyes, much less do this in a consistent manner in all specimens.

Secondly, in less common cases there may be plastic distortion during or after the fossilization process while the insect is embedded within the substrate. Geological shear forces within the sediment may stretch the sediment with its whole insect along a discrete angle, extending it in one direction and compressing it at the right angle to this. Such plastic distortion is not an issue with the fossils that we have examined from these Okanagan Highlands localities, and has not been noted in other formations where the fossils of this group with heads have been recovered in differing depositional settings with varying diagenetic processes (Laiyang Formation, Green River Formation, Florissant Formation). In any case, such distortion would be evident in the rest of the fossil and in other insects, fish, and plants, *etc*. from these beds, which it is not.

By the consistency of the distinctive head and eye shape and eye positioning among all known heads of the Dysagrionidae across a variety of species and genera and the variety of formations spanning some 90 million years from the Aptian to the Priabonian, we believe this to be their true morphologies. By their distinctive differences with the conservative head and eye morphology generally agreed to be of primary importance in defining the Zygoptera, we believe this is compelling evidence that the Dysagrionidae are not members of that suborder.

Some other traits that contradict Bechly's and Rehn's definitions of the Zygoptera are seen in Dysagrionidae specimens where they might be detected by preservation. As mentioned above, these further traits are, however, subject to homoplasy or reversal or may be plesiomorphic; none are unambiguously diagnostic of the suborder in themselves.

According to Bechly (1996) and Rehn (2003), crossvein Ax0 is obliterated or covered by a rather extensive sclerotization of the wing base in Zygoptera (character state 7). It is seen in some Zygoptera, however, see *Litheuphaea coloradensis* Petrulevičius *et al.,* and *Labandeiraia americaborealis* Petrulevičius *et al*. (Petrulevičius *et al*. 2007) (both Eocene Euphaeidae). In the Dysagrionidae, it is seen in published drawings of the wings of *Primorilestes violetae* (Nel *et al*. 2005b: Fig. 1, and see Fig. 7, here), *Electrophenacolestes serafini* (Nel & Arillo 2006: Fig. 2, and see their photograph Fig. 1) (Fig. 7) and *Phenacolestes parallelus* specimen YPMIP-220974 (see Fig. 3E) (and see above, specimen NHMUK I.9866/I.9718 of Nel & Fleck 2014). Ax0 is seen in the new species *Dysagrion pruettae* (Fig. 11B), *Okanagrion beardi* (specimen F-790, Fig. 11A), *Okanopteryx jeppesenorum* new species (paratype 3, SR 15-003-001, Fig. 11C) and possibly in some others. It may be seldom present in the Dysagrionidae as in these specimens, but it might also be more common or even ubiquitous, as the very wing base where it occurs is almost always either poorly or not preserved, or is obscured in some other fashion. For example, it is seen in the well-preserved new Okanagan Highlands species *Dysagrion pruettae*, but is unknown in any previous *Dysagrion* specimens, all of which are missing the proximal-most wing where it might be found.

Rehn (2003) found the origin of IR2 at less than a quarter wing length in many Zygoptera, with reversals and convergences. In 16 Dysagrionidae specimens that we measured, this ranged from about 30% to 38% wing length, averaging about 33%.

Garrouste & Nel (2015) found that the legs of the specimen of *Petrolestes hendersoni* examined bear spines shorter and stronger than in the Zygoptera, more like those present in many odonates outside of the suborder. In the Okanagan Highlands specimens, they are also relatively short, but generally weak.

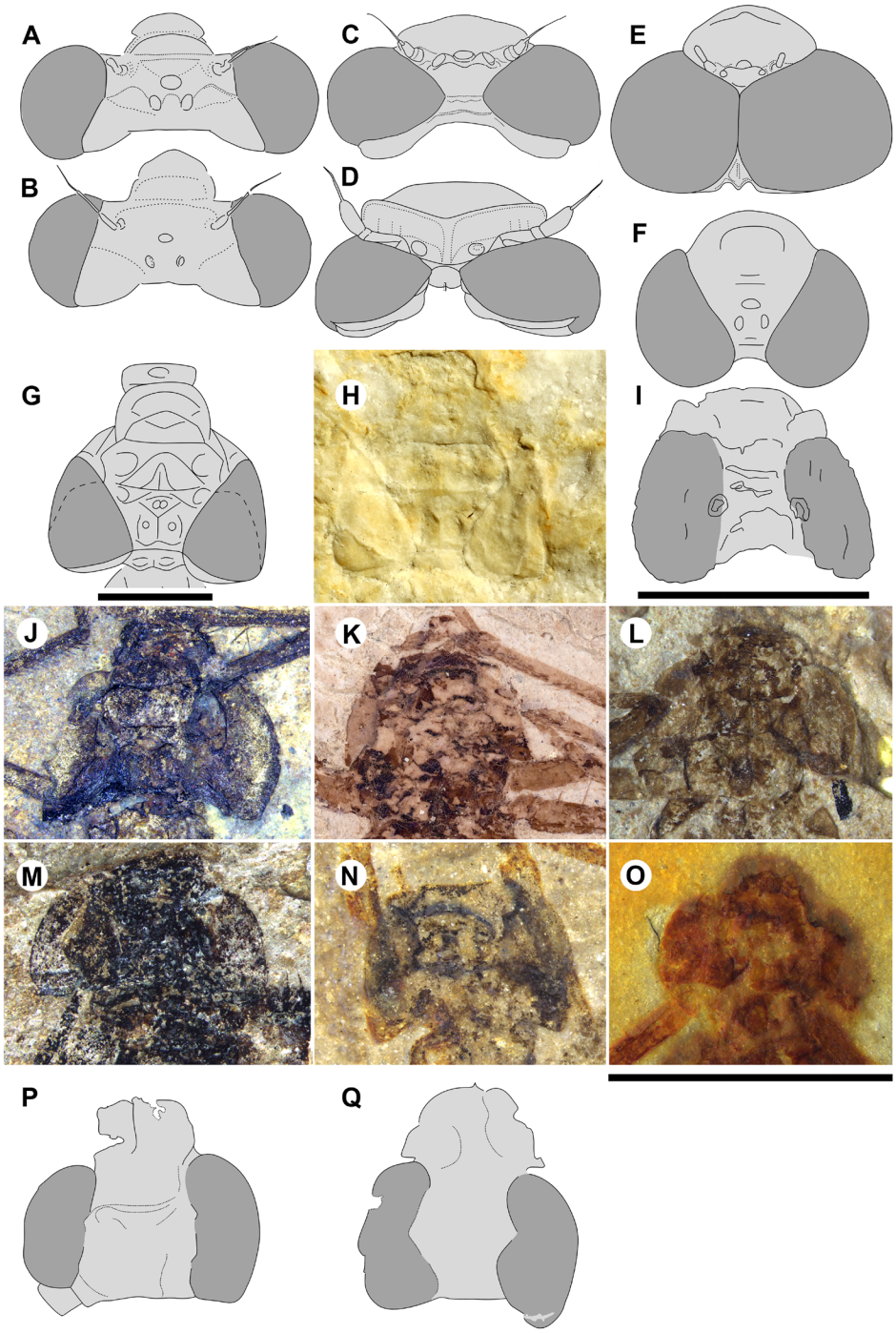

FIGURE 10. Heads of Zygoptera (A, B) and comparative Anisoptera, Anisozygoptera, Tarsophlebiidae, Stenophlebiidae (C–H); and Cephalozygoptera (I–Q). A, Zygoptera, *Heteropodagrion superbum* Ris redrawn from Fig. 318 of Garrison *et al*. (2010); B, Zygoptera, *Minagrion ribeiroi* (Santos) redrawn from Fig. 1842 of Garrison *et al*. (2010); C, Anisoptera, Gomphidae, *Cyanogomphus waltheri* Selys redrawn from Fig. 383 of Garrison *et al*. (2006); D, Anisozygoptera, *Epiophlebia laidlawi* Tillyard redrawn from Fig. 2 of Büsse (2016); E, Anisoptera, Aeshnidae, *Limnetron antarcticum* Förster redrawn from Fig. 16 of Garrison *et al*. (2006); F, *Stenophlebia* sp. redrawn from Tillyard & Fraser 1940, Fig, 4C; G, Tarsophlebiidae, *Tarsophlebia eximia* Hagen redrawn from Fleck *et al*. (2004) Fig. 1C; H, photograph of *Tarsophlebia eximia* in MCZ collections; I, *Sieblosia jucunda* redrawn from Hagen (1858, Plate 24, Fig. 1); J, Cephalozygoptera *incertae sedis* SR 14-003-004; K, *Phenacolestes parallelus* UCM-4545; L, *Okanopteryx macabeensis*, GSC 141101; M, *Okanagrion beardi* paratype 1, RBCM P1546; N, *Okanopteryx fraseri* GSC 141104; O, *Okanopteryx macabeensis* F-790; P, *Dysagrion fredericii* redrawn from Scudder 1890, plate 6, Fig. 10; Q, *Dysagrion fredericii* redrawn from Scudder 1890, plate 6, Fig. 2. G and H, I, J to O to scales, all 5 mm; others, originals without scales.

TABLE 1. Head measurements of Cephalozygoptera and measurement ratios: WH, width of head; WBE, width between eyes; WE, width of one eye; LE, length of one eye; LH, length of head. See Fig. 10 for head images and text for measurement details.

	Specimen	WH mm	WBE mm	WE mm	LE mm	LH mm	WH/ LH	WH/ WBE	LH/ WBE	WBE/ WE	LE/WE
Dysagrionidae											
Okanagrion beardi	RBCM P1546 Fig. 10 (M)	4.1	1.2	1.5	2.0	1.5	2.7	3.4	1.3	0.8	1.3
Okanopteryx fraseri	GSC 141104 F-778 Fig. 10 (N)	3.6	1.2	1.1	2.3	1.8	2.0	3.1	1.6	1.1	2.1
Okanopteryx macabeensis	F-790 Fig. 10 (O)	3.8	1.1	1.3	2.2	1.7	2.3	3.5	1.5	0.9	1.8
Okanopteryx macabeensis	GSC 141101 Fig. 10 (L)	3.7	1.0	1.2	1.8	1.5	2.4	3.9	1.6	0.8	1.5
Cephalozygoptera *incertae sedis*	SR-14-003-004 Fig 10. (J)	4.1	1.3	1.4	2.3	2.0	2.0	3.3	1.6	0.9	1.6
mean (n=5)		3.9	1.6	1.3	2.1	1.7	2.3	3.4	1.5	0.9	1.7
range		3.6–4.1	1.0–1.3	1.1–1.5	1.8–2.3	1.5–2.0	2.0–2.7	3.1–3.9	1.3–1.6	0.8–1.1	1.3–2.1
Congqingia rhora	Zhang (1992)	3.9	1.2	1.3	1.9	1.8	2.2	3.4	1.6	0.9	1.4
Dysagrion fredericii	Scudder (1890) Fig. 10 (P)	5.5	2.7	1.4	3.4	3.3	1.7	2.1	1.2	1.9	2.4
Dysagrion fredericii	Scudder (1890) Fig. 10 (Q)	5.5	2.4	1.5	3.5	3.3	1.7	2.3	1.3	1.6	2.3
Petrolestes hendersoni	Garrouste & Nel (2015)	5.2	2.0	1.6	2.7	2.5	2.0	2.6	1.2	1.3	1.7
Phenacolestes parallelus	UCM-4545 Fig. 10 (K)	3.3	1.7	1.1	1.7	1.9	1.7	2.0	1.2	1.5	1.8
Sieblosiidae											
Sieblosia jucunda	Hagen (1858) Fig. 10 (I)	5.0	1.4	1.7	3.1	2.9	1.7	3.6	2.1	0.8	1.8
Total mean (n=11)		4.4	1.6	1.4	2.5	2.2	2.1	3.0	1.5	1.0	1.8
Total range		3.3–5.5	1.0–2.7	1.1–1.7	1.7–3.5	1.5–3.3	1.7–2.8	2.0–3.9	1.2–2.1	0.8–1.9	1.3–2.4

TABLE 2. Head measurements of extant Zygoptera and measurement ratios: S, sex; RBCM #, Royal British Columbia Museum specimen number; WH, width of head; WBE, width between eyes; WE, width of one eye; LE, length of one eye; LH, length of head. See text for details.

	S	RBCM #	WH mm	WBE mm	WE mm	LE mm	LH mm	WH/ LH	WH/ WBE	LH/ WBE	WBE/WE	LE/WE
Amphipterigidae												
Amphipteryx agrioides Selys	m	991-052065	6.4	3.0	1.7	2.7	1.5	4.3	2.2	0.5	1.8	1.7
Argiolestidae												
Argiolestes griseus Tillyard	f	991-052103	4.6	2.9	1.0	1.6	1.3	3.6	1.6	0.4	3.0	1.6
Calopterygidae												
Calopteryx aequabilis Say	f	999-002177	5.4	2.7	1.1	1.9	1.9	2.9	2.0	0.7	2.5	1.7
Vestalis amaryllis Lieftinck	f	991-052062	5.3	2.4	1.3	1.9	1.3	4.2	2.2	0.5	1.9	1.6
Chlorocyphidae												
Cyrano unicolor (Hagen in Selys)	m	988-017083	5.5	2.6	1.9	2.6	1.9	2.8	2.2	0.8	1.4	1.4
Rhinocypha tincta Rambur	m	991-052014	3.9	1.7	0.9	1.8	1.4	2.8	2.2	0.8	2.0	1.1
Coenagrionidae												
Acanthagrion lancea Selys	m	991-052186	3.3	2.1	0.8	1.3	1.0	3.3	1.6	0.5	3.9	1.7
Agriocnemis femina (Brauer)	m	988-017270	2.7	1.6	0.5	1.1	0.7	3.8	1.7	0.5	3.2	2.3
Argia emma Kennedy	f	999-002173	4.6	2.6	1.0	1.7	1.5	3.1	1.8	0.6	2.6	1.7
Coenagrion pulchellum (Vander Linden)	m	991-050943	3.9	2.6	0.7	1.5	1.0	3.8	1.5	0.4	3.8	2.2
Enallagma boreale Selys	m	998-017433	3.9	2.7	0.7	1.4	1.2	3.3	1.5	0.5	4.0	2.0
Erythromma najas (Hansemann)	m	991-050013	4.5	2.6	0.9	1.7	1.3	3.5	1.7	0.5	2.9	1.9
Ischnura senegalensis (Rambur)	f	988-011601	3.7	2.5	0.6	1.5	1.2	3.0	1.5	0.5	4.0	2.4
Mecistogaster ornata Rambur	f	991-052124	5.6	3.2	1.1	2.1	1.5	3.7	1.8	0.5	2.9	1.9
Pseudagrion kersteni (Gerstäcker)	f	991-052380	3.5	2.2	0.7	1.4	1.2	3.0	1.6	0.5	3.0	2.0
Telebasis salva (Hagen)	m	011-001340	3.6	2.4	0.7	1.4	1.1	3.3	1.5	0.5	3.4	2.0
Dicteriadidae												
Heliocharis amazona Selys	m	991-052064	5.4	2.7	1.4	2.0	1.5	3.7	2.0	0.5	1.9	1.5
Euphaeidae												
Euphaea impar Selys	m	988-017096	5.0	2.5	1.0	1.8	1.1	4.6	2.0	0.4	2.4	1.8
Euphaea ochracea Selys	f	988-011791	5.5	2.8	1.2	1.9	1.3	4.2	2.0	0.5	2.3	1.6

.....continued on the next page

TABLE 2. (Continued)

	S	RBCM #	WH mm	WBE mm	WE mm	LE mm	LH mm	WH/ LH	WH/ WBE	LH/ WBE	WBE/WE	LE/WE
Isostictidae												
Isosticta robustior Ris	m	988-017713	4.5	2.6	0.8	1.9	1.2	3.8	1.8	0.5	3.2	2.5
Lestidae												
Austrolestes leda (Selys)	f	988-017111	4.4	2.4	0.9	1.6	1.4	3.2	1.8	0.6	2.6	1.7
Indolestes gracilis (Hagen in Selys)	m	991-052-070	3.9	2.2	0.7	1.4	1.0	3.8	1.8	0.5	2.9	1.9
Lestes dryas Kirby	m	999-000026	4.7	2.7	0.9	1.6	1.3	3.7	1.8	0.5	3.0	1.8
Sympecma fusca (Vander Linden)	f	988-016980	4.3	2.6	0.8	1.4	1.2	3.7	1.7	0.5	3.2	1.7
Perilestidae												
Perissolestes remotus (Vander Linden)	m	991-052100	4.1	1.9	1.1	1.6	1.0	4.3	2.2	0.5	1.7	1.5
Philogeniidae												
Philogenia minteri Dunkle	f	990-000502	5.7	2.5	1.7	1.9	1.4	4.1	2.2	0.5	1.5	1.2
Philosinidae												
Rhinagrion borneense (Selys)	m	988-017260	5.2	2.3	1.2	1.9	1.2	4.4	2.3	0.5	1.9	1.6
Platycnemididae												
Platycnemis pennipes (Pallas)	m	991-050199	4.6	2.7	0.8	1.4	1.1	4.1	1.7	0.4	3.3	1.7
Risiocnemis serrata (Hagen in Selys)	m	988-017716	3.9	2.1	0.8	1.3	0.7	5.5	1.8	0.3	2.7	1.7
Platystictidae												
Palaemnema paulirica Calvert	f	991-052138	4.0	1.8	1.1	1.5	1.1	3.5	2.2	0.6	1.7	1.4
Polythoridae												
Polythore derivate (McLachlan)	m	991-052006	5.8	3.2	1.3	2.2	1.7	3.5	1.9	0.5	2.4	1.7
Synlestidae												
Ecchlorolestes nylephtha (Barnard)	m	012-012189	4.9	2.0	1.3	1.9	1.3	3.9	2.4	0.6	1.6	1.5
Thaumatoneuridae												
Paraphlebia zoe Selys in Hagen	m	991-052116	7.00	3.5	1.6	2.4	1.4	4.9	2.0	0.4	2.2	1.5
Mean of ratio (n=33)								3.7	1.8	0.5	2.6	1.7
Range of ratio								2.8–5.5	1.5–2.4	0.3–0.8	1.4 –4.0	1.1–2.5

The following morphology of the Dysagrionidae conforms with that of Zygoptera. The ocelli are arranged in a close equilateral triangle in the same plane, the "zygopterid type" configuration of Fleck *et al*. (2004). This orientation is apparently ubiquitous in Zygoptera. Ocelli in Anisoptera form triangles which are usually far from equilateral, often strongly flattened (with the lateral ocelli farther apart and the median one moved rearward, closer to the lateral ones). However, a few, *e.g*., *Hypopetalia* McLachlan and *Phyllopetalia* Selys (Austropetaliidae) may have the ocelli arranged almost equilaterally (Dennis Paulson, pers. comm.). In Anisozygoptera, although the ocelli of *Epiophlebia* are more or less arranged equilaterally, they are much more widely separated than in Zygoptera, and the median and lateral ocelli are on different planes, with a high ridge between them. The head of *Stenophlebia latreillei* (Germar) (see Fleck *et al*. 2003; called *S. aequalis* by Tillyard & Fraser 1940) (Stenophlebioptera: see Fleck *et al.* 2004, and most recently considered in the fossil Infrasuperorder Stenophlebioptera Bechly by Huang *et al*. 2019) bears ocelli in this "zygopterid" arrangement (Fig. 10F). This condition appears plesiomorphic with regard to the Odonata, present in the Late Jurassic and Early Cretaceous Tarsophlebiidae (Fleck *et al*. 2003), sister to Odonata according to Bechly (1996) and Fleck *et al*. (2004) (what looks like a joined pair of median ocelli in Fig. 10G appears to be a preservational artefact).

Male anal appendages are known in *Okanopteryx macabeensis* paratype 1 (GSC 141101, Fig. 54) and *Okanagrion hobani* new species paratype 7 (F-1044, Fig. 31), which bear distinctly preserved well-developed paraprocts, consistent with Zygoptera. Such paraprocts are, however, plesiomorphic to Odonata, a groundplan structure in insects. The Tarsophlebiidae possess uniquely extended appendages at the terminus of the male abdomen: either they lost paraprocts; these appendages are modified paraprocts; or they are present but not visible by chance preservation (Fleck *et al*. 2004).

The fore- and hind wings of Dysagrionidae are petiolate, with very close shape and venation, including quadrangles closed and not crossed, CuA is simple, the arculus is positioned at or immediately proximal to Ax2, and with a well-developed nodus; their thorax is oblique; and their bodies gracile, although these or similar conditions are present in other groups. Rehn (2003) considered the midfork at less than a quarter of wing length a derived condition, present in the Calopterigoidea and some other Zygoptera. In the remaining Zygoptera and all Anisoptera and Anisozygoptera it is in the plesiomorphic, more distal, position. In the 16 complete to reasonably complete Dysagrionidae wings as above (assuming missing bases and tips), all midforks were at about 21% to 30% of wing length, averaging about 25%. Interestingly, the eight species of the new Okanagan Highlands genera *Okanagrion* and *Okanopteryx* all had values of 26% and below, averaging 23%. According to Bechly (1996) and various subsequent authors, Dysagrionidae is in the Amphipterygoidea, *i.e*., in the Calopterygoidea *sensu* Rehn, with which this condition then mostly conforms.

Order Odonata Fabricius

Cephalozygoptera Archibald, Cannings & Erickson, new suborder

To expand the Zygoptera concept to include the head and eye morphologies of the Dysagrionidae and Sieblosiidae (see below) would result in the loss of these few primary, unambiguous, and easily observable diagnostic character states defining the suborder. We, therefore, group these families and possibly the Whetwhetaksidae, whose wings indicate a close relationship with them, as the new suborder Cephalozygoptera. If a future fossil (presumably in amber, as this is highly unlikely to be seen in any compression fossil) shows that the ligula differs from that of Zygoptera, this may be considered a synapomorphy of the Cephalozygoptera; if it is consistent with the Zygoptera, it would be a synapomorphy of Zygoptera+Cephalozygoptera.

Diagnosis. Cephalozygoptera are odonates most like Zygoptera by a combination of: fore- and hind wings petiolate, with similar shape and venation including quadrangles that are closed and not crossed, CuA simple, and a well-developed nodus; an oblique thorax; gracile body; male clasping anal appendages comprised of a pair of dorsal cerci (without paddle-shaped extensions) and a pair of well-developed ventral paraprocts; and ocelli arranged in an equilateral triangle; but may be easily distinguished from them by any of:

1- head width across eyes about twice the length from anterior margin of antefrons to posterior of occiput; [Zygoptera: usually about three to five times as wide]; and compound eyes that are:

2- more or less adpressed to head, posterolateral corners protruding posteriorly to varying degrees, more or less rounded, sometimes acutely [Zygoptera: distinctly bulging laterally from head capsule];
3- separated by about one eye's width dorsally (ratio of width between eyes/width eye has a range of 0.8–1.9 and a mean 1.0), n=11 (Table 1) [Zygoptera: usually more than twice an eye's width].

Included taxa. The families Dysagrionidae and Sieblosiidae, and possibly the Whetwhetaksidae, new family.

Description. With character states of the diagnosis and further of the wings: Ax0 present; nodus at about a quarter wing length or more; anterior anal vein separates at a right angle from the posterior anal vein briefly before joining CuP (*i.e*., is briefly free distal to petiole); RP3-4 origin (midfork) in middle third between arculus and subnodus; antesubnodal space without crossveins; distinctive quadrangle (closed, distal side longer than proximal, posterior longer than anterior); long to very long pterostigmata (2.5 to about 10 times width if the Whetwhetaksidae is a member).

Etymology. The name Cephalozygoptera is derived from the Greek *κεφάλή*, *kefáli*, "head", and Zygoptera (*ζυγός*, *zugós*, even + *πτερόν*, *pterón*, wing, referring to the similar-shaped fore- and hind wings), indicating that they are distinguished from damselflies by their heads.



FIGURE 11. Crossvein Ax0 indicated by arrows in: A, *Okanagrion beardi* holotype, F-791; B, *Dysagrion pruettae* holotype, SR 13-005-012: C, *Okanopteryx jeppesenorum* paratype 3, SR 15-003-001. Scale bar is 1 mm.

Discussion. *Sieblosiidae and Whetwhetaksidae*. Handlirsch (1907) excluded *Sieblosia jucunda* from the Zygoptera, believing that it belongs to the Anisozygoptera without explanation. This view was later rejected by Fischer (1974) and Nel *et al*. (1993), who restored it to the Zygoptera. The type specimen (apparently lost: Fischer 1974)

was rather complete, including the head, which Hagen noted is almost as wide as long. In his drawing (Hagen 1858: his Plate 24, Fig. 1), although lacking detail, the head closely matches those of the Dysagrionidae (reproduced here as our Fig. 10 I). He assumed, however, that it was compressed post mortem (page 121: "kopf platt gedrückt"). Fleck *et al*. (2004) recognised that the head of Sieblosiidae is not transversely elongate with the compound eyes placed far apart. They further found that their wings do not share any unambiguous apomorphy with the Zygoptera and that particularly with their nodal morphology and curved CuP they may not belong to the suborder. Following this, Bechly (2015) treated the family as "Anisozygoptera".

The wings of Sieblosiidae and Dysagrionidae have strong similarities (Nel *et al*. 2005a) (Fig. 12). They share with Dysagrionidae character states 2 through 7 of its diagnosis, notably the distinctive quadrangle shape, character state 3. The wings of both are broad, with a short petiole and bear a long pterostigma. Crossvein Ax0 has been found in numerous species, see *Germanostenolestes lutzi* (2012, their Fig. 3), *Stenolestes fischeri* Nel, holotype MNHN-LP-R.06677 (Nel *et al*. 1997, their Fig. 6), and in *Stenolestes fasciata* Nel *et al*. (Nel *et al*. 2005a, their Fig. 9), *Stenolestes cerestensis* Nel *et al*. (Nel *et al*. 2005a, their Fig. 14), and *Miostenolestes zherikhini* (Nel *et al*. 2005a, their Fig. 5). As in the Dysagrionidae, the wing base of most published Sieblosiidae fossils where Ax0 might be found is missing or damaged, and so this represents a minimum of specimens where this may be present; judging from published drawings and photographs, none may be excluded as possessing it. As in Petrolestinae but not the Dysagrioninae, the origin of IR2 is in the middle third between the arculus and nodus, close to that of RP3-4. Nel & Paicheler (1994) suggested that Sieblosiidae and Dysagrionidae might be an example of convergent evolution.

Sieblosiidae differ from the above diagnosis of the Dysagrionidae by character state 8, width of the CuA–A space, which is usually two or more cells wide as in Dysagrionidae, but may be one cell wide (*e.g.*, see Fig. 12B, *Miostenolestes zherikhini*); by 9, CuA terminates on the margin proximal to the mid-wing; and 1, crossvein O is present. The nodus of Sieblosiidae differs as well by ScP passing through it and terminating on the anterior margin at an oblique angle. Although the pterostigmata of Dysagrionidae are long, those of the Sieblosiidae are longer.

The new family Whetwhetaksidae is only known by wings, which share character states 1 and 3 through 9 of the Dysagrionidae diagnosis and their general shape is like that of the Dysagrionidae and Sieblosiidae: broad, with a short petiole. The origin of IR2 is in the middle third between the arculus and nodus as in Sieblosiidae and the Petrolestinae, but not the Dysagrioninae.

These wings are notably distinct, however, as the arculus is in a proximal position near Ax1 as is found in some odonates outside of the Zygoptera. This feature is unknown in extant Zygoptera except in the Amazonian *Heliocharis amazona* Selys (Calopterygoidea, Dicteriadidae), and is present in two Paleogene Euphaeidae (the Priabonian *Litheuphaea ludwigi* Bechly and the Chattian *Parazacallites aquisextanea* Nel: Bechly 1998; Nel 1988). Whetwhetaksidae possess an extremely long pterostigma, unknown in Zygoptera, but like those found in the anisopteran Petaluridae. It is up to about ten times longer than wide, and is about a quarter to almost a third the length of the nodus to the wing apex. Further, the nodus is distant from the wing base, at about 38–40% wing length.

Groups with similar wings that are excluded. The Frenguelliidae are odonates from the Ypresian and Lutetian of Patagonia, Argentina, known only from wings (Fig. 12C, D). They are considered by some authors not to belong to the Zygoptera by their curved CuP (Petrulevičius & Nel 2003, 2007, 2013; Petrulevičius 2017, 2019). The wing of *Treintamilun vuelvenlucha* Petrulevičius resembles those of the Dysagrionidae in many aspects, but differs by its vertical subnodus and—importantly—its curved CuP. Those of *Nelala chori* Petrulevičius lack the characteristic Cephalozygoptera quadrangle shape. The suborder affinity of Frenguelliidae is unclear, and we follow Petrulevičius (2017, 2019) and Petrulevičius & Nel (2003, 2007, 2013) in treating it as Odonata suborder indet., pending more complete specimens.

The wings of *Oligolestes grandis* (Statz) from the Chattian of Rott, Germany and *Italolestes stroppai* Nel *et al.* from the Messinian (late Miocene) of Italy (Gentilini & Bagli 2004; Nel *et al*. 2005a, 2005c) share many traits with the Sieblosiidae (Fig. 13) but differ in important ways, *e.g*., the quadrangle of *Oligolestes* Schmidt is somewhat narrower and the bases of RP3-4 and IR2 are in a distinctly different position. Both genera differ significantly from the Sieblosiidae in possessing a subnodus of normal obliquity and ScP not passing through the nodus (see Nel *et al*. 2005a). We agree with Nel *et al*. (2005a) that they might be best treated as of uncertain position pending the discovery of more complete fossils.

Cephalozygoptera terminal appendages. Only the male terminal appendages in Cephalozygoptera are known, unless those of the female are present on some Sieblosiidae fossils of which we are not aware. The well-developed cerci and paraprocts at the apex of the abdomen are used in extant Zygoptera to grasp the female during mating. As

the terminal appendages of male Cephalozygoptera are so like those of Zygoptera, we predict that their female genitalia will be found to be correspondingly similar. We are not aware of any Cephalozygoptera fossil that preserves secondary male genitalia.

Cladistic analyses. Searches performed using morphological data (Appendix C) recovered a single most-parsimonious tree (MPT). Analysis 1, of the relationships of the suborders of Odonata, Burmese amber genera not assigned to suborder, and Tarsophlebiidae, produced one MPT (Fig. 14). Constraining Tarsophlebiidae as the outgroup recovers Anisoptera and Anisozygoptera as sister taxa with high support, consistent with other recent analyses (Westfall *et al*. 2014 and references therein). Cephalozygoptera and Zygoptera are recovered as sister taxa with high support, while *Burmadysagrion*, *Electrodysagrion*, and *Paleodysagrion*, formerly considered to belong to the Dysagrionidae, are recovered as members of Zygoptera with moderate to high support. Zygoptera, therefore, was used as an outgroup in Analyses 2 and 3.

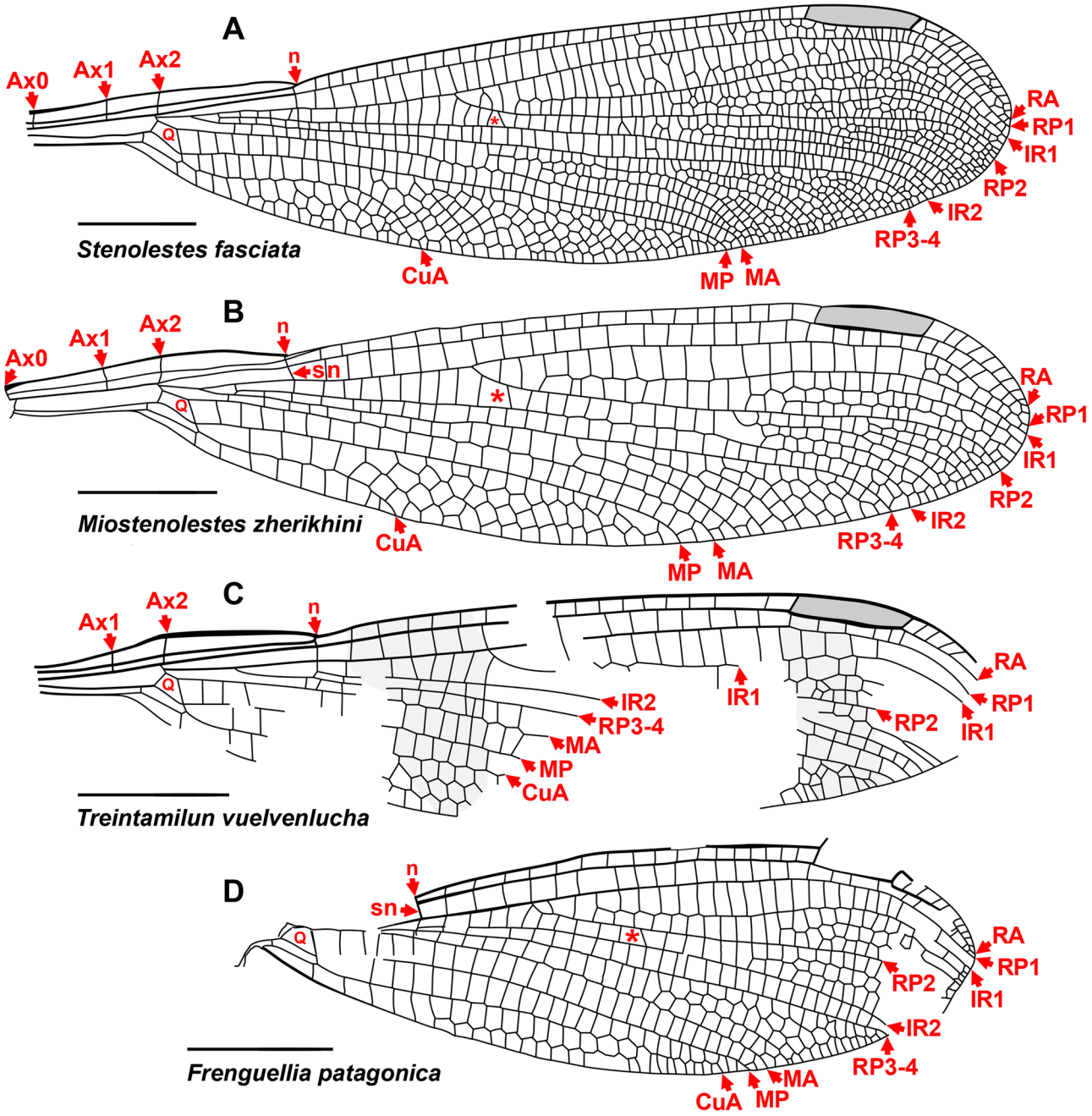

FIGURE 12. Representative Sieblosiidae, A, *Stenolestes fasciata* Nel *et al*.; B, *Miostenolestes zherikhini*; and Frenguelliidae, C, *Treintamilun vuelvenlucha*; D, *Frenguellia patagonica* Petrulevičius & Nel. Redrawn from: A, B, Nel *et al*. (2005a); C, Petrulevičius (2017); D, Petrulevičius & Nel (2007). An asterisk indicates the oblique vein "O" immediately to its right. Scale bars, 5 mm.

In Analysis 2, the relationship of Whetwhetaksidae to Cephalozygoptera and its families, produced a single MPT (Fig. 15) that provides weak support for Dysagrionidae and Whetwhetaksidae as sister taxa.

Analysis 3, the internal phylogeny of Dysagrionidae, is discussed below.

History and biogeography of the Cephalozygoptera. The Cephalozygoptera has been found in localities across the Northern Hemisphere (Table 3) from the Aptian of China; possibly the Thanetian of France (*Valerea*, *Thanetophilosina*) and the Thanetian or Ypresian of Alaska, United States of America (Garrouste & Nel 2019: unnamed); the Ypresian of Denmark, Canada, and the United States of America; the Lutetian of Germany; the Priabonian of Colorado, United States of America, the United Kingdom, and Russia (European and Pacific); the Rupelian (early Oligocene) of Russia (Caucasus) and Germany; Chattian (late Oligocene) of France; Langhian/Serravallian (middle Miocene) of Russia (Caucasus) and Bulgaria; Serravallian (middle Miocene) of Croatia and Germany; Tortonian (late Miocene) of Spain and France.

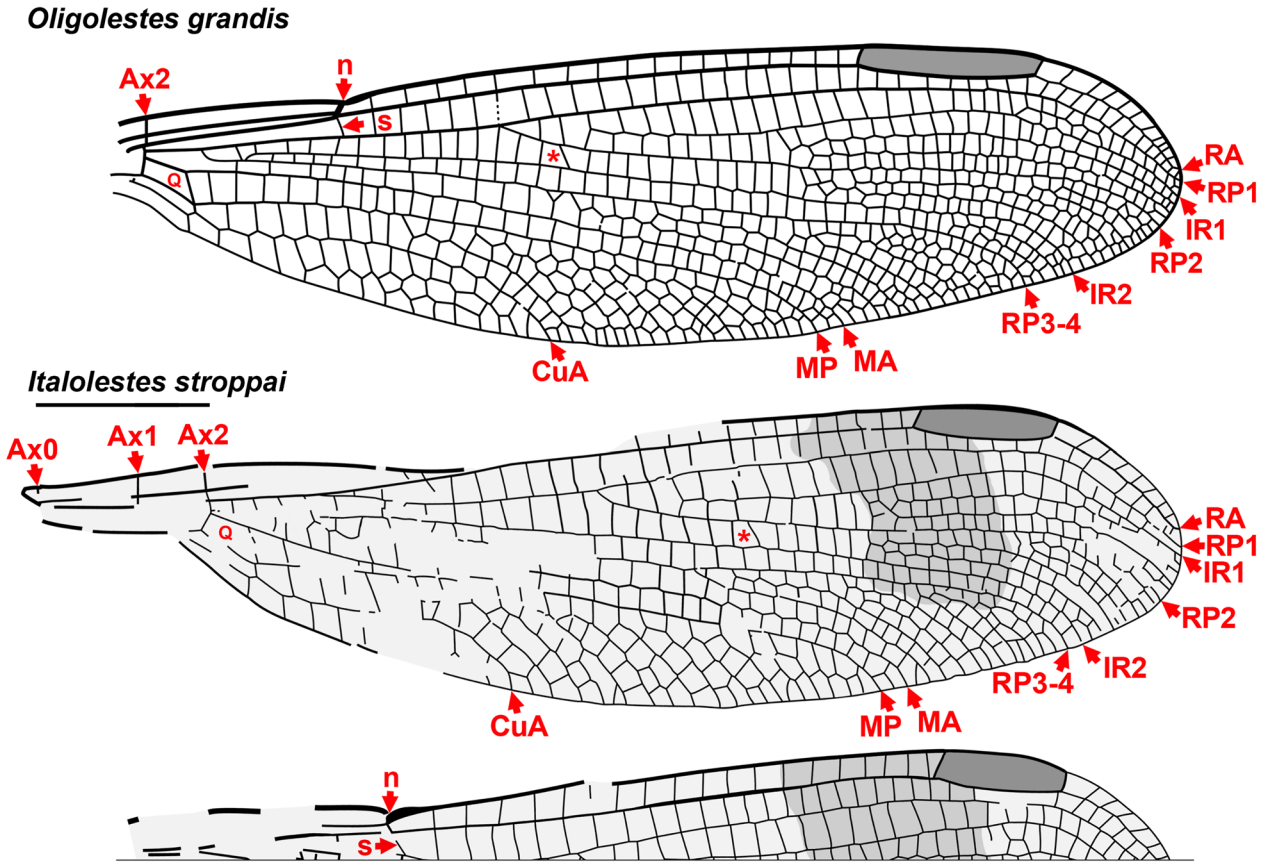

FIGURE 13. Drawings of wing of *Oligolestes* and wings of *Italolestes stroppai*. *Oligolestes* is redrawn from Schmidt (1985, Fig. 2), which appears accurate, *cf*. his photograph (his Fig. 1). Carpenter's drawing (1992, Fig. 52.4) correctly reproduced this, but Statz's drawing (1930, unnumbered figure) appears inaccurate in part and includes some presumptive morphology not on the fossil. These had no scale bar. Drawings of *Italolestes stroppai* wings are redrawn from Nel *et al*. (2005a, Figs. 2, 3, there called genus and species A), bottom wing portion reproduced to show nodal region morphology contrary to Sieblosiidae that is damaged in the more complete wing reproduced above it, scale bar is 5 mm. An asterisk indicates the oblique vein "O" immediately to its right; "s", subnodus.

Bechly (pers. comm.) reports a specimen from the Ypresian Green River Formation that bears the distinctive Cephalozygoptera head morphology, but is in ways quite different from the families that we include, suggesting that the suborder may have been larger and more diverse than we understand it here.

The Dysagrionidae dominanted the Eocene Cephalozygoptera across the Holarctic (see Table 3 and references therein). They were by far the dominant Odonata in more temperate far-western montane North America, the Okanagan Highlands (in upper microthermal mean annual temperatures, *i.e.* 13°C and below: Wolfe & Wehr 1987; Archibald & Farrell 2003; Greenwood *et al*. 2005; Archibald *et al*. 2014), with 70 fossils in seventeen species assigned to four genera and one genus-level parataxon genus, contrasted with seven specimens of the single species of

Whetwhetaksidae; nine fossil dragonflies there in two families, seven genera and eight species; and one undescribed fossil damselfly wing. It is unclear if the larger wings of dragonflies depress their fossil abundance relative to their community abundance by taphonomic bias through increased floating time before deposition on the substrate (Martínez-Delclòs & Martinell 1993, Wagner *et al*. 1996).

They were less common, but still well-represented in the hot lowlands of mid-continental Ypresian Colorado and Wyoming (mean annual temperatures upper mesothermal to megathermal, megathermal = 20°C and over: Archibald *et al*. 2011b), and are fewer yet in the upland Priabonian of Colorado (likely similar mean annual temperature as the Okanagan Highlands: Allena *et al.* 2020), where they were mixed with a variety of dragonflies and damselflies, and were present to lesser degrees in the Eocene of Europe and Asia.

After the Eocene, the Dysagrionidae become rare, with one (*Primorilestes magnificus*), perhaps two (*Phenacolestes*? *coloratus*) occurrences in the Miocene. Sieblosiidae dominate the Cephalozygoptera in the Oligocene and Miocene, the globally cooler post-Eocene icehouse world climatic regime (Zachos *et al*. 2001), restricted to the Palearctic Realm. Their last record, and so that of the suborder, is in the late Miocene.

The cool, higher elevations of the Okanagan Highlands is where we see many of the earliest occurrences of the floral taxa and community associations of modern temperate Northern Hemisphere forests that later descended to lower elevations and spread throughout and predominate in much of the Holarctic as temperature seasonality increased outside of the tropics bringing colder winters, the latitudinal gradient of mean annual temperature steepened, and cooler global temperatures were established following the close of the Eocene (*e.g*., Graham 1999; Zachos *et al*. 2001, 2008). As the Cephalozygoptera genera *Okanagrion* and *Okanopteryx* were the dominant Odonata of the montane Okanagan Highlands forests, why did they not spread with them and flourish across the Holarctic to the present? There is no obvious explanation.

TABLE 3. Cephalozygoptera and tentative Cephalozygoptera occurrences.

Mesozoic		
Cretaceous		
Early Cretaceous		
Aptian		
Laiyang Formation, Shandong, China		
	Dysagrionidae	*Congqingia rhora* Zhang
Cenozoic		
Paleogene		
Paleocene		
Thanetian		
Menat, France		
	Dysagrionidae?	*Thanetophilosina menatensis** Nel *et al.*
		*Valerea multicellulata** Garrouste *et al.*
Paleocene or Eocene		
Thanetian or Ypresian		
Chickaloon Formation, Alaska, USA		
	Dysagrionidae?	Chickaloon specimen* (Garrouste & Nel 2019)
Eocene		
Ypresian		
Fur Formation, Denmark		
	Dysagrionidae	*Primorilestes madseni* Rust *et al*.
		Furagrion jutlandicus (Henriksen)
		Furagrion morsi Zessin
Okanagan Highlands, British Columbia, Canada and Washington, USA		
	Dysagrionidae	*Dysagrion pruettae* n. sp.

.....continued on the next page

		Okanagrion threadgillae n. gen., n. sp.
		Okanagrion hobani n. sp.
		Okanagrion beardi n. sp.
		Okanagrion lochmum n. sp.
		Okanagrion angustum n. sp.
		Okanagrion dorrellae n. sp.
		Okanagrion liquetoalatum n. sp.
		Okanagrion worleyae n. sp.
		Okanopteryx jeppesenorum n. gen., n. sp.
		Okanopteryx fraseri n. sp.
		Okanopteryx macabeensis n. sp.
		Stenodiafanus westersidei n. gen., n. sp.
		Dysagrionites delinei n. coll. gen., n. sp.
		Dysagrionites sp. A (herein)
		Dysagrionites sp. B (herein)
	Whetwhetaksidae*	*Whetwhetaksa millerae* n. gen., n. sp.
	Green River Formation, Colorado, Wyoming, USA	
	Dysagrionidae	*Petrolestes hendersoni* Cockerell
		Dysagrion fredericii Scudder
		Dysagrion lakesii Scudder
		Dysagrion packardii Scudder
Lutetian		
	Grube Messel, Germany	
	Dysagrionidae	*Petrolestes messelensis* Garrouste & Nel
	Dysagrionidae?	*cf*. Dysagrionidae gen. *et* sp. A*† (Petrulevičius *et al*. 2008)
Priabonian		
	Florissant Formation, Colorado, USA	
	Dysagrionidae	*Phenacolestes mirandus* Cockerell
		Phenacolestes parallelus Cockerell
	Bembridge Marls, Isle of Wight, United Kingdom	
	Dysagrionidae?	Dysagrioninae? species A*‡ (Nel & Fleck 2014)
	Baltic amber	
	Dysagrionidae	*Electrophenacolestes serafini* Nel & Arillo
	Bol'shaya Svetlovednaya (Biamo), Primorye, Russia	
	Dysagrionidae	*Primorilestes violetae* Nel *et al*.
Oligocene		
Rupelian		
	Sieblos, Germany	
	Sieblosiidae	*Sieblosia jucunda* (Hagen)
	Belaya river, Adygeia, Russia	
	Sieblosiidae	*?Stenolestes adygeianensis* Nel *et al*.
	Dauphin, Bois d'Asson, Alpes-de-Haute, France	
	Sieblosiidae	*Stenolestes dauphinensis* Nel *et al*.
		Sieblosiidae sp. 1 (Nel 1991)
	Ronzon, France	*Stenolestes ronzonense* (Maneval)

.....continued on the next page

	Céreste, France	*Stenolestes cerestensis* Nel *et al*.
		Stenolestes coulleti Nel & Papazian
		Stenolestes falloti (Théobald)
		Stenolestes sp. 1 (Nel & Paicheler 1994)
		Stenolestes? sp. 2 (Nel & Paicheler 1994)
		Stenolestes sp. 3 (Nel & Paicheler 1994)
Chattian		
	Bouches-du-Rhone, France	
	Sieblosiidae	*Parastenolestes oligocenicus* Nel & Paicheler
		Stenolestes belligaudi Nel *et al*.
		Stenolestes camoinsi Nel
		Stenolestes sp. 4§ (Nel 1991)
		Stenolestes sp. (Nel 1991)
	Malvezy, Narbonne, Aude, France	
	Sieblosiidae	
		Stenolestes fischeri Nel
Neogene		
Miocene		
Burdigalian		
	Radoboj, Croatia	
	Dysagrionidae?*	*Phenacolestes*? *coloratus* (Hagen)
"Middle Miocene"		
	Sivik Formation, Bulgaria	
	Dysagrionidae	*Primorilestes magnificus* Nel *et al*.
Serravallian/Langhian		
	Satovcha Graben, Bulgaria	
	Sieblosiidae	*Stenolestes rhodopensis* Nel *et al*.
	Stavropol Russia	
	Sieblosiidae	*Stenolestes fasciata* Nel *et al*.
		Miostenolestes zherikhini Nel *et al*.
		Paraoligolestes stavropolensis Nel *et al*.
Serravallian		
	Oeningen, Germany	
	Sieblosiidae	*Stenolestes iris* Scudder
		Germanostenolestes lutzi Nel & Fleck
Tortonian		
	Bellver-en-Cerdaña, Spain	
	Sieblosiidae	*Stenolestes hispanicus* Nel
	Montagne d'Andance, France	
	Sieblosiidae	*Stenolestes sp.* indt. (Riou & Nel 1995)
		Stenolestes andancensis Riou & Nel
		Paraoligolestes miocenicus Nel & Escuillié

*Possible and tentative Cephalozygoptera; †Megapodagrionidae genus and species A of Petrulevičius *et al*. (2008); ‡Dysagrionini species A of Nel & Fleck (2014); §*Stenolestes* sp. 4 of Nel & Paicheler (1994), *Stenolestes* sp. indéterminée of Nel (1991).

Family Dysagrionidae Cockerell

Subfamily Dysagrioninae Cockerell

Genus *Dysagrion* Scudder
Figs. 4–6, 14–16.

Diagnosis (emended). Wings distinguished from those of other Dysagrionidae genera by subnodus with reverse obliquity [all others and tentative Dysagrionidae as below (where known), normal]; and from all Dysagrioninae by: from *Okanopteryx*, *Furagrion* by pterostigma long (4–7 times its width) [*Okanopteryx*: 2.5 times; *Furagrion*: 3; not from *Okanagrion*: 3–4; *Stenodiafanus*: 4; *Primorilestes*: 3.5–4; *Phenacolestes*: 5; *Dysagrionites* species: unknown]; with oblique brace vein joining posterior-proximal corner of pterostigma in forewing, hind wing [not present in *Okanagrion*, *Phenacolestes* (both known from fore-, hind wings), not known in *Primorilestes* (fore- or hind wings?); known in *Furagrion*, *Okanoptyeryx*, *Stenodiafanus*; wing region not preserved in *Electrophenacolestes*, *Dysagrionites* species]; costal space distal to pterostigma 1 cell wide [distinct from *Primorilestes*, *Okanopteryx*, *Stenodiafanus*: all 2; *Okanagrion*: 3–5; shared with *Furagrion*, *Phenacolestes*: 1; *Electrophenacolestes*, *Dysagrionites* species: not known]; IR2 origin between RP1-2, RP3-4, closer to RP3-4, connected to RP1-2 notably more distally than to RP3-4 [other genera: origin close to or on RP1-2 (some *Okanagrion*), or between RP1-2, RP3-4 as in *Dysagrion* (all others), but connected with RP1-2 similar level as RP3-4]; MA linear from quadrangle to zigzagged roughly mid-wing or further, linear again near, to margin [*Furagrion*: similar (but differs by distinct curve beyond mid-wing); *Phenacolestes*: very slightly zigzagged or not in mid-portion; *Primorilestes*, *Okanagrion*: not zigzagged; *Okanopteryx*, *Stenodiafanus*, *Dysagrionites* species: linear to mid-wing, somewhat to strongly zigzagged to margin (in portions known); MA, MP close, 1–2 cells apart at margin [distinct from *Electrophenacolestes*, *Furagrion*, *Primorilestes*, *Okanagrion*, *Phenacolestes*: widely separated; not clearly distinct from *Okanopteryx*, *Stenodiafanus*, difficult to be sure of identity of MA near margin by strong zigzag, probably separated by two cells; *Dysagrionites* species also difficult, perhaps one cell]; CuA increasingly zigzagged distal to level of nodus [distinct from *Furagrion*: slightly zigzagged distal to about level of origin of RP2; *Phenacolestes*: very slightly zigzagged in parts; *Electrophenacolestes*, *Primorilestes*, *Okanagrion*: linear or only very slightly zigzagged; not clearly distinct from *Okanoptyeryx*, *Stenodiafanus*: zigzagged to various degrees distal to about mid-wing]; CuA–A space 4 cells wide [separated from *Furagrion*: 2; *Stenodiafanus*: 2 (most likely, wing incomplete); *Dysagrionites delinei*: 3; *Dysagrionites* sp. A: 2; *Dysagrionites* sp. B: probably 3 but unclear; not separated from *Phenacolestes*: 4; *Primorilestes*: 3–6; *Okanagrion*: 4–7; *Okanopteryx*: 2–4; not distinct from *Electrophenacolestes*: 4 except 5 in one column]; further from *Electrophenacolestes* by shorter petiole; further from *Primorilestes* by no linear intercalary veins in CuA–A space. Postnodal, postsubnodal crossveins not aligned at least in proximal half [separated from *Stenodiafanus*, *Okanopteryx*, *Primorilestes violetae*, *Electrophenacolestes*, *Furagrion*: all aligned or somewhat so in proximal half; not distinct from *Phenacolestes*, *Primorilestes madseni*, *Okanagrion*: all not]. Separated from *Valerea* (tentative Dysagrioninae) by no linear supplementary sector between RP1, IR1 [*Valerea*: with such sector]; by one cell wide in costal space distal to pterostigma [*Valerea*: up to 5]. Most easily separated from other genera regarded here as possible Dysagrionidae as follows: from the Chickaloon specimen (Garrouste & Nel 2019) by CuA increasingly zigzagged from level of nodus [linear at least to well past level of origin of IR1 (distal-most portion not preserved)]; MA, MP close [widening in distal-most preserved portion]; from *Thanetophilosina* by proximal side of quadrangle more than half length of distal side [less than half], IR2 originates between RP1-2, RP3-4 [originates on RP1-2]; from NHMUK I.9866/I.9718 by origin of RP3-4 [distinctly closer to subnodus]; from *cf*. Dysagrionidae genus A, species A (Petrulevičius *et al*. 2008) by hyaline membrane [preserved portion infuscate except apex distal to pterostigma], by MA zigzagged mid-wing, CuA zigzagged distally [both linear to margin].

Discussion. *Dysagrion fredericii* was designated the type species of *Dysagrion* by Scudder (1878). His diagnosis of the genus distinguished it from *Philogenia* Selys, a genus currently in need of revision (Garrison *et al*. 2010). *Philogenia* had been placed in the polyphyletic Megapodagrionidae, which was recently divided into several families (Dijkstra *et al*. 2014), including the Philogeniidae, where it now resides. We, therefore, provide an emended diagnosis of *Dysagrion*, above.

An oblique brace vein between RA and RP1 at the posterior-proximal corner of pterostigma is seen in the fore- and hind wings of *D. pruettae* (Figs. 17, 18), and in the wings of *D. lakesii* (Fig. 5, slightly, but distinctly oblique),

D. fredericii (see Scudder 1890 plate 6 Fig. 9), *D. packardii* (a portion preserved, but distinct: Fig. 4, redrawn from the original by Scudder 1890 plate 6 Fig. 3).

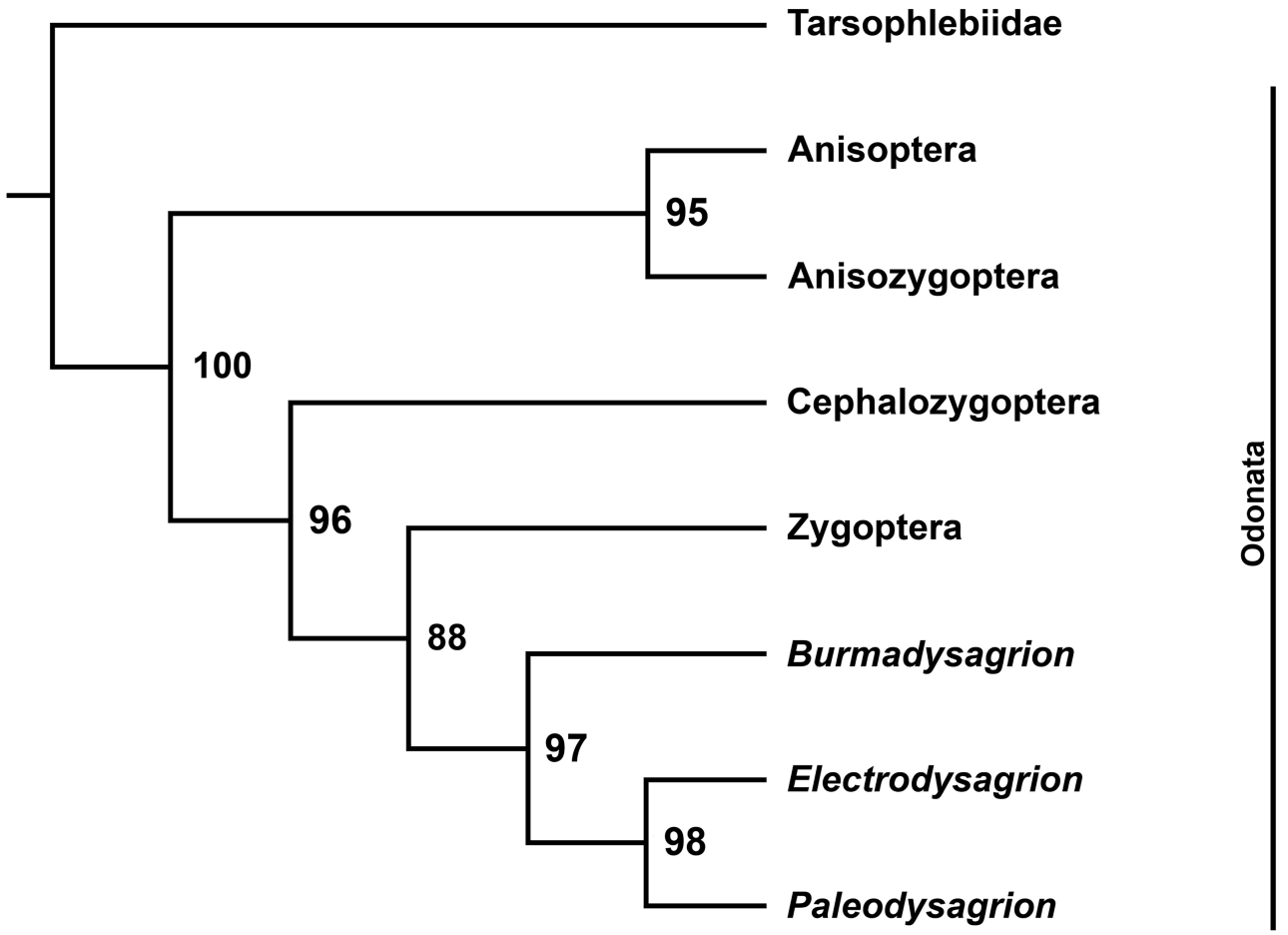

FIGURE 14. Tree resulting from parsimony-based analyses for Analysis 1: Tarsophlebiidae, the suborders of Odonata and former members of Dysagrionidae (*Burmadysagrion*, *Electrodysagrion*, *Paleodysagrion*). One single most-parsimonious tree (MPT) based on 23 continuous and 79 discrete characters. Symmetrical resampling values ≥70 are labelled at the nodes.

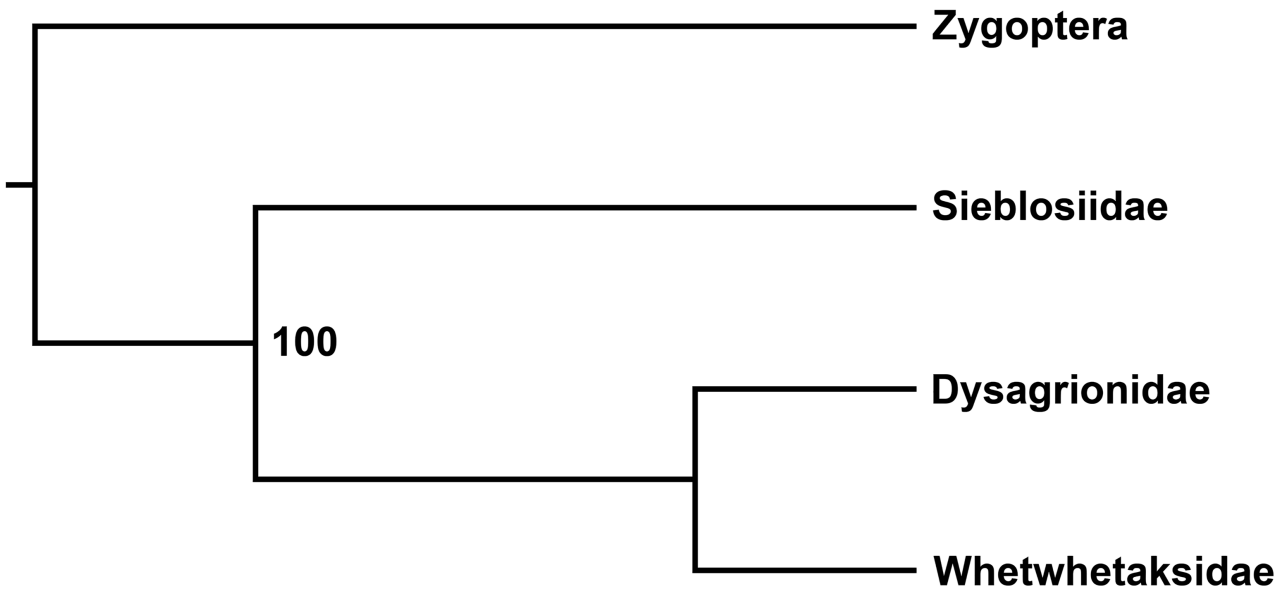

FIGURE 15. Tree resulting from parsimony-based analyses for Analysis 2 (relationship Whetwhetaksidae to confirmed families of Cephalozygoptera). One single most-parsimonious tree (MPT) based on 23 continuous and 79 discrete characters. Symmetrical resampling values ≥70 are labeled at the nodes.

The subnodus appears to be of reverse obliquity in one specimen of *Okanagrion hobani*, paratype 1, however, given that all other of its numerous specimens have normal obliquity, we consider this adventitious in this individual.

Dysagrion pruettae Archibald & Cannings, new species

Figs. 16–18.

Diagnosis. Wings most easily distinguished from those of other *Dysagrion* species by pterostigma 6–7 times longer than wide [*D. packardii*: 4 times; *D. fredericii*: 5; *D. lakesii*, 5]; by maximum width 7.4 mm (forewings), 7.0 mm (hind wings) [*D. packardii*: 8.7 mm; *D. lakesii*: 8.4 mm; *D. fredericii*: about 9.0 mm]; maximum width 24–25% length arculus to apex, (fore-, hind wings) [*D. fredericii*: 30%; *D. packardii*: 27%; *D. lakesii* 28%]. Further from *D. packardi* by anterior of quadrangle longer than base [*D. packardi*: about equal]; from *D. fredericii* by no accessory antenodal crossveins [*D. fredericii*: one (see above)].

Type material. *Holotype*: SR 13-005-012A, B, collected at Republic B4131 by Katrina Pruett, 24.vi.2013: a specimen preserved in lateral aspect, missing much of the head and the abdomen distal to segment 3 with portions of the legs present; all wings present, overlapping. Housed in the Stonerose Interpretive Center collection.

Description. Holotype, SR 13-005-012A, B, female. Head missing. Prothorax more or less oval in lateral aspect, 1.3 mm long, with leg attached; pterothorax in lateral aspect, about 8.2 mm long, mostly dark coloured with narrow pale stripes on mesopleural (humeral) suture and (probably) metapleural suture. Preservation of metepimeron unclear. Best preserved leg is the mesothoracic or metathoracic one, probably the latter; rather short, femur only 5.7 mm long, about as long as the tibia and abdominal segment 3; spines on femur and tibia short, weak and irregulary spaced.

Wings: forewing 1 (blue in Figs. 16B, 18A): petiolate; 35.0 mm long, about 21.7 mm nodus to apex; 7.4 mm wide; hyaline throughout. Nodus at 37% wing length. Pterostigma long, approximately seven times as long as wide, subtending unknown number of cells (preservation); oblique proximal margin, strikingly more oblique distal margin; with oblique brace vein. Few crossveins preserved in postnodal, postsubnodal spaces, not aligned. One cell wide distal to pterostigma in costal space. RA meets margin slightly anterior to apex. RA–RP1, RP1–IR1 spaces one cell wide to margin. Linear supplementary sectors in IR1–RP2 space (2), RP2–IR2 space (2), IR2–RP3-4 space (4), RP3-4–MA space (4–5) as in Fig. 18A (small blue arrows). Possible area of crossvein O not preserved. IR1 origin unclear; origins of supplementary sectors in IR1–RP2 space unclear. RP2 origin not definable relative to IR2 by preservation; IR2; origin unclear. RP3-4: origin unclear. MA zigzags distal to level of origin of RP2, linear again near wing margin. MP linear, with light curves from quadrangle to terminus; MP–CuA space widens near terminus. CuA becomes zigzagged around presumed level of origin of RP3-4, increasingly so to terminus. CuA–A space five cells wide at widest proximal to level of origin of RP2.

Forewing 2 (red in Figs. 16B, 17A): as for forewing 1 except pterostigma six times as long as wide; subtends unknown number of cells (preservation); oblique brace vein present. All crossveins preserved in postnodal space, 18; 15 in postsubnodal space, but apparently not all, these not aligned. IR1 origin five cells distal to origin of RP2; IR1–RP2 space become two cells wide six cells distal to origin. RP2 origin about three cells distal to subnodus. No crossvein O. IR2 origin not preserved. RP3-4: origin in middle third between arculus and nodus. CuA–A space maximum width unclear (posterior margin missing in this region), probably maximum four cells wide.

Hind wing 1 (orange in Figs. 16B, 18B): small anterior portions discernable. Petiolate, 33 mm long, 21.4 mm nodus to apex; hyaline throughout. Nodus at 36% of wing length. Pterostigma width not accurately measurable (RA bent); oblique proximal margin, more oblique distal margin; oblique brace vein present; apparently two cells subtend pterostigma (?). Crossveins in postnodal, postsubnodal spaces incompletely preserved, not aligned. Costal space one cell wide distal to pterostigma. RA meets margin slightly anterior to apex. RA–RP1 space one cell wide to margin; RP1–IR1 space one cell wide but two right at margin. Undetermined number of supplementary sectors in IR1–RP2 space.

Hind wing 2 (green in Figs. 16B, 17B): more complete than hind wing 1. As for hind wing 1, except: 7.0 mm wide; length of pterostigma approximately seven times width; oblique brace vein present. Few crossveins preserved in postnodal space, 12 in postsubnodal space, not complete; these not aligned. Linear supplementary sectors in IR1–RP2 space (2), RP2–IR2 space (2), IR2–RP3-4 space (4), RP3-4–MA space (4). IR1 origin five cells distal

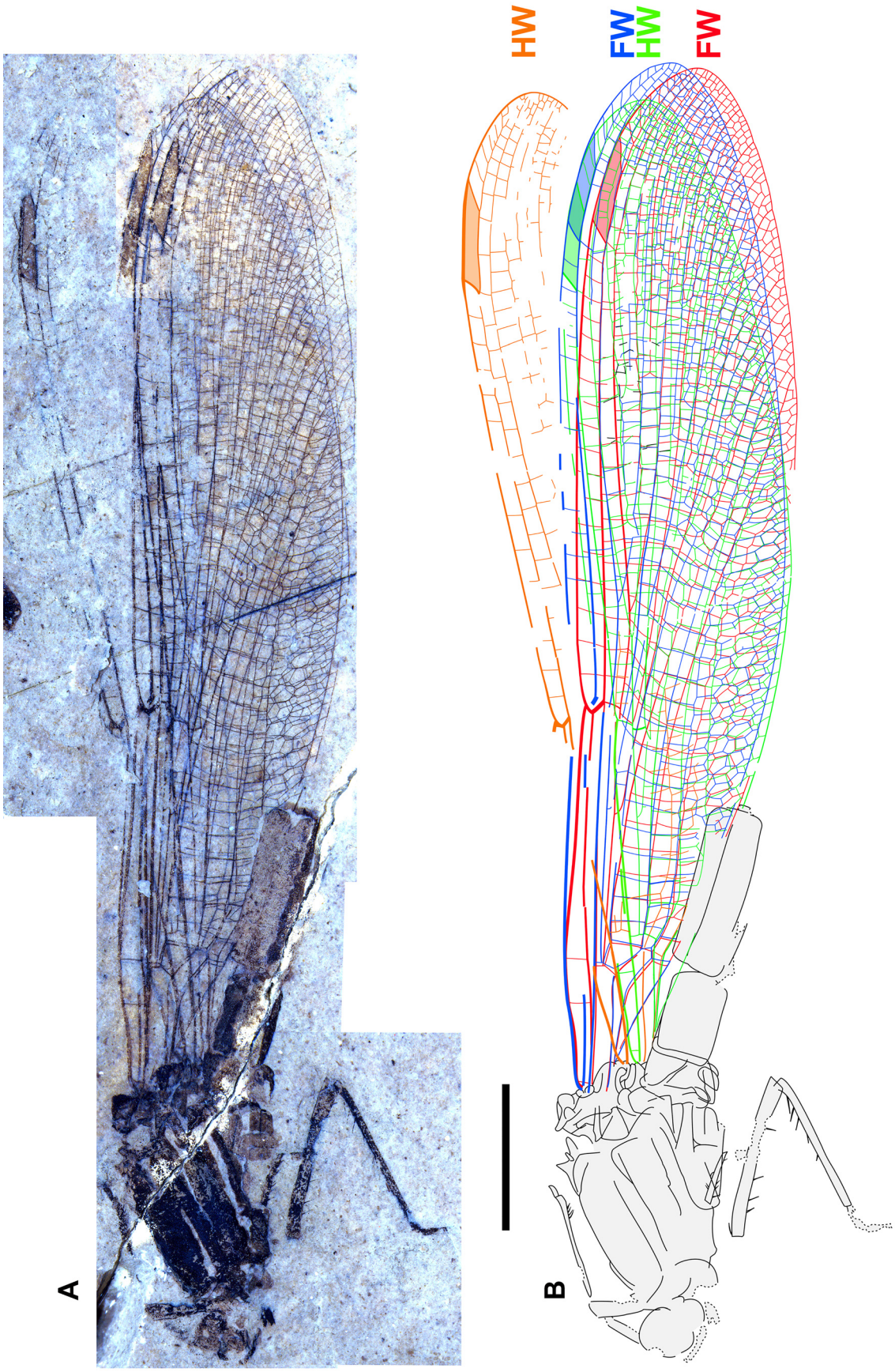

FIGURE 16. *Dysagrion pruettae*, new species holotype, SR 13-005-012. A, photograph; B, drawing. Wings and labels (FW, forewing; HW, hind wing) colour-coded to match Figs. 17 and 18. Both to scale, 5 mm.

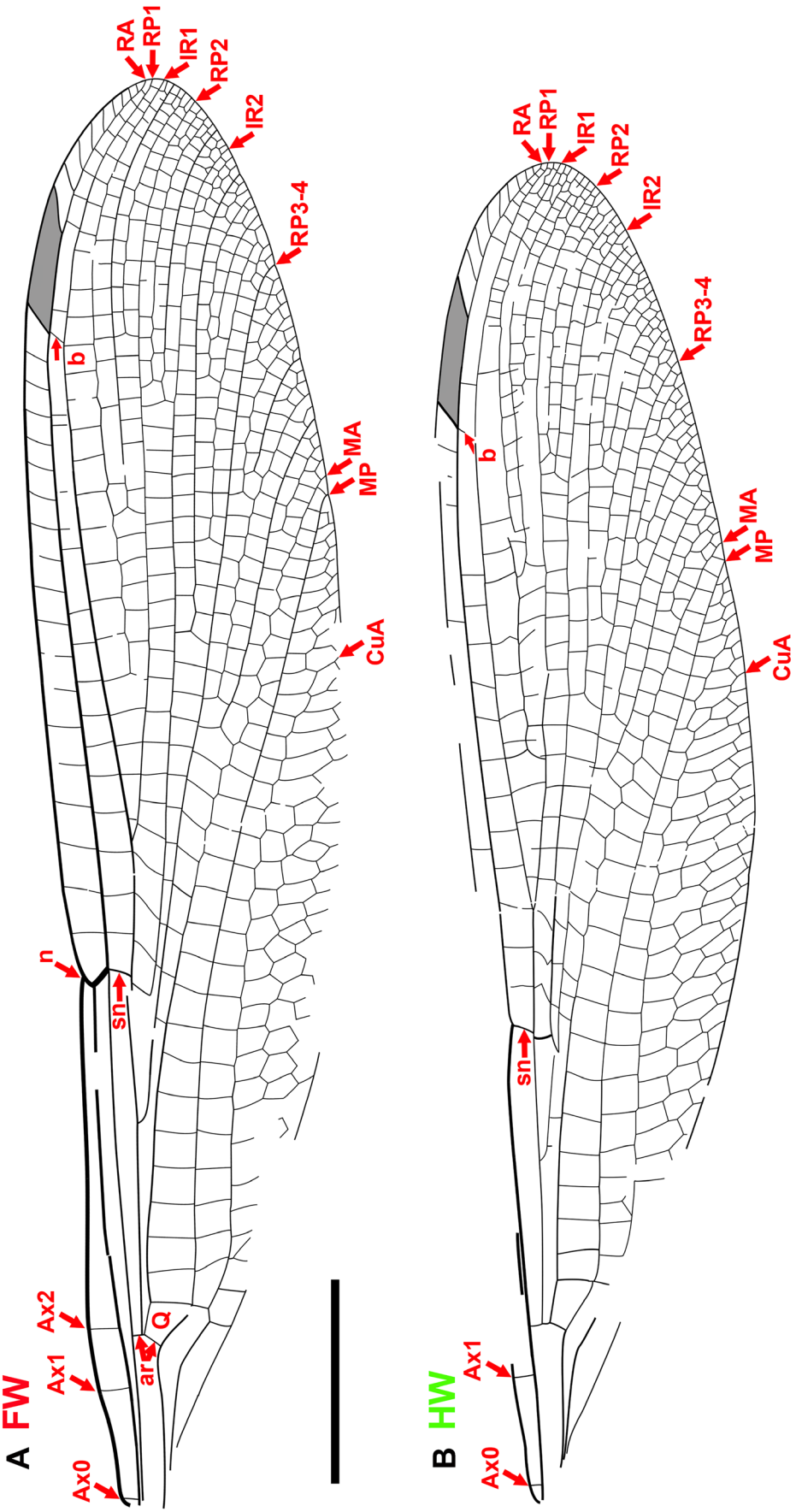

FIGURE 17. *Dysagrion pruettae* holotype, SR 13-005-012. A, drawing of forewing (FW); B, drawing of hind wing (HW). FW, HW label colours refer to those in Fig. 16. Both to scale, 5 mm.

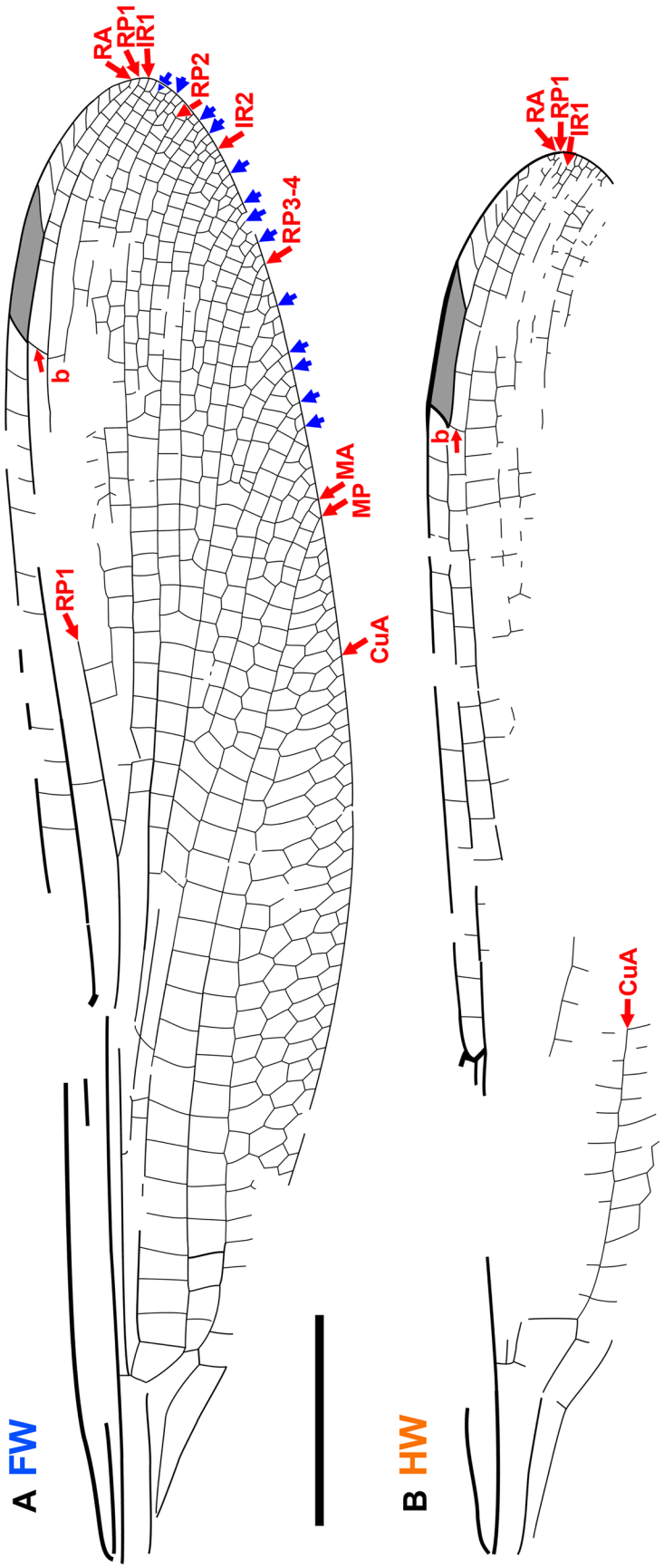

FIGURE 18. *Dysagrion pruettae* holotype, SR 13-005-012. A, drawing of forewing (FW); B, drawing of hind wing (HW). FW, HW label colours refer to those in Fig. 16. Small, blue arrows indicate supplementary sectors. Both to scale, 5 mm.

to that of RP2; becomes two cells wide seven cells distal to origin. RP2 origin three cells distal to origin of IR1. IR2 origin very close to subnodus. RP3-4: origin in middle third between arculus and nodus. No crossvein O. MA zigzags increasingly beyond level of nodus, linear again near margin. MP linear, evenly curved from quadrangle to terminus. CuA increasingly zigzagged from level of nodus; CuA–A space maximum four cells wide.

Abdomen: dark coloured dorsally, pale ventrally; segments 1 to 2 preserved in lateral aspect, segment 3 in ventral aspect; thickness of abdomen and lack of secondary genitalia on venter of segment 2 indicate a female specimen.

Etymology. The specific epithet is a patronymic formed from the surname of Katrina Pruett, the collector of the holotype, recognising her contribution.

Range and age. Republic locality B4131 of the Tom Thumb Tuff Member of the Klondike Mountain Formation; latest Ypresian.

Discussion. If the Green River specimens are hind wings, they are notably longer: *D. pruettae* arculus to apex: 28.4 mm, *D. packardii*: 31.7 mm, *D. lakesii*: 30.0 mm, *D. fredericii*: about 30.5 mm. If they are forewings, their lengths match those of *D. pruettae* more closely, 30.7 mm long arculus to apex.

Okanagrion Archibald & Cannings, new genus

Figs. 19–43.

Diagnosis. Wings distinct from all other genera of Dysagrioninae by: pterostigma 3–3.5, rarely 4 times longer than wide [separated from *Okanopteryx*: 2.5 times; *Stenodiafanus*: 4; *Phenacolestes*: 5; not separated from *Furagrion*: 3; *Primorilestes*: 3.5–4; *Dysagrion*: 4–7.5; *Dysagrionites* species: unknown]; no oblique brace vein [separated from *Dysagrion*, *Furagrion*, *Okanoptyeryx*, *Stenodiafanus*; wing region not preserved in *Electrophenacolestes*, *Dysagrionites* species; not separated from *Phenacolestes*, *Primorilestes*]; costal space 3–5 cells wide distal to pterostigma [distinct from *Primorilestes*, *Okanopteryx*, *Stenodiafanus*: all 2; *Dysagrion*, *Furagrion*, *Phenacolestes*: all 1; *Electrophenacolestes*, *Dysagrionites* species: not known]; subnodus with normal obliquity (reverse in one specimen of *Okanagrion hobani*, paratype 1, which we consider adventitious) [separated from *Dysagrion*, reversed obliquity; all others: normal obliquity, slight to notable]; no accessory antenodal crossveins [distinguished from *Phenacolestes*, *Electrophenacolestes*, some *Dysagrion* species: present; not separated from all others: also none]; IR2 origin rather evenly between RP1-2, RP3-4, connected to RP1-2, RP3-4 at similar level (some species IR2 origin close to or on RP1-2) [*Dysagrion* rather evenly between RP1-2, RP3-4, but connected with RP1-2 distinctly more distally than to RP3-4; other genera IR2 origin rather evenly between RP1-2, RP3-4, connected to RP1-2, RP3-4 at similar level]; MA linear from quadrangle to margin [separated from *Dysagrion*: MA linear from quadrangle to zigzagged roughly mid-wing or further, linear again near margin; *Furagrion*: similar to *Dysagrion* but deeply curved in distal portion; *Phenacolestes*: very slightly zigzagged or not in mid-portion; *Okanopteryx*, *Stenodiafanus*, *Dysagrionites* species (known portions, none known to margin): linear to mid-wing, somewhat to strongly zigzagged to margin; not separated from *Primorilestes*: linear]; MA, MP far apart at margin [distinct from *Dysagrion*: MA, MP close, 1–2 cells apart at margin; not clearly distinct from *Okanopteryx*, *Stenodiafanus* as difficult to be sure of identity of MA near margin by strong zigzag, but close, probably separated by two cells; *Dysagrionites* species also difficult, perhaps one cell; not separated from *Furagrion*, *Primorilestes*, *Electrophenacolestes*: MA, MP widely separated]; CuA not zigzagged (or only very slightly so), linear to margin [distinct from *Dysagrion*: CuA increasingly zigzagged distal to level of nodus; *Furagrion*: slightly zigzagged distal to level of origin of RP2; *Phenacolestes*: may be very slightly zigzagged in parts; *Okanoptyeryx*, *Stenodiafanus*: zigzagged to various degrees distal to about mid-wing; not clearly distinct from *Electrophenacolestes*, *Primorilestes*: linear or very slightly zigzagged]; CuA–A space 4–7 cells wide [separated from *Furagrion*: 2; *Stenodiafanus*: 2 (most likely, wing incomplete); *Dysagrionites delinei*: 3; *Dysagrionites* sp. A: 2; *Dysagrionites* sp. B: probably 3 but unclear; not separated from *Dysagrion*: 4; *Phenacolestes*: 4; *Primorilestes*: 3–5; *Electrophenacolestes*: 4 (one column 5); *Okanopteryx*: 2–4]; postnodal, postsubnodal crossveins not aligned at least in proximal half [separated from *Stenodiafanus*, *Okanopteryx*, *Primorilestes violetae*; *Electrophenacolestes*; *Furagrion*: all aligned or somewhat so in proximal half; not distinct from *Phenacolestes*, *Primorilestes madseni*, *Dysagrion*: all not]; further from *Dysagrion* by nodus at 25–30% wing length [*Dysagrion*: ≥ 35%]; further from *Primorilestes* by no intercalary vein in CuA–A space. Separated from *Valerea* (tentative Dysagrioninae) by no linear supplementary sector between RP1, IR1 [*Valerea*: with such sector]; origins of IR1,

RP2 further from nodus; origin of IR2 between RP1-2, RP3-4 or near or on RP1-2 [IR2 origin not preserved, only preserved to level of nodus, where it is closer to RP3-4]. Most easily separated from genera regarded here as possible Dysagrionidae as follows: from *Thanetophilosina* by pterostigma 3–3.5, rarely 4 times longer than wide [about 6 times width], by no linear supplementary sectors between RP1, IR1, between IR1, RP2 [*Thanetophilosina*: with such sectors]; from Chickaloon specimen by MA linear [beginning to zigzag in distal-most portion preserved]; from NHMUK I.9866/I.9718 by origin of RP3-4 [distinctly closer to subnodus]; from *cf*. Dysagrionidae genus A, species A ("Megapodagrionidae" genus A, species A of Petrulevičius *et al*. 2008) by width of CuA–A space [two cells wide, preserved portion, likely maximum], by crossvenation in apical third [not as dense, *e.g*., costal space apical to pterostigma two cells wide, RA–RP1, RP1–IR1 spaces one cell wide to apex]; no brace vein [present].

Type and included species. Type species: *Okanagrion threadgillae* new species; included: *O. hobani*, *O. beardi*, *O. lochmum* new species, *O. angustum* new species, *O. dorrellae* new species, *O. liquetoalatum* new species, and *O. worleyae* new species.

Description. As in diagnosis and the following. Colouration of wings varies: broad regions of dark or light fasciae or may be completely hyaline. Pterostigma 3–3.5 (rarely four) times longer than wide; four–seven cells subtend pterostigma (usually six); no accessory crossvein proximal to or distal to CuP; no well-defined supplementary sector between IR1, RP2; CuP proximal to arculus, between levels of Ax1, Ax2; petiole ends proximal to CuA, proximal to CuP; no oblique brace vein; postnodal, postsubnodal crossveins not aligned; CuA–A space maximum four–seven cells wide; origin of RP3-4 proximal to subnodus; no crossvein O; origin of IR2 at (or immediately proximal to) subnodus; IR1 zig-zagged in proximal half, CuA may be slightly zigzagged briefly about nodal level, apart from this all major veins linear (except MP zigzagged distally in *O. dorrellae*), well defined; usually one–two hyperstigmal crossveins, less often none; two antenodal crossveins (Ax1, 2), rarely Ax0, no accessory antenodal crossveins; Ax2 at or very close to, immediately distal to arculus; CuA long, terminating on posterior margin beyond half length of arculus to apex.

Etymology. The genus name is a toponym derived from "Okanagan Highlands" and *-agrion*, the Greek *ἄγριος*, often used as a suffix in forming damselfly genus names. Gender neuter.

Range and age. McAbee, BC, Canada and the Klondike Mountain Formation at Republic, Washington, USA; second half of the Ypresian.

Discussion. Valerea *and the Chickaloon specimen. Okanagrion* wings share distinctive character states with that of the Thanetian *Valerea multicellulata* from Menat, France (Garrouste *et al*. 2017). That insect has a notably large number of small cells in the costal and RA–RP1 spaces distal to the pterostigma, up to five cells wide, a condition that is only approached in the RA–RP1 space by some Mesozoic Aeschnidiidae, in which it is up to three cells wide (Fleck & Nel 2003; Garrouste *et al*. 2017). In *Okanagrion*, there are usually three, and sometimes four, cells in the costal space, but this space does reach five cells wide in *O. worleyae* (see paratype 1, SR 16-006-001, Fig. 40). The *Okanagrion threadgillae* (Figs. 19, 20) and *O. lochmum* (Fig. 23) holotypes have five cells wide in the RA–RP1 space, and while *O. hobani* specimens usually have a maximum of four cells wide in this space, it does reach this remarkable number in paratype 3 (SR 94-05-22, Fig. 27), paratype 4 (SRUI 99-96-55, Fig. 28), and paratype 6 (SR 00-04-05, Fig. 30). Garrouste *et al*. (2017) noted that five cells width in these two spaces distal to the pterostigma was then only known in the Odonata in *V. multicellulata*.

The pterostigma of *V. multicellulata* is also distinct by its shape, the distal side is strongly curved and the proximal side is very long and oblique to C and RA, with two crossveins between the Costa and proximal side of the pterostigma, *i.e*., hyperstigmal crossveins. Hyperstigmal crossveins are uncommon in extant Zygoptera (Garrouste *et al.* 2017). The pterostigmata of *Okanagrion* species are shaped like this, and the majority of specimens of *O. hobani*, and one each of *O. worleyae* and *O. beardi* have a hyperstigmal crossvein, and the holotype hind wing of *O. threadgillae* bears two (Fig. 20B). The pterostigma of *Valerea* is about three times longer than wide, within the lower range of *Okanagrion*. The vein fragment of *V. multicellulata* that we interpret as CuA is linear at least well proximal to the origin of IR1, as in *Okanagrion*.

The proximal portion of IR2 in *V. multicellulata* is not preserved from immediately distal to the level of the nodus. Unlike the condition in *Okanagrion* species where IR2 originates at this level either closer to RP1-2 or on RP1-2, the proximal-most preserved portion in *V. multicellulata* is relatively far from RP1-2 and closer to RP3-4, indicating that it likely originates well proximal to the nodus, or if at that level, then on or near RP3-4.

The Thanetian of Menat and the Ypresian Okanagan Highlands are probably about three to six million years apart, and would have been connected by continuous land at that time, with mild climates reaching high latitudes facilitating intercontinental dispersal (reviewed: Archibald & Makarkin 2006; Archibald *et al***.** 2011b).

The specimen of undetermined genus and species from the Thanetian or Ypresian Chickaloon Formation of Alaska (Garrouste & Nel 2019) appears quite close to *Okanagrion* with its dense venation, including an expanded CuA–A space four cells wide at its widest, between the levels of origins of RS2 and IR1. In its diagnosis, above, we cite the MA beginning to zigzag in the distal-most portion of preserved in the Chickaloon specimen as distinguishing it from *Okanagrion* (where this is linear), although this is not a great difference, and they might be congeners or closely related genera. It is clearly not a species of *Valerea* as, *e.g*., the crossvenation is much more dense and the origins of IR1 and RP2 are nearer to the nodus in that genus.

Species richness. It is not surprising that there is high species richness of *Okanagrion* at two localities: eight in total, with four at McAbee and five at Republic (one of these shared between them). High alpha diversity was established at McAbee by Archibald *et al*. (2010), who found insect and woody dicotyledon species richness there to be equivalent to that of a modern lowland tropical rainforest in Costa Rica. That this richness is not an artefact of splitting was confirmed by the independent assessments of experts in individual insect orders (see Archibald *et al*. 2010). Such high, tropical levels of alpha diversity for woody dicotyledons have also been established at Republic (Wilf *et al*. 2003).

This is also consistent with the findings of Archibald *et al*. (2013) that insect beta diversity is high between site pairs in the Okanagan Highlands. They extended Janzen's hypothesis "Mountain passes are higher in the tropics" to mid-latitude mountainous regions of the Eocene by their "greenhouse world" extra-tropical climatic equability. This diversity pattern is then expected with climate-driven high alpha diversity, and climate and topography-driven high beta diversity. Other genera described here are less speciose.

Wing colour patterning. There is sexual dimorphism in wing colouration in a variety of extant Zygoptera and this may also be true in Cephalozygoptera. Further, there may be differences in patterning between the hind wings and forewings. In some Zygoptera species, there is also colour polymorphism in a single sex (*e.g*., clear-winged and pattern-winged males of *Paraphlebia* (Thaumatoneuridae), but this is uncommon.

There are 17 specimens of *Okanagrion hobani* illustrated and discussed here, one of which we know is a male. While it seems unlikely that all 17 would be males, still, this is possible. *Okanagrion* species concepts are defined by other wing traits, with wing colouration as supplementary. Taking a conservative stance, we identify wing colouration as male in the *O. hobani* diagnosis, with female colouration unknown, and in other species specify that the sex is unknown. Colouration is consistent between wings identified as fore- and hind wings, and in the articulated fore- and hind wings of *O. hobani* paratype 7, F-1044.

Forewings and hind wings. Although forewings are close in shape to hind wings in Cephalozygoptera, Anisozygoptera and Zygoptera, they may in cases be somewhat different (*e.g*., slightly in *Paraphlebia zoe* Selys in Hagen see Figs. 470 and 436 and 437 of Garrison *et al*. 2010, more so in *Thaumatoneura inopinata* McLachlan, their Figs. 470 and 471). We base our assignment of fore- and hind wings on those of the holotype (and only specimen) of *O. threadgillae*, where two wings that conform to the differences seen in some modern species are in close association: the wing that we presume to be a forewing is slightly wider at the base, with the posterior margin slightly convex, widened at the level of the distal portion of the quadrangle (Fig. 35, red arrows), and the anterior margin is slightly curved between the nodus and the pterostigma. In the presumptive hind wing, the proximal posterior margin is smoothly curved through the level of the quadrangle (Fig. 35, blue arrow), the anterior margin is rather straight from the nodus to the pterostigma, and the posterior margin is more deeply curved. We compare this difference to that of the fore- and hind wings of *Thaumatoneura* species, although not as pronounced as in some of those. Unfortunately, in the male specimen F-1044 of *O. hobani* with all four wings preserved, these are somewhat damaged, precluding meaningful comparison of details of shape. Rather complete and undamaged wings of *Okanagrion* species appear to vary in the same manner as do those that we presume to be the fore- and hind wing of *O. threadgillae*, and so we assume these identities where possible.

Okanagrion threadgillae Archibald & Cannings, new species

Figs. 19–20.

Diagnosis. Wings separated from those of *O. beardi*, *O. dorrellae* by MP, CuA sub-parallel at terminus on posterior margin [*O. beardi*: distinctly wider, *O. dorrellae*: widening, but less distinctly as CuA zigzagged distally (*O. angustum*, not known); from *O. dorrellae* by MP linear to margin [*O. dorrellae*: zigzagged near margin]; from *O. angus-*

tum, *O. beardi* by IR2 origin between RP1-2, RP3-4 [*O. angustum*, *O. beardi*: origin on RP1-2]; from *O. dorrellae* by wider wing: length (arculus to apex)/ maximum width, 3.1 [*O. dorrellae*: 3.7], nodus to apex 2.5 times maximum width [although the wing of *O. angustum* is less complete, it is distinctly narrower, compare angle of posterior margin to anterior margin preserved between levels of nodus, origin of RP2]; width at level of two cells proximal to origin of RP2 in *O. angustum* 75% that of *O. threadgillae*; from *O. liquetoalatum* by wing shape: while length of arculus to nodus is equivalent, arculus to apex is about 2 mm longer in *O. threadgillae*; from *O. liquetoalatum*, *O. dorrellae* by wing shape: length (arculus to apex) / maximum width 3.1 [*O. liquetoalatum*: 2.6; *O. dorrellae* 3.7; others similar to *O. threadgillae* (*O. lochmum*, *O. worleyae*, *O. angustum* not comparable by preservation)]; wing length (arculus to apex) / maximum width, *O. dorrellae* 3.7; from *O. hobani* by main veins less deeply curved near margin; from *O. worleyae* further by shape: posterior margin more deeply curved; from *O. lochmum* by RA–RP1 space becomes two cells wide about two cells proximal to pterostigma [*O. lochmum* over seven cells proximal]. Further separated by colouration (sex unknown): proximal approx. 2/5 hyaline, dark apical to this except narrow lighter fascia just distal to mid-way between nodus, pterostigma, extending from anterior margin to mid-wing; size and extent of light fascia differs from: *O. hobani* about three times as wide, extending to or almost to posterior margin; *O. angustum* apparently similar to *O. hobani* as preserved; *O. beardi*, *O. lochmum*, wider than in *O. threadgillae* by small but definite amount, extending closer to posterior margin; *O. dorrellae* similar width as *O. beardi*, *O. lochmum*, probably extending to mid-wing (but damage in this region); *O. liquetoalatum*: hyaline throughout; *O. worleyae*: lightly infuscate throughout known wing.

Type material. *Holotype*: SR 98-12-10 (Republic A0307, collected by Carolyn Threadgill 8.iv.1998): two well preserved, complete wings; disarticulated, in close association; with colour patterning clearly preserved; housed in the Stonerose Interpretive Center collection.

Description. Holotype, SR 98-12-10, forewing (Figs. 19A, 20A): distal to nodus rather wide-oval, symmetrical around longitudinal line from apex; posterior margin slightly widens about level of quadrangle; 30.5 mm long, 27.6 mm arculus to apex, 22.5 mm nodus to apex; 18.0 mm origin of RP2 to apex, 21.5 mm arculus to base of pterostigma, 16.5 mm nodus to base of pterostigma; 9.0 mm wide. Nodus at 28% wing length. Colouration as in diagnosis. Pterostigma anterior, posterior margins oblique; length 3.5 times width; subtends 5.5 cells; no oblique brace vein. 40 crossveins in postnodal space (complete), the distal-most one joining pterostigma (hyperstigmal crossvein); not aligned with postsubnodal crossveins. Maximum three cells wide in much of costal space distal to pterostigma. RA meets margin at apex; RA–RP1 space narrows near margin. RP1–IR1 space goes to two cells wide 10 cells distal to origin of IR1. Cells in apical portion increasingly dense, many small cells along margin. IR1 origin nine cells distal to origin of RP2; IR1–RP2 space becomes two cells wide about ten cells distal to origin. RP2 origin 6.5 cells distal to origin of IR2. No crossvein O. IR2 origin at subnodus. R3-4 origin less than 2/3 distance between arculus, nodus. Arculus immediately proximal to Ax2. Ax0 not detected. All main veins linear except proximal portion of IR1. MP, CuA slightly divergent at terminus on posterior margin. CuA ends at level about half way between nodus, pterostigma; CuA–A space maximum five cells wide.

Hind wing (Figs. 19B, 20B): As for forewing, except: Posterior margin evenly curved about level of quadrangle, does not slightly widen; 26.5 mm arculus to apex, 21.7 mm nodus to apex, 17.7 mm origin of RP2 to apex, 20.6 mm arculus to base of pterostigma, 15.7 mm nodus to base of pterostigma; 8.5 mm wide. Nodus at 30% wing length. Pterostigma length 3.5 times width; subtends six cells. 35 crossveins preserved (presume 36 total) in postnodal space, distal-most three hyperstigmal. One column four cells wide, mostly three in costal space distal to pterostigma. RP1–IR1 space goes to two cells wide 11 cells distal to origin of IR1. IR1 origin six cells distal to origin of RP2; IR1–RP2 space becomes two cells wide eleven cells distal to origin. RP2 origin probably five cells distal to origin of IR2. Origin of RP3-4 slightly proximal to position in forewing. MP, CuA sub-parallel at terminus on posterior margin. CuA–A space maximum six cells wide.

Etymology. The specific epithet is a patronymic formed from the surname of Carolyn Threadgill, the collector of the holotype, recognising her contribution.

Range and age. Republic locality A0307 of the Tom Thumb Tuff Member of the Klondike Mountain Formation; latest Ypresian.

Discussion. We presume the top wing of Figs. 19A and 20A to be a forewing and the bottom wing of these (Figs. 19B and 20B) to be a hind wing, as discussed above.

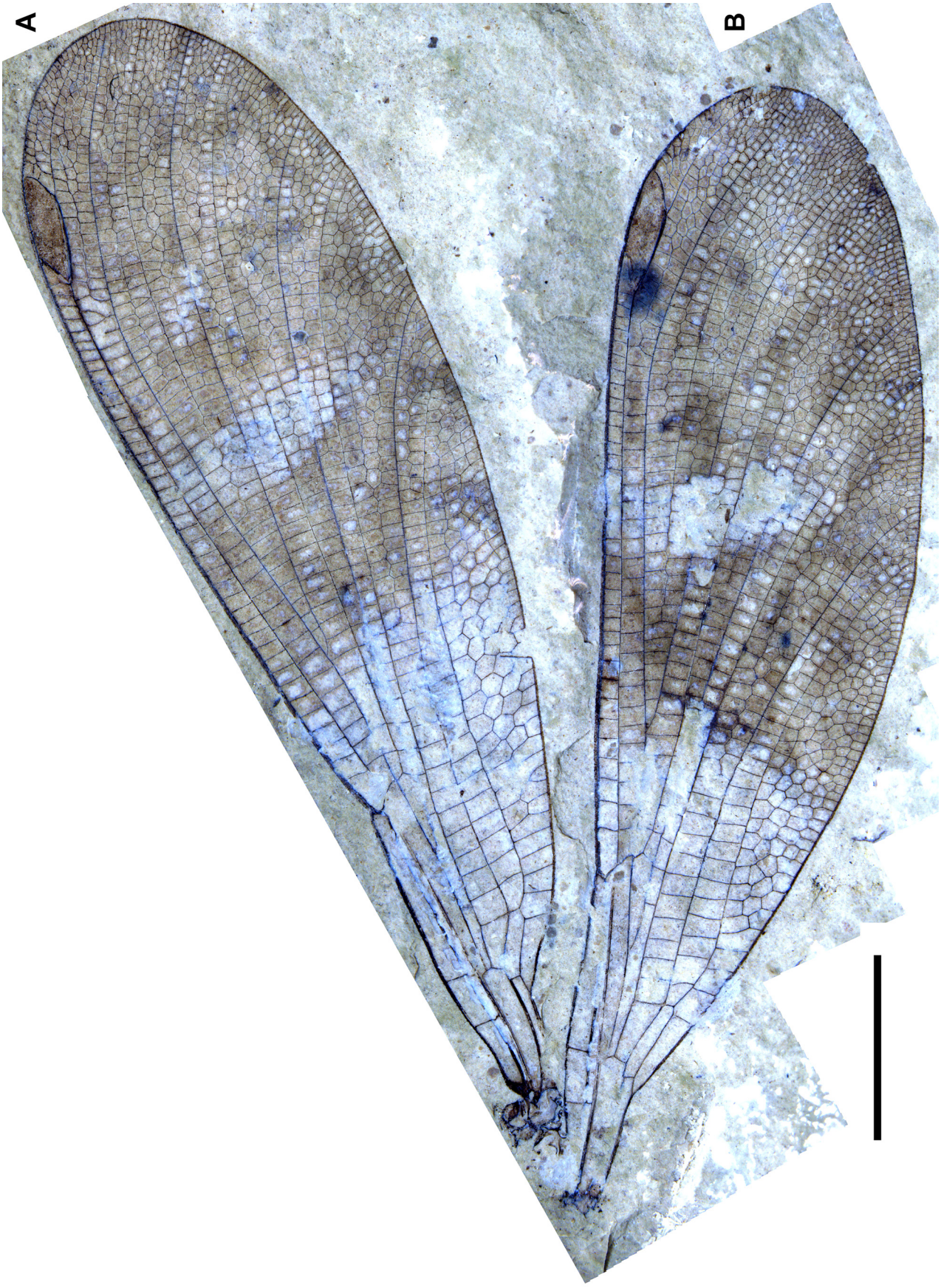

FIGURE 19. *Okanagrion threadgillae* holotype, SR 98-12-10. Photograph. A and B refer to drawings in Fig. 20. Scale bar is 5 mm.

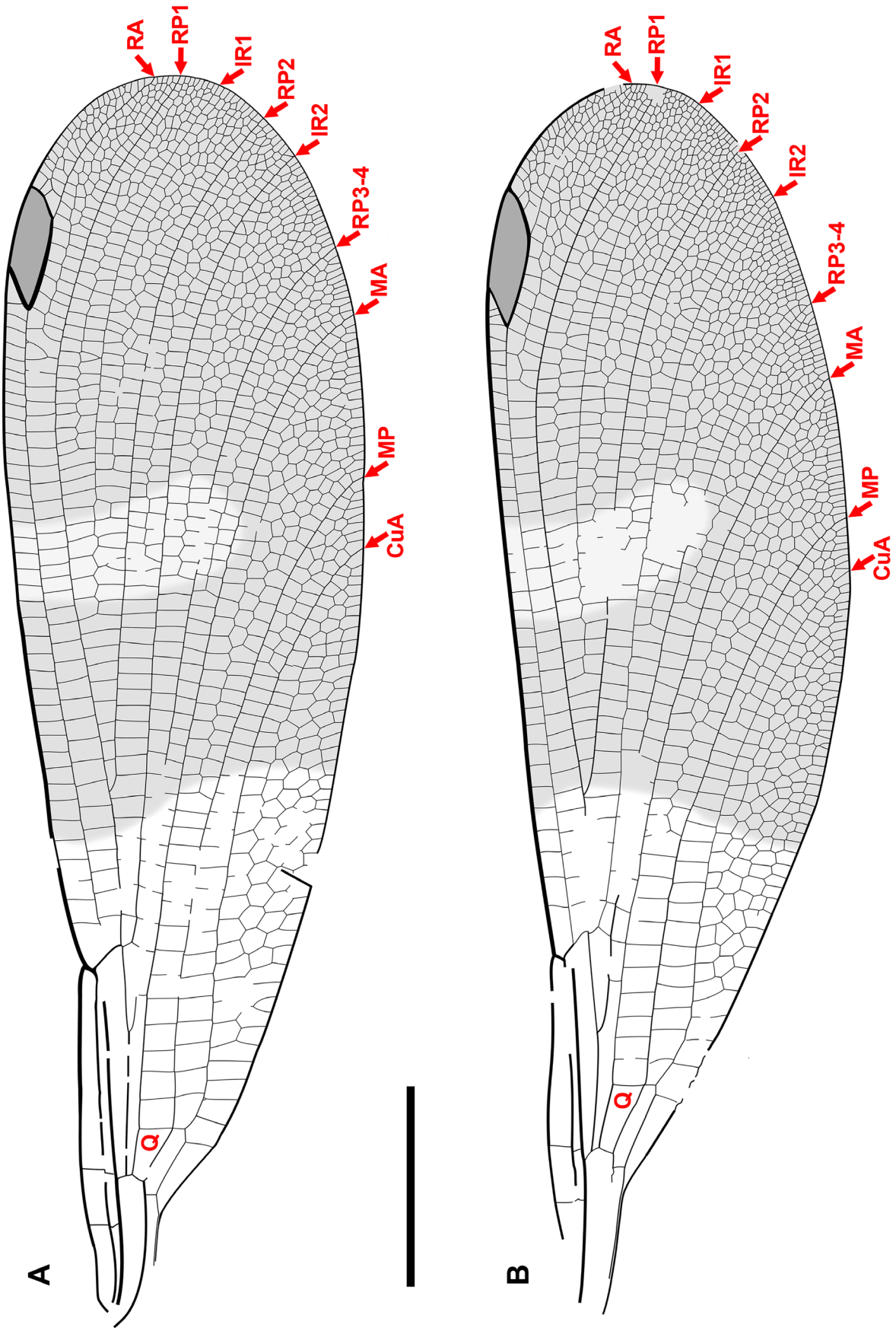

FIGURE 20. *Okanagrion threadgillae* holotype, SR 98-12-10. A, drawing of wing A of Fig. 19; B, drawing of wing B of Fig. 19. Both to scale, 5 mm.

***Okanagrion beardi* Archibald & Cannings, new species**
Figs. 21–22.

Diagnosis. Wings separated from those of all other *Okanagrion* species but *O. dorrellae* by MP, CuA distinctly divergent near margin [others: MP-CuA space remaining narrow; *O. dorrellae*: widening, but less distinctly as CuA zigzagged distally (*O. angustum*, not known)]; from all others except *O. angustum* by IR2 originating on RP1-2 [others: between RP1-2, RP3-4]; from *O. angustum* by Ax1 to nodus shorter, 6.5 mm (holotype; paratype 1: almost 6 mm, smaller wing, but proportions match holotype) [*O. angustum*: 7.5 mm]; from *O. dorrellae* by MP linear to margin [*O. dorrellae*: zigzagged near margin]; from *O. liquetoalatum*, *O. dorrellae* by wing shape: length (arculus to apex) / maximum width 3.1 [*O. liquetoalatum*: 2.6; *O. dorrellae* 3.7; others similar to *O. beardi* (*O. lochmum*, *O. worleyae*, *O. angustum* not comparable by preservation)].

Further separated by colouration (sex unknown): proximal approx. 2/5 hyaline, dark apical to this except narrow lighter fascia just distal to mid-way between nodus, pterostigma, extending from anterior margin to close to posterior margin; size and extent of light fascia differs from: *O. hobani* about twice or more as wide, extending to or almost to posterior margin; *O. angustum* apparently similar to *O. hobani* as preserved; *O. threadgillae* notably narrower, extending to mid-wing; *O. dorrellae* similar width, probably extending to mid-wing (but damage in this region); *O. lochmum*, similar to *O. beardi*; *O. liquetoalatum*: hyaline throughout; *O. worleyae*: lightly infuscate throughout known wing.

Type material. *Holotype*: F-791 (part only) (Fig. 21): One complete wing and portions of two or three others; possibly part of one eye; part of damaged thorax preserved in lateral aspect; at least two pieces of abdomen present; collected at the McAbee Hoodoo Face beds, collector and date unknown; housed in the Thompson Rivers University collections. *Paratype 1*: RBCM P1546 (Fig. 22): a head, thorax, bits of some legs, proximal-most portion of the abdomen, well-preserved forewing and proximal portion of a hind wing; coated with shellac; collected at the McAbee Hoodoo Face beds, vi.1998 by unknown grade 8 or 9 student, donated by Graham Beard; in the Royal British Columbia Museum collections.

Description. Holotype, F-791, forewing. Almost complete, missing tiny portions of the apex and proximal to the nodus. Shape: oval distal to nodus, symmetrical from lateral mid-line; length: 31.5 mm, arculus to apex: about 27.7 mm, nodus to apex: about 22.7 mm, origin of RP2 to apex: 18.2 mm, arculus to base of pterostigma: 22.0 mm, nodus to base of pterostigma: 16.8 mm, nodus at 29% wing length; width 8.3 mm. Colouration as in diagnosis. Pterostigma anterior, posterior margins oblique, 3.5 times longer than wide, subtends 6.5 cells, no oblique brace vein. 35 crossveins in postnodal space (complete), none hyperstigmal, crossveins in postsubnodal space not aligned. Maximum three cells wide distal to pterostigma in costal space (partially preserved). RA–RP1 space narrows near margin. RP1–IR1 space becomes two cells wide unknown number of cells from origin by preservation. IR1 origin eight cells distal to origin of RP2. IR1–RP2 space becomes two cells wide unknown number of cells origin by preservation. RP2 origin six cells distal to origin of IR2. IR2 origin very close to subnodus; close to, appears to arise from RP1-2. RP3-4 origin about 2/3 from arculus to nodus. Ax0 present. Arculus close to, immediately proximal to Ax2. No crossvein O. All main veins linear other than IR1 proximally. MP, CuA divergent at terminus on posterior margin. CuA–A space with maximum five cells wide.

Paratype 1, RBCM P1546. Head (Fig. 10 M, Table 1): relatively well preserved in dorsal aspect but details obscure; labrum/clypeus area damaged. In dorsal view about 4.1 mm across eyes at widest part, with rear margin expanded somewhat postero-laterally; approximate length from anterior edge of antefrons to posterior of occiput 1.5 mm; at level of hind ocelli distance between eyes about 1.2 mm, single eye roughly 1.5 mm wide, 2.0 mm long. Thorax: lateral view; colouration dark, apparently with narrow pale stripe on mesopleural suture, any other patterns obscure; pieces of legs poorly preserved. Forewing: as in holotype except length: 31.6 mm, arculus to apex: 26.5 mm, nodus to apex: 21.7 mm, origin of RP2 to apex: 16.6 mm, arculus to base of pterostigma: 21.0 mm, nodus to base of pterostigma: 16.2 mm; width 7.7 mm; nodus at 25% wing length. Colouration mostly obscured by applied shellac, but as apparent is consistent with holotype. Pterostigma: 5.5 cells subtend, length 3.5 times width. Postnodal space with 36 crossveins (probably complete), distal-most one hyperstigmal. IR1 origin seven cells distal to origin of RP2; IR1–RP2 space becomes two cells wide six or seven cells (unclear by preservation) distal to origin by preservation. RP2 origin nine cells distal to origin of IR2. Ax0 not detected. CuA–A space unknown number of cells wide by preservation, but appears similarly wide as holotype. Abdomen: segments 1 and 2 preserved in lateral aspect; base of abdomen relatively slender; irregular ventral margin of segment 2 may indicate presence of secondary male genitalia but sex of specimen undetermined.

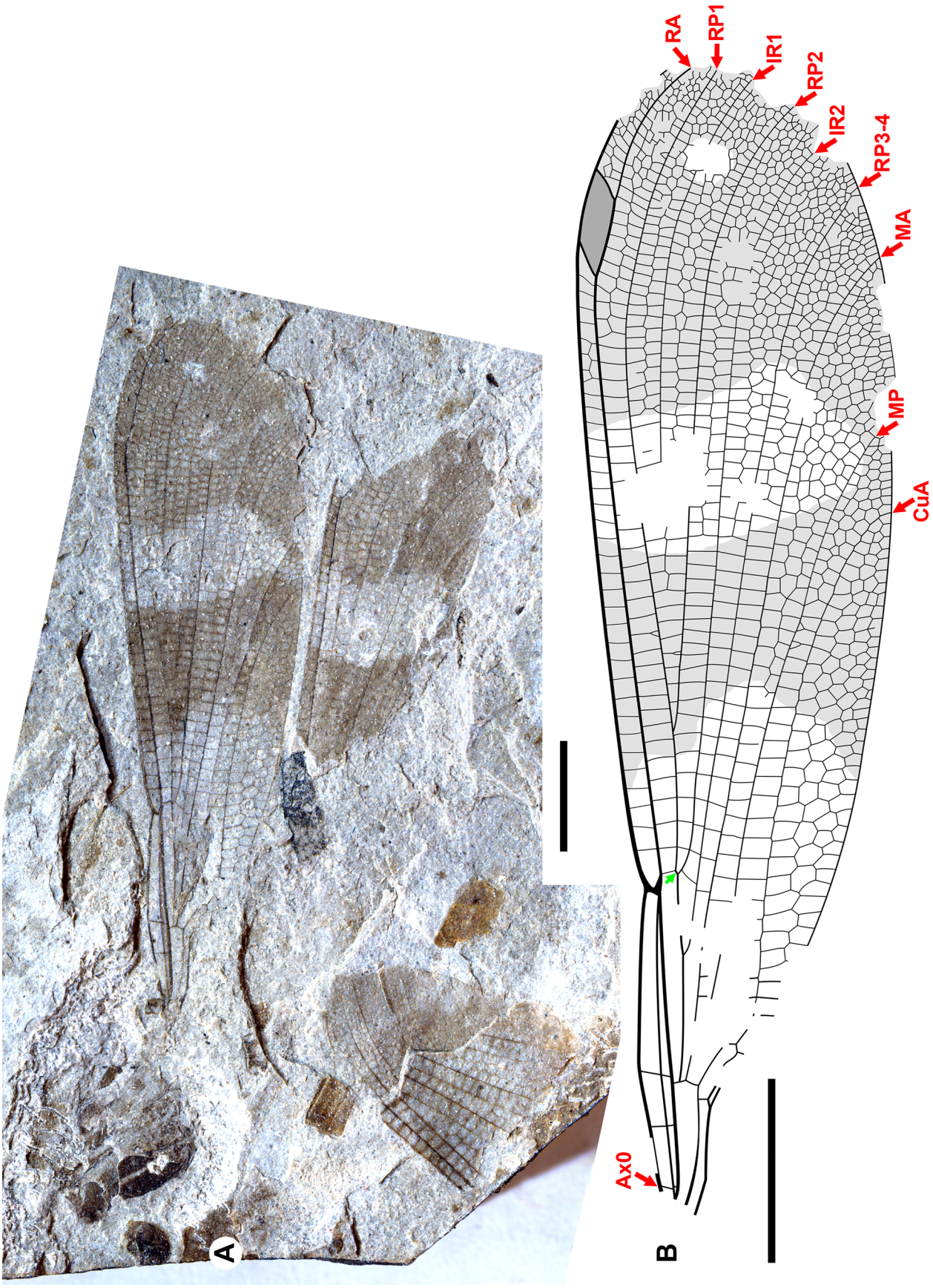

FIGURE 21. *Okanagrion beardi* holotype, F-791. A, photograph; B, drawing. Small green arrow indicates IR2 originating on RP1-2. Both to scale, 5 mm.

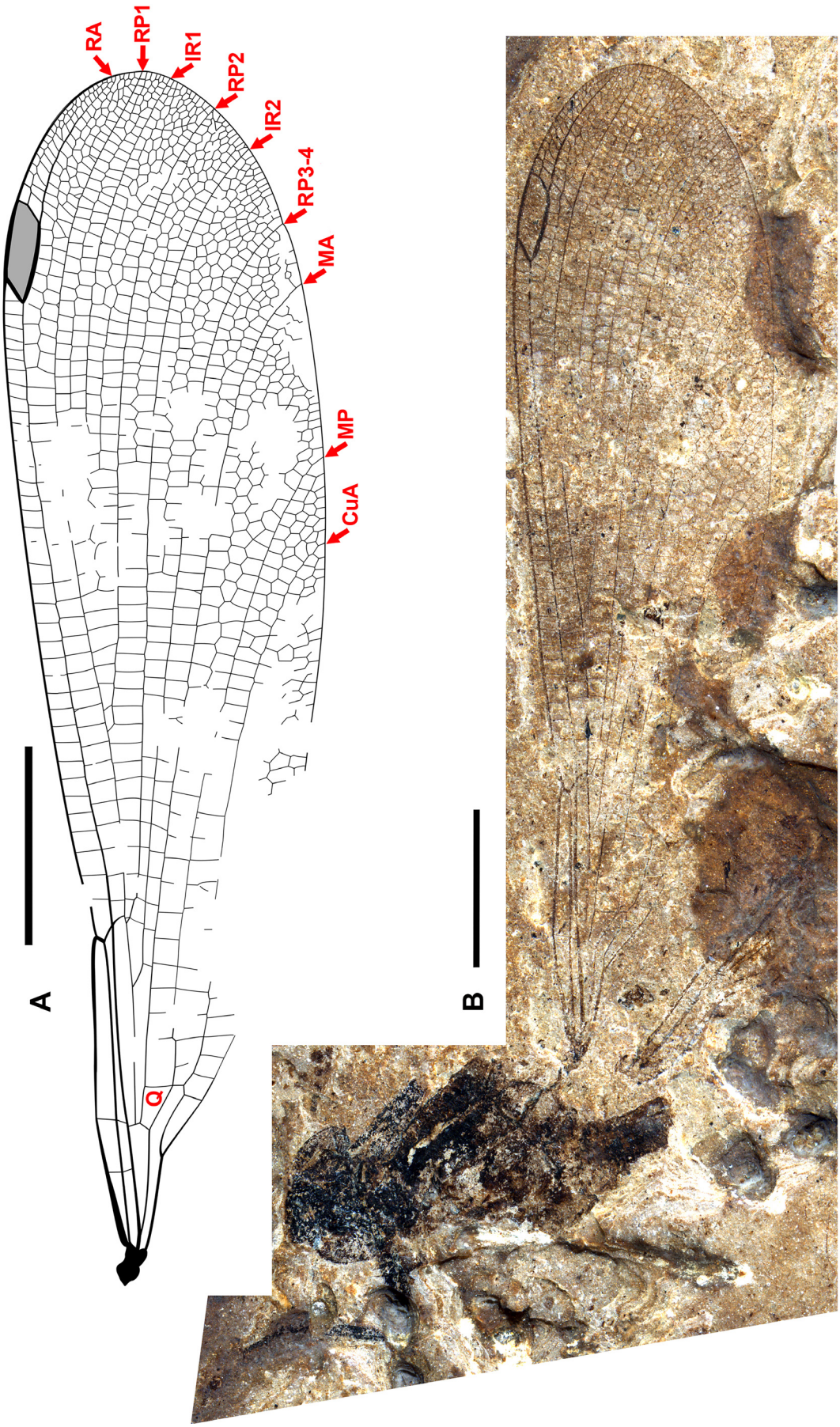

FIGURE 22. *Okanagrion beardi* paratype 1. RBCM P1546. A, drawing; B, photograph. Both to scale, 5 mm.

Etymology. The specific epithet is a patronymic formed from the surname of Graham Beard, the donor of paratype 1, recognising his contribution.

Range and age. McAbee, BC, Canada; mid-Ypresian.

Okanagrion lochmum Archibald & Cannings, new species

Fig. 23.

Diagnosis. Wings separated from those of *O. worleyae* by shape: posterior margin more deeply curved (*O. angustum* not known by preservation); from *O. beardi*, *O. dorrellae* by MP, CuA sub-parallel at terminus on posterior margin [*O. beardi*: distinctly wider, *O. dorrellae*: widening, but less distinctly as CuA zigzagged distally (*O. angustum*, not known); from *O. hobani* by RP2, IR2, RP3-4, MA, MP not as strongly curved at margin (veins anterior to these not preserved at margin); from *O. hobani* by main veins less deeply curved near margin; from *O. threadgillae* by IR2–RP3-4 space at wing margin about half width as in *O. threadgillae*; from *O. angustum*, *O. dorrellae* by width measured two cells proximal to origin of RP2 perpendicular to apical margin [*O. angustum*, *O. dorrellae*: 75% width of *O. lochmum*]; from *O. dorrellae* by MP linear to margin [*O. dorrellae*: zigzagged near margin]; from *O. angustum*, *O. beardi* by IR2 origin between RP1-2, RP3-4 [*O. angustum*, *O. beardi*: origin on RP1-2]; from *O. threadgillae*, *O. beardi*, *O. dorrellae*, *O. hobani*, *O. liquetoalatum*, *O. worleyae* by cells denser in apical wing: RA–RP1 space becomes two cells wide just over seven cells proximal to pterostigma [*O. threadgillae*, *O. beardi*, *O. dorrellae*: about three cells proximal to it; *O. hobani*: about two to four; *O. liquetoalatum*: one; *O. worleyae* four]; RA–RP1 space three cells wide from about one cell proximal to pterostigma [*O. threadgillae*, *O. hobani*, *O. liquetoalatum*, *O. worleyae*: at or one cell from apical corner of pterostigma; *O. beardi*: two–three cells apical to pterostigma; *O. angustum*, *O. dorrellae*: not known]; RA–RP1 space becomes four/five cells wide at distal corner of pterostigma [*O. hobani*: from about half distance from pterostigma to margin; *O. beardi*: becomes maximum four wide about four–five cells distal to pterostigma; *O. liquetoalatum*: five cells wide over half distance from pterostigma to margin; *O. worleyae*: maximum four wide from about four or more cells distal to pterostigma; *O. angustum*, *O. dorrellae*: not known by preservation].

Further separated by colouration (sex unknown): similar to that of *O. beardi*, and differing from other species of the genus as in their diagnoses.

Type material. *Holotype*: RBCM 11799.001 (Fig. 23), collected at the McAbee Hoodoo Face beds by John Leahy, date unknown: a mostly complete wing missing the apical-most portion and small damage proximally; housed in the Royal British Columbia Museum collections.

Description. Holotype, RBCM 11799.001, hind wing. Shape generalised for *Okanagrion* hind wing, *i.e.*, anterior margin nodus to pterostigma rather straight, posterior margin deeply curved; length arculus to base of pterostigma: 20.4 mm; nodus to base of pterostigma: 15.4 mm; nodus estimated at about 28% wing length; maximum width 8.5 mm; colouration as in diagnosis; pterostigma anterior, posterior margins oblique (anterior margin more), three times longer than wide, subtends 5.5 cells; no oblique brace vein; crossveins in postnodal, postsubnodal spaces not aligned; maximum four cells wide distal to pterostigma in costal space (but region damaged); RA–RP1 space maximum five cells wide in preserved portion; IR1 origin six cells distal to origin of RP2; RP2 origin five cells distal to origin of IR2; IR2 origin close to subnodus, immediately proximal to it; RP3-4 origin in distal part of middle third between arculus, nodus; arculus at Ax2; Ax0 not detected; no crossvein O; MA linear (very slight, short zigzag); MP linear, hardly curved from quadrangle to terminus about two-thirds distance from nodus to pterostigma; MP, CuA sub-parallel at terminus on posterior margin; CuA linear; CuA–A space with seven cells at widest (between levels of origins of IR1, RP2).

Etymology. The specific epithet *lochmum* is the Latinized neuter adjective form of the Greek Λόχμη, *lóchmi*, meaning *thicket*, referring to the denseness of the crossvenation.

Range and age. McAbee, BC, Canada; mid-Ypresian.

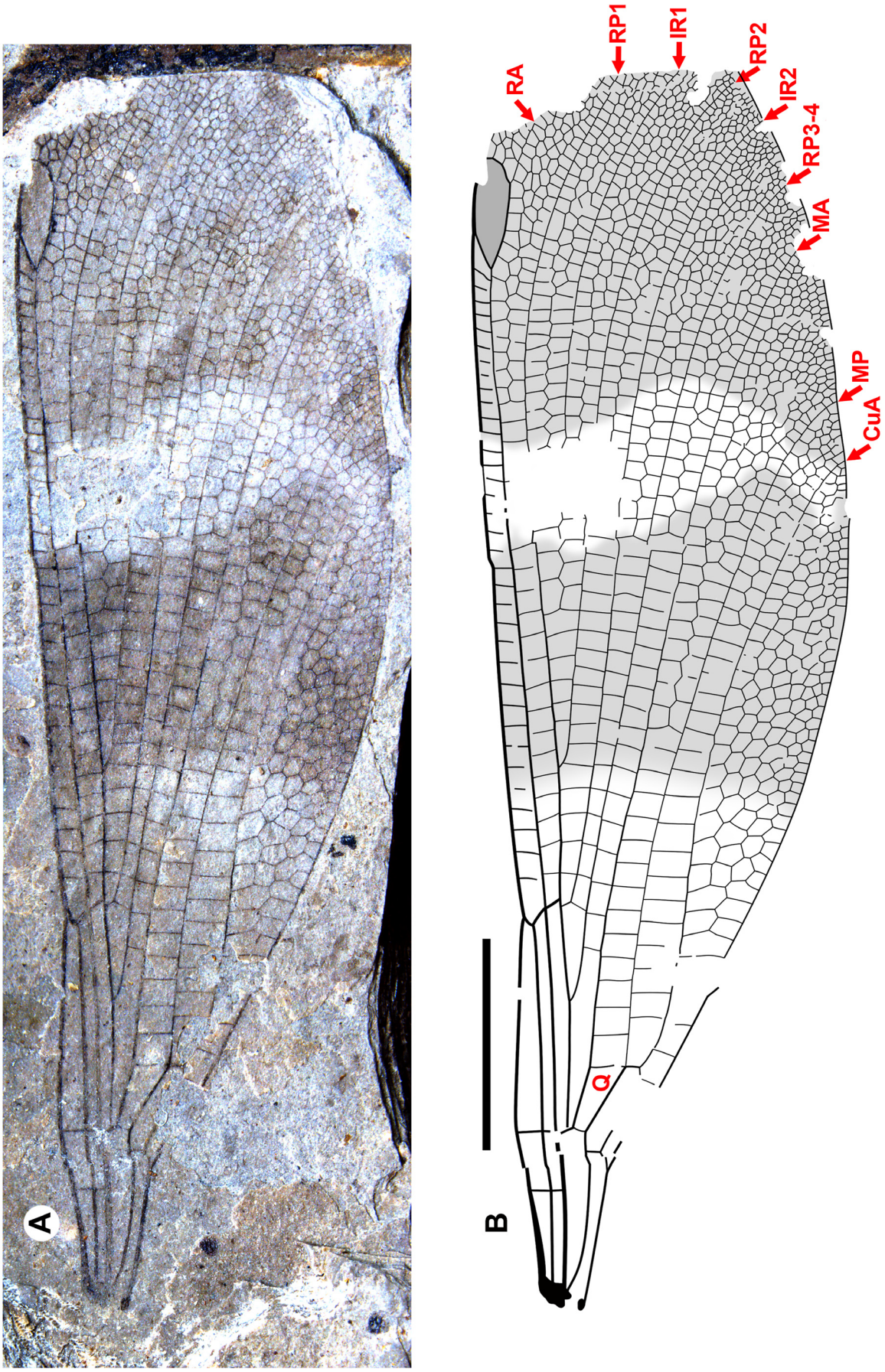

FIGURE 23. *Okanagrion lochmum* holotype, RBCM 11799.001. A, photograph; B, drawing. Both to scale, 5 mm.

***Okanagrion hobani* Archibald & Cannings, new species**
Figs. 24–35.

Diagnosis. Wings separated from those of all other *Okanagrion* species by some or all main veins anterior to CuA more deeply curved near margin (*O. angustum* not known); from *O. lochmum* by cells less dense in apical portion of the wing: see RA–RP1 space becomes two cells wide, three cells wide, four–five cells wide as it its diagnosis; from *O. angustum*, *O. beardi* by IR2 origin between RP1-2, RP3-4 [*O. angustum*, *O. beardi*: origin on RP1-2]; from *O. beardi*, *O. dorrellae* by MP, CuA sub-parallel at terminus on posterior margin [*O. beardi*: distinctly wider, *O. dorrellae*: widening, but less distinctly as CuA zigzagged distally (*O. angustum*, not known); from *O. dorrellae* by MP linear to margin [*O. dorrellae*: zigzagged near margin]; from *O. dorrellae*, *O. angustum*, *O. liquetoalatum* by wing shape [*O. dorrellae*, *O. angustum*: relative width measured two cells proximal to origin of RP2 perpendicular to apical margin, see their diagnoses; *O. liquetoalatum*: measured length (arculus to apex) / maximum width; others similar, see diagnosis of *O. liquetoalatum*]; from *O. liquetoalatum*, *O. dorrellae* by wing shape: length (arculus to apex) / maximum width 3.2 [*O. liquetoalatum*: 2.6; *O. dorrellae* 3.7; others similar to *O. hobani* (*O. lochmum*, *O. worleyae*, *O. angustum* not comparable by preservation)]; from *O. worleyae* by shape: posterior margin more deeply curved.

Further separated by colouration (male, female unknown): proximal approx. 2/5 hyaline, dark apical to this except wide lighter fascia with mid-point just distal to mid-way between nodus, pterostigma, extending from anterior margin to or almost to posterior margin; size and extent of light fascia differs from: *O. threadgillae* about a third as wide, extending to mid-wing; *O. dorrellae*, *lochmum*, *O. beardi*: about half as wide or less, extending apparently to mid-wing (*O. dorrellae*) or close to posterior margin (*lochmum*, *O. beardi*); *O. angustum* apparently similar in portion preserved; *O. liquetoalatum*: hyaline throughout; *O. worleyae*: lightly infuscate throughout known wing.

Type and additional material. *Holotype*: F-1052 (Fig. 24), McAbee, unknown collector and date, housed in the Thompson Rivers University collections. *Paratype 1*: SR 11-21-33A, B (Fig. 25), collected at Republic B4131 by Suzie Brazee, 12.vi.2008, housed in the Stonerose collections; *Paratype 2*: SR 02-24-14A, B (Fig. 26), collected at Republic B4131 by Stonerose staff, 29.viii.2002, housed in the Stonerose collections: a well preserved disarticulated wing; *Paratype 3*: SR 94-05-22A, B (Fig. 27), collected at Republic B4131 by Shay Hoban 15.v.1994, housed in the Stonerose collections; *Paratype 4*: SRUI 99-96-55A, B (Fig. 28), collected at Republic A0307 by Joanne West, 28.iv.2013, housed in the Stonerose collections; *Paratype 5*: F-1140 (Fig. 29), collected at McAbee, collector and date unknown, housed in the Thompson Rivers University collections; *Paratype 6*: SR 00-04-05 (Fig. 30), collected at Republic B4131 by Janelle Bush, 1-x-2000, housed in the Stonerose collections; *Paratype 7*: F-1044 (Fig. 31) collected at McAbee, unknown collector and date, housed in the Thompson Rivers University collections; *Paratype 8*: RBCM P1547 (Fig. 32) collected at McAbee by John Leahy, date unknown, housed in the Royal British Columbia Museum collections; *Paratype 9*: RBCM P1548 (Fig. 32), collected at McAbee by John Leahy, date unknown date, housed in the Royal British Columbia Museum collections. Additional material: SR 95-03-30 (Fig. 33) collected at Republic A0307B by Dorothy Anthony 25.ix.1994, housed in the Stonerose Interpretive Center collections; SR 10-72-03 (Fig. 33), collected Republic B4131 by Heather Johns, 29.viii.2010, housed in the Stonerose Interpretive Center collections; SR 06-62-06 (Fig. 30), collected at Republic B4131 by Karl Volkman, 8.vi.2006, housed in the Stonerose Interpretive Center collections; SR 13-005-017 (Fig. 28), collected at Republic B4131 by Dustin Bellin, 3.vi.2011, housed in the Stonerose Interpretive Center collections; SR 17-006-001 (Fig. 32), collected at Republic B4131 by Toni Brender, 30.iv.2017, housed in the Stonerose Interpretive Center collections; SRUI 99-71-07 (Fig. 34), collected Republic B4131 by Karl Volkman, 28.iv.2017, housed in the Stonerose Interpretive Center collections; RBCM P1549 (Fig. 34), collected at McAbee by John Leahy, date unknown, housed in the Royal British Columbia Museum collections.

Description. Holotype, F-1052, forewing (Fig. 24). Oval distal to nodus, symmetrical from lateral mid-line to apex. Length arculus to apex: 27.9 mm, nodus to apex: 22.2 mm, origin of RP2 to apex: 18.5 mm, arculus to base of pterostigma: 22.0 mm, nodus to base of pterostigma: 16.0 mm; maximum width 8.8 mm. Colouration as in diagnosis. Pterostigma 3.5 times longer than wide; anterior, posterior margins oblique; subtends seven cells; no oblique brace vein. Crossveins preserved in postnodal, postsubnodal spaces not aligned. Costal space distal to pterostigma maximum (mostly) three cells wide in area preserved. RA meets margin near, posterior to apex; slightly upturned near margin. Wing dense with cells throughout, increasingly dense apically. RP2: origin 5.5 cells distal to origin of IR2. IR2: origin near, proximal to subnodus. RP3-4: origin about 2/3 from arculus to subnodus. Arculus very close to, immediately proximal to Ax2

(effectively same level). All major veins linear (proximal portion of IR1 not preserved). No crossvein O. CuA terminates on posterior margin at level of mid-point between nodus, pterostigma; CuA–A space five wide cells at widest.

Paratype 1, SR 11-21-33A, B, hind wing (Fig. 25). Portions proximal to nodus not preserved (arculus, quadrangle). As for holotype except: shape: anterior margin straighter than posterior margin, which is deeply curved; without slight bulge on posterior margin at level of distal edge of quadrangle; not symmetrical from lateral mid-line to apex. Length Ax2 to base of pterostigma: 22.7 mm, nodus to base of pterostigma: 17.2 mm; maximum width 9.5 mm. Pterostigma approximately 4 times longer than wide. Subnodus with reversed obliquity. 34 crossveins preserved in postnodal space (complete number), distal-most one hyperstigmal. Costal space distal to pterostigma maximum four cells wide in area preserved. Apex not preserved: RA at margin unknown. Proximal-most portion of IR1 zigzagged (most of proximal half of IR1 not preserved). RP2: origin six cells distal to origin of IR2. IR2: origin at subnodus. RP3-4: origin closer to middle between Ax2, subnodus. CuA terminus missing, but apparently as in holotype; CuA–A space eight wide cells at widest.

Paratype 2, SR 02-24-14A, B, forewing (Fig. 26). Missing mid-posterior margin region, portions proximal to nodus (arculus, Ax2, quadrangle). As for holotype except: length nodus to apex: 19.3 mm, origin of RP2 to apex: 15.6 mm, nodus to base of pterostigma: 14.6 mm; maximum width estimated 8.3 mm. Pterostigma three times longer than wide; subtends 5.5 cells. RA meets margin at apex. RP2: origin six cells distal to origin of IR2. RP3-4: origin apparently positioned similar to that of holotype (arculus, Ax2 not preserved). CuA terminus not preserved, but preserved portion as in holotype; most of CuA–A space not preserved, four wide cells at level of nodus (holotype, similar).

Paratype 3, SR 94-05-22A, B, forewing (Fig. 27). Missing base of wing: proximal to nodus in anterior region, from level just distal to quadrangle in posterior region. As for holotype except: length nodus to apex: 22.0 mm, origin of RP2 to apex: 18.0 mm, nodus to base of pterostigma: 16.4 mm; maximum width 9.1 mm. Pterostigma four times longer than wide; subtends 6.5 cells; no oblique brace vein. 38 crossveins in postnodal space (complete number), distal-most one hyperstigmal. RA meets margin at apex. Small portion of proximal region of IR1 preserved, zigzagged. RP2: origin relative to IR2 not preserved. IR2, RP3-4 origins, arculus not preserved. CuA–A space six wide cells at widest.

Paratype 4, SRUI 99-96-55A, B hind wing (Fig. 28). Missing most of wing proximal to nodus, middle portions of remaining, slightly torn in region of pterostigma. As for holotype except: shape of preserved portion like that of paratype 1. Length nodus to apex: 19.7 mm, origin of RP2 to apex: 16.4 mm, nodus to base of pterostigma: 14.7 mm; width 8.2 mm. Pterostigma incomplete. 31 crossveins preserved in postnodal space (complete), distal-most hyperstigmal. RA meets margin at apex. Basal portion of IR1 preserved, zigzagged. RP3-4 origin, arculus, Ax2 not preserved. CuA–A space six wide cells at widest.

Paratype 5, F-1140, hind wing (Fig. 29). Missing nodal region to base. Shape relative to holotype, paratype 1 not determinable. As for holotype except: origin of RP2 to apex: 19.0 mm, width estimated 8.8 mm. Pterostigma subtends 6.5 cells; no oblique brace vein. One hyperstigmal crossvein. RP2 origin relative to that of IR2 not preserved. IR2, RP3-4 origins, arculus, Ax2 not preserved. Nodus not preserved, but CuA terminates on posterior margin at similar level as holotype; CuA–A space at least six cells wide cells at widest, probably one or two more.

Paratype 6, SR 00-04-05, hind wing (Fig. 30). Missing or very damaged proximal to subnodus, missing small portion of posterior margin mid-wing. As for holotype except: shape more like paratype 1: anterior (costal) margin straight between level of origin of RP2, subnodus, or proximal to it, near pterostigma. Length subnodus to apex: about 20.0 mm, origin of RP2 to apex: 16.9 mm, subnodus to base of pterostigma: about 14.5 mm; width 9.2 mm. Pterostigma subtends six cells. 30 crossveins preserved in postnodal space, probably 31 total, distal-most one hyperstigmal. RA not slightly upturned at margin. RP2: origin 4.5 cells distal to origin of IR2. IR2 origin poorly preserved, apparently as in holotype. RP3-4 origin, arculus, Ax2 not preserved. CuA terminus not preserved, preserved portion as in holotype; CuA–A space six wide cells at widest.

Paratype 7, F-1044, male (Fig. 31). Almost complete specimen preserved in lateral aspect: missing head, legs; all wings present, mostly overlapping, missing apical portions of two; abdomen present, segments 1 to 3 articulated to thorax; segments 4 to 10 (latter rotated so that dorsal margin is apical) and anal appendages present, disarticulated from rest of fossil, positioned closely. Wings: much of colouration of all four wings comparable, same for all. Wings somewhat crumpled, measurements not taken. Arculus immediately proximal to Ax2 (also in other two wings where preserved). Origin of RP3-4 near middle between arculus, nodus. Abdomen: about 34 mm long, about as long as wing; thick (segment 3 is 4.8 mm long, 2.4 mm wide in lateral view); segment 10 apparently displaced, rotated so

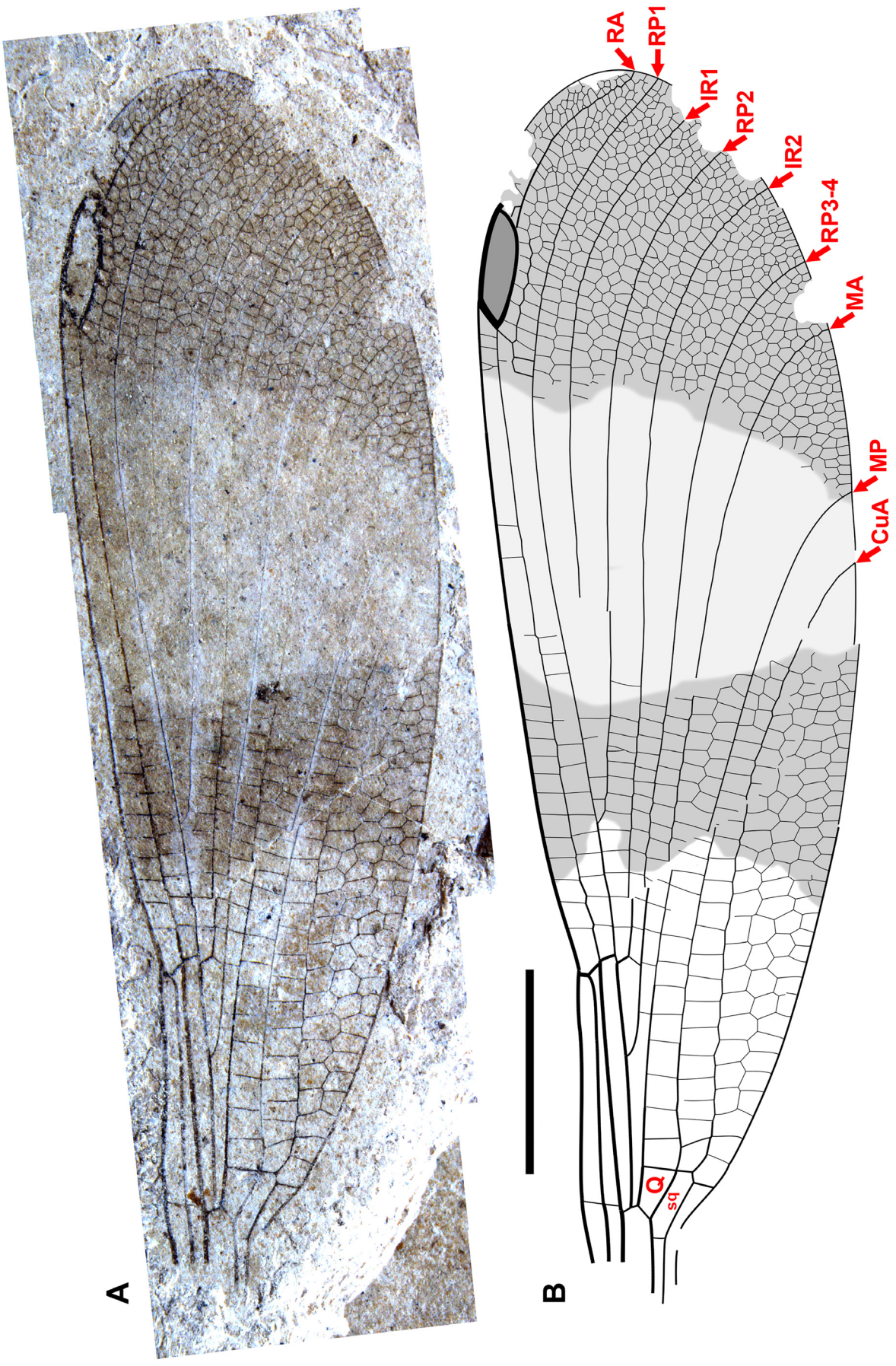

FIGURE 24. *Okanagrion hobani* holotype, F-1052. A, photograph; B, drawing. Both to scale, 5 mm.

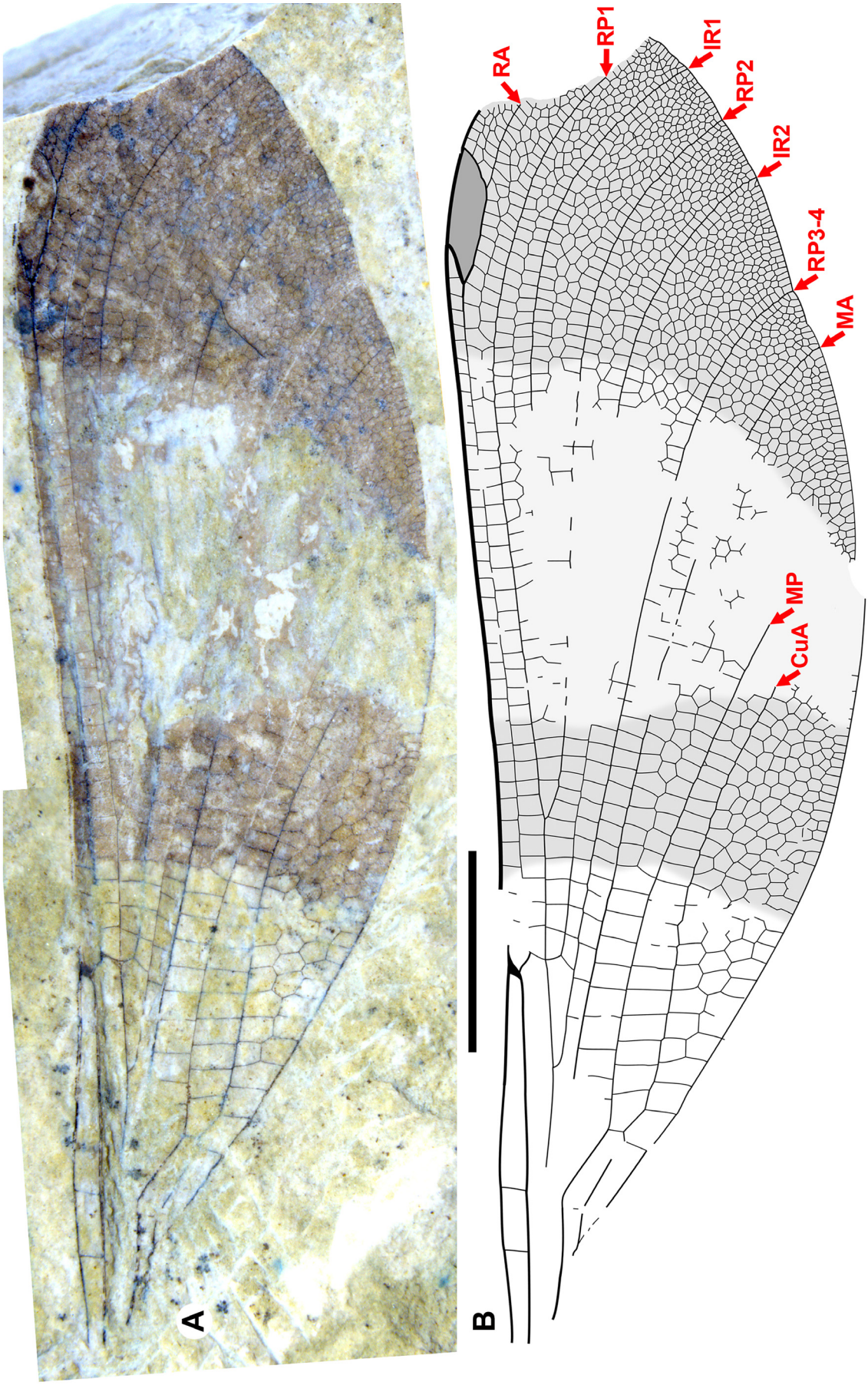

FIGURE 25. *Okanagrion hobani* paratype 1, SR 11-21-33. A, photograph; B, drawing. Both to scale, 5 mm.

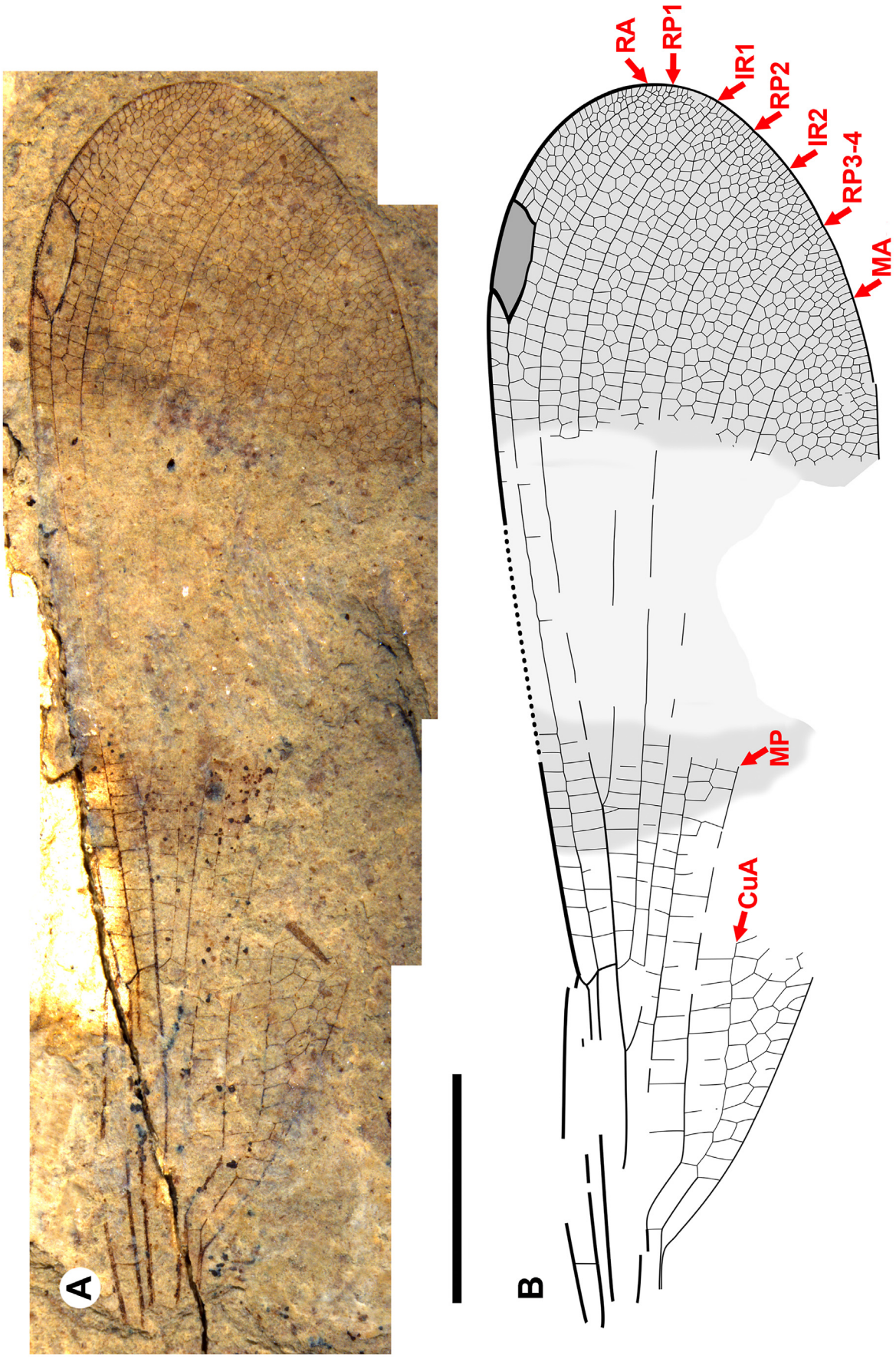

FIGURE 26. *Okanagrion hobani* paratype 2, SR 02-24-14. A, photograph; B, drawing. Both to scale, 5 mm.

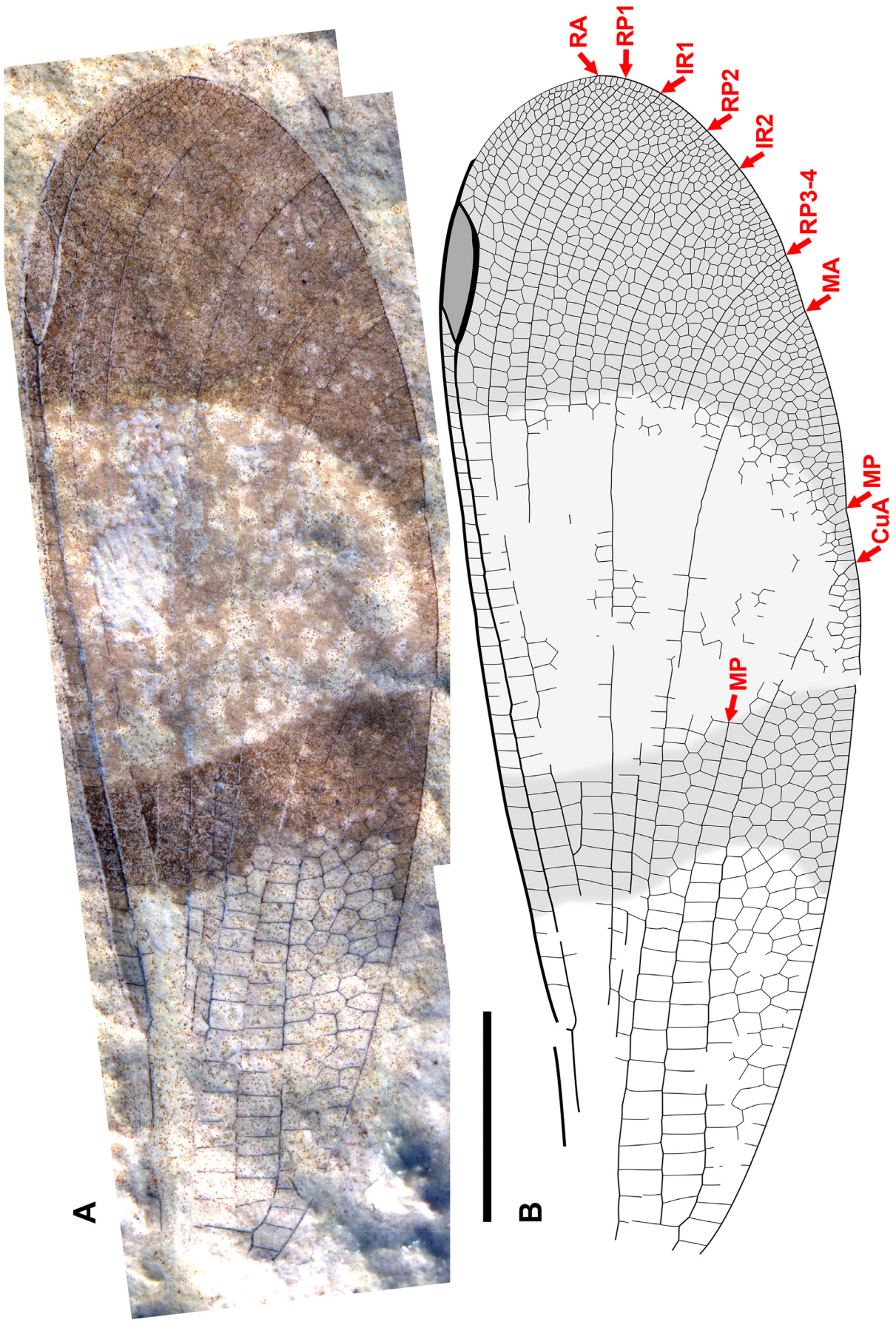

FIGURE 27. *Okanagrion hobani* paratype 3, SR 94-05-22. A, photograph; B, drawing. Both to scale, 5 mm.

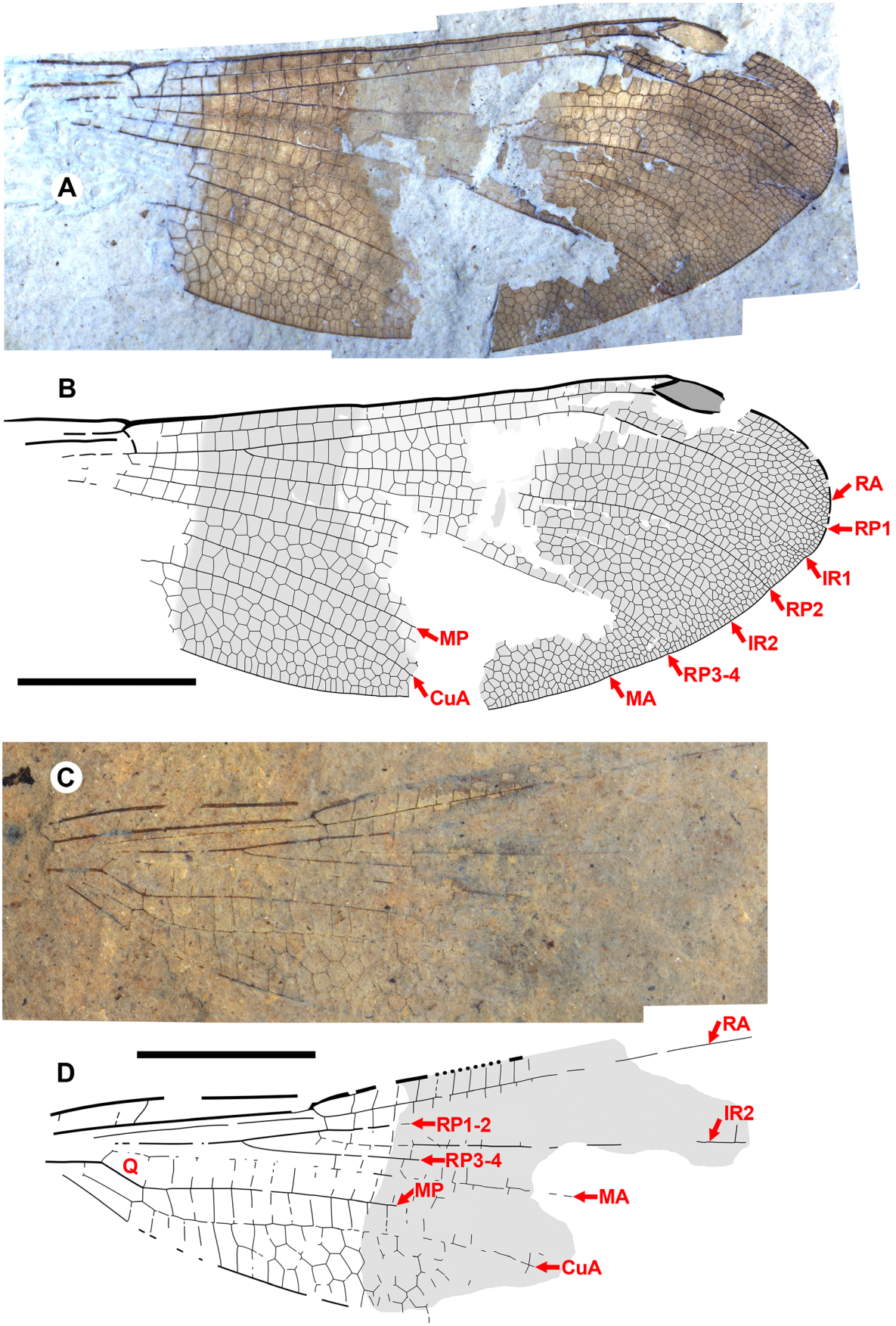

FIGURE 28. *Okanagrion hobani*. Paratype 4, SRUI 99-96-55: A, photograph; B, drawing; SR 13-005-017: C, photograph; D, drawing. All to scale, 5 mm.

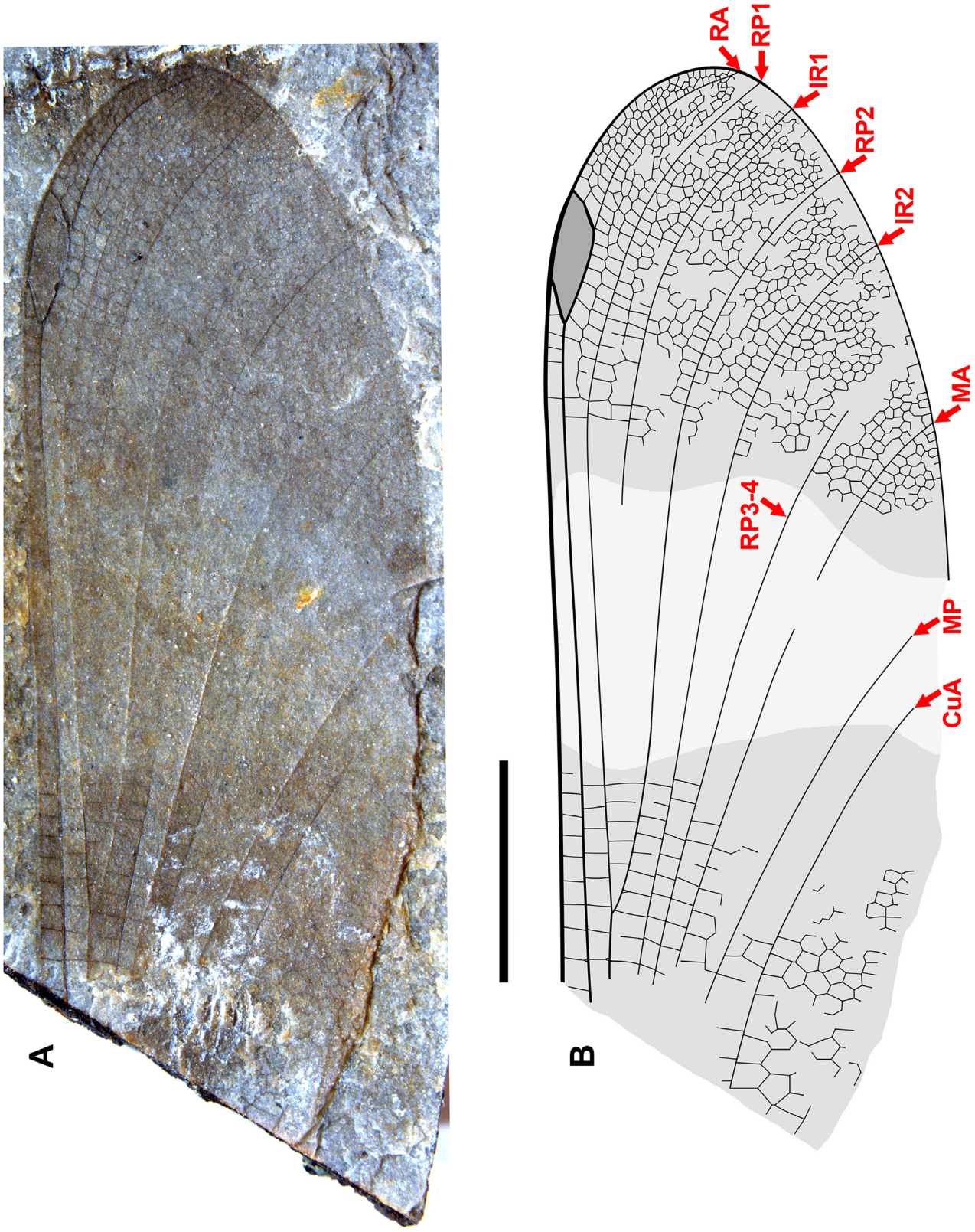

FIGURE 29. *Okanagrion hobani* paratype 5, F-1140. A, photograph; B, drawing. Both to scale, 5 mm.

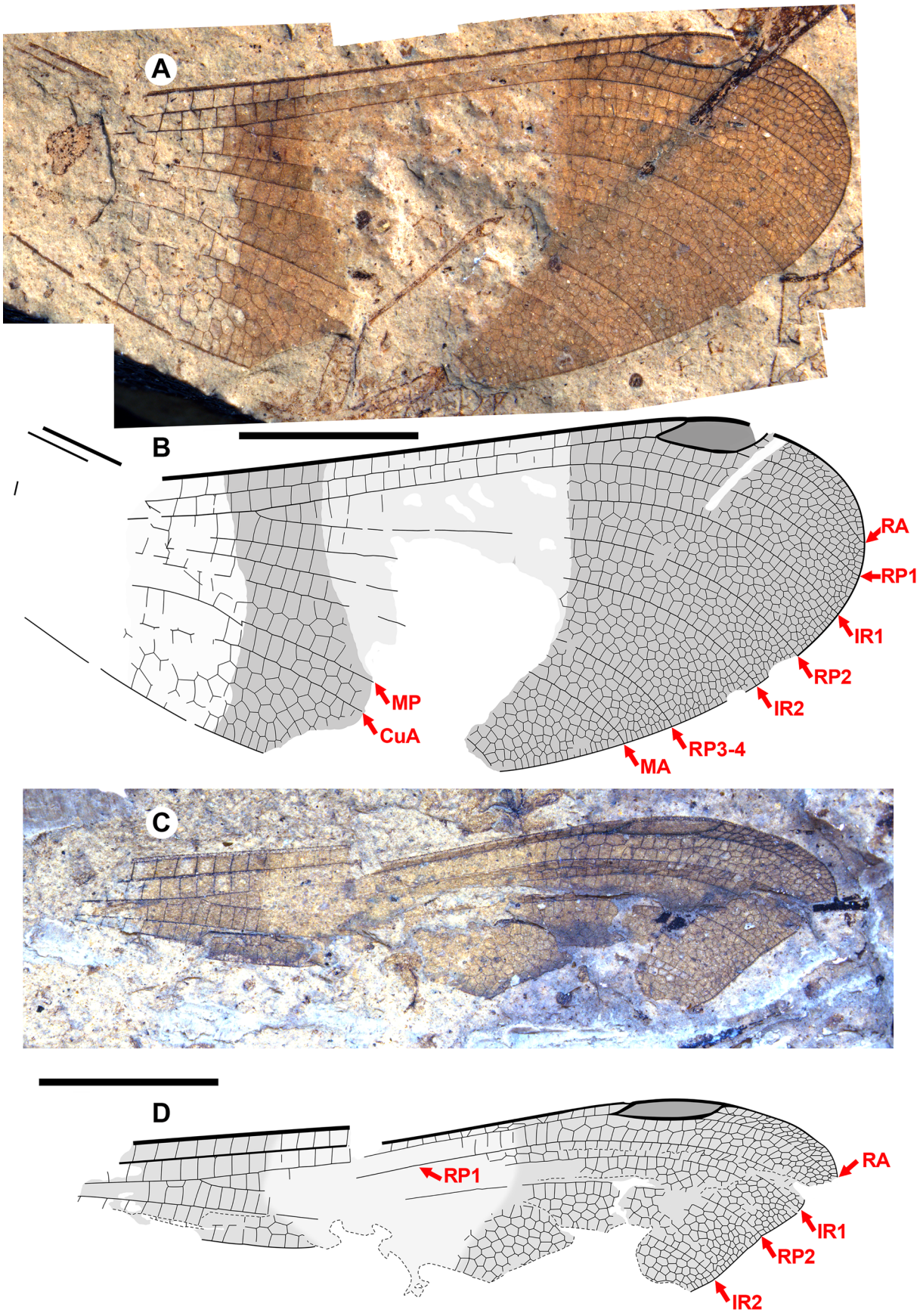

FIGURE 30. *Okanagrion hobani*. Paratype 6, SR 00-04-05: A, photograph; B, drawing; SR 06-62-06: A, photograph; B, drawing. Both to scale, 5 mm

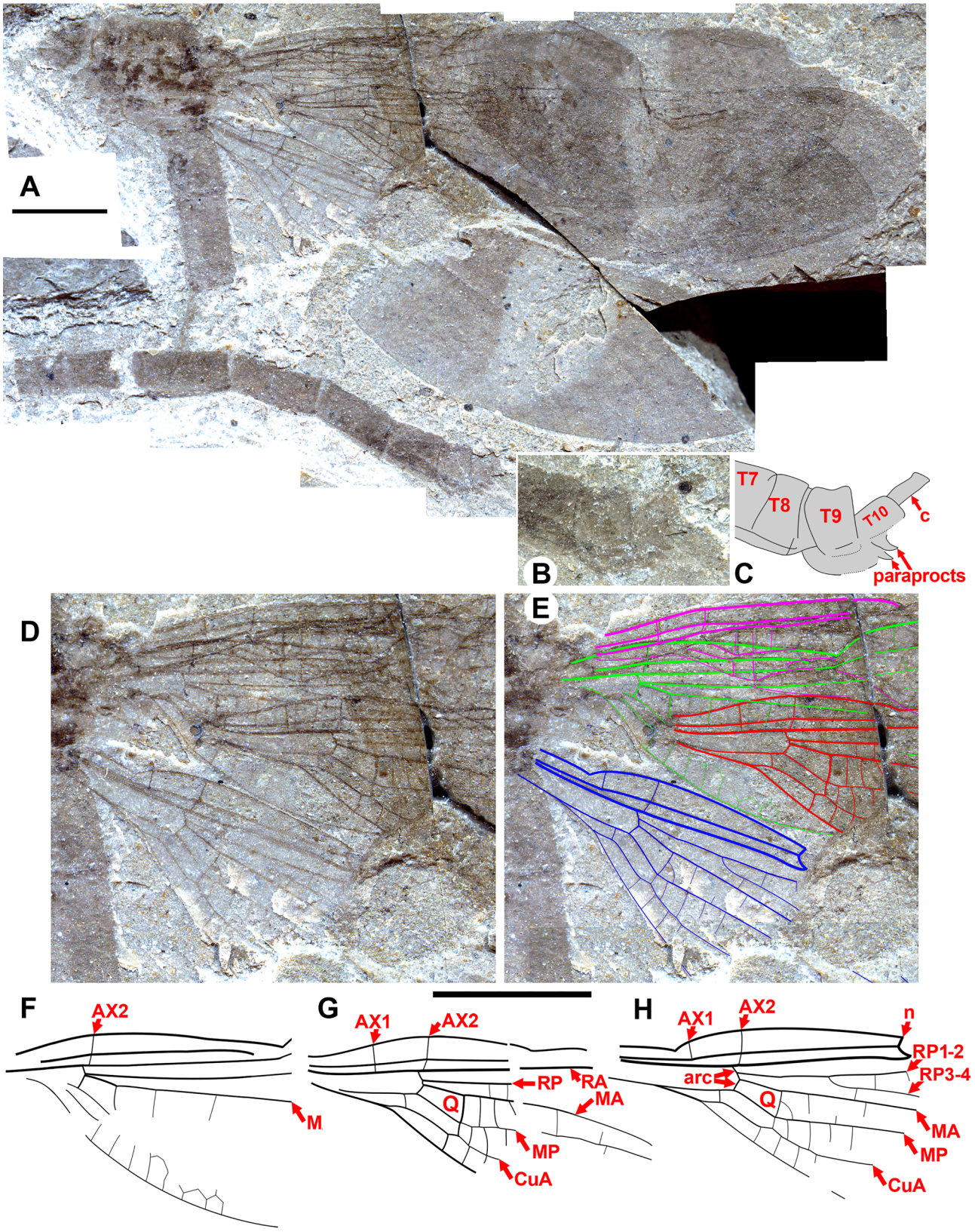

FIGURE 31. *Okanagrion hobani* paratype 7, F-1044. A, photograph of complete specimen; B, close-up of anal appendages; C, drawing of abdominal showing segments 8 to 10 (10 apparently displaced and rotated somewhat clockwise in the view), paraprocts and one cercus; D, close-up showing proximal portions of wings; E, colour-coded wings referring to 22F through H; F, G, H: drawings of wings indicated in 22E: F, green wing, G, red wing; H, blue wing (purple wing very damaged, not informative). A to scale, B–H to scale; scale bars are 5 mm

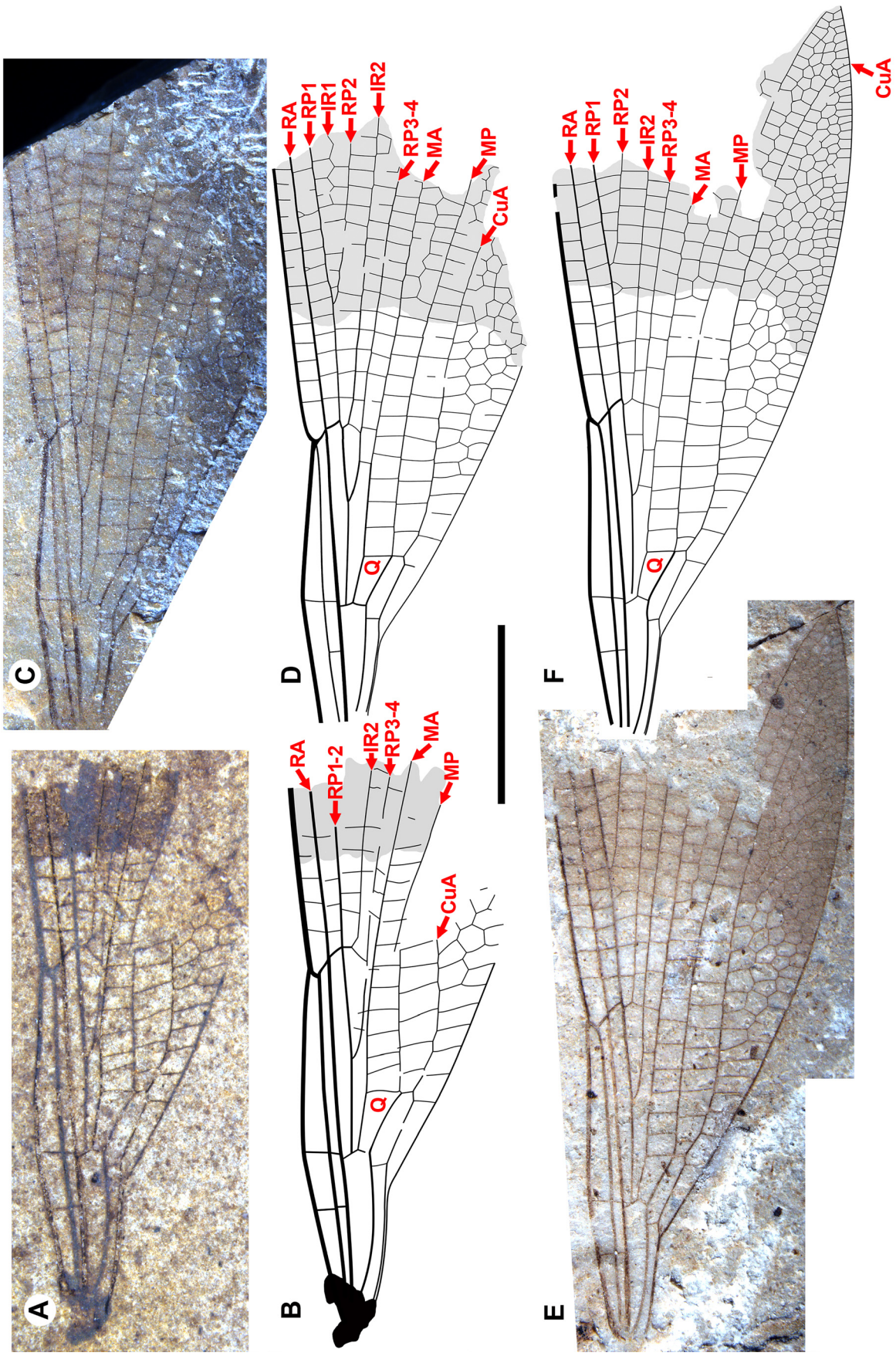

FIGURE 32. *Okanagrion hobani*. Paratype 9, RBCM P1548: A, photograph; B, drawing. Paratype 8, RBCM P1547: C, photograph; D, drawing. SR 17-006-001: E, photograph; F, drawing. All to scale, 5 mm.

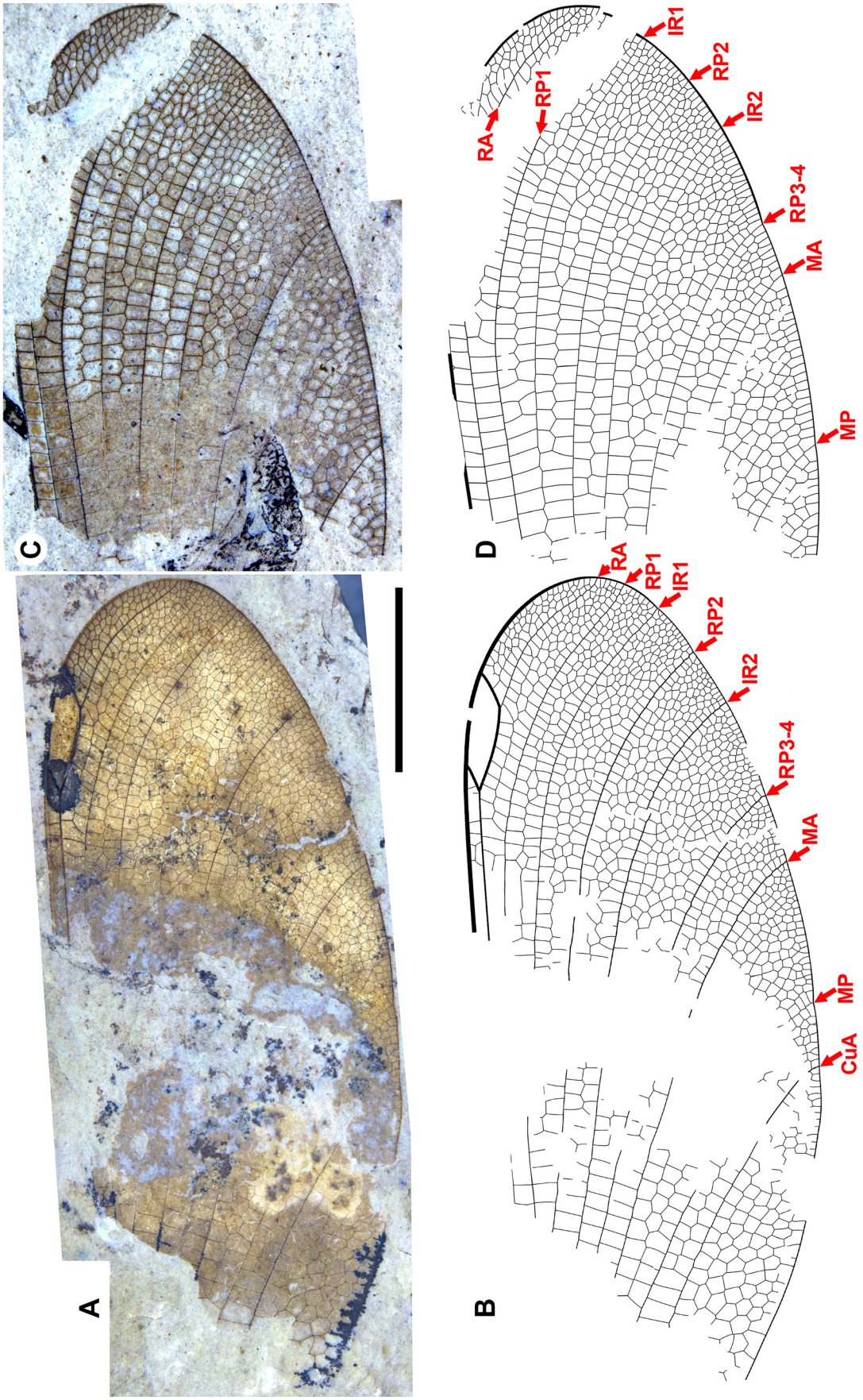

FIGURE 33. *Okanagrion hobani*. SR 10-72-03: A, photograph; B, drawing. SR 95-03-30: C, photograph; D, drawing. All to scale, 5 mm.

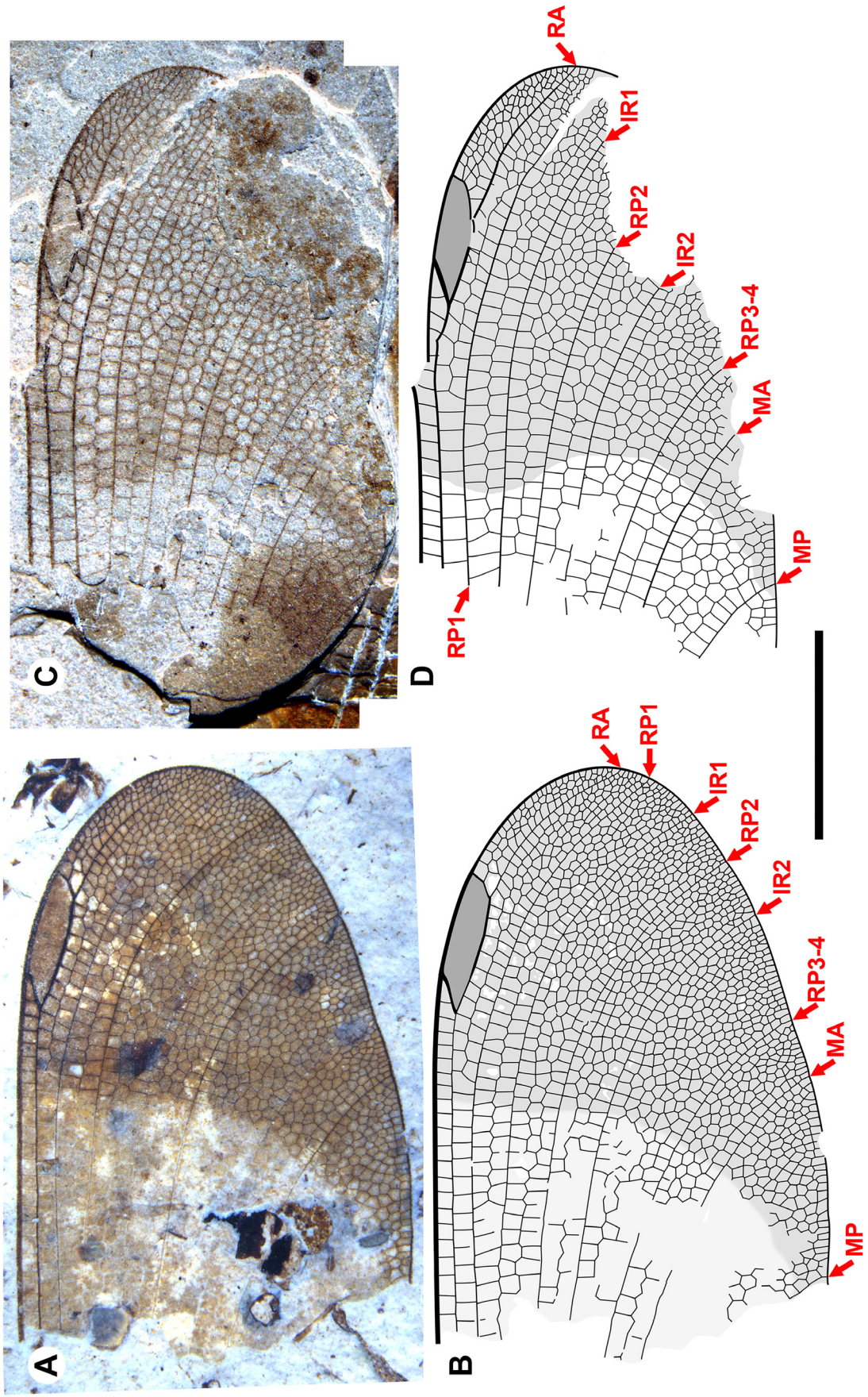

FIGURE 34. *Okanagrion hobani*. SRUI 99-71-07: A, photograph; B, drawing. RBCM P1549: C, photograph; D, drawing. All to scale, 5 mm.

that dorsal margin lies apically (about 0.5 mm long, 0.9 mm wide in lateral view), proximal parts of anal appendages thus somewhat obscured; cercus elongate, straight, slender, parallel-sided, the ventral margin slightly longer than the dorsal one, estimated at 1.3 mm long from its tip to the point it is obscured by segment 10; paraproct roughly triangular, the ventral margin about 0.8 mm long, the apical margin emarginate, more or less bifid, the ventral tooth slightly curved dorsally and acute.

Paratype 8, RBCM P1547, hind wing (Fig. 32). Proximal half of a wing. All preserved portion as for holotype except: shape more like paratype 1: posterior margin around level of distal margin of quadrangle not slightly expanded. RP2: origin five cells distal to origin of IR2. IR2: origin near, proximal to subnodus. RP3-4: origin near, slightly distal to middle between arculus, subnodus. CuA–A space six wide cells at widest.

Paratype 9, RBCM P1548, hind wing (Fig. 32). Proximal portion of a wing. All preserved portion as for holotype except: shape more like paratype 1: posterior margin around level of distal margin of quadrangle not slightly expanded. Proximal portion of IR1 preserved, zigzagged. RP3-4: origin in middle third between arculus to subnodus. CuA–A space five wide cells at widest in preserved portion.

Additional material:

SR 10-72-03, fore- or hind wing (Fig. 33). Much of the apical half of a wing, with sections not preserved, and colouration poorly preserved. As preserved, colouration agrees with holotype. All preserved portion as for holotype except: maximum width estimated as about 9.0 mm. Pterostigma four times longer than wide; subtends 6.5 cells. Few postnodal crossveins preserved, distal-most one hyperstigmal (a second joins RA at the base of the pterostigma). Costal space distal to pterostigma maximum four cells wide. Proximal portion of IR1 preserved, zigzagged. CuA–A space six wide cells at widest.

SR 13-005-017, forewing (Fig. 28). Damaged proximal portion of a wing, as for holotype except: colouration faintly preserved but apparently like that of holotype. What appears to be a possible accessory antenodal crossvein is most likely damage. RP3-4: origin in middle third between arculus, subnodus. CuA–A space apparently five wide cells at widest.

SR 17-006-001, hind wing (Fig. 32). Proximal portion of a wing, as for holotype except: IR2: origin at subnodus. RP3-4: origin half way between arculus, subnodus. CuA–A space at level of subnodus three cells wide, not preserved posterior to this.

SRUI 99-71-07, fore- or hind wing (Fig. 34). Apical portion of a wing. Colouration as in holotype. All other preserved morphology agrees with holotype except: distal-most postnodal crossvein hyperstigmal; pterostigma four times longer than wide; costal space distal to pterostigma maximum four cells wide. Part of proximal portion of IR1 preserved, zigzagged.

RBCM P1549, fore- or hind wing (Fig. 34). Apical portion of a wing. Colouration as in holotype. All other preserved morphology agrees with holotype except: distal-most postnodal crossvein hyperstigmal; pterostigma about 3.5 times longer than wide; costal space distal to pterostigma maximum four cells wide.

SR 95-03-30, fore- or hind wing (Fig. 33). An apical portion of a wing, torn, missing the pterostigmal region. As preserved, colouration agrees with holotype. Part of proximal portion of IR1 preserved, zigzagged.

SR 06-62-06, fore- or hind wing (Fig. 30). Much of an apical half or a wing from just distal to nodus, crushed, crumpled, torn. Colouration agrees with holotype.

Etymology. The specific epithet is a patronymic formed from the surname of Shay Hoban, the collector of the first of the specimens of this species (paratype 2) in May of 1994, recognising his contribution.

Range and age. Republic localities B4131 and A0307 of the Tom Thumb Tuff Member of the Klondike Mountain Formation, latest Ypresian; McAbee, BC, Canada, mid-Ypresian.

Discussion. Colour patterning is well preserved in a number of fore- and hind wings. This appears consistent throughout, including McAbee and Republic specimens, except for a slight variation in the light fascia along the posterior margin from a rather evenly "U" shape (*e.g*., SR 94-05-22) to being slightly curved proximally (*e.g*., SR 11-21-33). As discussed above, we can only be confident that this is male colouration.

They also vary by size: the forewing SR 02-24-14 is smaller than the forewing SR 94-05-22 and the hind wing SRUI 99-96-55 is smaller than the hind wing SR 11-21-33. This might be explained by sexual dimorphism (*e.g*., Serrano-Meneses *et al*. 2008).

Forewings with complete CuA–A spaces are five to six cells wide (SR 94-05-22, F-1052), and hind wings vary from six to eight cells wide (SRUI 99-96-55, SR 11-21-33), consistent with their more deeply curved posterior margin. The costal space distal to the pterostigma is a maximum three cells wide, except in RBCM P1549, SR 10-72-03, SRUI 99-71-07, and SR 11-21-33, where it reaches four cells wide.

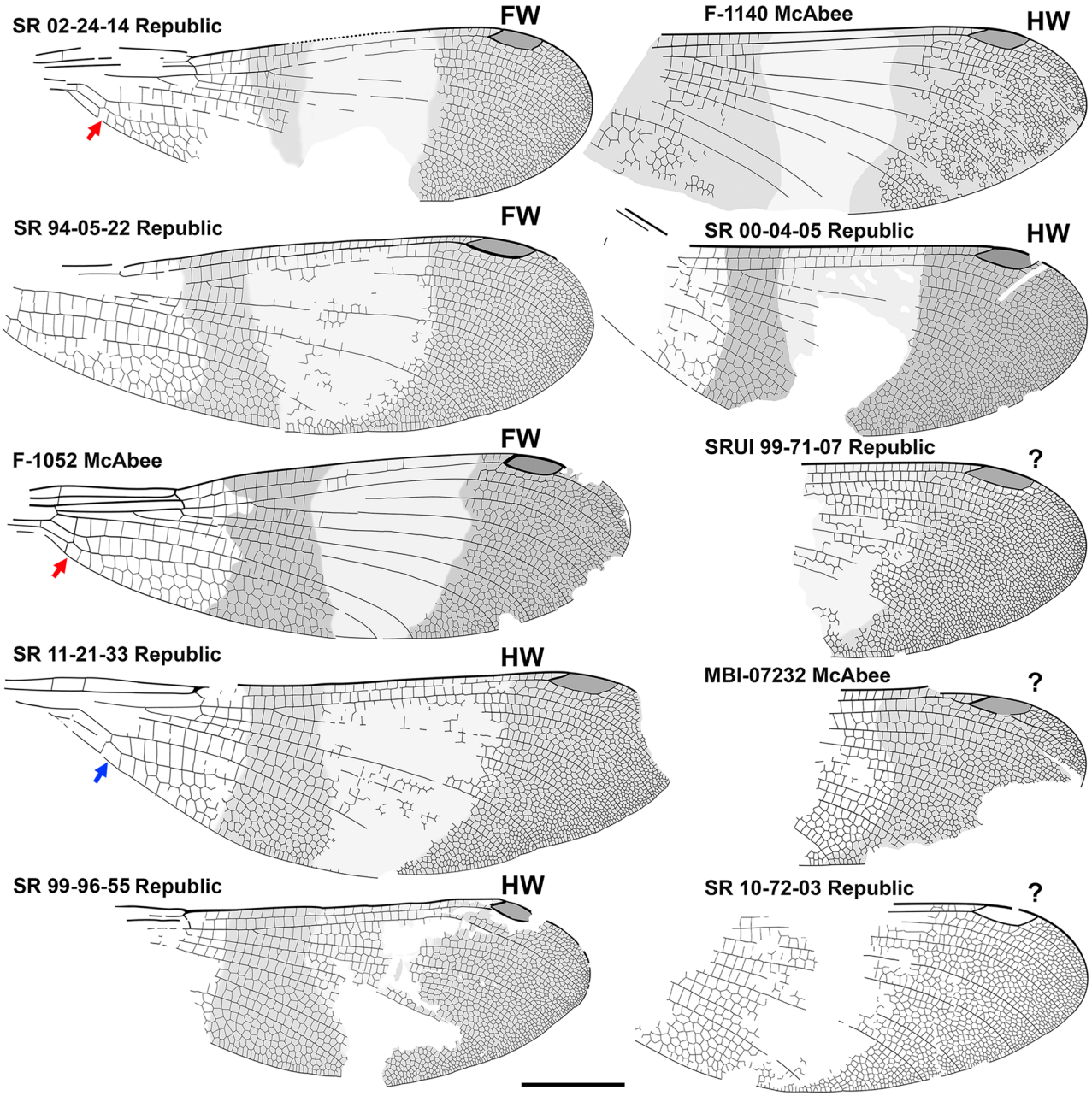

FIGURE 35. *Okanagrion hobani* relatively complete wings, comparative forewings (FW) and hind wings (HW). Red, blue arrows, see text. All to scale, 5 mm.

Okanagrion angustum Archibald & Cannings, new species

Fig. 36.

Diagnosis. Wings separated from those of all others but *O. beardi* by IR2 origin on RP1-2 [all others: origin between RP1-2, RP3-4]; from *O. beard*, *O. dorrellae* by Ax1 to nodus 1–1.5 mm longer than for *O. beardi*: 1.5 mm longer than for *O. dorrellae*; from *O. worleyae*, *O. dorrellae* by narrower at level of nodus: *O. angustum* about 5.5 mm wide [*O. worleyae*: about 4.5 mm, *O. dorrellae* 4 mm].

Further separated by colouration (sex unknown): similar to that of *O. hobani* in preserved portions (much of posterior margin, apical portion not preserved), differs from others as in its diagnosis.

Type material. *Holotype*: RBCM.EH2017.050.11.2491 (Fig. 36), collected at McAbee by John Leahy, date unknown. Much of the proximal three-quarters of a wing. Housed in the Royal British Columbia Museum collections.

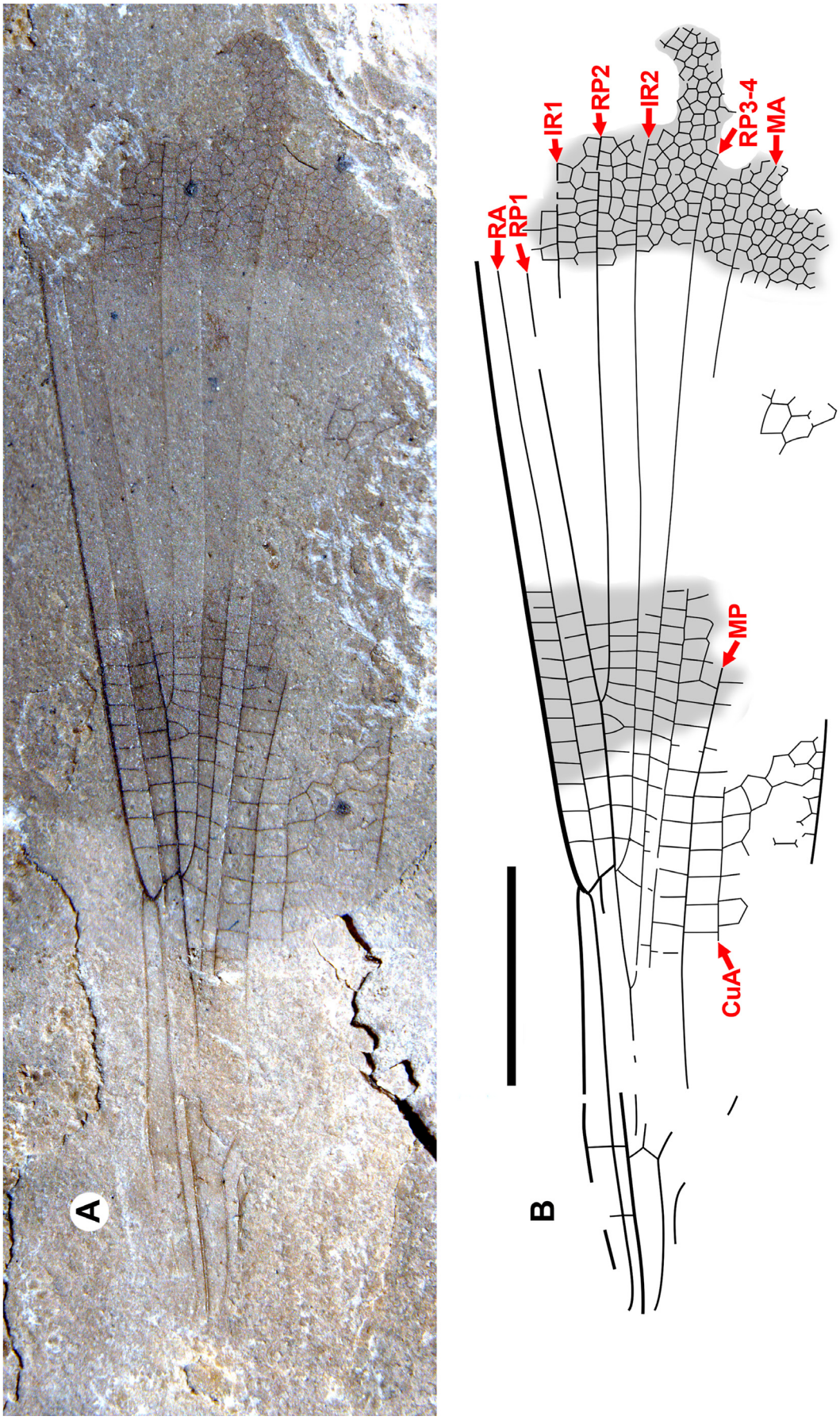

FIGURE 36. *Okanagrion angustum* holotype, RBCM.EH2017.050.11.2491. A, photograph; B, drawing. Both to scale, 5 mm.

Description. Holotype, RBCM.EH2017.050.11.2491, wing. Shape: wing narrow, as in diagnosis; colour (preserved portion) as in *O. hobani*, see diagnosis; few crossveins in postnodal, postsubnodal spaces preserved, mostly not aligned; RP2 origin 6.5 cells distal to origin of IR2; IR2 origin at subnodus, on RP1-2 as in diagnosis; RP3-4: origin in distal part of middle third between arculus, nodus; arculus just proximal to Ax2; Ax0 not detected; no crossvein O in preserved portion; no major vein zigzags in preserved portions; CuA–A space with four, possibly five cells wide at widest (between levels of origins of IR1, RP2).

Etymology. The specific epithet is the neuter form of the Latin *angustus* (*-a*, *-um*) meaning "narrow", referring to the distinctive wing shape of the species.

Range and age. McAbee, BC, Canada, mid-Ypresian.

Okanagrion dorrellae Archibald & Cannings, new species

Fig. 37.

Diagnosis. Wings separated from those of all other species of *Okanagrion* by MP zigzagged in distal portion [all others: linear (but not known in *O. angustum*)]; from all but *O. angustum* by narrower shape, especially in the proximal portion: maximum width 7.0 mm [*O. threadgillae*: forewing, hind wing: 9.0 mm; *O. hobani* all wings: 8.2–9.5 mm; *O. beardi*: 7.7, 8.3 mm; *O. liquetoalatum*: forewing 8.5 mm; *O. worleyae*: about 7.8 mm], wing length (arculus to apex) / width, 3.7 [*O. hobani*: 3.2; *O. threadgillae*: forewing 3.0, hind wing 3.1; *O. beardi*: forewings 3.3, 3.4, *O. liquetoalatum*: forewing 2.6 (*O. lochmum*, *O. worleyae*, *O. angustum* not comparable by preservation)]; from *O. hobani* by main veins less deeply curved near margin; from *O. angustum*, *O. beardi* by IR2 origin between RP1-2, RP3-4 [*O. angustum*, *O. beardi*: origin on RP1-2]; from *O. lochmum* by cells less dense in apical portion of wing: see RA–RP1 space becomes two cells wide, three cells wide, four–five cells wide as it its diagnosis; from all other *Okanagrion* species but *O. beardi* by MP, CuA divergent near margin [others: MP-CuA space remaining narrow; *O. beardi*: distinctly divergent, *O. dorrellae*: less distinctly as CuA zigzagged distally (*O. angustum*, not known)].

Further separated by colouration (sex unknown): proximal near half hyaline, dark apical to this except lighter fascia just distal to mid-way between nodus, pterostigma, extending from anterior margin to apparently mid-wing (some damage); size and extent of light fascia differs from: *O. hobani* about twice or more as wide, extending to or almost to posterior margin; *O. angustum* apparently similar to *O. hobani* as preserved; *O. threadgillae* narrower, extends to mid-wing; *O. beardi*, *O. lochmum*, similar width, apparently extends closer to posterior margin; *O. liquetoalatum*: hyaline throughout; *O. worleyae*: lightly infuscate throughout known wing.

Type material. *Holotype*: SR 93-11-02 (Fig. 37), collected Republic B9201 by Laurie Dorrell, 31.x.1992, a complete wing except for diagonal break across mid-section, with colour patterning; SR collection.

Description. Holotype, SR 93-11-02, wing. Shape: oval distal to nodus, symmetrical to lateral mid-line, but apex slightly posterior to this. Length: arculus to apex: 25.6 mm, nodus to apex: 21.1 mm, origin of RP2 to apex: 16.5 mm, arculus to base of pterostigma: 19.7 mm, nodus to base of pterostigma: 15.3 mm, nodus at 26% wing length; width 7.0 mm. Colouration as in diagnosis. Pterostigma incompletely preserved, region of possible oblique brace vein not preserved. 35 crossveins in postnodal space (total), those in postsubnodal space not aligned. At least three cells wide maximum in costal space distal to pterostigma, but most of space not preserved. RA meets margin anterior to apex. RA–RP1 space narrows near margin. IR1: origin nine cells distal to origin of RP2, IR1 two cells wide probably (poorly preserved) eight cells distal to origin. RP2: origin seven cells distal to origin of IR2 (one very small). IR2: origin at subnodus. RP3-4 origin in distal part of middle third between arculus, nodus. Arculus just proximal to Ax2. No crossvein O. All main veins linear except base of IR1, MP distal to mid-wing between nodus, pterostigma. CuA–A space apparently (by preservation) five cells wide at widest.

Etymology. The specific epithet is a patronymic formed from the surname of Laurie Dorrell, the collector of the holotype, recognising her contribution.

Range and age. Republic locality B9201 of the Tom Thumb Tuff Member of the Klondike Mountain Formation; latest Ypresian.

Discussion. Although the holotype wing and sole specimen of *O. dorrellae* has a diagonal break across it, we are confident of the shape as the veins are not shifted across this break. The wing has not been compressed, as internal elements such as the shape of cells are not deformed.

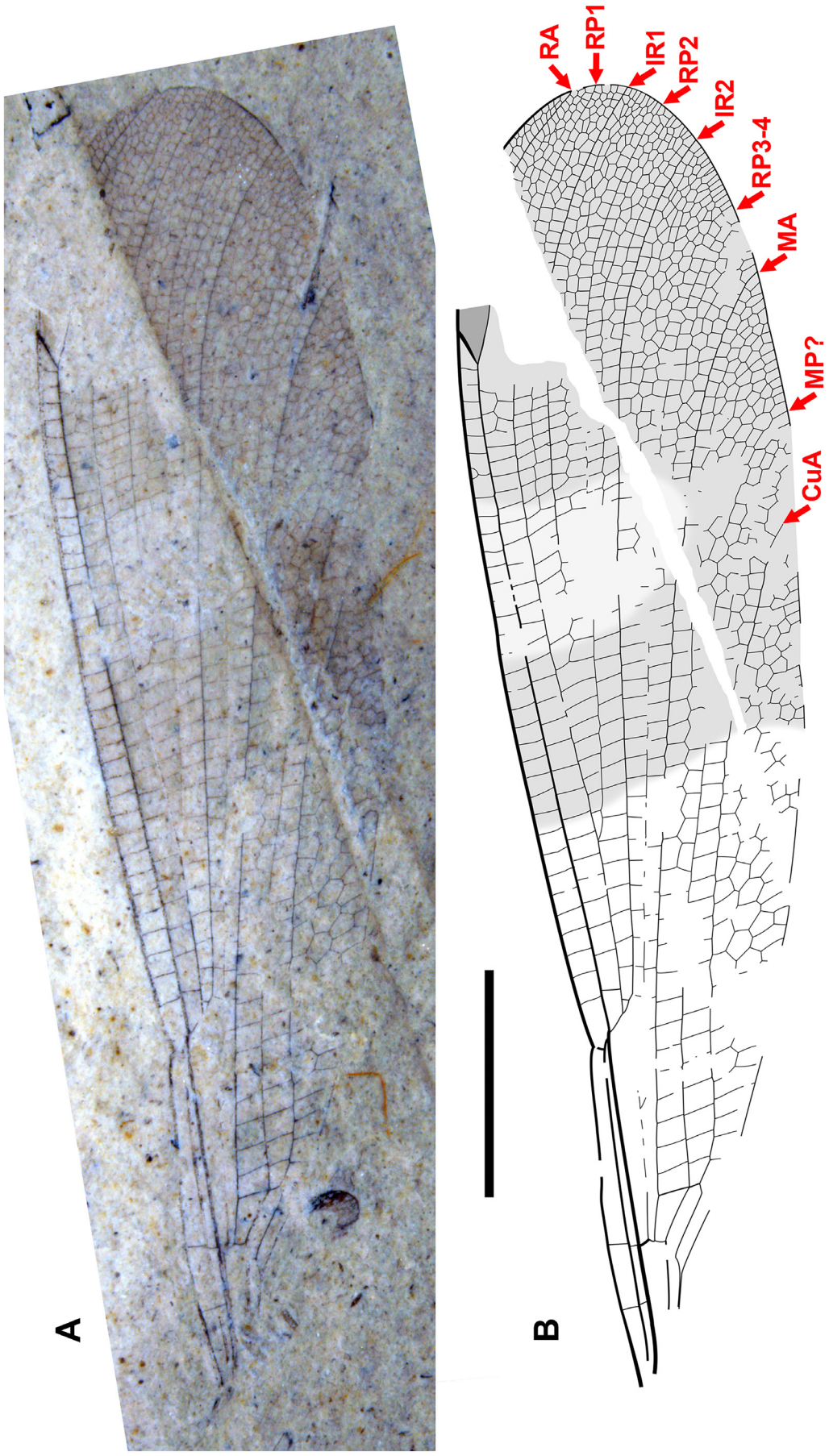

FIGURE 37. *Okanagrion dorrellae* holotype, SR 93-11-02. A, photograph; B, drawing. Both to scale, 5 mm.

***Okanagrion liquetoalatum* Archibald & Cannings, new species**
Fig. 38.

Diagnosis. Wings separated from those of *O. hobani*, *O. threadgillae*, *O. worleyae*, *O. dorrellae*, *O. beardi* by shape: length (arculus to apex) / maximum width 2.6 [*O. hobani*: 3.2; *O. threadgillae*: 3.0, 3.1; *O. worleyae* holotype: 2.8, paratype: 3.1; *O. dorrellae*: 3.7; *O. beardi*: 3.3, 3.4]; from *O. angustum* by shape [*O. lochmum*, *O. worleyae*, *O. angustum* apical region not preserved, but *O. angustum* distinctly narrower, see width, angle of posterior to anterior margin preserved between levels of nodus, origin of RP2]; from *O. beardi*, *O. dorrellae* by MP, CuA sub-parallel at terminus on posterior margin [*O. beardi*: distinctly wider, *O. dorrellae*: widening, but less distinctly as CuA zigzagged distally (*O. angustum*, not known); from *O. lochmum* by cells less dense apically: RA–RP1 space two cells wide distal to 1–2 cells proximal to pterostigma [*O. lochmum* from 7–8 cells proximal to pterostigma], RA–RP1 space three cells wide distal from apical corner of pterostigma or one cell distal from that [*O. lochmum* from about one cell proximal to pterostigma], RA–RP1 space becomes five cells wide over half distance from pterostigma to margin [*O. lochmum*: from distal end of pterostigma]; from *O. hobani* by main veins less deeply curved near margin; from *O. dorrellae* by MP linear to terminus [*O. dorrellae*: zigzagged distally]; from *O. angustum*, *O. beardi* by IR2 origin between RP1-2, RP3-4 [*O. angustum*, *O. beardi*: origin on RP1-2].

Further separated by colouration (sex unknown): *O. liquetoalatum*: hyaline throughout; others with distinct colour patterning as in their diagnoses; *O. worleyae*: lightly infuscate throughout known wing.

Type material. *Holotype*: SR 06-69-17A, B (Fig. 38), collected at Republic B4131 by Gregg Wilson, 29.iv.2006: a well preserved disarticulated wing, housed in the Stonerose Interpretive Center collections.

Description. Holotype, SR 06-69-17A, B, wing. Shape: oval distal to nodus, anterior margin rather straight between nodus, pterostigma, posterior margin evenly curved apical to petiole. Hyaline throughout. Length 30.5 mm, arculus to apex: 25.2 mm, nodus to apex: 20.3 mm, origin of RP2 to apex: 16.6 mm, arculus to base of pterostigma: 20.4 mm, nodus to base of pterostigma: 15.4 mm, nodus at 29% wing length; maximum width 8.5 mm. Pterostigma 3.5 longer than wide, subtends 5.5 cells, no oblique brace vein. Costal space distal to pterostigma maximum 3 cells wide; RA terminates at apex, slightly upturned at margin. 31 crossveins in postnodal space, none hyperstigmal, those in postsubnodal spaces not aligned. Maximum three cells wide distal to pterostigma in costal space. RA–RP1 space hardly narrows near margin. RP1–IR1 space goes to two cells wide eight cells distal to origin of IR1. IR1: origin eight cells distal to origin of RP2, zigzagged proximally. IR1 two cells wide six (or ten?) cells distal to origin. RP2: origin 5.5 cells distal to that of IR2. IR2: origin very close proximal to subnodus. RP3-4 origin near, distal to middle between arculus, nodus. Arculus at Ax2. No crossvein O. All main veins except base of IR1 linear. CuA–A space with five cells wide at widest.

Etymology. The specific epithet *liquetoalatum* is formed from the Latin *liquet* for clear and *alatus* (*-a, -um*) meaning winged.

Range and age. Republic locality B4131 of the Tom Thumb Tuff Member of the Klondike Mountain Formation; latest Ypresian.

Discussion. Wing falsely appears mottled in Fig. 38 photo by wetting with ethanol.

***Okanagrion worleyae* Archibald & Cannings, new species**
Figs. 39–41.

Diagnosis. Wings separated from those of *O. threadgillae*, *O. beardi*, *O. liquetoalatum*, *O. lochmum*, *O. hobani*, by shape: posterior margin less deeply curved; further from *O. threadgillae* by shape, nodus to apex 3.0 times maximum width [*O. threadgillae*: 2.5]; further from *O. angustum* by narrower wing, about 4.5 mm wide at levels of nodus [*O. angustum* about 5.5 mm]; from *O. dorrellae* by MP linear near margin (but partially known by preservation) [*O. dorrellae*: zigzagged]; from *O. beardi*, *O. dorrellae* by MP, CuA sub-parallel at terminus on posterior margin [*O. beardi*: distinctly wider, *O. dorrellae*: widening, but less distinctly as CuA zigzagged distally (*O. angustum*, not known); from *O. angustum*, *O. beardi* by IR2 origin between RP1-2, RP3-4 (clearly preserved in holotype, not clear by damage in paratype 2, region not preserved in paratype 1) [*O. angustum*, *O. beardi*: origin on RP1-2]; from *O. hobani* by main veins less deeply curved near margin; from *O. lochmum* by cells less dense in apical portion of wing: RA–RP1 space two cells wide distal to four cells proximal to pterostigma [*O. lochmum*: 7–8 cells proximal],

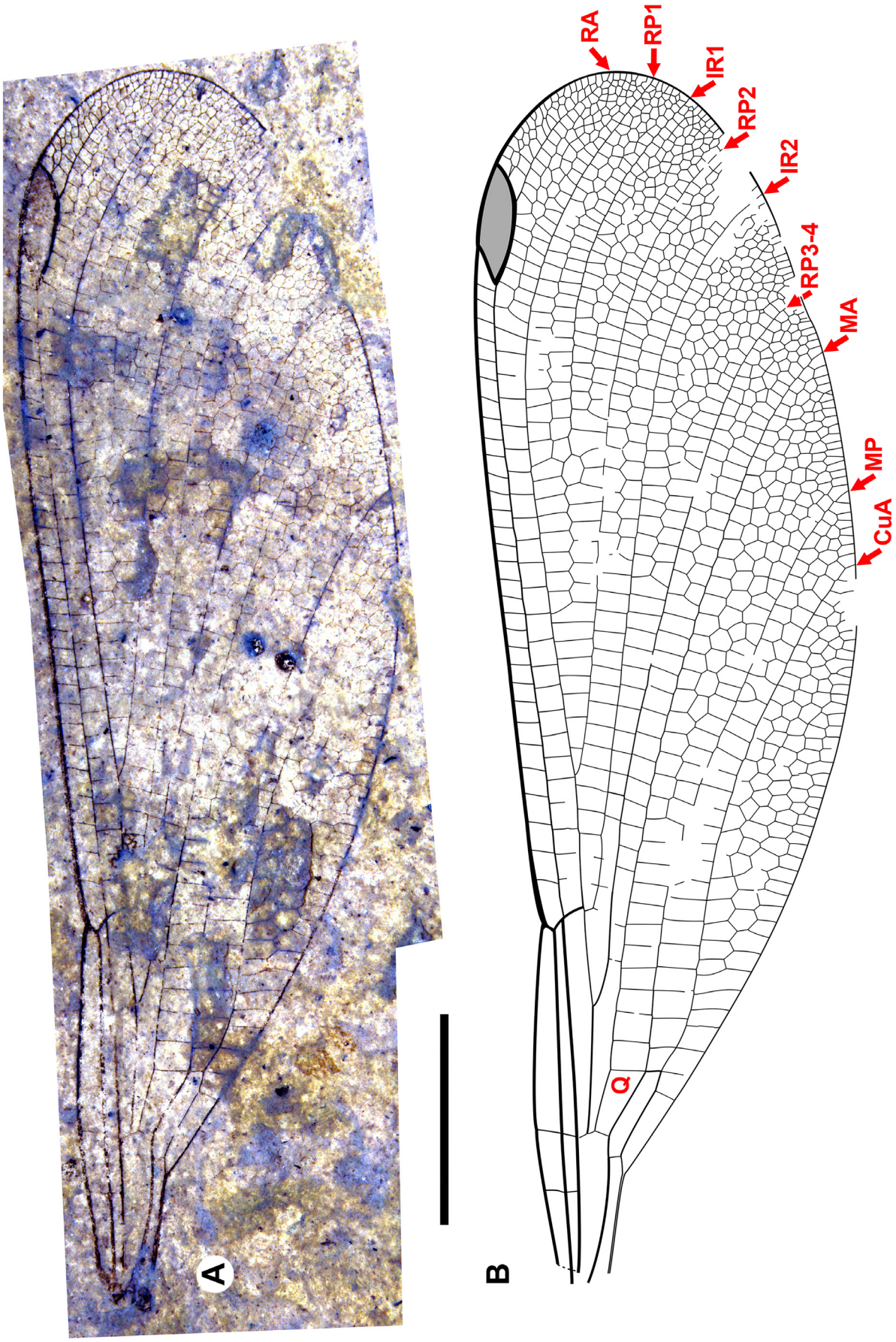

FIGURE 38. *Okanagrion liquetoalatum* holotype, SR 06-69-17. A, photograph; B, drawing. Both to scale, 5 mm.

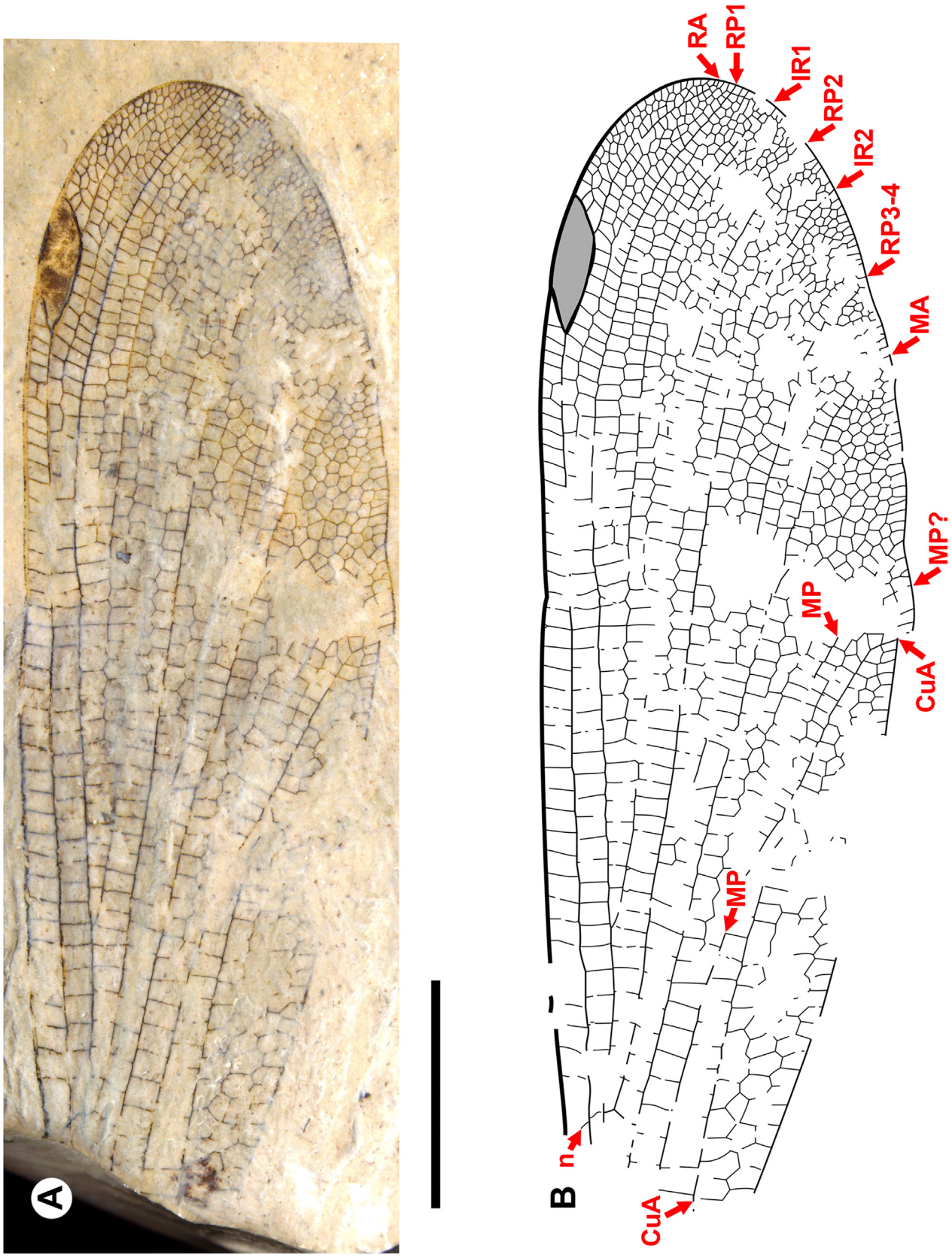

FIGURE 39. *Okanagrion worleyae* holotype, SR 99-14-02: A, photograph; B, drawing. Both to scale, 5 mm.

RA–RP1 space three cells wide about one cell distal to pterostigma [*O. lochmum*: at base of pterostigma], RA–RP1 space maximum four wide from about four cells distal to pterostigma [*O. lochmum*: four, then five cells wide about distal corner of pterostigma].

Further separated by colouration (sex unknown): wing lightly, uniformly infuscate across all known portions as preserved (might appear almost hyaline by preservation).

Type material. *Holotype*: SR 99-14-02 (Fig. 39), collected at Republic A0307 by Providence Worley, 23.viii.1998, housed in the Stonerose Interpretive Center collections; *paratype 1*: SR 16-006-001 (Fig. 40), collected at Republic A0307 by Kattia Rojas, 9.x.2016, in the Stonerose Interpretive Center collections; *paratype 2*: SR 11-21-09 (Fig. 41), collected at Republic B4131 by Eric Blumhagen, 2.viii.2008, in the Stonerose Interpretive Center collections.

Description. Holotype, SR 99-14-02, wing (Fig. 39). Missing portion proximal to nodus. Shape: narrow oval distal to nodus, mostly symmetrical from lateral mid-line, except apex slightly anterior to this. Length: nodus to apex: 22.7 mm, origin of RP2 to apex: 18.5 mm, nodus to base of pterostigma: 17.2 mm; width 7.8 mm. Lightly infuscate throughout. Pterostigma anterior, posterior margins oblique, 3.5 longer than wide, subtends seven cells, no oblique brace vein. 37 crossveins preserved in postnodal space (probably two not preserved), distal-most one hyperstigmal; those in postsubnodal spaces not aligned. Three cells wide distal to pterostigma in costal space. RA meets margin close to, posterior to apex, RA slightly curved forward near margin. RA–RP1 space narrows at margin. RP1–IR1 space goes to two cells wide nine cells distal to origin of IR1. IR1 origin eight cells distal to origin of RP2; IR1 two cells wide eight cells distal to origin. RP2: origin apparently (by preservation) seven cells distal to origin of IR2. IR2 origin at subnodus. No crossvein O. All major veins linear except proximal portion of IR1. CuA–A space four cells wide at widest.

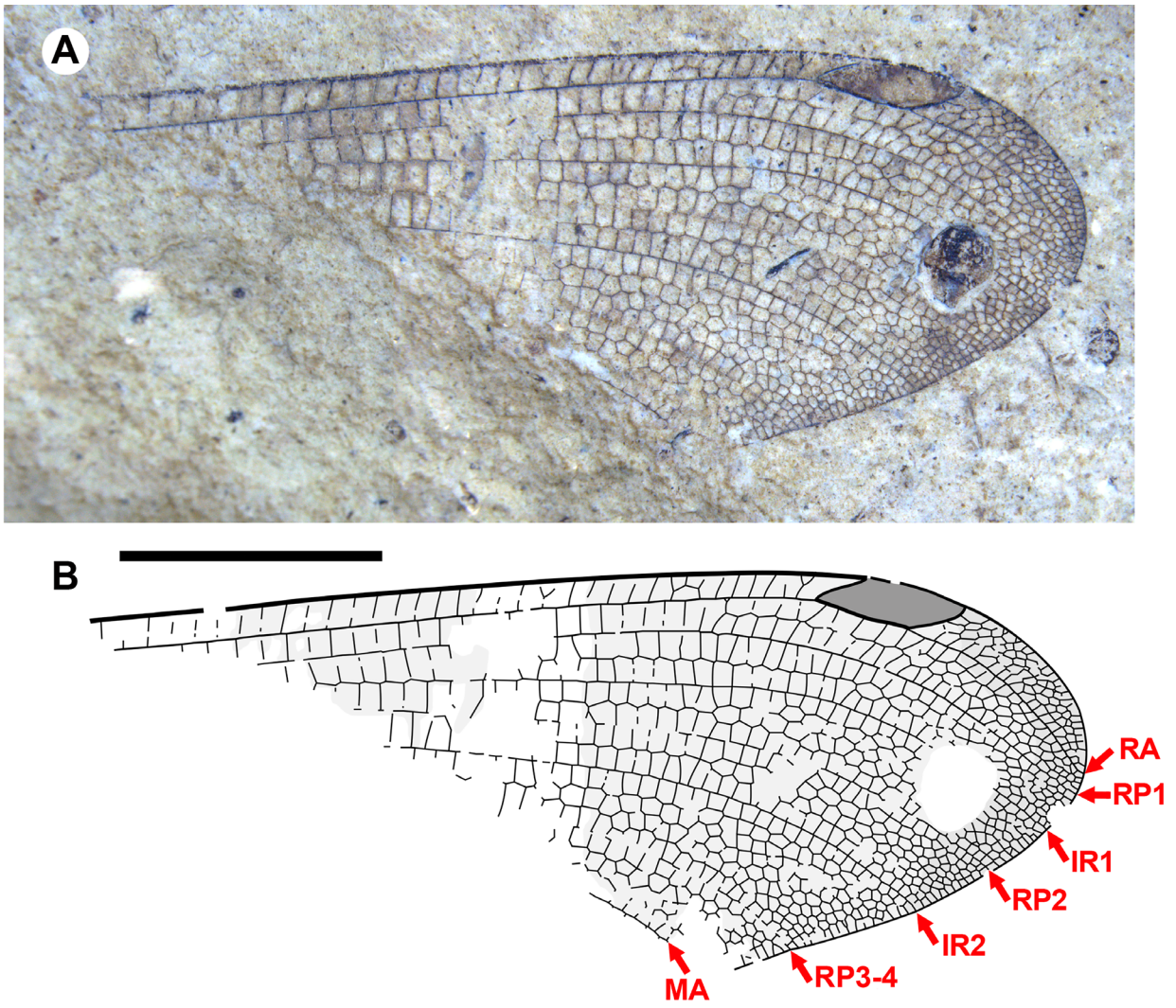

FIGURE 40. *Okanagrion worleyae* paratype 1, SR 16-006-001. A, photograph; B, drawing. Both to scale, 5 mm.

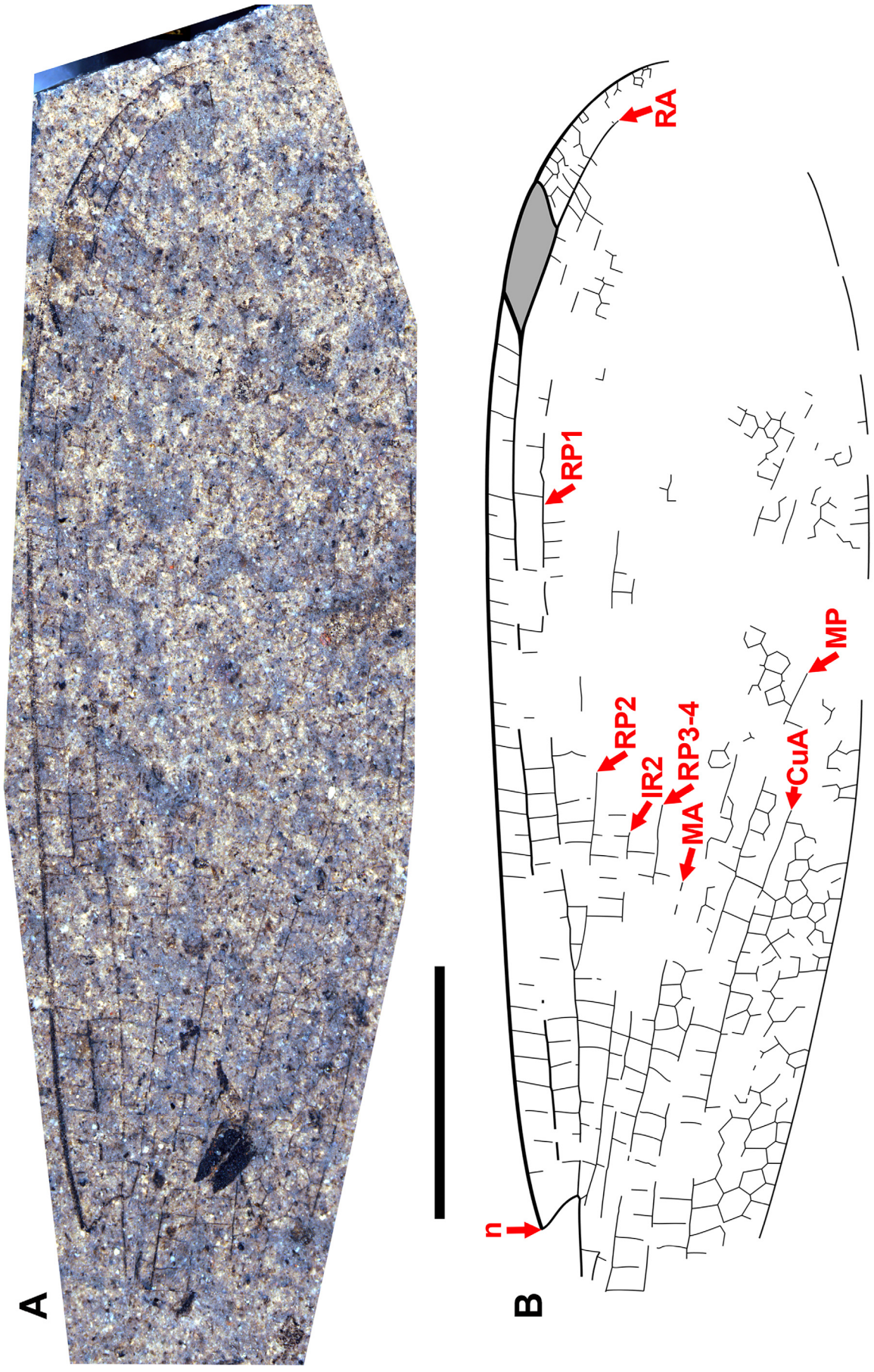

FIGURE 41. *Okanagrion worleyae* paratype 2, SR 11-21-09. A, photograph; B, drawing. Both to scale, 5 mm.

Paratype 1, SR 17-006-001, wing (Fig. 40). Apical portion, from about termination of MA on posterior margin to apex; diagonally to near nodus on anterior margin. As for holotype except: pterostigma subtends 4.5 cells; four cells wide distal to pterostigma in costal space; RA terminates a bit further posteriad.

Paratype 2, SR 11-21-09, wing (Fig. 41). Preserved from about level of nodus, missing portion of posterior-apical region, partly indistinctly preserved. As in holotype, except: length: nodus to apex: about 22.7 mm, origin of RP2 to apex: 17.9 mm, nodus to base of pterostigma: about 17.2 mm. Pterostigma almost four longer than wide, subtends unknown number of cells. Crossveins in postnodal space partially preserved, appear as dense as in holotype, none hyperstigmal. RA not preserved at margin. RP1-2–IR2, RP1–IR1, IR1–RP2, IR2–RP3-4 spaces partially preserved, IR1, RP2 origin distances appear similar to holotype. IR2 origin at subnodus. No crossvein O. All major veins linear except proximal portion of IR1. CuA–A space five cells wide at widest (but region poorly preserved).

Etymology. The specific epithet is a patronymic formed from the surname of Providence Worley, the collector and donor of the holotype, recognising her contribution.

Range and age. Exposures B4131 and A0307 of the Tom Thumb Tuff Member of the Klondike Mountain Formation at Republic, Washington, USA; late Ypresian.

Okanagrion incertae sedis

Figs. 42–43.

Material. SR 11-60-17AB (Fig. 42), collected at Republic A0307 by Karl Volkman, 15.vii.2006, housed in the Stonerose Interpretive Center collections; SR 94-05-30 (Fig. 43), collected at Republic A0307B by Wes Wehr, 31.x.1994 and SR 11-51-07AB (Fig. 43) collected at Republic B4131 by Dennis Vickerman, 22.viii.2008, both in the Stonerose Interpretive Center collections; SR 06-08-18 (Fig. 42), collected at Republic B4131 by Don Volkman, 4.vi.2004, in the Stonerose Interpretive Center collections; UWBM-74307 (Fig. 42), collected at Republic A0307B by Wesley Wehr, 1993, in the Burke Museum collections; RBCM P1550, three wing portions (Fig. 43) collected by John Leahy at the McAbee Hoodoo Face beds, unknown date, in the Royal British Columbia Museum collections.

Discussion. SR 11-60-17: The dense crossvenation and colouration indicates that this specimen belongs to one of the infuscate *Okanagrion* species. SR 94-05-30 and SR 11-51-07: these two apical-anterior wing fragments could belong to any *Okanagrion* species that are infuscate in this region, although SR 94-05-30 does not belong to *O. lochmum* by its crossvenation in the RA–RP1 space. SR 06-08-18: colouration indicates that this specimen belongs to one of the infuscate *Okanagrion* species; the light fascia, although poorly preserved, suggests *O. threadgillae*. UWBM-74307: the infuscation does not reach the nodus as in some *Okanagrion* species, and IR2 originating on RP1-2 restricts it within these to *O. beardi*, *O. dorrellae*, and *O. angustum*. Many crossveins are closer together than in any of these, however. RBCM P1550 belongs to an infuscate species, although this is preserved too poorly to clarify which one; IR2 originates rather evenly between RP1-2 and RP3-4, ruling out *O. beardi*; and it is neither *O. dorrellae* nor *O. augustum* by shape. It likely either belongs to *O. hobani* or to *O. lochmum*; the CuA–A space five or six cells wide is consistent with these.

Okanopteryx Archibald & Cannings, new genus

Figs. 44–60.

Diagnosis. Wings separated from other genera of Dysagrioninae by a combination of pterostigma 2.5 times longer than wide [separated from *Okanagrion*: 3–3.5, rarely 4 times; *Stenodiafanus*: almost 4; *Phenacolestes*: 4.5–5; *Furagrion*: 3; *Primorilestes*: 3.5; *Dysagrion*: 3–7.5; *Dysagrionites* species: unknown]; with oblique brace vein [separated from *Okanagrion*, *Phenacolestes*, *Primorilestes*; not separated from *Dysagrion, Furagrion*, *Stenodiafanus*: present; unknown in *Electrophenacolestes*, *Dysagrionites* as wing region not preserved]; costal space 2 cells wide distal to pterostigma [distinct from *Dysagrion*, *Furagrion*, *Phenacolestes*: all 1; *Okanagrion*: 3–5; shared by *Primorilestes*, *Stenodiafanus*: both 2; *Electrophenacolestes*, *Dysagrionites* species: not known by preservation]; subnodus with normal obliquity [separated from *Dysagrion*: reversed obliquity; all others: normal obliquity, slight to notable]; no accessory antenodal crossveins [distinct from *Phenacolestes*, *Electrophenacolestes*, some *Dysagrion* species: with; not separated from others: also without]; IR2 origin rather evenly between RP1-2, RP3-4, connected to RP1-

2, RP3-4 at similar level [*Dysagrion*: between RP1-2, RP3-4, closer to RP3-4, connected with RP1-2 distinctly more distally than to RP3-4; other genera as in *Okanopteryx*, except some *Okanagrion* species: IR2 origin close to or on RP1-2]; MA linear to mid-wing, somewhat to strongly zigzagged to margin [separated from *Okanagrion*: MA linear or only slightly zigzagged from quadrangle to margin; *Primorilestes*: MA not zigzagged; *Dysagrion*: MA linear from quadrangle to zigzagged roughly mid-wing or further, linear again near, to margin; *Furagrion*: similar to *Dysagrion* (but deeply curved distally); *Phenacolestes*: very slightly zigzagged or not in mid-portion; not separated from *Stenodiafanus*, *Dysagrionites* species (known portions, none known to margin): also linear to mid-wing, somewhat to strongly zigzagged to margin]; MA, MP close at margin (difficult to be sure of exact identity of MA near margin by strong zigzag) [distinct from *Okanagrion*, *Furagrion*, *Primorilestes*, *Electrophenacolestes*: MA, MP widely separated; not distinct from *Dysagrion*: 1–2 cells apart at margin; not distinct from *Stenodiafanus*: also identity of MA near margin unsure by strong zigzag, but close, probably separated by two cells; *Dysagrionites* species: also difficult, perhaps one cell]; CuA increasingly zigzagged from to about mid-wing to strongly near margin [distinct from *Electrophenacolestes*, *Primorilestes*, *Okanagrion*: linear or very slightly zigzagged; *Furagrion*: slightly zigzagged distal to level of origin of RP2; *Phenacolestes*: slightly zigzagged in parts; not distinct from *Stenodiafanus*: zigzagged to various degrees distal to about mid-wing; from *Dysagrion*: increasingly zigzagged distal to level of nodus; or from *Dysagrionites* species as known, but distal portions not preserved]; further from *Okanagrion* by wing apical region with less dense crossvenation; distinct from all other Dysagrionidae genera except *Okanopteryx* by RA, RP1, IR1, RP2 distinctly converge, almost meeting at apex; postnodal, postsubnodal crossveins mostly aligned at least in proximal half [distinct from *Phenacolestes*, *Primorilestes madseni*, *Dysagrion*: all not; not separated from *Stenodiafanus*, *Primorilestes violetae*, *Electrophenacolestes*, *Furagrion*]; further from *Primorilestes* by no intercalary vein in CuA–A space. Separated from *Valerea* (tentative Dysagrioninae) by no linear supplementary sector between RP1, IR1 [*Valerea*: with such sector]; costal space 2 cells wide distal to pterostigma [*Valerea*: maximum 5]; origins of IR1, RP2 further from nodus; origin of IR2 between RP1-2, RP3-4 [IR2 origin not preserved, only preserved to level of nodus, where it is closer to RP3-4]. Most easily separated from fossil genera regarded here as possible Dysagrionidae as follows: from *Thanetophilosina* by no linear sectors between RP1, IR1, between IR1, RP2 [*Thanetophilosina*: with], by pterostigma 2.5 times longer than wide [about 6]; from Chickaloon specimen (Garrouste & Nel 2019) by CuA becoming zigzagged mid-wing to margin [linear in all preserved portion to near margin]; from NHMUK I.9866/I.9718 by origin of RP3-4 [distinctly closer to subnodus: subnodus to anterio-distal corner of quadrangle about 4.5 times distance to origin of RP3-4]; from *cf*. Dysagrionidae genus A, species A ("Megapodagrionidae" genus A, species A of Petrulevičius *et al*. 2008) by colouration [preserved portion infuscate except apex distal to pterostigma], MA, CuA zigzagged in distal portion to margin [linear].

Okanopteryx males also separated from those of other Dysagrioninae genera by colouration, mostly hyaline with broad, dark fascia across mid-wing from level of nodus to just apical to mid-distance between nodus, pterostigma (see discussion, below).

Type and included species. Type species: *Okanopteryx macabeensis*; other included species: *Okanopteryx jeppesenorum*, and *Okanopteryx fraseri*.

Description. Wing. RA terminates on margin at or posterior to apex. MP, RP3-4, IR2 rather straight (at most very gently curved in part except at very base); IR1 almost straight, slightly zigzagged to origin; pterostigma stout for Dysagrionidae (length 2.5 times width), subtending 2.5 cells (but pterostigma not known in *O. fraseri*).

Etymology. The genus name is a toponym formed from Okan- from "Okanagan Highlands" and the Greek πτέρυξ, *pteryx*, meaning wing. Gender feminine.

Range and age. Okanagan Highlands localities of McAbee, BC, Canada and the Klondike Mountain Formation, at Republic, Washington, USA; second half of the Ypresian.

Discussion. We describe 22 specimens of three species of *Okanopteryx*: six of *O. jeppesenorum*, five of *O. fraseri*, four of *O. macabeensis*, and seven unassigned to species. Colouration is consistent throughout all 22 specimens (in a few poorly preserved). We know that paratype 1 of *O. macabeensis* is a male. As in *O. hobani*, although we expect that the chances that there are only males in this collection seem small, this could be true. We, therefore, conservatively treat this wing patterning as male, with female colouration unknown.

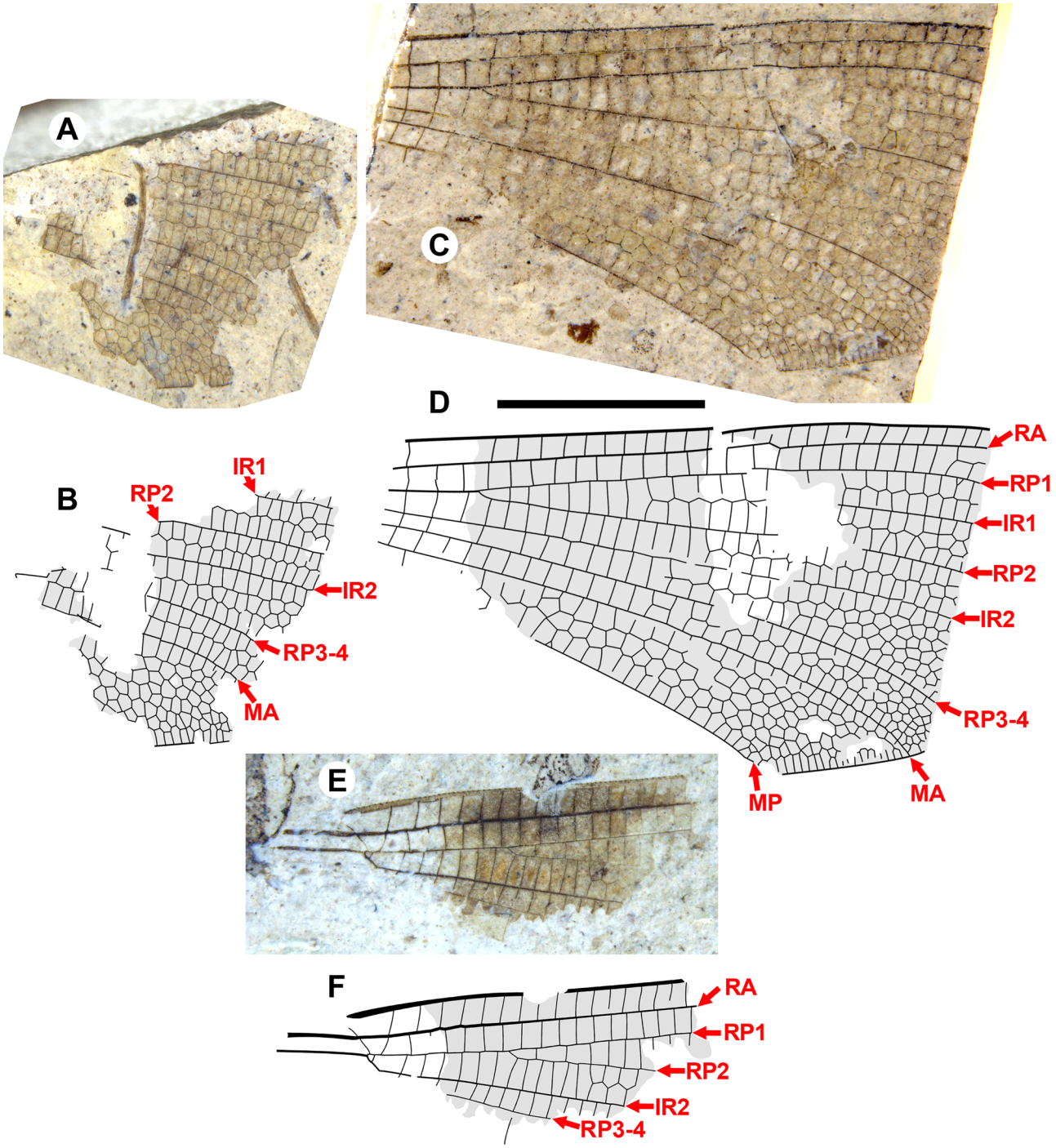

FIGURE 42. *Okanagrion incertae sedis*. SR 11-60-17. A, photograph; B, drawing; SR 06-08-18: C, photograph; D, drawing; UWBM-74307: E, photograph; F, drawing. All to scale, 5 mm.

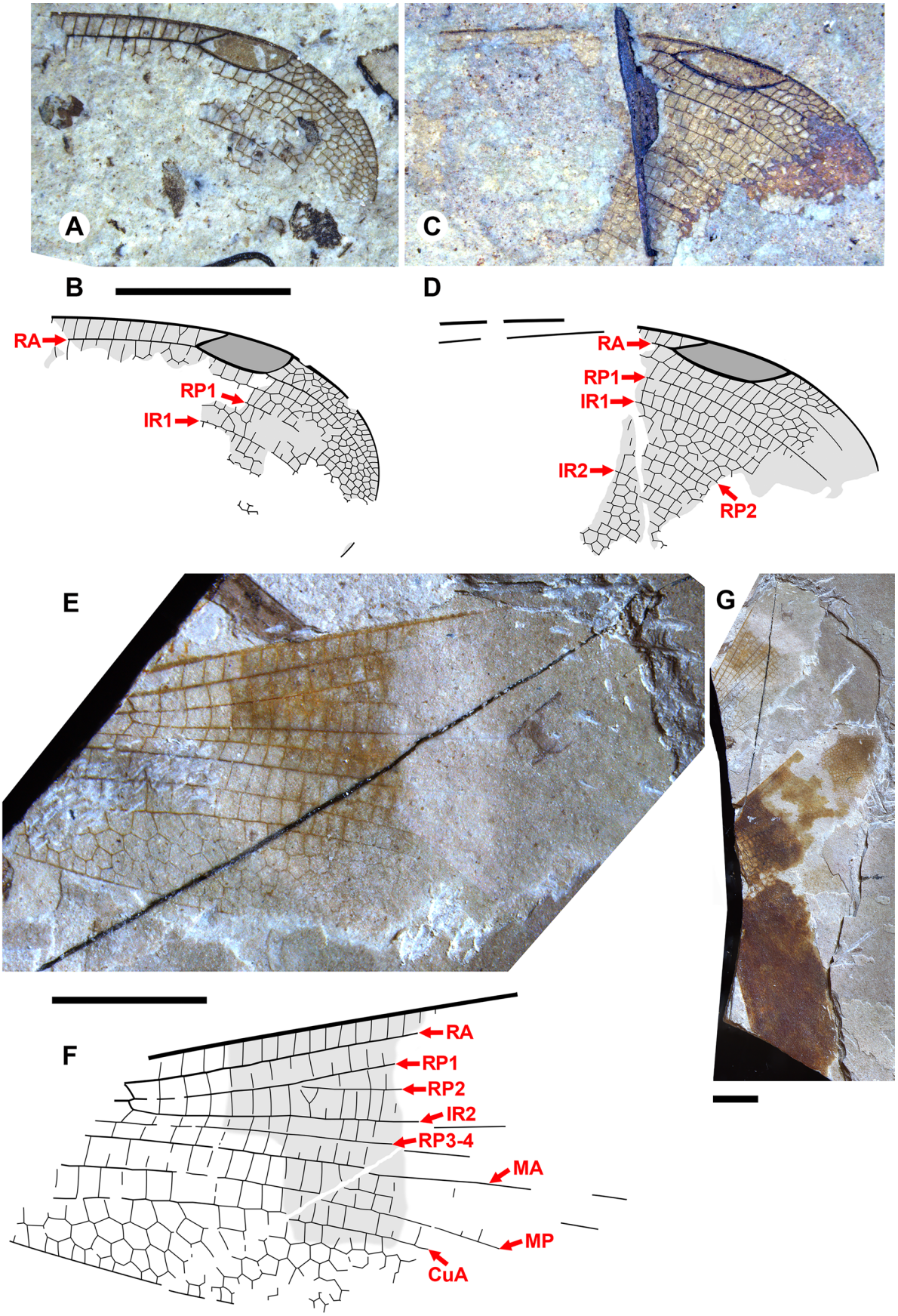

FIGURE 43. *Okanagrion incertae sedis*. SR 94-05-30: A, photograph; B, drawing; SR 11-51-07: C, photograph; D, drawing; RBCM P1550: E, photograph of top wing in G; F, drawing of wing in E; G, all three wings. A–D to scale; E, F to scale; G to scale; all scales 5 mm.

***Okanopteryx jeppesenorum* Archibald & Cannings, new species**
Figs. 44–48.

Diagnosis. Wings distinct from those of *O. macabeensis*, *O. fraseri* by CuA–A space wider, four cells wide at widest (difficult to count number of columns by preservation), between the levels of origins of IR1, RP2 [*O. macabeensis*: 5–10 columns of three cells wide; *O. fraseri*: all two cells wide, but sometimes a single column of three]; further from *O. macabeensis*, by longer wing, holotype, 22.4 mm nodus to apex; paratype 1 (SR 11-43-09): 23.5 mm [*O. macabeensis* holotype: estimated 18.4 mm] (all *O. fraseri* wings missing apex).

Material. *Holotype*: SR 13-005-013 (Fig. 44), collected at B4131 by Jackie and Tim Jeppesen, 15.vii.2013, housed in the Stonerose Interpretive Center collections; *paratype 1*: SR 11-43-09, (Fig. 45), collected at Republic B4131 by Christin Gustafson, 15.vi.2011, in the Stonerose Interpretive Center collections; *paratype 2*: SR 18-002-001 (Fig. 46), collected at Republic B4131 by Valerie Paquin, 28.iv.2018, in the Stonerose Interpretive Center collections; *paratype 3*: SR 15-003-001 (Fig. 47), collected at Republic B4131 by Ethan Fisher, 30.v.2015, in the Stonerose Interpretive Center collections; *paratype 4*: SR 02-32-23 (Fig. 48), collected at Republic B4131 by Chris Engle, 6.vi.2002, in the Stonerose Interpretive Center collections; *paratype 5*: SR 07-22-05AB (Fig. 47), collected at Republic B4131 by Kathleen Malloch 13.viii.2006, in the Stonerose Interpretive Center collections; *paratype 6*: SR 19-005-002AB (Fig. 48), collected at Republic B4131 by Gregg Wilson, 1.v.2019, in the Stonerose Interpretive Center collections.

Description. Holotype, SR 13-005-013, wing (Fig. 44). Mostly complete, with portions of mid-posterior not preserved. Petiolate. Evenly oval distal to nodus, nodus to apex 22.4 mm, maximum width mid-wing 7.7 mm. Hyaline except for broad dark fascia across wing between level of nodus, just over half way to pterostigma. Pterostigma broad, about 2.5 times longer than wide, proximal side nearly vertical; subtends 2.5 cells. Oblique brace vein joins RA at proximal corner of pterostigma. Most crossveins roughly aligned in proximal half of postnodal, postsubnodal spaces. Costal space distal to pterostigma two cells wide. RA meets margin posterior to apex, RA slightly sigmoidal near margin. RA–RP1, RP1–IR1 spaces narrow near margin. RA–RP1 space mostly one cell wide, briefly two near apex. RP1–IR1 space two cells wide four cells distal to origin of IR1. Origin of IR1 presumed four cells distal to origin of RP2, mid-way between arculus, pterostigma. IR1–RP2, RP2–IR2 spaces two cells wide shortly proximal to level of pterostigma. Origin of RP2 about 5–6 cells distal to subnodus. RP2 mostly rather straight, curved slightly posteriorly in distal quarter. IR2: origin at subnodus; mostly rather straight, linear, slightly zigzagged in distal quarter, strongly so near margin. Origin of RP3-4 about 2/3 between arculus, nodus; mostly rather straight. MA linear, straight at least to half way from quadrangle (partially not preserved), strongly zigzagged at least distal third. MP linear, rather straight from quadrangle to terminus. CuA linear until shortly after level of nodus, then increasingly zigzagged. CuA–A space with 4 cells at widest (from just proximal to, distal to level of RP2 origin as preserved).

Paratype 1, SR 11-43-09, wing (Fig. 45). Petiolate. Evenly oval distal to nodus; nodus to apex 23.5 mm: maximum 7.2 mm wide. Hyaline except for broad dark fascia across wing between level of nodus, just over half way to pterostigma. Pterostigma broad, about 2.5 times longer than wide; proximal side with shallow angle to costa. Region of oblique brace vein not preserved. Crossveins in postnodal, postsubnodal spaces mostly rather aligned. Two cells wide distal to pterostigma in costal space. RA–RP1 space one cell wide. RA meets margin posterior to apex. RP1–IR1 space goes to two cells wide five cells distal to origin of IR1; narrows near margin. Origin of IR1 four cells distal to origin of RP2, mid-way between arculus, pterostigma. IR1–RP2, RP2–IR2 spaces mostly not preserved. RP2: origin about 3 cells distal to subnodus; proximal half linear, rather straight; distal half not preserved. IR2: origin at subnodus; mostly rather straight, liner, slightly zigzagged in distal quarter, missing by preservation near margin. RP3-4: origin < 2/3 between arculus, nodus; mostly rather straight (not preserved near margin). MA linear, straight at least to half way from quadrangle; slightly zigzagged in small portion preserved distal to this. MP linear, rather straight from quadrangle to terminus in regions preserved. CuA slightly zigzagged from level of quadrangle to level of origin of RP2, mostly not preserved apical to this. CuA–A space with 4 cells wide shortly proximal to level of origin of RP2 (portion distal to this missing)

Paratype 2, SR 18-002-001, wing (Fig. 46). Petiolate. Evenly oval distal to nodus (missing apical region), nodus to base of pterostigma 16.5 mm, maximum width mid-wing 7.2 mm. Hyaline except for broad dark fascia across wing between level of nodus, to about presumed 2/3 distance to pterostigma. Pterostigma not preserved. Most crossveins roughly aligned in proximal half of postnodal, postsubnodal spaces, not in distal half. RP1–IR1 space two cells wide eight cells distal to origin of IR1. IR1 origin two cells distal to origin of RP2. RP2: origin apparently

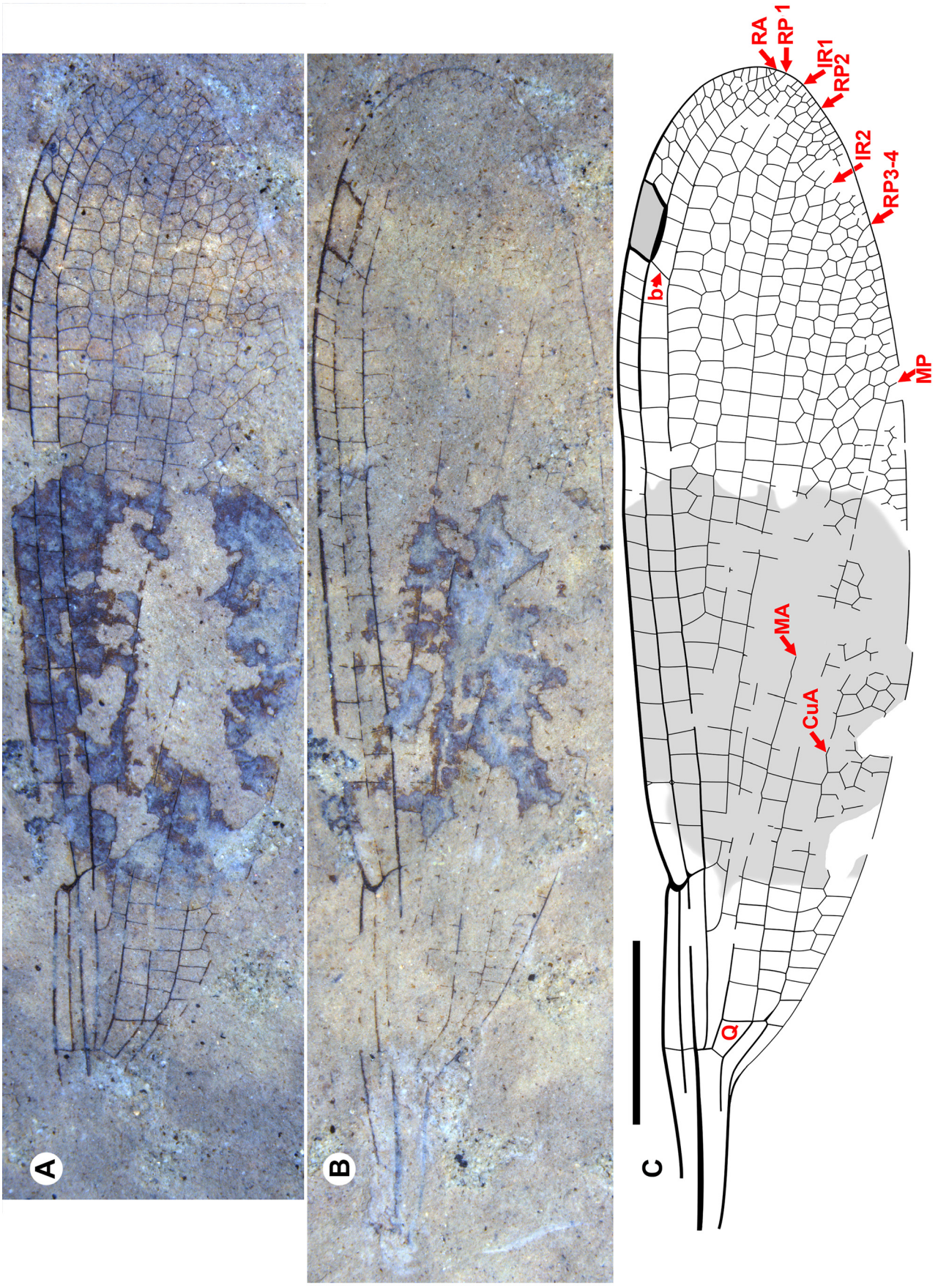

FIGURE 44. *Okanopteryx jeppesenorum* holotype, SR 13-005-013. A, photograph of part SR 13-005-013A; B, photograph of counterpart SR 13-005-013B; C, drawing from part and counterpart. All to scale, 5 mm

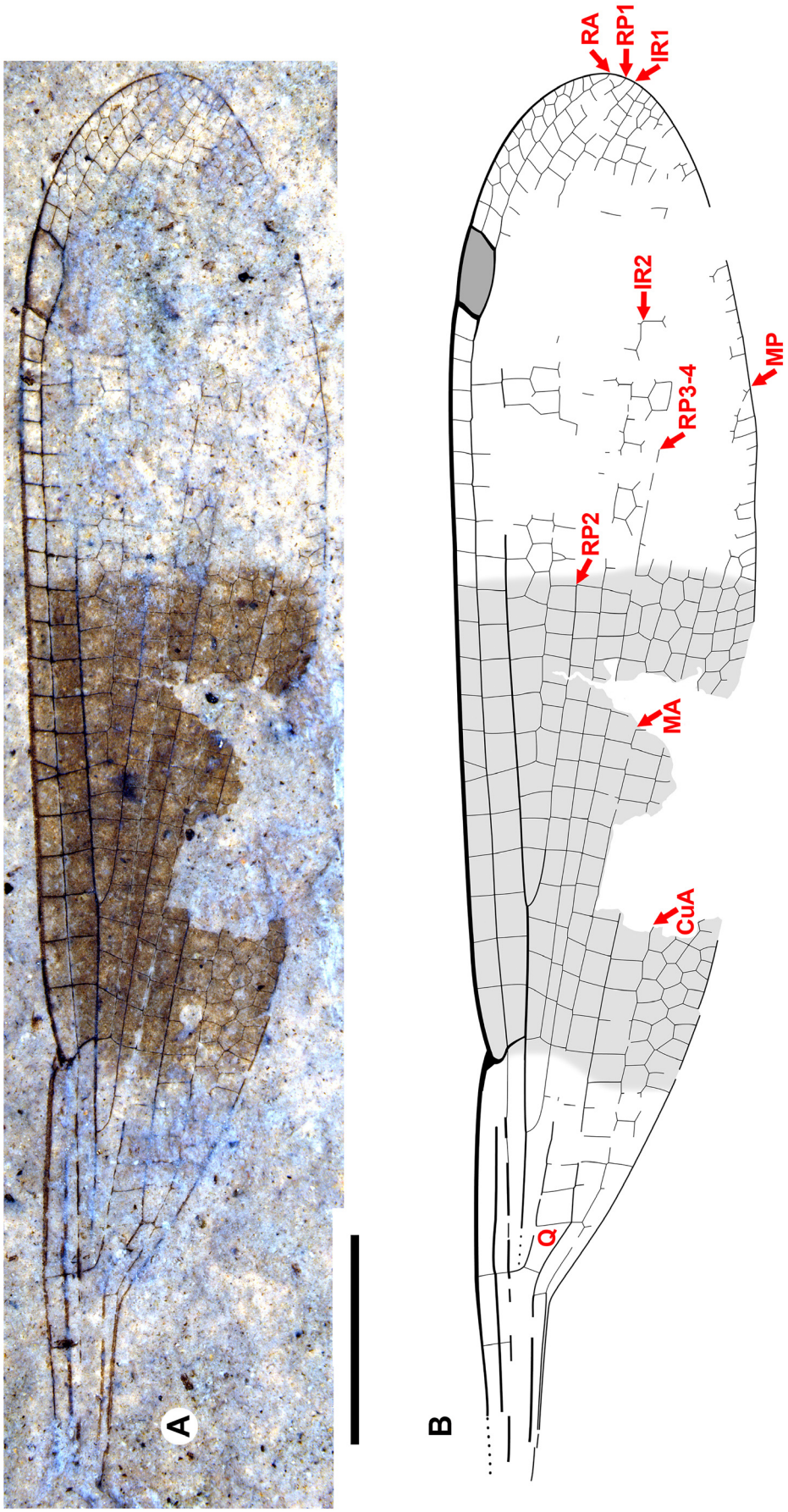

FIGURE 45. *Okanopteryx jeppesenorum* paratype 1, SR 11-43-09. A, photograph; B, drawing. Both to scale, 5 mm.

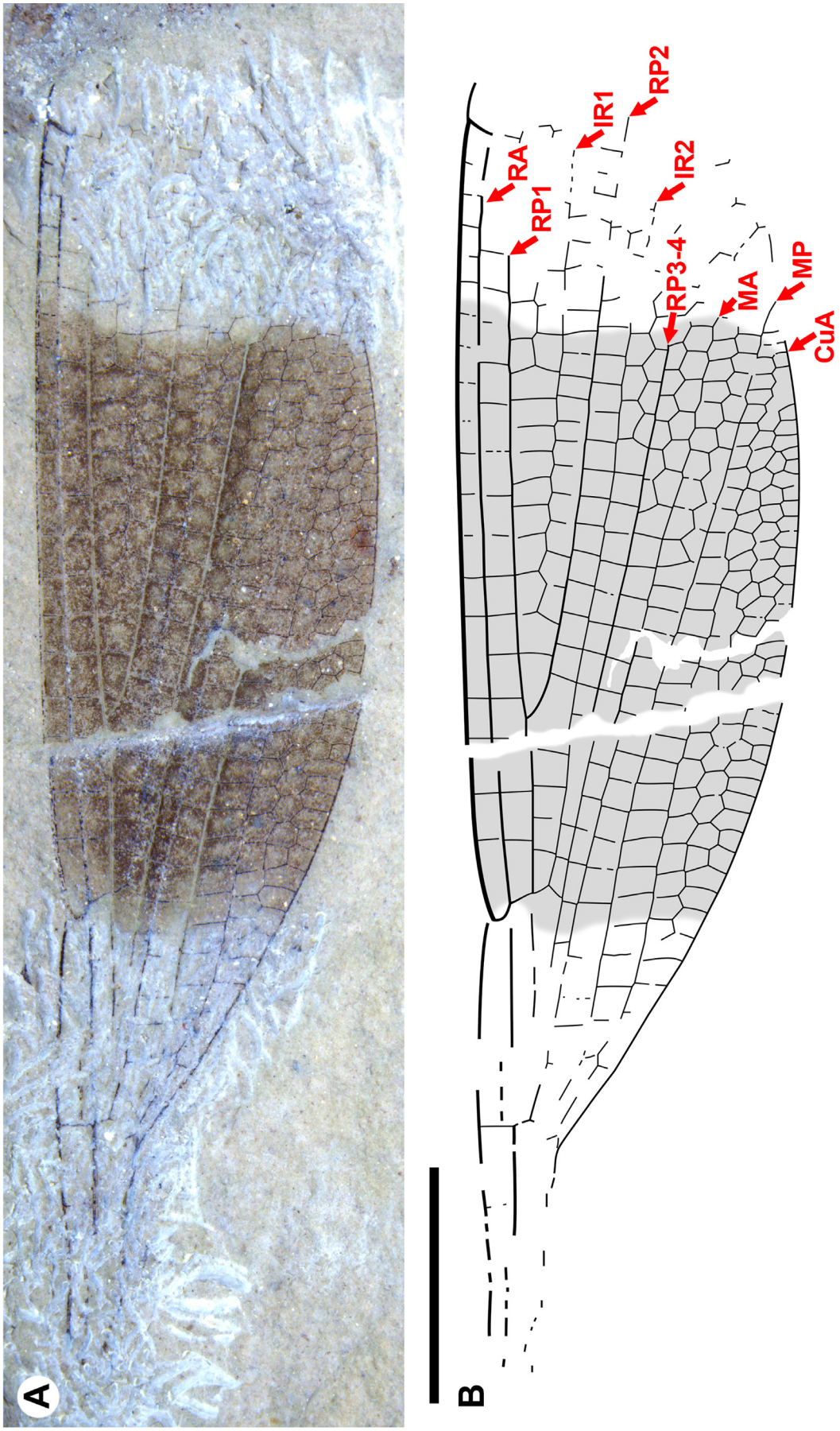

FIGURE 46. *Okanopteryx jeppesenorum* paratype 2, SR 18-002-001. A, photograph; B, drawing. Both to scale, 5 mm.

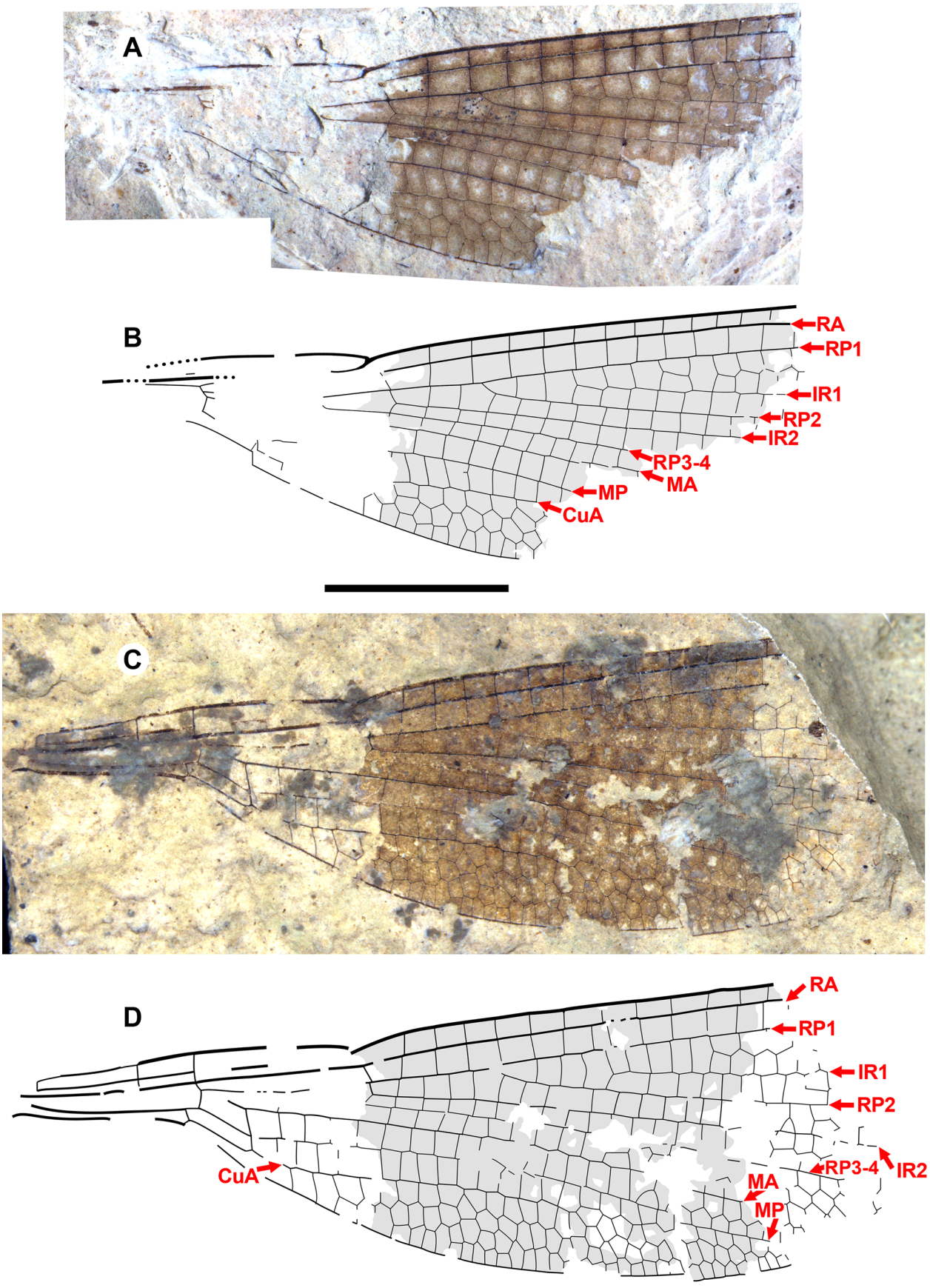

FIGURE 47. *Okanopteryx jeppesenorum* paratype 5, SR 07-22-05. A, photograph; B, drawing; paratype 3, SR 15-003-001: C, photograph; D, drawing. All to scale, 5 mm.

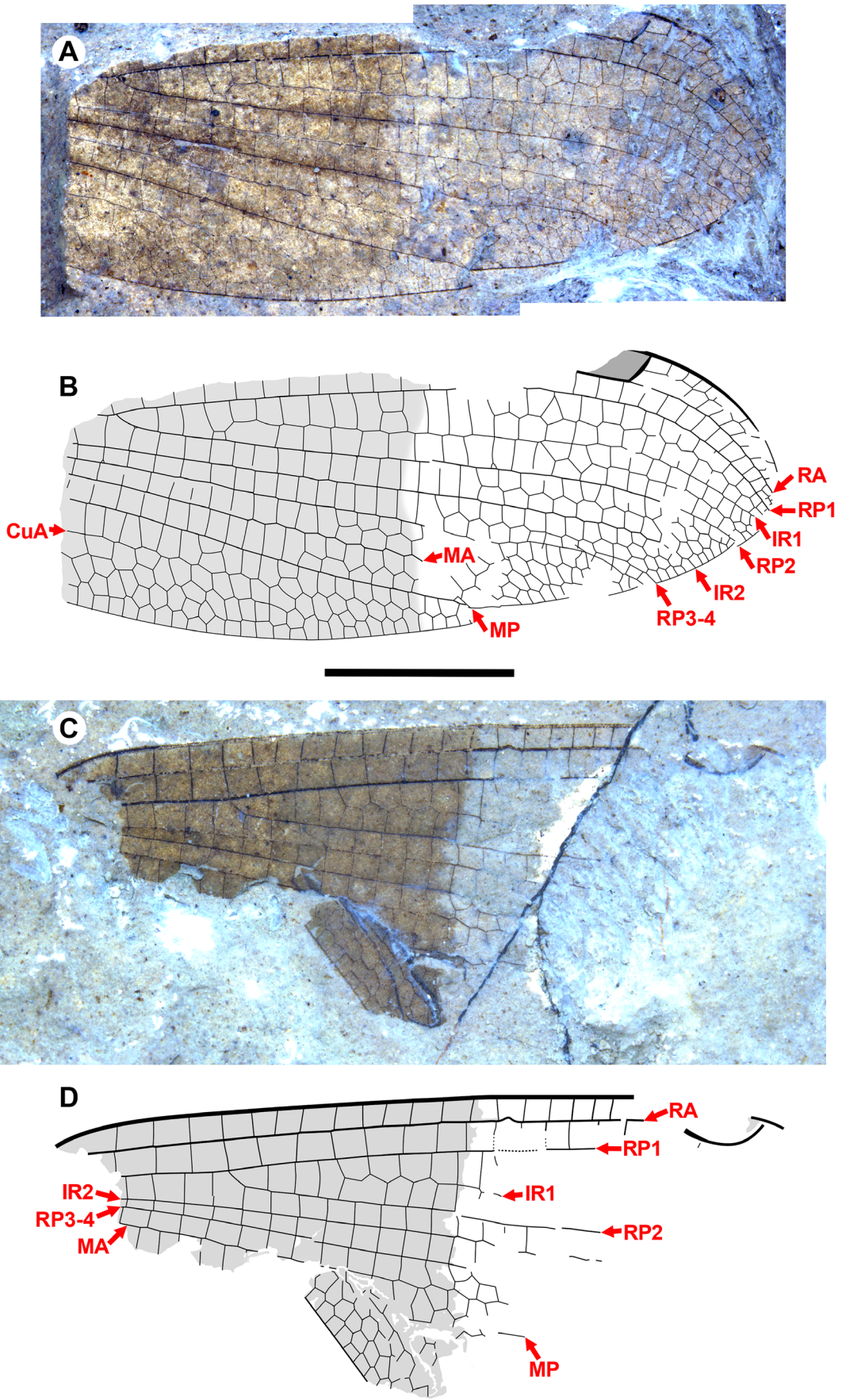

FIGURE 48. *Okanopteryx jeppesenorum* paratype 4, SR 02-32-23. A, photograph; B, drawing; paratype 6, SR 19-005-002: C, photograph; D, drawing. All to scale, 5 mm.

five cells distal to subnodus; mostly rather straight in region preserved. IR2: origin at subnodus; mostly rather straight, linear, apical quarter missing. RP3-4: origin missing; mostly rather straight, missing apical quarter. MA linear, straight at least to half way between nodus, presumed level of pterostigma. MP linear, rather straight from quadrangle to terminus. CuA linear until shortly after level of nodus, then slightly zigzagged to distal quarter, then increasingly so. CuA–A space four cells at widest from just proximal to level of origin of RP2 to about level IP2 origin.

Paratype 3, SR 15-003-001, wing (Fig. 47). Proximal two-thirds. Petiolate. Maximum width 7.7 mm. Hyaline proximal to level of nodus, darkly infuscate distal to it. Most crossveins roughly aligned in proximal half preserved of postnodal, postsubnodal spaces. RP1–IR1 space two cells wide five cells distal to origin of IR1. IR1: origin four cells distal to origin of RP2. RP2: origin five cells distal to subnodus; mostly rather straight in region preserved. IR2: origin at subnodus; mostly rather straight, linear, apical half missing. RP3-4: origin missing; mostly rather straight, missing apical third. MA mostly linear, slightly zigzagged around levels of origin of RP2 to IR1, mostly not preserved distal to that. MP mostly linear, slightly zigzagged in portions, gently curved from quadrangle, near terminus not preserved. CuA rather linear to level of origin of RP2, then increasingly zigzagged. CuA–A space four cells at widest from just proximal to, to just distal to level of origin of RP2.

Paratype 4, SR 02-32-23, wing (Fig. 48). Apical half, missing much of anterior region. Apical portion hyaline from about half way between origin of IR1, pterostigma; darkly infuscate proximal to this. Pterostigma broad, proximal portion not preserved. Postnodal, most of postsubnodal spaces not preserved. Costal space distal to pterostigma two cells wide. RA meets margin posterior to apex. RA–RP1, RP1–IR1 spaces narrow near margin. RA–RP1 space mostly one cell wide, briefly two near apex. RP1–IR1 space constantly two cells wide twelve cells distal to origin of IR1. Origin of IR1 presumed three cells distal to origin of RP2. IR1–RP2 space two cells wide at presumed level of proximal side of pterostigma; IR2–RP3-4 space two cells wide from a few cells proximal to this. RP2: linear, mostly rather straight, slightly curved posteriorly in apical quarter. IR2 straight, linear to level RP2–IR2 space becomes two cells wide, then slightly zigzagged, curves posteriorly near terminus. RP3-4: mostly rather straight, wing damaged near margin. MA preserved portion linear to about level of origin of IR1, then increasingly zigzagged. MP preserved portion linear, slightly curved to terminus. CuA increasingly zigzagged in region preserved, strongly so apically. CuA–A space four cells wide from just proximal to level of RP2 origin to just distal to level of origin of IR1.

Paratype 5, SR 07-22-05A, B, wing (Fig. 47). Parts of proximal half. Petiolate. Hyaline proximal to level of nodus, darkly infuscate distal to it. Most crossveins in postnodal, postsubnodal spaces roughly aligned in region preserved. Origin of IR1 three cells distal to origin of RP2. RP2: origin 2.5 cells distal to subnodus; portion preserved rather straight, linear. IR2: origin at subnodus; straight, linear. RP3-4, MA, MP: origins, distal portions missing; preserved portion mostly rather straight, rather linear. CuA–A space 4 cells wide just proximal to level of RP2 origin, not preserved distal to this.

Paratype 6, SR 19-005-002A, B, wing (Fig. 48). Broken up middle portion from closely distal to nodus to base of pterostigma, posterior region missing or damaged. Proximal portion darkly infuscate, distal portion hyaline. Many crossveins roughly aligned in preserved portion of postnodal, postsubnodal spaces. IR1 origin four cells distal to origin of RP2. RP2, IR2, RP3-4, MA: preserved portions mostly linear, rather straight, except MA zigzagging in distal portion preserved. Small portions of MP reserved. Disarticulated fragment of CuA–A space preserved, four cells wide.

Etymology. The specific epithet is a patronymic formed from the surname of Jackie and Tim Jeppesen, the collectors and donors of the holotype, recognising their contribution. The Latin suffix *–orum* indicates the genitive case of plural nouns.

Range and age. Tom Thumb Tuff Member of the Klondike Mountain Formation, locality B4131 [and other maybe?] at Republic, Washington, USA; second half of the Ypresian.

Okanopteryx fraseri Archibald & Cannings, new species

Figs. 49–52.

Diagnosis. Separated from other *Okanopteryx* species by: abdomen longer, 29.5 mm from proximal end of abdominal segment 3 to distal end of segment 7 [*O. macabeensis*: 20.0 mm]. We have compared the abdomen lengths using segments 3 to 7 only, as the *O. fraseri* abdomen is missing from the middle of segment 8 distally and the margins

of the two proximal segments are difficult to interpret (*O. jeppesenorum* only known from wings). Wings distinct from *O. jeppesenorum*, *O. macabeensis* by CuA–A space narrower, usually two cell rows at widest between levels of origins of IR1, RP2, sometimes a single column of three [*O. jeppesneorum*: always four; *O. macabeensis*: always three].

Material. *Holotype*: GSC 141104, part, housed in the Geological Survey of Canada collections, and F-778, counterpart, in the Thompson Rivers University collections (Fig. 49), collected at the McAbee Hoodoo Face beds, Geological Survey of Canada locality code V-016800, collected by John Fraser, unknown date; *paratype 1*: RBCM P1551 (Fig. 50), collected at the McAbee Hoodoo Face beds by John Leahy, date unknown, in the Royal British Columbia Museum collections; *paratype 2*: F-1091 (Fig. 51), collected at the McAbee Hoodoo Face beds, date and collector unknown, in the Thompson Rivers University collections; *paratype 3*: PB-4157 (Fig. 51), collected at the McAbee Hoodoo Face beds, date and collector unknown, in the Thompson Rivers University collections; *paratype 4*: F-1045 (Fig. 52), collected at the McAbee Hoodoo Face beds, date and collector unknown, in the Thompson Rivers University collections; *paratype 5*: RBCM P1552 (Fig. 52), collected at the McAbee Hoodoo Face beds, John Leahy, date unknown, in the Royal British Columbia Museum collections.

Description. Holotype, GSC 141104, F-778 (Fig. 49). A mostly complete specimen in dorsal aspect but with the bases of some of the legs possibly displaced to a lateral or dorsal position; one leg, at least, with part lying above the thorax. Abdomen distal to middle of segment 8 missing; two wings lacking the apical portions and only partially, mostly poorly, preserved, the other two wings fragmented; all legs mostly complete but poorly preserved. As in diagnosis and: Head (Fig. 10 N, Table 1): in dorsal view, about 3.6 mm across eyes at widest point; approximate length from anterior edge of antefrons to posterior of occiput 1.8 mm; at level of hind ocelli distance between eyes 1.2 mm, width of eye about 1.1 mm, length 2.3 mm; eyes rather compressed laterally, with acute but rounded postero-lateral corners; protuberance of clypeus and labrum not evident. Thorax: pterothorax about 7.5 mm long, 3.8 mm wide in dorsal view, prothorax 1.3 mm long. Wing (Fig. 43B): CuA–A space two cells wide between level of origin of RP2, IR1. Legs. No spines or other setae visible; some coxae evident; metafemur 5.6 mm, metatibia 5.0 mm, twice as long as abdominal segment 2. Wing 1. Mid-portion well preserved. Abdomen: colouration pale dorsally, extrapolated total length about 45 mm; segment 2, 2.5 mm long; segment 3, 6.3 mm long x 1.3 mm wide.

Paratype 1, RBCM P1551, wing (Fig. 50). Missing the apical quarter and parts proximal to the nodus. Maximum width 6.8 mm. Hyaline with broad dark fascia between level of nodus, level of terminus of CuA (presumably to half of wing distal to nodus, as in *O. jeppesenorum*). Pterostigma not preserved. Most crossveins in postnodal, postsubnodal spaces aligned in region preserved (proximal half of these spaces). RP1–IR1 space becomes two cells wide three cells distal to origin of IR1. IR1: origin four cells distal to origin of RP2; two cells wide ten cells distal to origin. RP2: origin three cells distal to origin of IR2; linear, rather straight (distal quarter missing). IR2 origin at subnodus; straight, linear but slight zigzag near end of preserved portion (small portion missing near end). RP3-4: origin half way between anterior-distal corner of quadrangle, nodus; almost complete: straight, linear. MA linear proximally, slight zigzag beginning between levels of origins of RP2, IR1, increasingly zigzagged to extreme apical to this. MP linear, rather straight from quadrangle to terminus. CuA slightly zigzagged from level of quadrangle, increasing from about level of origin of RP2; CuA–A space two cells wide at widest (between levels of origins of IR1, RP2).

Paratype 2, F-1091, wing (Fig. 51). As RBCM P1551, except: antenodal space preserved, no accessory crossveins. Width 6.6 mm. IR1: origin six cells distal to that of RP2. CuA–A space two cells wide at widest except one column of three.

Paratype 3, PB-4157, wing (Fig. 51). As RBCM P1551, except the following. Much of antenodal space preserved, no accessory crossveins. RP3-4: origin two thirds distance between anterior-distal corner of quadrangle, nodus. IR1: origin two cells distal to origin of RP2. RP1–IR1 space two cells wide six cells distal to origin. RP2: origin 3.5 cells distal to origin of IR2. CuA–A space two cells wide at widest except one column of three.

Paratype 4, F-1045, wing (Fig. 52). As RBCM P1551, except: almost all antenodal space missing. Width 6.4 mm. RP1–IR1 space goes to two cells wide six cells distal to origin of IR1. IR1: origin three cells distal to origin of RP2. RP3-4 origin: quadrangle not preserved, but similar distance from nodus. MP missing near terminus. CuA slightly zigzagged from level of origin of RP3-4, increasing from about level of origin of IR1; two cells wide at widest except one column of three.

Paratype 5, RBCM P1552, wing (Fig. 52). Smallest portion, from about base of IR1 to RP1–IR1 space becoming two cells wide. Width 6.8 mm. Darkly infuscate throughout. Preserved portion as for RBCM P1551,

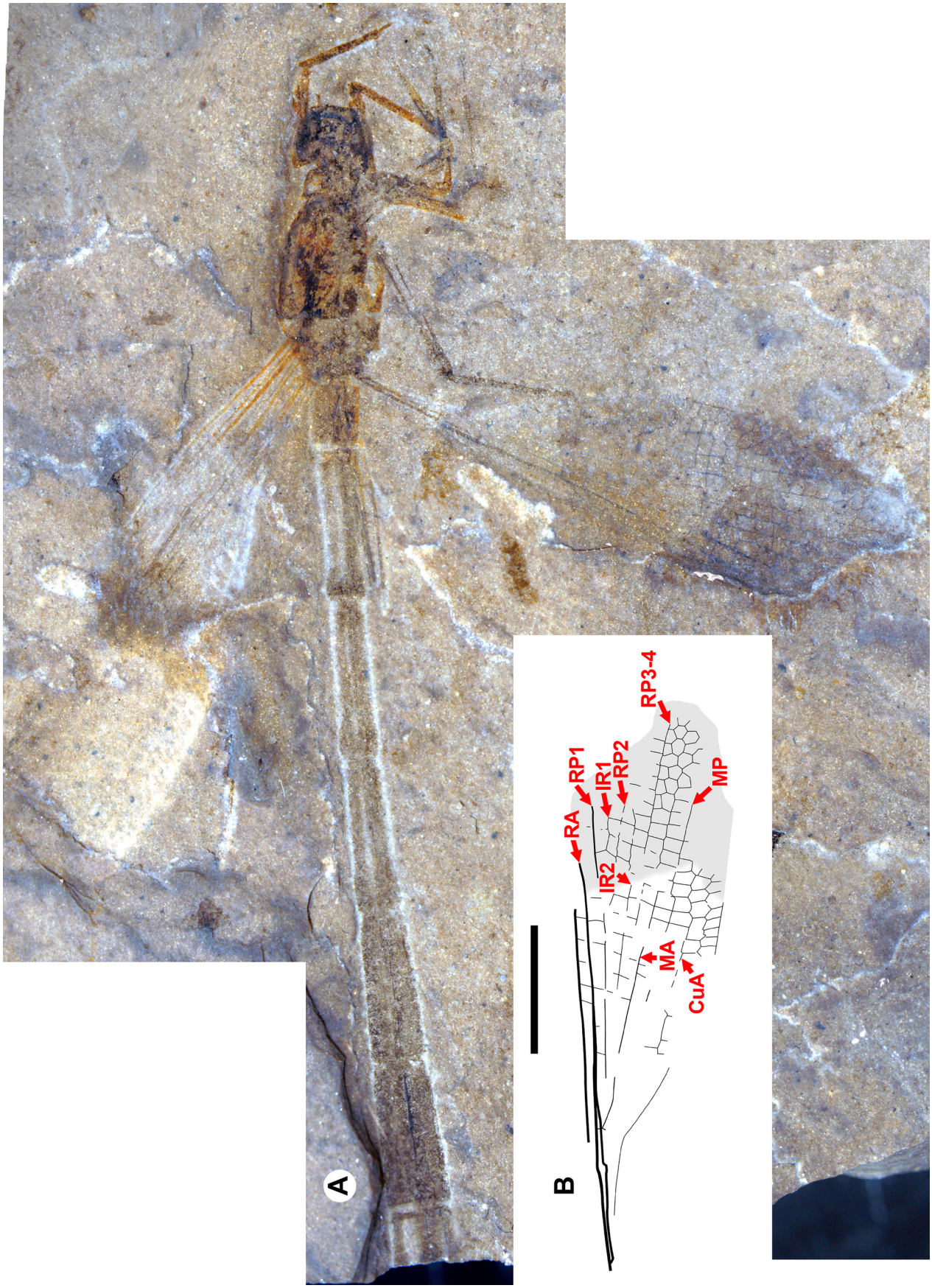

FIGURE 49. *Okanopteryx fraseri* holotype, GSC 141104/F-778. A, photograph of entire specimen (part: GSC 141104); B, drawing of wing. Both to scale, 5 mm.

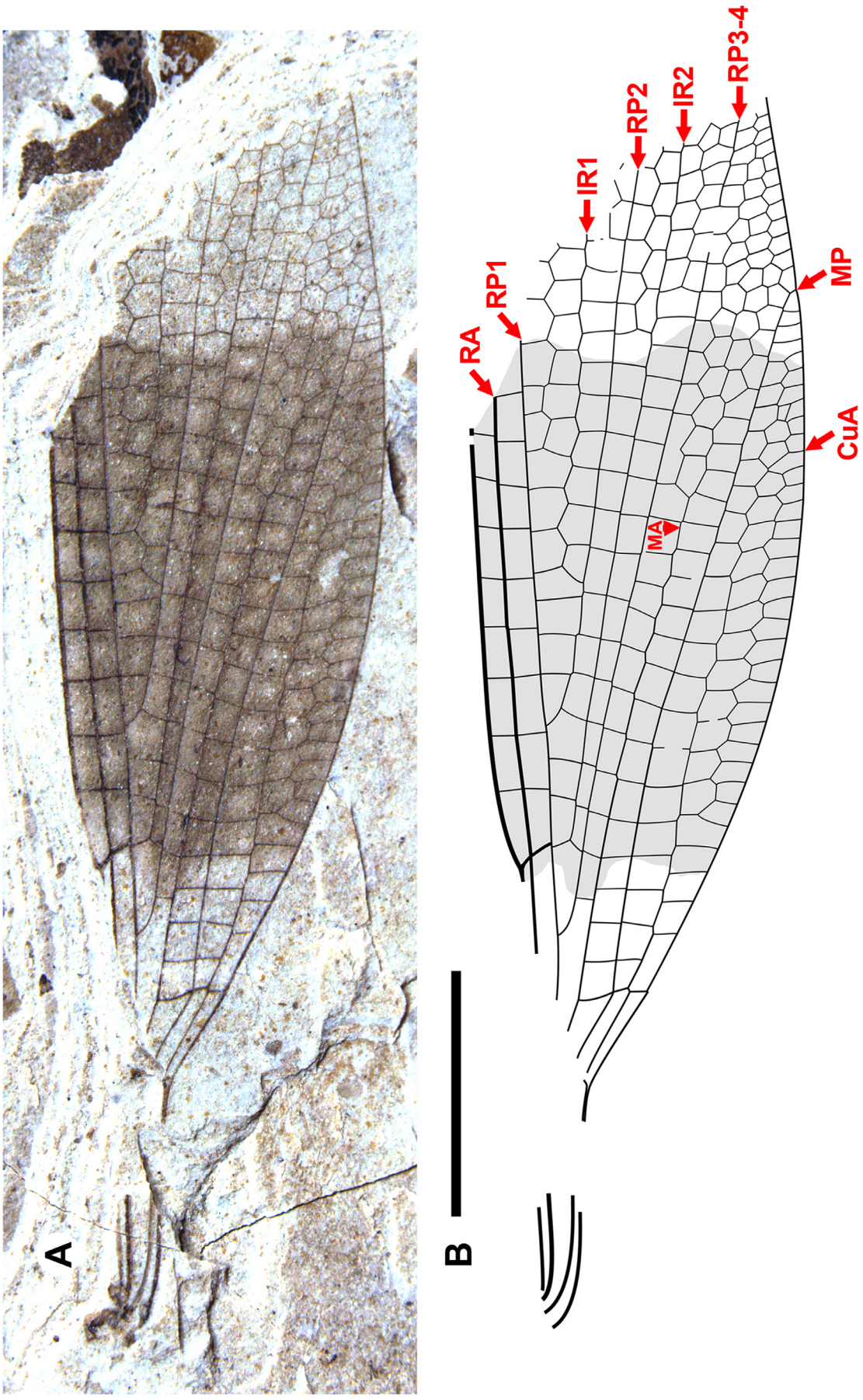

FIGURE 50. *Okanopteryx fraseri* paratype 1, RBCM P1551. A, photograph; B, drawing. Both to scale, 5 mm.

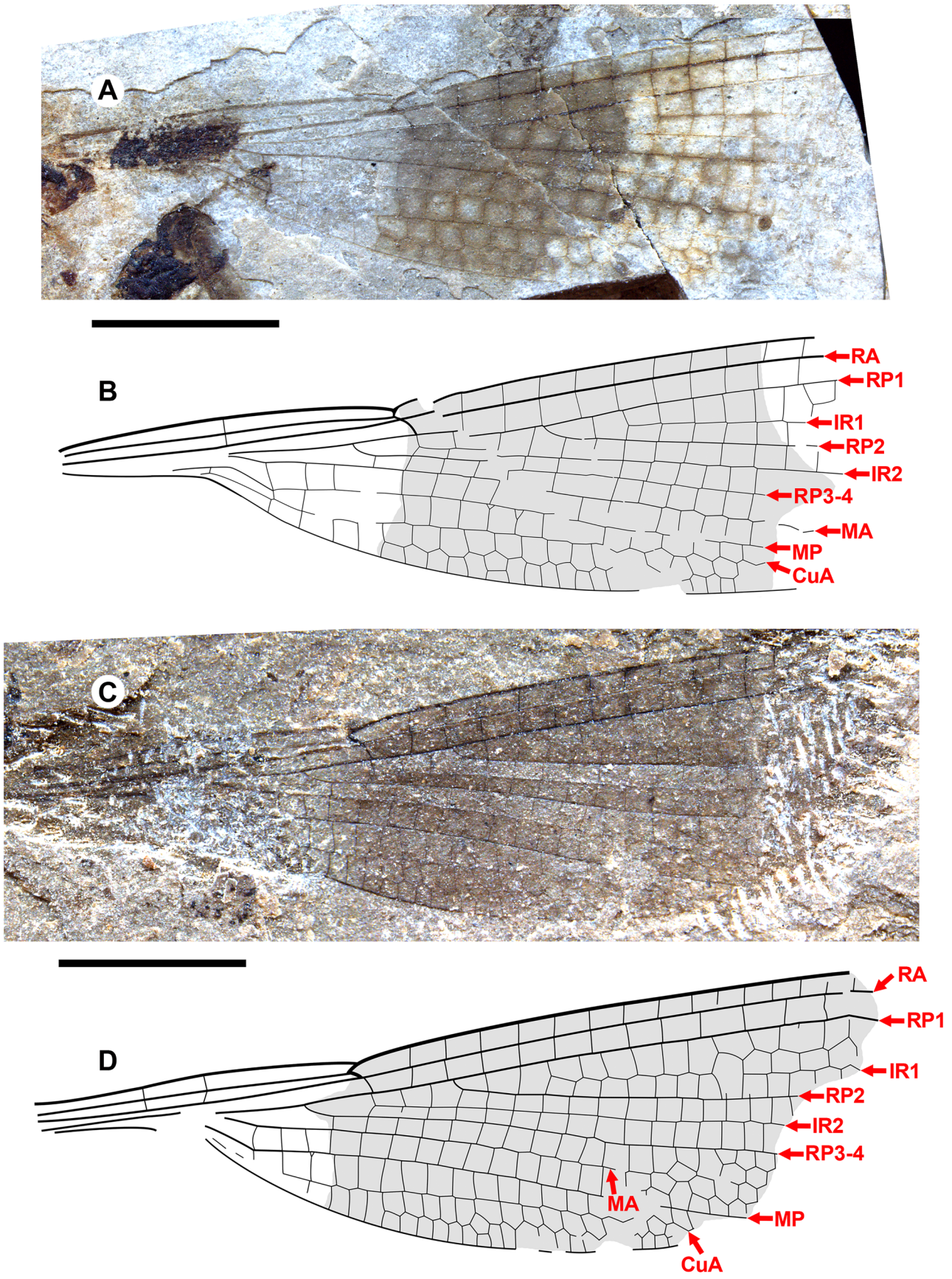

FIGURE 51. *Okanopteryx fraseri* paratype 3, PB-4157. A, photograph; B, drawing; paratype 2, F-1091: C, photograph; D, drawing. All to scale, 5 mm.

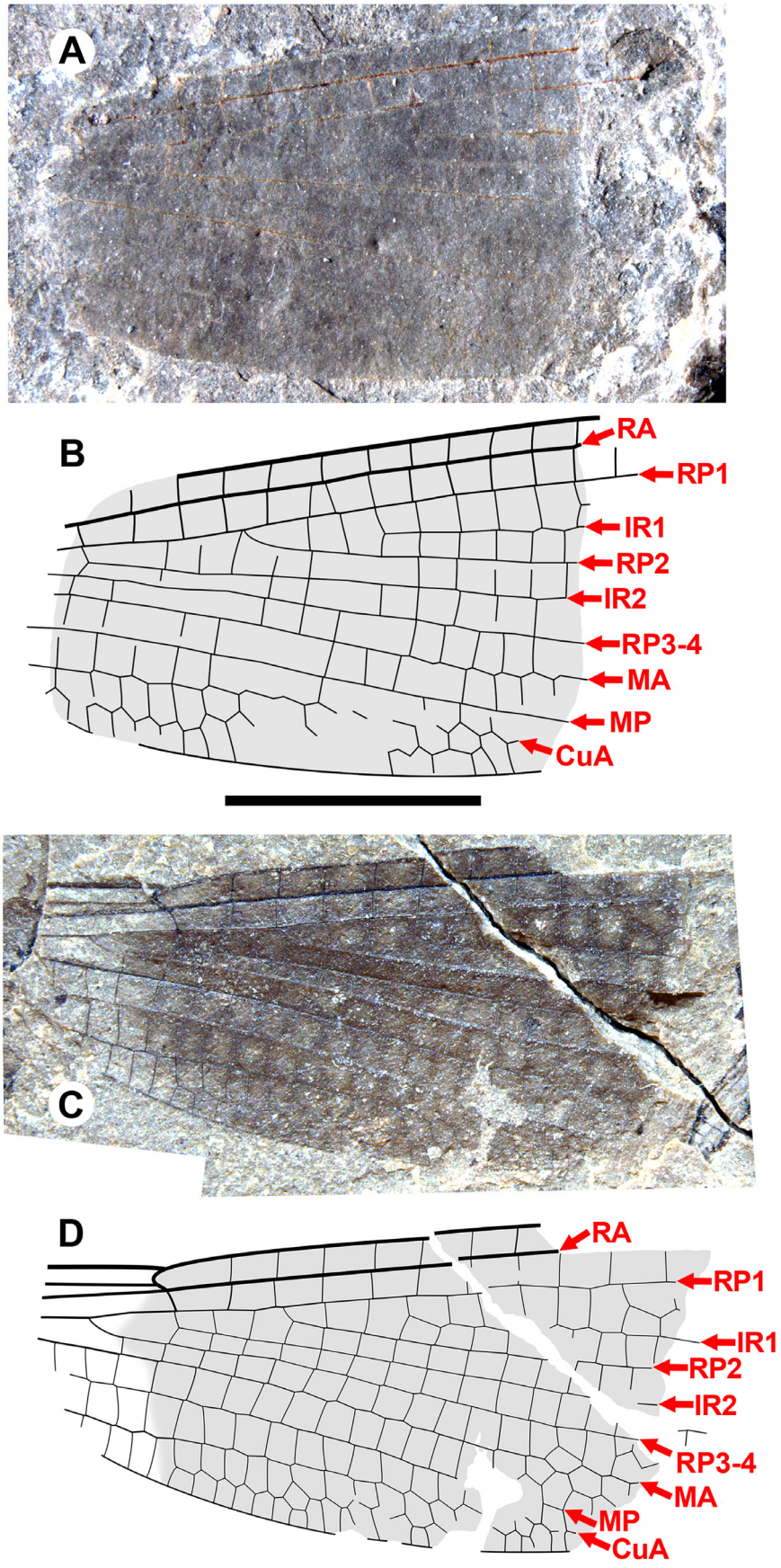

FIGURE 52. *Okanopteryx fraseri* paratype 5, RBCM P1552. A, photograph; B, drawing; paratype 4, F-1045: C, photograph; D, drawing. All to scale, 5 mm.

except: RP1–IR1 space becomes two cells wide five cells distal to origin of IR1. IR1: origin three cells distal to origin of RP2. RP2: origin three cells distal to origin of IR2 by preservation, but probably four. MA becoming zigzagged about level of origin of IR1. CuA probably becoming zigzagged about level of origin of IR2, increasing distal to it. CuA–A space apparently two cells wide at widest, unsure by preservation if a third cell wide as in F-1091, PB-4157, F-1045.

Etymology. The specific epithet is a patronymic formed from the surname of John Fraser, the collector and donor of the holotype, recognising his contribution.

Range and age. McAbee, BC, Canada; mid-Ypresian.

Discussion. The abdomen of the holotype is much longer than that of *O. macabeensis*; indeed, the specimen as a whole is likely about 1.7 times longer than *O. macabeensis*, confidently setting these two species apart (see diagnosis). Based on known variation in extant species, this size difference is unlikely to be the result of intraspecific variation or sexual dimorphism.

Although the wing of the holotype of *O. fraseri* is only partially preserved, its CuA–A space is only two cells wide at this level, with an occasional single column of three. By this, we associate wings which share the colouration and other venational character states with either *O. fraseri* or *O. macabeensis* based on the number of cells across the CuA–A space between the levels of IR1 and RP2: three in *O. macabeensis* and two (sometimes a single column of three) in *O. fraseri*.

The thorax of *O. fraseri* may be more robust than that of *O. macabeensis*, however, it might also be that they are preserved at slightly different angles.

Okanopteryx macabeensis Archibald & Cannings, new species

Figs. 53–57.

Diagnosis. Wings distinct from those of *O. fraseri*, *O. jeppesenorum* as in their diagnoses; further from *O. fraseri* by abdomen/body length as in its diagnosis.

Material. *Holotype*: GSC 141100 (collector number SBA-2801) (Fig. 53), collected at the McAbee Hoodoo Face beds, Geological Survey of Canada locality code V-016800, by SBA, 10.vii.2000, housed in the Geological Survey of Canada collections; *paratype 1*: GSC 141101 (Fig. 54, 55A, 55C–55F), collected at the McAbee Hoodoo Face beds, Geological Survey of Canada locality code V-016801 by Rod Bartlett, vii.1991, in the Geological Survey of Canada collections; *paratype 2*: F-790 (Fig. 56), collected at the McAbee Hoodoo Face beds, date and collector unknown (this is the much less complete counterpart; the part, with the almost entire insect preserved, was last seen in the inaccessible private collection of a commercial fossil dealer), in the Thompson Rivers University collections; *paratype 3*: GSC 141102 (collector number SBA-5928) (Fig. 57), collected at the McAbee Hoodoo Face beds, Geological Survey of Canada locality code V-016800, by SBA, date unknown, in the Geological Survey of Canada collections; *paratype 4*: RBCM 3087 (Fig. 53), collected at the McAbee Hoodoo Face beds by John Leahy, date unknown in the Royal British Columbia Museum collections.

Description. Holotype, GSC 141100, wing (Fig. 53). Almost complete, missing petiole, small portion of the posterior margin in the apical quarter. Oval distal to nodus. Nodus to apex estimated 18.4 mm (presumed: small portion of apex missing), nodus to pterostigma 14.2 mm; width 6.5 mm wide. Hyaline except for broad, darkly infuscate fascia from level of nodus to about half distance to apex (similar to other *Okanopteryx* species). Pterostigma broad, 2.5 times longer than wide. Region of possible oblique brace vein missing. Crossveins in postnodal, postsubnodal spaces mostly aligned. Two cells wide distal to pterostigma in region of costal space preserved except one wide at pterostigma. RA–RP1 space one cells wide (apical-most portion not preserved). RP1–IR1 space goes to two cells wide seven cells distal to origin of IR1. IR1: origin two cells distal to origin of RP2; two cells wide close before level of pterostigma. RP2: origin 3.5 cells distal to origin of IR2; two cells wide same level as IR1–RP2 space; linear, straight to slight, even curve posteriorly near margin. IR2 origin at subnodus, mostly straight, linear except near margin slightly zigzag with slight, even curve posteriad. RP3-4: origin about half way between anterior-distal corner of quadrangle, nodus; straight, linear to slight, even curve posteriorly near margin. MA straight, linear, begins slight zigzag shortly beyond level of origin of IR1, increasingly so, but missing close to margin. MP linear, slightly curved from quadrangle, missing near terminus. CuA slightly zigzagged distal to level of origin of RP2; CuA–A space about six columns of three cells wide; otherwise two distal to level of nodus.

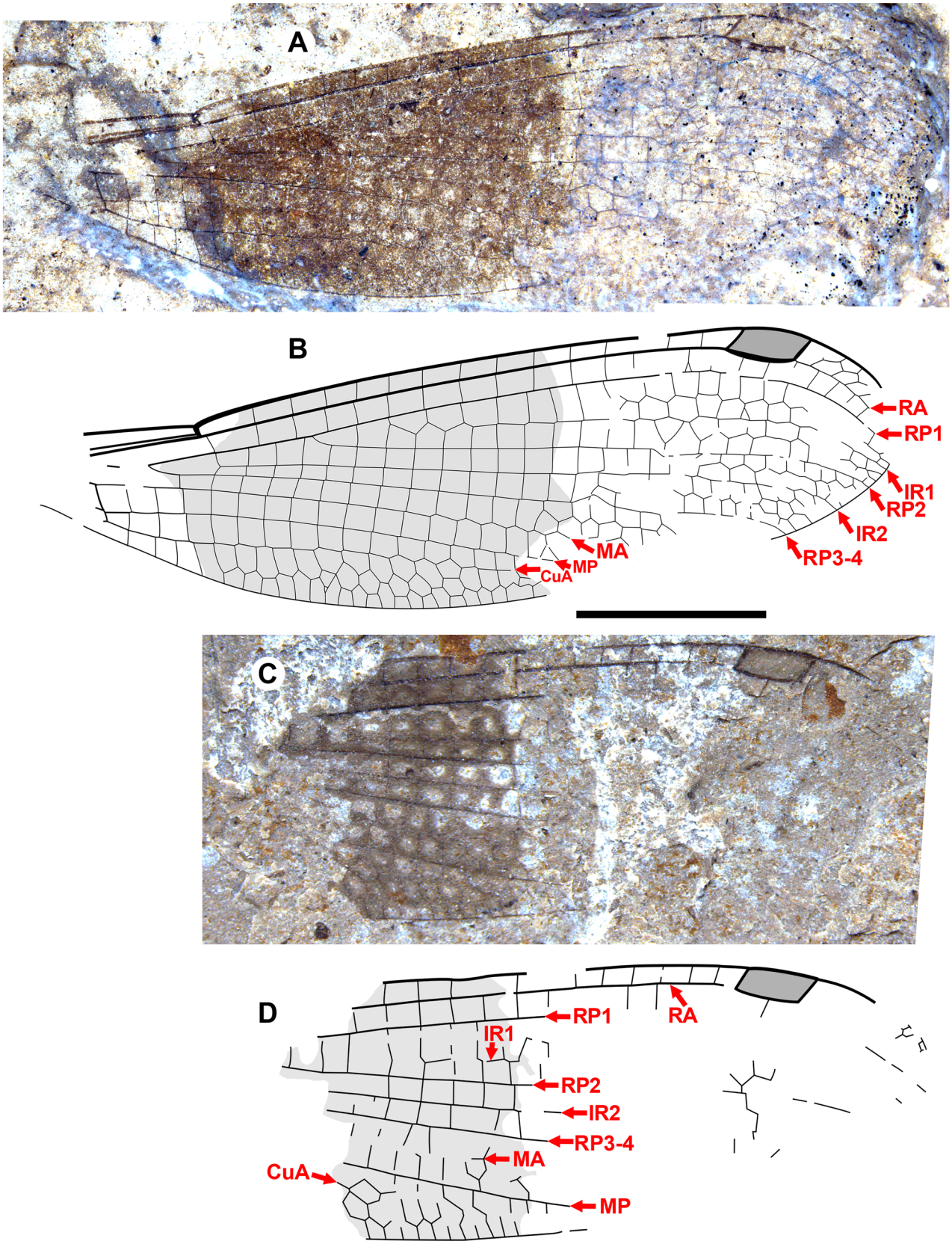

FIGURE 53. *Okanopteryx macabeensis* holotype, GSC 141100: A, photograph; B, drawing. Paratype 4: RBCM 3087: C, photograph; D, drawing. All to scale, 5 mm.

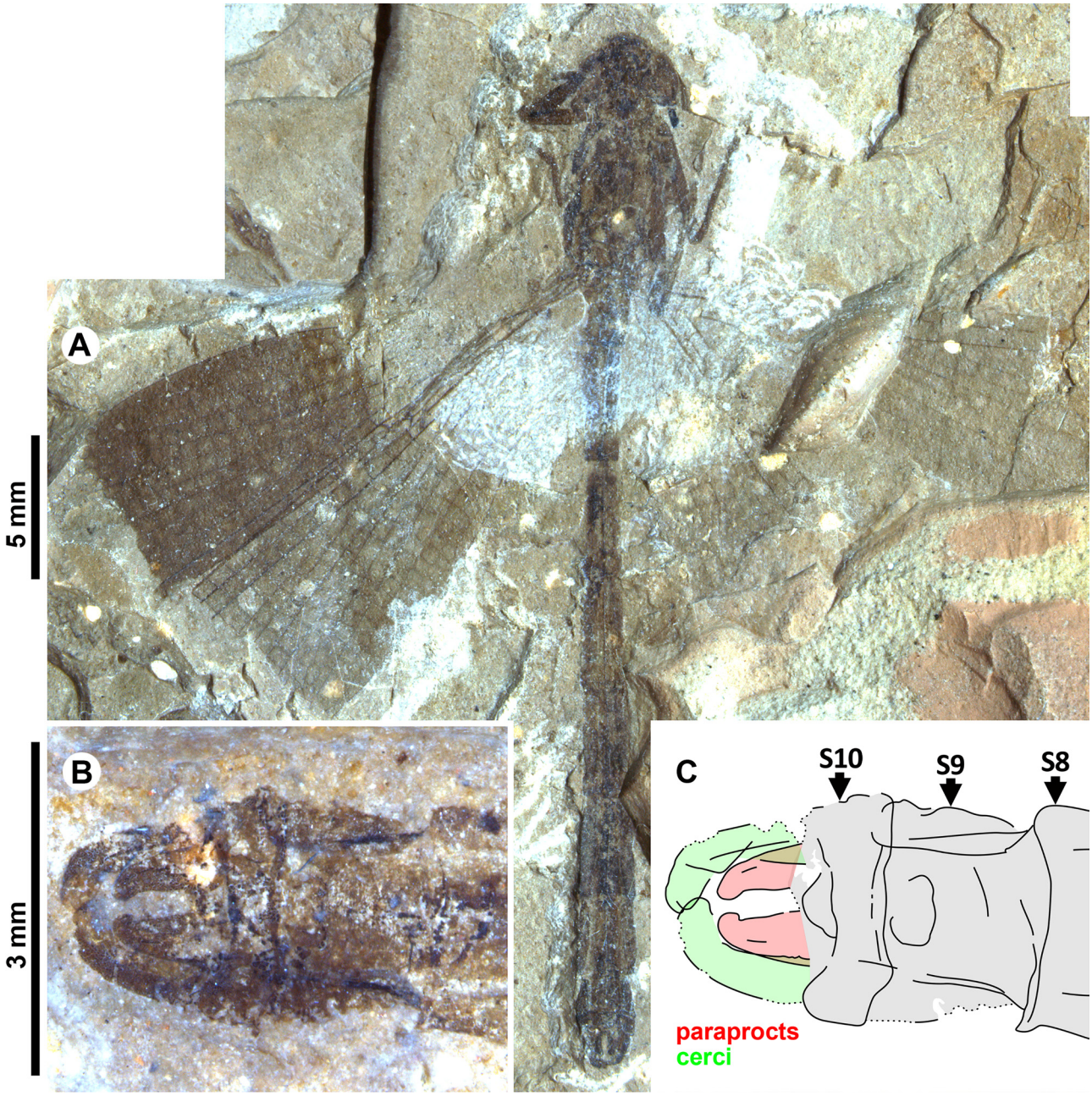

FIGURE 54. *Okanopteryx macabeensis* paratype 1, GSC 141101. A, photograph of specimen; B close-up photograph of male anal appendages; C, drawing of male anal appendages labelling abdominal segments 8–10 and indicating paraprocts (red) and cerci (green). A, to 5mm scale, B, C, to 3 mm scale.

Paratype 1, GSC 141101, male (Figs. 54, 55A, 55C–55F). Complete body, total length 37.7 mm; abdomen preserved in ventral aspect, at least distal to segment 4; thorax and head in dorsal aspect; portions of four legs, portions of all four wings. Head (Fig. 10 L, Table 1). In dorsal view about 3.7 mm across eyes at widest point; approximate length from anterior edge of antefrons to posterior of occiput about 1.5 mm; at level of hind ocelli distance between medial margins of eyes about 1.0 mm, width of eye about 1.2 mm, length 1.8 mm. Thorax. Dorsum of prothorax oval, 2.1 mm wide, 1.1 mm long; pterothorax about 6.0 mm long. Legs. Lengths of leg segments unclear, not measured. Wings. Left fore(?)wing. Proximal portion to presumed (based on holotype) half distance between nodus, apex. Darkly infuscate from nodus to distal portion preserved, hyaline proximal to nodus. Maximum width 6.9 mm. Crossveins aligned in postnodal, postsubnodal spaces (portion preserved). RP1–IR1 space goes to two cells wide three cells distal to origin of IR1. IR1: origin two cells distal to origin of RP2. RP2: origin three cells distal to origin of IR2. IR2 origin very close to subnodus; straight, linear. RP3-4: origin not preserved; linear, straight where

reserved. MA linear, slightly curved from quadrangle to zigzag increasingly from about level of origin of IR1. MP linear, slightly curved from quadrangle. CuA with slight zigzag beyond level of nodus, increasing beyond level of origin of RP2, CuA–A space about 10 columns with 3 cells wide, the rest two distal to level of origin of PR3-4. Left hind(?) wing. Same region preserved as left fore(?)wing, but more complete in antenodal region. Petiole partially preserved. Shape as for left fore(?)wing. Width 6.9 mm. Hyaline, infuscate in same regions, but infuscation notably lighter. Crossveins in postnodal, postsubnodal spaces aligned. RP1–IR1 space goes to two cells wide four cells distal to origin of IR1. IR1: origin three cells distal to origin of RP2. RP2: origin four cells distal to origin of IR1; straight, linear. IR2 origin very close to subnodus; straight, linear. RP3-4: origin at level of Ax2, half way between anterior-distal corner of quadrangle, nodus, in middle third between arculus, nodus. MA slightly zigzagged from level of origin of IR1, increasingly so distal to it. MP linear, slightly curved from quadrangle through preserved portion near terminus. CuA linear from level of quadrangle until slight zigzag from nodus level increasingly so after level of origin of RP2; CuA–A space with about ten columns of three cells at widest, otherwise two from level of origin of RP3-4. Right wings fragmentary, preserved portions do not disagree with left wings; presumed hind(?) wing with same lighter infuscation as left hind(?) wing. Presumed fore(?)wing colouration as in holotype. Abdomen approximately 20.0 mm long. Anal appendages: cerci 1.3 mm long, 0.4 mm wide, evenly curved medially, the rounded apices nearly touching; paraprocts about 0.8 mm long, 0.4 mm wide at base tapering to 0.2 mm at apex, extending about 0.7 the length of cerci; medial side straight, lateral side curved medially; apex slightly hooked medially, rounded.

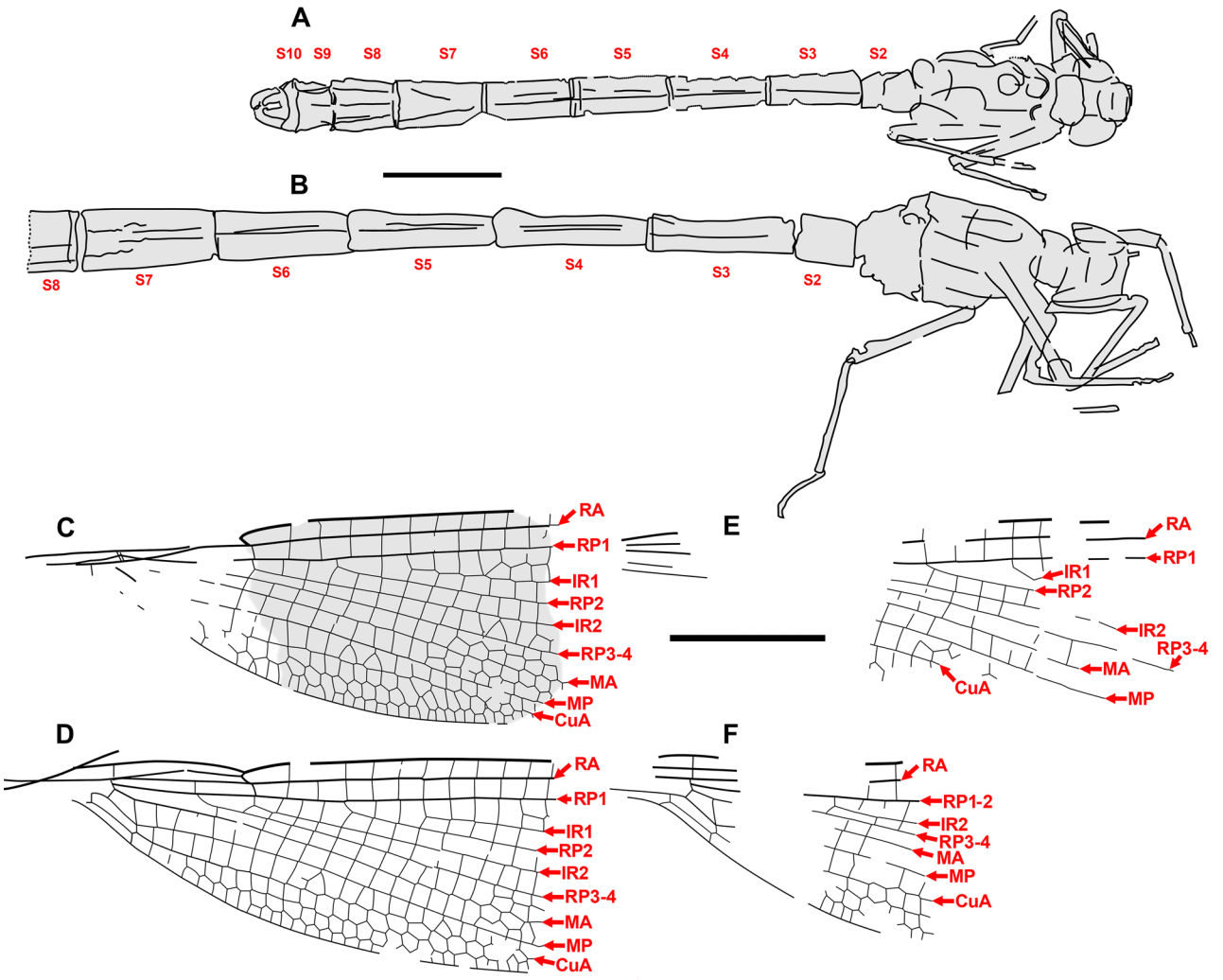

FIGURE 55. *Okanopteryx macabeensis* and *O. fraseri*. A, *O. macabeensis* paratype 1, drawing of body; B, holotype *O. fraseri* drawing of body; abdominal segments labelled; C–F, wings of *O. macabeensis* paratype 1. A, B and C–F to scales, 5 mm.

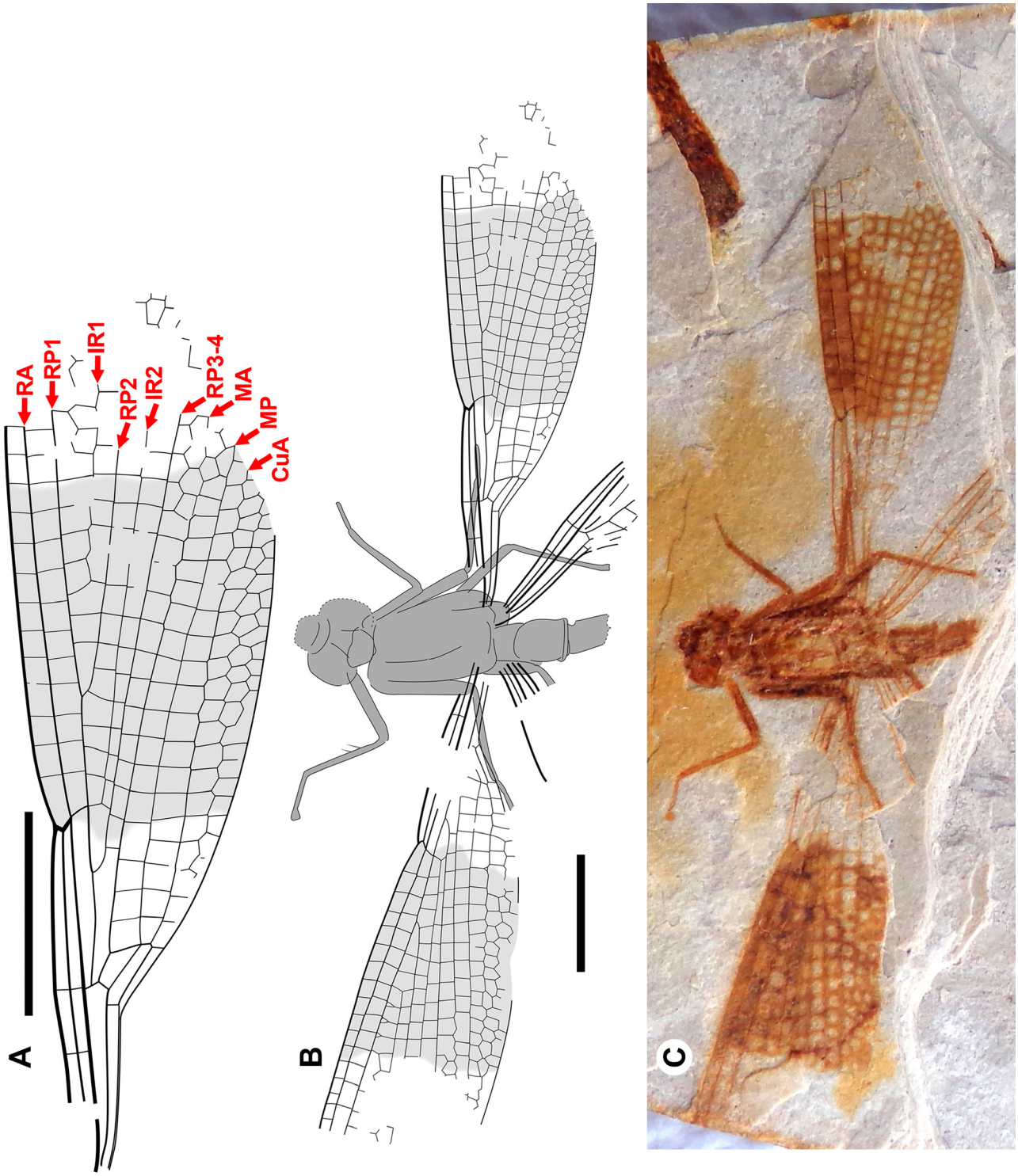

FIGURE 56. *Okanopteryx macabeensis* paratype 2, F-790. A, labelled drawing of wing; B, drawing of specimen; C, photograph of specimen. A to scale, B, C to scale, both scales 5 mm.

Paratype 2, F-790 (Fig. 55). Head; thorax, parts of five legs, both forewings missing the apical quarters, the proximal portions of both hind wings; the abdomen to part of segment 3; preserved in dorsal aspect. Head (Fig. 10 O, Table 1). Relatively well preserved; in dorsal view about 3.8 mm across eyes at widest point; approximate length from anterior edge of antefrons to posterior of occiput about 1.7 mm; at level of hind ocelli distance between medial margins of eyes about 1.1 mm, width of eye about 1.3 mm, length 2.2 mm. Thorax. Prothorax roughly oval, about 1.5 mm wide, 1.0 mm long; pterothorax slightly deformed, especially posterior part, about 5.9 mm long, 3.2 mm wide. Legs. Left profemur 3.0 mm long, tibia 3.8 mm (setae 0.6 mm long, their bases separated by about half

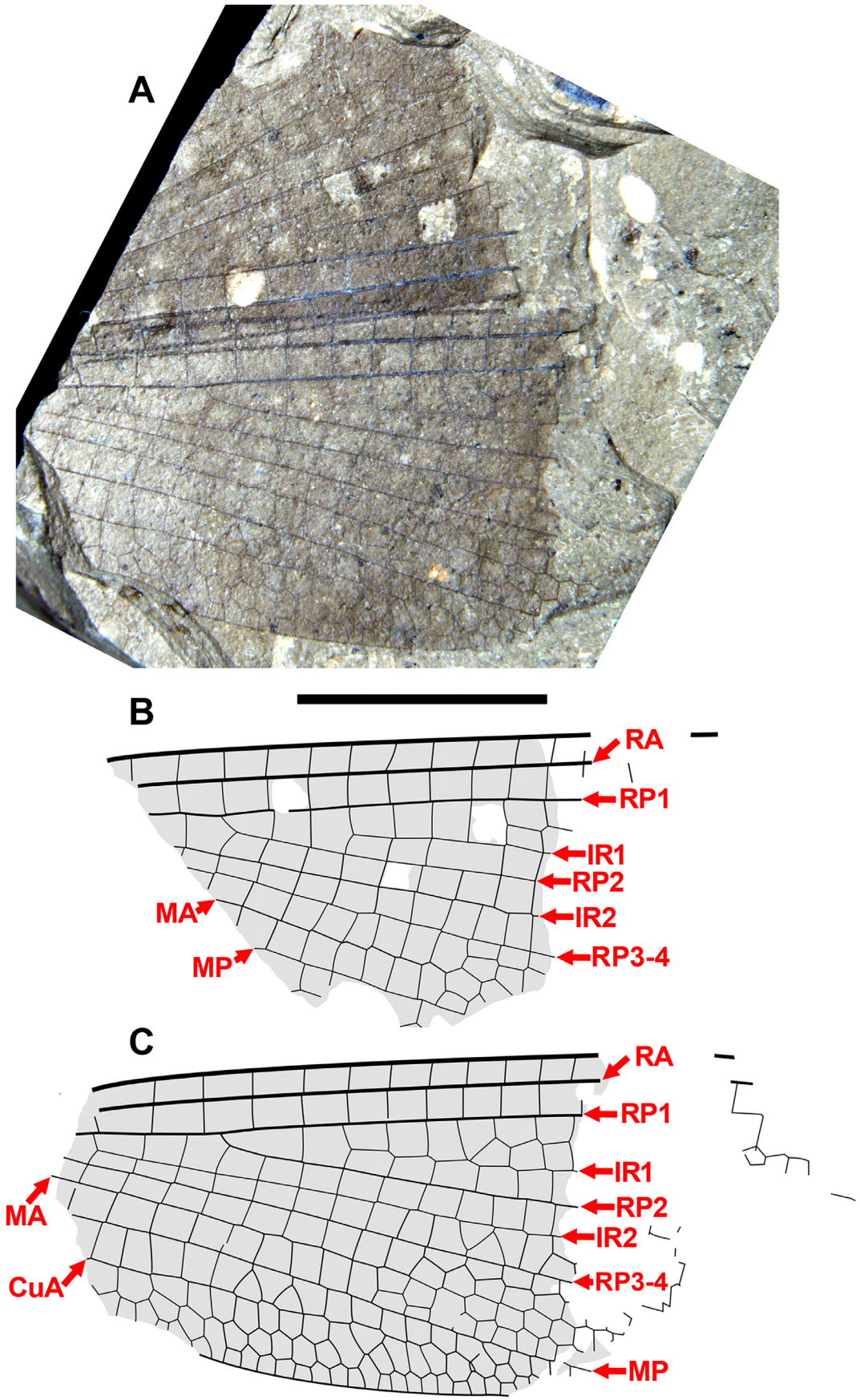

FIGURE 57. *Okanopteryx macabeensis* paratype 3, GSC 141102. A, photograph of specimen; B, drawing of upper wing in A, (vertically inverted for anterior margin on top); C, drawing of bottom wing in A. All to scale, 5 mm.

their length), tarsus 1.5 mm. Right forewing. Petiolate. no accessory antenodal crossveins. Maximum width 6.5 mm. Proximal portion hyaline, darkly infuscate from level of nodus to near level where RP1–IR1 space becomes two cells wide, hyaline in portion preserved distal to this. Crossveins in postnodal, postsubnodal spaces almost all aligned. RP1 space goes to two cells wide five cells distal to origin of IR1. IR1: origin three cells distal to origin of RP2. RP2: origin four cells distal to origin of IR2. IR2: origin at subnodus; linear, straight in portion preserved. RP3-4: origin about 2/3 from arculus to nodus; linear, straight in portion preserved. MA linear, slightly curved from quadrangle to about level of origin of IR1, increasingly zigzags distal to this. MP linear, slightly curved from quadrangle, small portion near terminus not preserved. CuA increasingly zigzagged from level of origin of RP3-4; CuA–A space about seven columns of three cells at widest, otherwise two beyond level of origin of RP3-4. Left forewing. Petiolate. no accessory antenodal crossveins in areas preserved. Width 6.6 mm. Proximal portion hyaline, darkly infuscate from level of nodus to near level where RP1–IR1 space becomes two cells wide, hyaline in portion preserved distal to this. Crossveins in postnodal, postsubnodal spaces almost all aligned. RP1–IR1 space becomes two cells wide four cells distal to origin of IR1. IR1: origin three cells distal to origin of RP2. RP2: origin 3.5 cells distal to origin of IR2. IR2: origin at subnodus; linear, straight in portion preserved. RP3-4: origin similar distance from nodus as right forewing; linear, straight in portion preserved. MA linear, slightly curved from quadrangle to about level of origin of IR1, zigzagged distal to this. MP linear, slightly curved from quadrangle, small portion near terminus not preserved. CuA increasingly zigzagged from level of origin of RP3-4; CuA–A space number of columns of three cells wide difficult to determine as preserved, two evident, likely more, otherwise two beyond level of origin of RP3-4. Right hind wing. Proximal part of wing from articulation to distal side of quadrangle present. Left hind wing. Only base of petiolate portion present. Abdomen mostly missing; only segments, 1, 2 and proximal part of 3 present.

Paratype 3, GSC 141102, two wings (Fig. 57). Middle portions. Wing 1 (Fig 57B) missing posterior portion. Darkly infuscate consistent with the holotype. Crossveins in preserved portion of postnodal, postsubnodal spaces aligned. RP1–IR1 space becomes two cells wide four cells distal to origin of IR1. IR1: origin three cells distal to that of RP2. RP2: origin not preserved. Preserved portions of IR1, RP2, IR2, RP3-4, MP linear, mostly rather straight. MA becoming, increasingly zigzagged distal to level of origin of IR1. MP linear, slightly curved. Wing 2 (Fig. 50C). As for wing 1, except: maximum width 6.8 mm. Crossveins in preserved portion of postnodal, postsubnodal spaces aligned, at most slightly not. RP1–IR1 space becomes two cells wide three cells distal to origin of IR1. IR1: origin two cells distal to that of RP2. RP2: origin 2.5 cells distal to that of IR2. CuA increasingly zigzagged about distal to level of origin of RP2; >7 columns of cells three cells deep, the rest two, then one apically.

Paratype 4, RBCM 3087, wing (Fig. 53). Parts of apical half, missing much of apical-most posterior portion. Maximum width 6.9 mm. Proximally-preserved portion infuscate, hyaline apical to this as in holotype. Pterostigma broad, 2.5 times longer than wide. Preserved crossveins in postnodal, postsubnodal spaces aligned or almost so. Two (possibly more?) cells wide distal to pterostigma in costal space (fragmentarily preserved). RP1–IR1 space becomes two cells wide four cells distal to origin of IR1. Preserved portions of RP2, IR2, RP3-4, MP linear, rather straight. MA indistinctly preserved. CuA zigzagged in portion preserved; at least a few columns of three cells wide.

Etymology. The specific epithet is a toponym referring to its only known locality.

Range and age. McAbee, BC, Canada; mid-Ypresian.

Okanopteryx incertae sedis

Figs. 58–60.

Material. Republic: SRUI 99-72-96AB (Fig. 58), collected at Republic B4131 by Rita Weikel, 27.iv.2019, housed in the Stonerose Interpretive Center collections; SRUI 99-97-44 (Fig. 58), collected at Republic A0307 by Wes Wehr, date unknown, in the Stonerose Interpretive Center collections; F-1046 (Fig. 58), collected at McAbee, collector and date unknown, in the Thompson Rivers University collections; UWBM-72324 (Fig. 60), collected by Wes Wehr at Republic A0307, date unknown, in the Burke Museum collections; SR 13-005-015 AB (Fig. 59), collected at Republic B4131 by Richard Dillhoff, 6.v.2008, in the Stonerose Interpretive Center collections; GSC 141103 (Fig. 59), collected at the McAbee Hoodoo Face beds, Geological Survey of Canada locality code V-016800, by SBA, July 31 2000, in the Geological Survey of Canada collections; RBCM P1553 (Fig. 60), collected at the McAbee Hoodoo Face beds by John Leahy, date unknown, in the Royal British Columbia Museum collections.

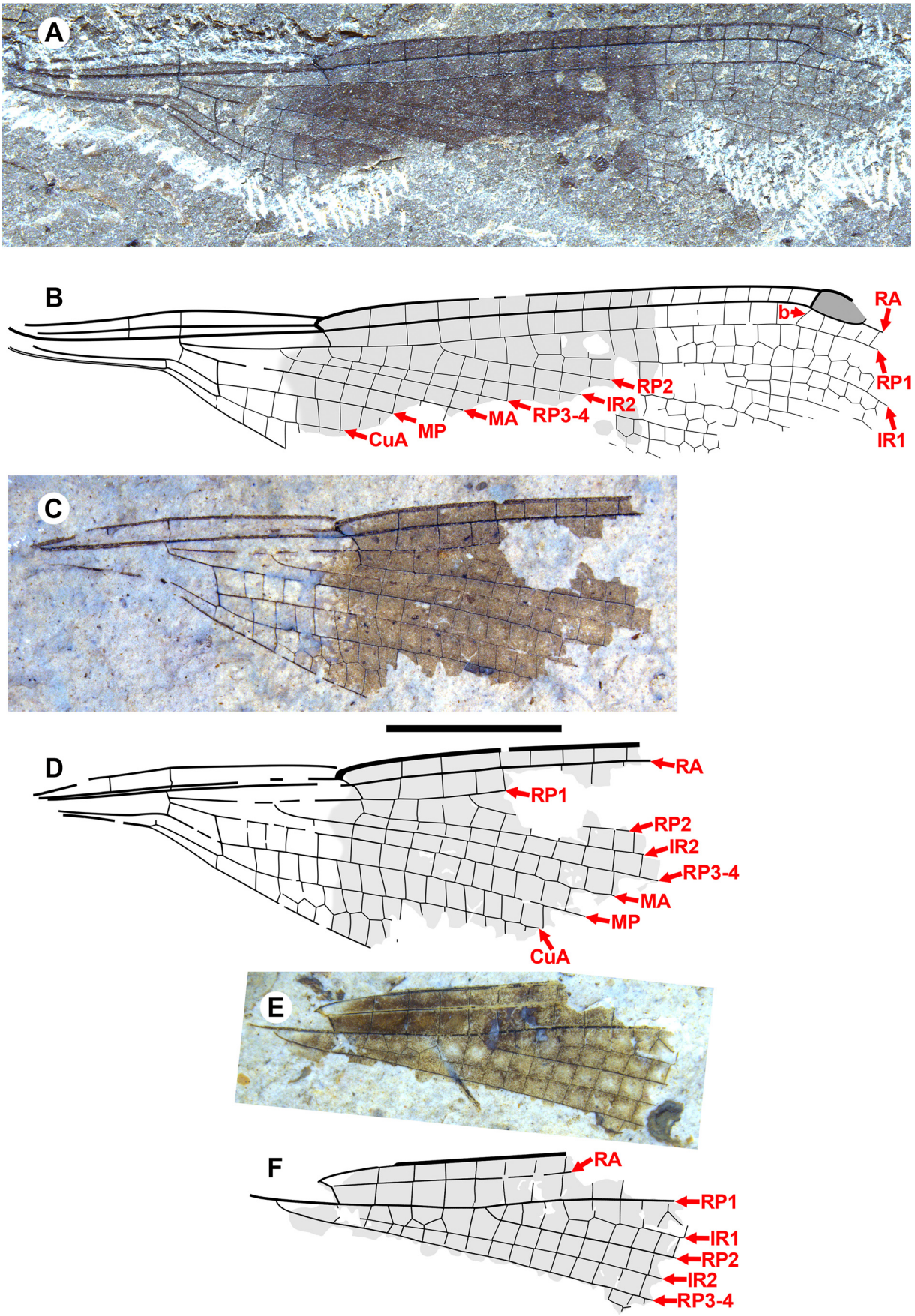

FIGURE 58. *Okanopteryx incertae sedis*. F-1046: A, photograph; B, drawing; SRUI 99-72-96: C, photograph; D, drawing; SRUI 99-97-44: E, photograph; F, drawing. All to scale, 5 mm.

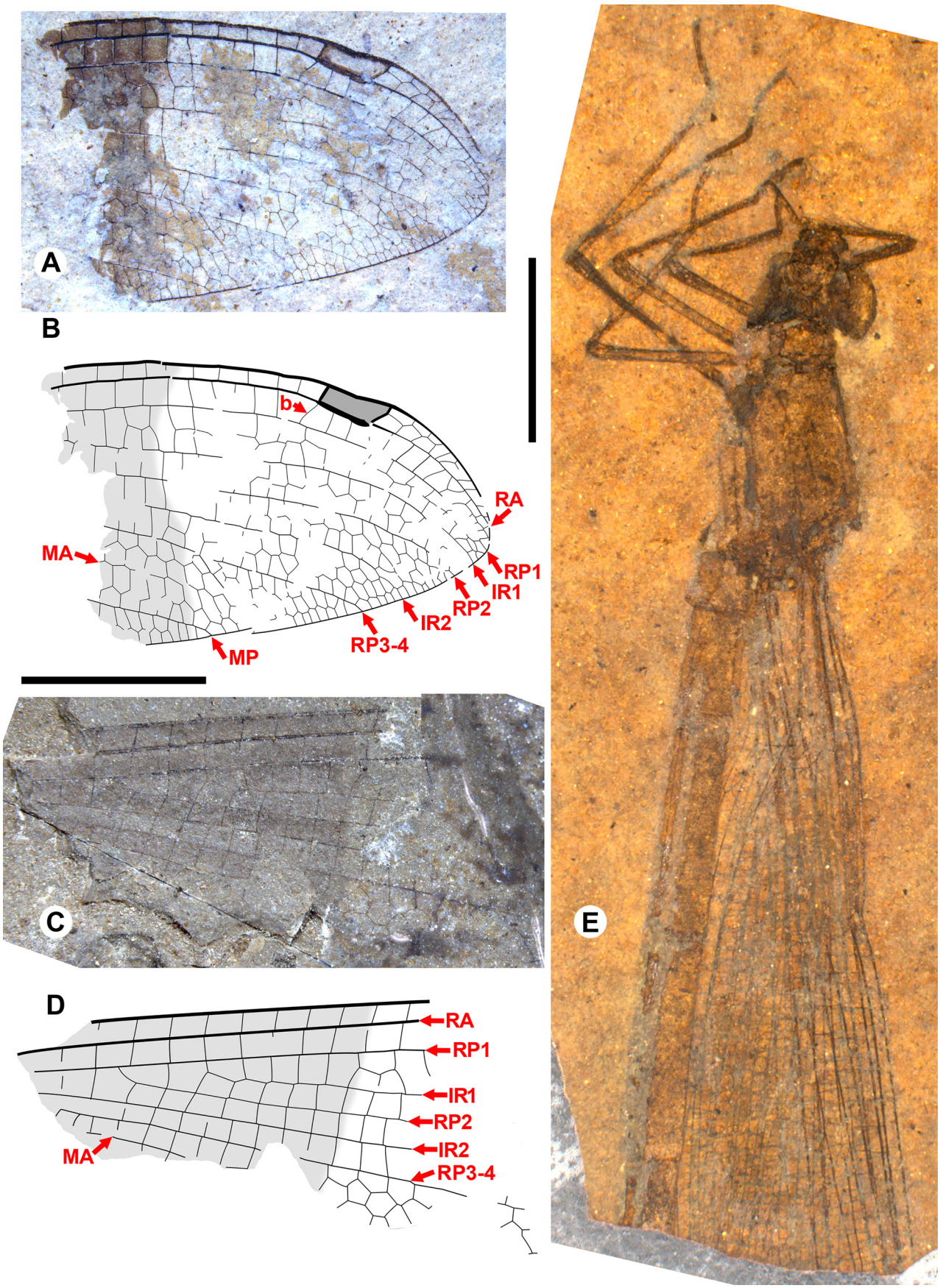

FIGURE 59. *Okanopteryx incertae sedis*, A–D, and Cephalozygoptera *incertae sedis*, E. GSC 141103: A, photograph; B, drawing; SR 13-005-015: C, photograph; D, drawing; E, photograph SR 14-003-004. A–D to scale, E to scale, scale bars are 5 mm.

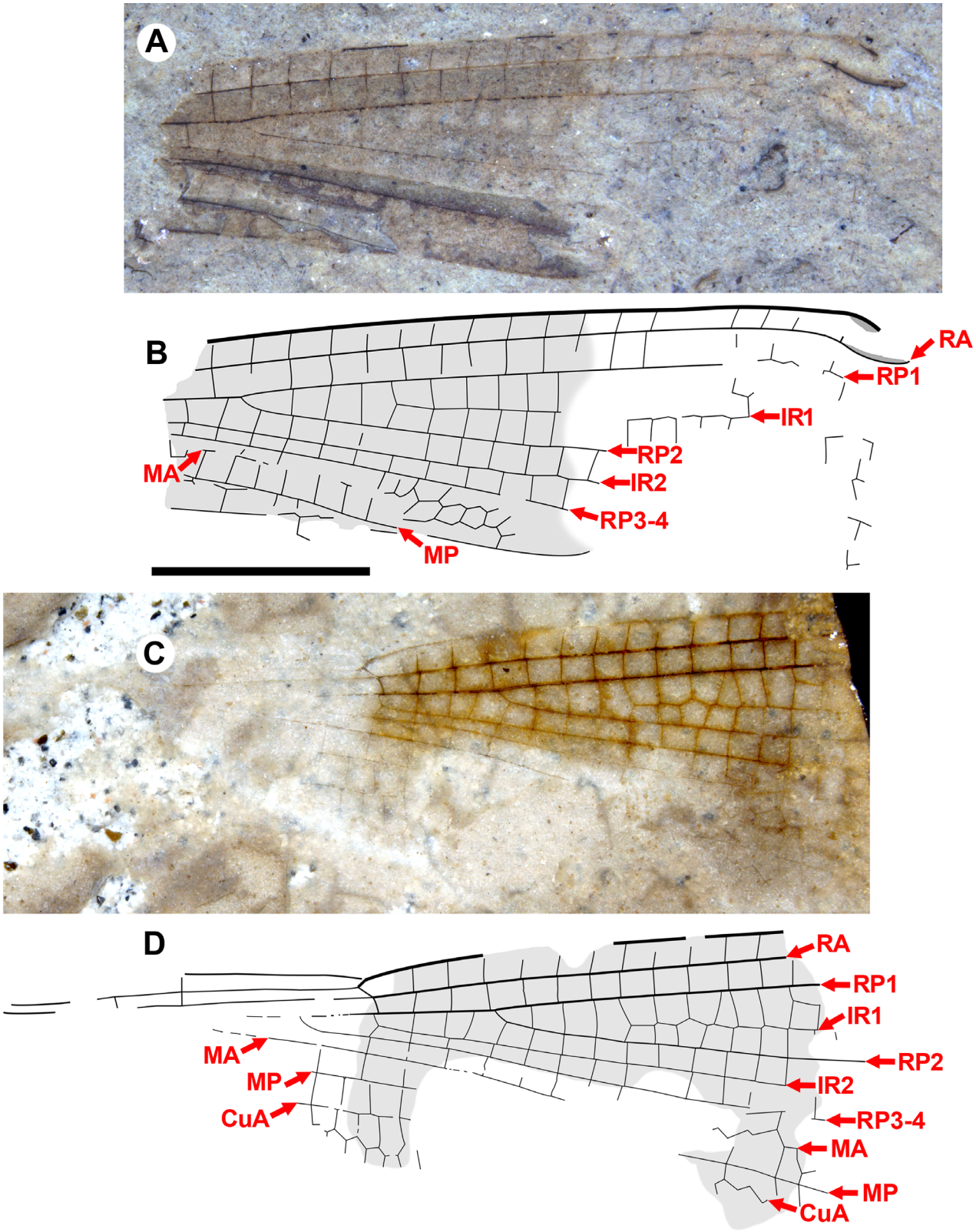

FIGURE 60. *Okanopteryx incertae sedis*. UWBM-72324: A, photograph; B, drawing; RBCM P1553: C, photograph; D, drawing. All to scale, 5 mm.

Discussion. These wing fragments of varying size appear to belong to one of the defined species of *Okanopteryx* by their distinctive colouration and all other preserved morphology, but diagnostic character states separating these species are not preserved. For example, F-1046 agrees with the *O. macabeensis* holotype in all aspects, *e.g.*, just over 14 mm nodus to pterostigma, but lacks almost the entire CuA–A space. The preserved region of specimen SR 13-005-015 AB is almost identical to that of the more complete *O. jeppesenorum* SR 02-32-23, also from Republic exposure B4131.

Stenodiafanus Archibald & Cannings, new genus

Fig. 61.

Diagnosis. Wings distinct from other Dysagrioninae except *Okanopteryx* by: pterostigma length 4 times width [distinct from *Okanopteryx*: 2–2.5 times; *Furagrion*: 3; *Primorilestes*: 3.5; *Phenacolestes*: 4.5–5; not distinct from *Dysagrion*: 3–7.5; *Stenodiafanus*: almost 4; *Okanagrion*: 3–3.5, rarely 4; *Dysagrionites* species: unknown]; oblique brace vein present [separated from *Okanagrion*, *Phenacolestes*, *Primorilestes*, not present; not distinct from *Dysagrion*, *Furagrion*, *Okanoptyeryx*: present; *Electrophenacolestes*, *Dysagrionites* species: unknown, wing region not preserved]; costal space 2 cells wide distal to pterostigma [distinct from *Dysagrion*, *Furagrion*, *Phenacolestes*: all 1; *Okanagrion*: 3–5; shared by *Primorilestes*, *Okanopteryx*: both 2; *Electrophenacolestes*, *Dysagrionites* species: not known]; subnodus with normal obliquity [separated from *Dysagrion*: reversed obliquity; all others: normal obliquity, slight to notable]; no accessory antenodal crossveins [distinguished from *Phenacolestes*, *Electrophenacolestes*, some *Dysagrion* species: with; not distinguished from others: without]; IR2 origin between RP1-2, RP3-4, connected to RP1-2, RP3-4 at similar level [*Dysagrion*: between RP1-2, RP3-4, but closer to RP3-4, connected with RP1-2 distinctly more distally than to RP3-4; not distinct from other genera, except some *Okanagrion* species: origin close to or on RP1-2]; MA zigzagged from mid-wing to margin [distinct from *Okanagrion*, *Primorilestes*, *Electrophenacolestes* (very end not preserved): linear or nearly so; *Phenacolestes*: very slight zigzag in middle; *Dysagrion*: MA becomes zigzagged mid-wing, then linear near margin; *Furagrion*: slightly zigzagged mid-wing then linear, deeply curved to margin]; MA, MP close at margin, probably separated by 1–2? cells (difficult to be sure of exact identity of MA near margin by strong zigzag) [distinct from *Okanagrion*, *Furagrion*, *Primorilestes*, *Electrophenacolestes*: widely separated; not distinct from *Dysagrion*: 1–2 cells apart; *Okanopteryx*: identity of MA near margin also unsure by strong zigzag, but close to MP; *Dysagrionites* species: also difficult to establish, perhaps one cell apart?]; CuA zigzagged from to about mid-wing to margin (but proximal to this not known) [distinct from *Electrophenacolestes*, *Primorilestes*, *Okanagrion*: linear or only very slightly zigzagged; *Furagrion*: slightly zigzagged distal to level of origin of RP2; *Phenacolestes*: very slightly zigzagged in parts or not; not distinct from *Dysagrion*, *Okanopteryx*: increasingly zigzagged distal to level of nodus or from *Dysagrionites* species as known, but distal-most portions not preserved]; CuA–A space 2 cells wide [separated from *Phenacolestes*, *Dysagrion*, *Electrophenacolestes*: 4; *Primorilestes*: 3–5; *Okanagrion*, 4–7; *Dysagrionites* sp. B: probably 3 but unclear; not separated from *Okanopteryx*: 2–4; *Furagrion*: 2; *Dysagrionites* sp. A: 2]; distinct from all other Dysagrionidae genera except *Okanopteryx* by RA, RP1, IR1, RP2 distinctly converge, almost meeting at apex; postnodal, postsubnodal crossveins mostly aligned at least in proximal half [distinct from *Phenacolestes*, *Primorilestes madseni*, *Dysagrion*: all not; not separated from *Okanopteryx*, *Primorilestes violetae*; *Electrophenacolestes*; *Furagrion*: similar]; hyaline throughout (sex unknown) [males (females unknown) of *Okanopteryx*, most *Okanagrion*: with various colour patterning; not separated from *Dysagrion*: hyaline (sex unknown)]; shape long, 24.8 mm nodus to apex, narrow, 5.8 mm wide, with a rather acute, elongate apex [*Okanopteryx* from holotype *O. macabeensis*: 18.4 mm nodus to apex, 6.5 mm wide to *O. jeppesenorum* paratype 1 (SR 11-43-09): 23.5 mm nodus to apex, 7.2 mm wide, holotype (SR 13-005-013): 7.7 mm wide]; further distinct from *Primorilestes* by no intercalary vein in CuA–A space. Separated most easily from *Valerea* (tentative Dysagrioninae) by no linear supplementary sector between RP1, IR1 [*Valerea*: with such sector]; costal space 2 cells wide distal to pterostigma [maximum 5]; origins of IR1, RP2 further from nodus; origin of IR2 between RP1-2, RP3-4 [IR2 origin not preserved, only preserved distal to level of nodus, where it is closer to RP3-4]. Most easily separated from genera regarded here as possible Dysagrionidae as follows: from Chickaloon specimen (Garrouste & Nel 2019) by CuA zigzagged distally to margin (proximal portion not preserved) [linear in all preserved portion to near terminus]; CuA–A space 2 cells wide [4]; from *Thanetophilosina* by no linear sectors between RP1, IR1, between IR1, RP2 [with], by pterostigma length 4 times width [about 6];

from NHMUK I.9866/I.9718 by origin of RP3-4 [distinctly closer to subnodus]; from *cf*. Dysagrionidae genus A, species A ("Megapodagrionidae" genus A, species A, Petrulevičius *et al*. 2008) by hyaline membrane [preserved portion infuscate except apex distal to pterostigma], by MA, CuA zigzagged distally to margin [linear to margin], by pterostigma length 4 times width [about 2.5], by width 23% length nodus to apex [37%].

Type and included species. *Stenodiafanus westersidei*, type and only species.

Description. As in diagnosis and the description of its only species, below.

Etymology. The genus name is formed from the Greek στενός, *stenos*, meaning "narrow", and Διαφανής, *diafanis*, meaning "transparent", referring to their slender, hyaline wings. Gender, masculine.

Range and age. Okanagan Highlands, Tom Thumb Tuff Member of the Klondike Mountain Formation, at Republic, Washington, USA; late Ypresian.

Stenodiafanus westersidei Archibald & Cannings, new species

Fig. 61.

Diagnosis. As for genus.

Material. *Holotype*: SR 06-01-42, collected at Republic B4131 by Steven Westerside, 15.viii.2005, housed in the Stonerose Interpretive Center collections.

Description. Holotype, sex unknown. SR-06-01-42, wing (Fig. 61). Hyaline, narrow; nodus to apex 24.8 mm, width 5.8 mm. 18 postnodal crossveins, about half aligned with postsubnodal crossveins, mostly the proximal third. Pterostigma pale, four times longer than wide. Costal space apical to pterostigma one cell wide for one cell, then two. Oblique brace vein present, connecting to proximal corner of pterostigma, oblique. RA–RP1 space one cell wide except for a few adventitious crossveins. RP1–IR1, RP2–IR2, IR2–RP3-4 spaces become two cells wide about half distance from origin of IR1 to pterostigma; IR1–RP2 space becomes two cells wide shortly distal to this. RA, RP1, IR1, RP2 converge, almost meeting at apex (only six cells likely along margin between RA, RP2). RP2 origin about quarter distance between nodus, pterostigma. IR2: origin at level of subnodus, slightly zigzagged in distal quarter. RP3-4: origin proximal to, near nodus; rather straight from level of nodus to terminus on margin at level of distal end of pterostigma. MA linear from level of nodus (not preserved proximal to that) to about half way to level of pterostigma, then zigzagged to margin, about 3-4 nodus to pterostigma levels. MP preserved from level of nodus: rather straight to slight curve near terminus on margin. CuA preserved from just proximal to origin of RP2, zigzagged to margin.

Etymology. The specific epithet is a patronymic formed from the surname of Steven Westerside, the collector and donor of the holotype, recognising his contribution.

Range and age. Tom Thumb Tuff Member of the Klondike Mountain Formation, locality B4131 at Republic, Washington, USA; late Ypresian.

Dysagrionites Archibald & Cannings, new collective genus

Fig. 62–64.

Definition. This genus-level collective group name is proposed for any fossil species referable to the Dysagrioninae that can be clearly defined at the species level, separating them from other species of the subfamily, but whose orthotaxon generic affinity is unclear by the preservation of its currently known specimens.

Etymology. The collective genus name is formed from *Dysagrion*, the name of type genus of the subfamily Dysagrioninae, and the suffix *–ites*, often used in the names of fossil genera, including parataxa. Gender masculine.

Discussion. As a collective group, a definition is provided, but not a diagnosis or description, and a type species is not designated (International Trust for Zoological Nomenclature 1999: article 42.3.1). Species are distinguished from all other species of the bounding group, the Dysagrioninae.

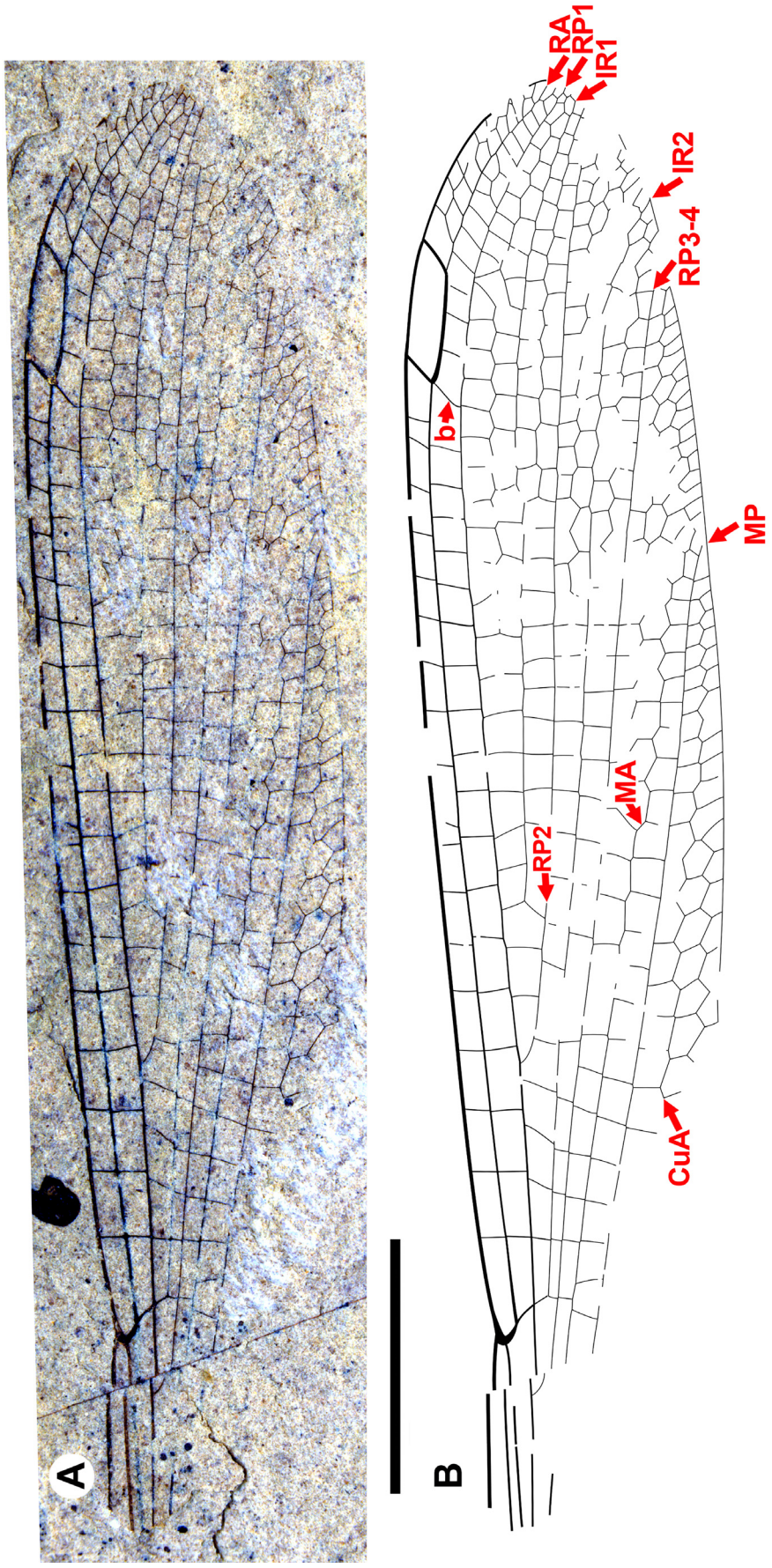

FIGURE 61. *Stenodiafanus westersidei* holotype, SR-06-01-42. A, photograph; B, drawing. Both to scale, 5 mm.

***Dysagrionites delinei* Archibald & Cannings, new species**
Figs. 62–63A.

Diagnosis. Wings of *Dysagrionites delinei* may be distinguished from those of all other species of Dysagrioninae except of *Okanopteryx*, *Stenodiafanus* by: Cu–A space 3 cells wide [*Okanagrion*: 4–7; *Furagrion*, *Dysagrionites* sp. A, *Stenodiafanus*: 2 (most likely, wing incomplete); *Dysagrion*, *Phenacolestes*: 4; *Electrophenacolestes*, 4 (one column 5); *Okanopteryx*: 2–4; not separated from *Primorilestes*: 3–5; *Dysagrionites* sp. B: probably 3 but unclear]. By CuA zigzagged beyond about level of origin of RP2 [*Electrophenacolestes*, *Primorilestes*, *Okanagrion*: linear; not separated from *Dysagrion*, *Okanopteryx*, *Phenacolestes*, *Stenodiafanus*]. Separated from the sole species of *Stenodiafanus* by wider wing, 6.5 mm wide [5.8 mm]; by CuA–A space maximum three cells wide [two]. Separated from males of *Okanopteryx*, *Okanagrion* (males of *O. hobani*, sex unknown in other species) except *O. liquetoalatum*, *Dysagrionites* species B (sex unknown) by wing hyaline throughout known portion (from base past presumed mid-way between nodus, pterostigma [*Okanopteryx*, *Okanagrion* except *O. liquetoalatum*, *Dysagrionites* species B: with infuscate regions]. Further distinct from *Primorilestes* by no intercalary vein in CuA–A space. Most easily separated from fossil genera regarded here as possible Dysagrionidae by: from Chickaloon specimen by cells of CuA–A evenly sized, spaced, maximum three wide [irregularly sized, spaced, four wide]; *Thanetophilosina* by all preserved crossveins in postnodal, postsubnodal spaces aligned or almost so [not]; from NHMUK I.9866/I.9718 by origin of RP3-4 about a third distance from subnodus to level of anterio-distal corner of quadrangle [about 20%]; distinct from *cf.* Dysagrionidae genus A, species A (Petrulevičius *et al*. 2008) by hyaline membrane [infuscate except apex distal to pterostigma]; CuA lightly zigzagged distal to level of origin of RP2 [linear].

Material. *Holotype*: SR 06-01-46AB (Fig. 62), collected at Republic B4131 by William Deline, 21.ix.2005, housed in the Stonerose Interpretive Center collections; *paratype 1*: UWBM 77612 (Fig. 63A), collected at Republic, no exposure, collector, or date recorded, in the Burke Museum collections; *paratype 2*: SR 94-05-26 (Fig. 62), collected at Republic B4131 by Analee Flowers, 18.x.1994, in the Stonerose Interpretive Center collections.

Description. Holotype, SR 06-01-46, wing. Missing apical portion from proximal to pterostigma. Approximately 6.5 mm maximum width. Hyaline throughout (sex unknown). All preserved crossveins in postnodal, postsubnodal spaces aligned or almost so. RP1–IR1, IR1–RP2 spaces do not become two cells wide in preserved portion. IR1: origin four cells distal to origin of RP2. RP2: origin almost five cells distal to origin of IR1. IR2: origin at subnodus. RP3-4: origin not preserved. MA with only slight zigzag around level of origin of IR1. MP linear, slightly curved from quadrangle (distal portion not preserved). CuA becomes slightly zigzagged around level of nodus, increasingly so apical to level of origin of RP2. CuA–A space three cells at widest (from close distal to level of nodus to level of origins of IR1), 9–10 columns; two cells wide proximal to this about 4 columns, distal to this a few columns of two cells wide, then not preserved.

Paratype 1, UWBM-77612, wing. Proximal portion missing apical portion from mid-wing. Maximum width not measurable, but preserved portions match SR 06-01-46. Hyaline throughout (sex unknown). Three preserved crossveins in proximal postnodal, postsubnodal spaces aligned. RP1–IR1, IR1–RP2 spaces do not become two cells wide in preserved portion. IR1 not preserved. RP2: origin probably five cells distal to origin of IR1. IR2: origin at subnodus. RP3-4: origin just over 2/3 distance from arculus to subnodus. MA with only slight zigzag around similar length as SR 06-01-46. MP linear, slightly curved from quadrangle (distal portion not preserved). CuA becomes slightly zigzagged around level of nodus, increasingly so apical to approximate level of origin of RP2. CuA–A space two cells wide from level of nodus to half way between level of nodus, presumed origin of RP2; three cells wide 6–7 columns, then briefly two for remaining preserved portion.

Paratype 2, SR 94-05-26, wing. Anterior portion missing apical region proximal region, much of posterior region. Hyaline throughout (sex unknown). All preserved crossveins in postnodal, postsubnodal spaces aligned or almost so, two in nodal space without matching subnodal space crossveins. RP1–IR1 space becomes two cells wide six cells distal to origin of IR1. IR1: origin three cells distal to origin of RP2; IR1–RP2 space does not become two cells wide in preserved portion. RP2: origin apparently 3.5 cells distal to origin of IR1. IR2: origin at subnodus. RP3-4: origin 2/3 length of arculus to subnodus. MA notably zigzagged beyond level of origin of IR1. MP: small portions preserved, linear. CuA slightly zigzagged around level of origin of RP2, then increasingly so in remaining preserved portion. CuA–A space at least three cells wide at least seven columns, maybe (many?) more, all preserved portion at least two.

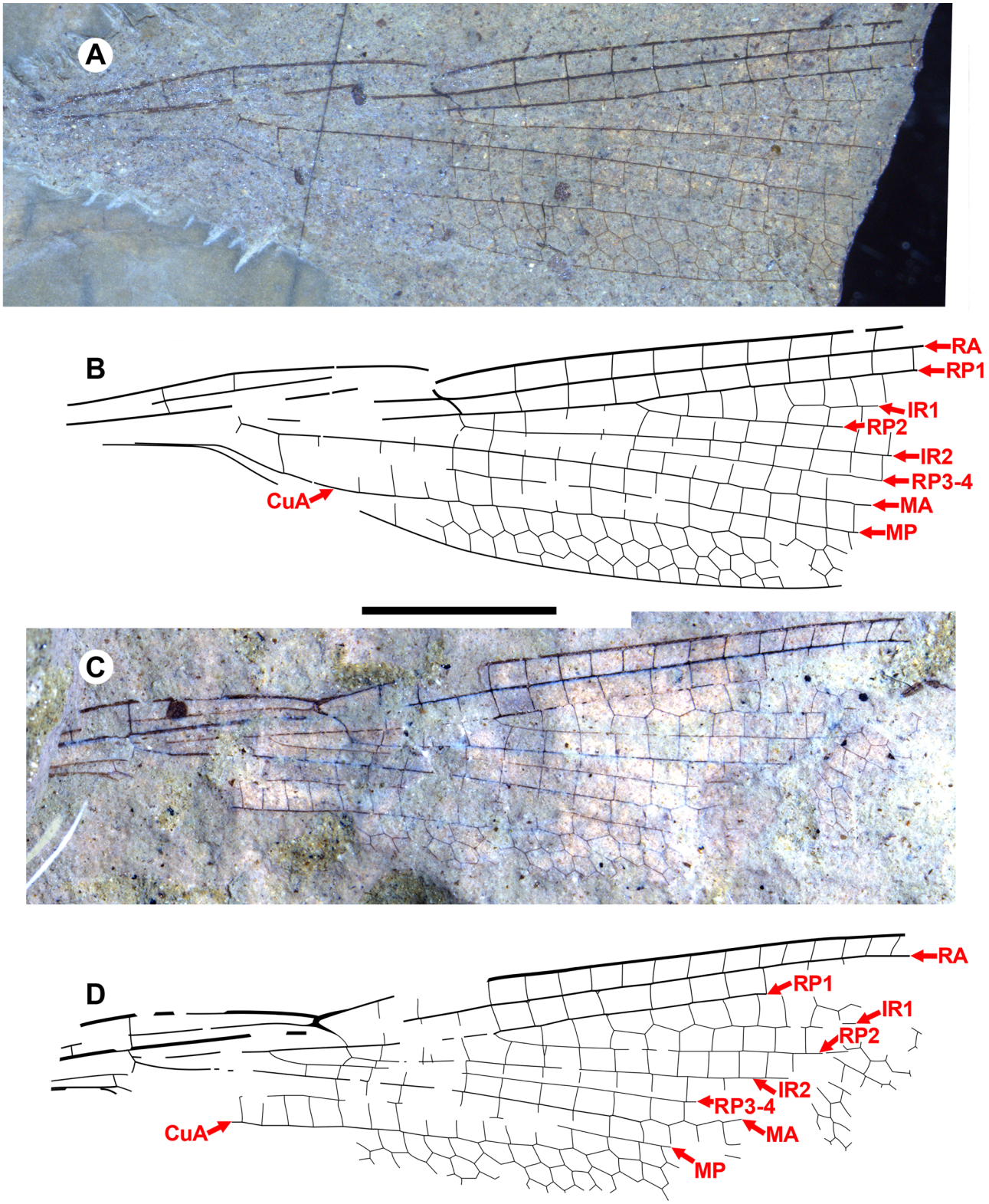

FIGURE 62. *Dysagrionites delinei* holotype, SR 06-01-46. A, photograph; B, drawing; paratype 2, SR 94-05-26: C, photograph; D, drawing. All to scale, 5 mm.

Etymology. The specific epithet formed from the surname of William Deline, collector and donor of the holotype, recognising his contribution.

Range and age. Tom Thumb Tuff Member of the Klondike Mountain Formation at Republic, Washington, USA, all with exposure information are from B4131; late Ypresian.

Discussion. This species might belong to either *Okanopteryx* or *Okanagrion*, expanding its genus concept, or may constitute a new orthotaxon genus.

These differ among themselves by the width of the CuA–A space: SR 06-01-46 is three cells wide between the origins of RP2 and IR1, SR 96-12-03 is three cells wide only briefly around the level of the origin of RP2, and in UWBM-77612 it is uniformly two cells wide except for one column of three. This suggests that there may be more than one species among these specimens.

Although SR 96-12-03 is the middle portion of a wing lacking almost all diagnostic character states of the Dysagrionidae listed above, its great similarity to the other two specimens in particular makes it possible to assign it to the family. It does differ in having almost the whole preserved CuA–A space two cells wide, whereas in the other specimens it has many columns of three. If this specimen is not a member of this species, we believe it likely closely related.

***Dysagrionites* sp. A**
Fig. 63B.

Material. SR 96-12-03 (Fig. 63B), collected at Republic B4131 by Les Larson, 15.x.1996, housed in the Stonerose Interpretive Center collections.

Description of SR 96-12-03. The mid-portion of wing apical to about origin of RP2 to shortly distal to origin of IR1 anteriorly diagonally to shortly proximal to terminus of RP3-4. Width estimated 6.5 mm. hyaline throughout. Few preserved crossveins in proximal postnodal, postsubnodal spaces aligned. RP1–IR1 space does not become two cells wide in preserved portion. IR1: origin three cells distal to that of RP2; RP2–IR2 space becomes two cells wide ten cells distal to origin. RP2 linear, rather straight through preserved portion. IR2, RP3-4 origins not preserved, rather linear, slightly zigzagged in places, rather straight through preserved portion. MA increasingly zigzagged through preserved portion. MP linear, slightly curved in portion preserved to near terminus. CuA zigzagged throughout preserved portion. CuA–A space mostly preserved, from just proximal to level of origin of RP2 almost to distal end; two cells wide throughout with one column of three.

Range and age. Okanagan Highlands, Thumb Tuff Member of the Klondike Mountain Formation at Republic, Washington, USA, exposure B4131; late Ypresian.

Discussion. This middle portion of a wing most resembles *Dysagrionites delinei* in that it is narrow, hyaline, three cells from origin of RP3-4 to origin of IR1 [*D. delinei* 3–4], CuA linear to mid-wing, then begins to zigzag (distal portion not known). It differs, however in the CuA–A space being two cells wide (one column three), whereas in *D. delinei* it is three cells wide. It differs from *Furagrion* and hyaline species of *Okanagrion* by CuA zigzagged in distal portion to the margin, whereas in *Furagrion* it is lightly zigzagged in mid-wing, returning to linear in the distal portion to the margin, and in *Okanagrion* it is linear throughout. It differs further from hyaline *Okanagrion* species by the narrow CuA space [four or more cells wide]. Although it is distinct in these ways, we prefer to wait to name this species until a more complete specimen is found that would allow a more through definition, and given the chance of sexual dimporphism in wing colouration.

***Dysagrionites* sp. B**
Fig. 64.

Material. RBCM P1554 (Fig. 64), the proximal half of a wing, damaged, apparently torn along or near RP3-4, which is missing or obscured. Collected at Driftwood Canyon Provincial Park by SBA, 10.viii.2002, housed in the Royal British Columbia Museum collections.

Description of RBCM P1554. A somewhat damaged proximal portion of a wing. Length, width undeterminable by preservation. As in diagnosis and the following. Crossveins in postnodal, postsubnodal spaces aligned in preserved region. IR1 originates two, maybe three cells distal to origin of RP2. RP2 originates 2.5 cells distal to origin of IR2. IR2 originates at subnodus. RP3-4 is missing, wing damaged. MA linear to level of origin of IR1, not preserved distal to this. MP linear, rather straight from quadrangle to level of origin of IR2, not preserved distal to this. CuA slightly zigzagged distal to level of subnodus, little preserved distal to this. CuA–A space at least three cells wide by level of subnodus, at least two briefly proximal to this.

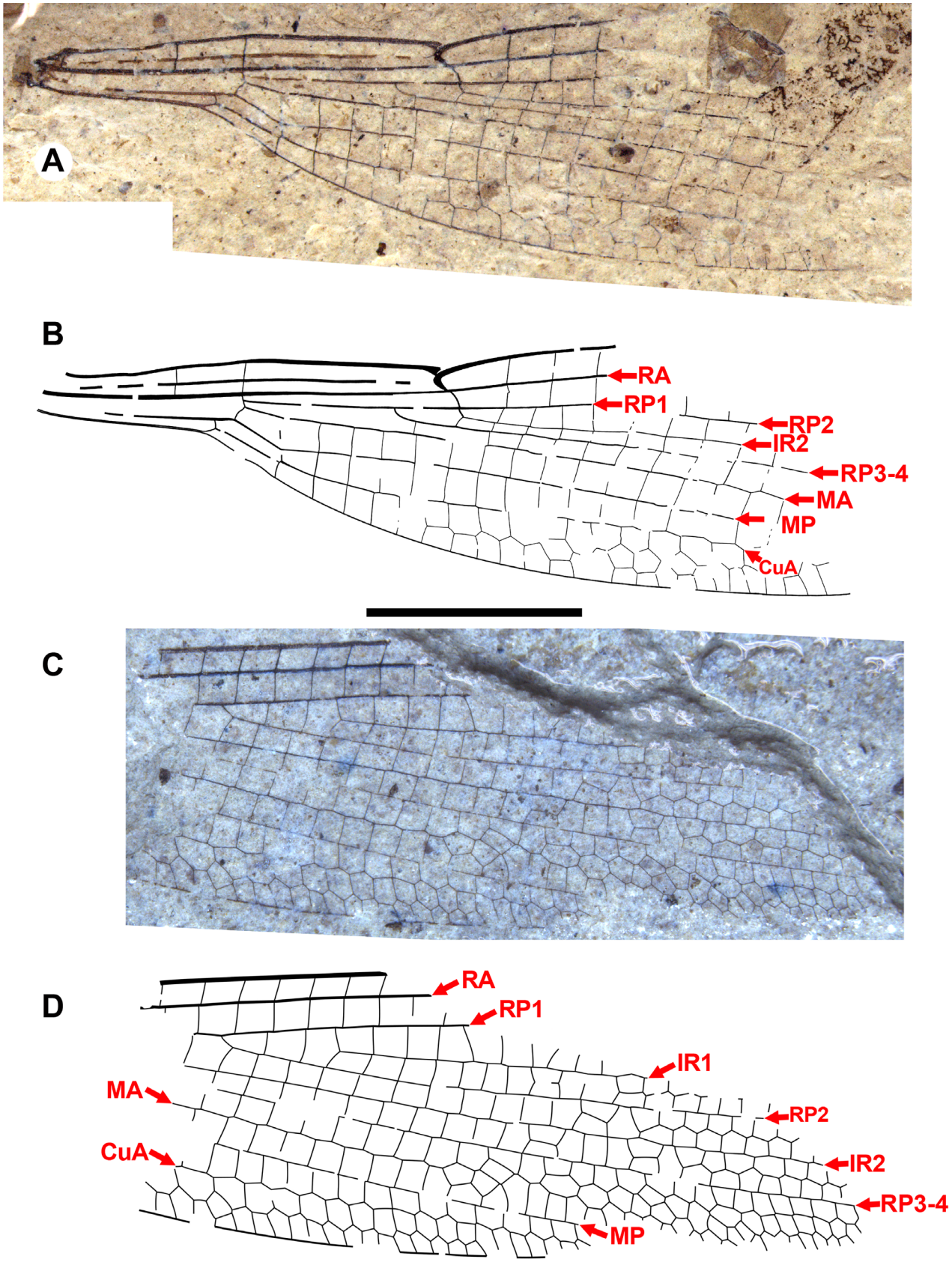

FIGURE 63. *Dysagrionites delinei* paratype 1, UWBM 77612. A, photograph; B, drawing; *Dysagrionites* sp. A, SR 96-12-03: C, photograph; D, drawing. All to scale, 5 mm.

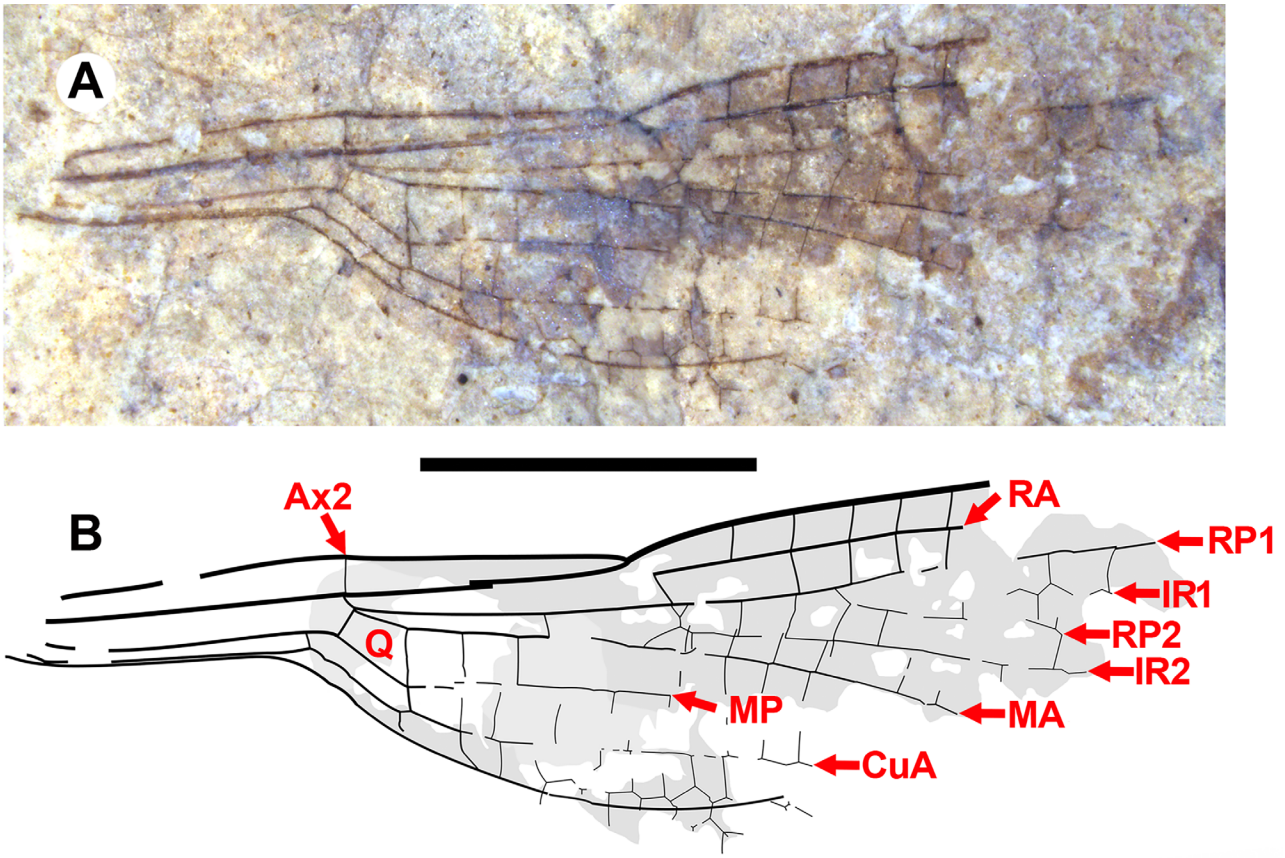

FIGURE 64. *Dysagrionites* sp. B, RBCM P1554. A, photograph; B, drawing. Both to scale, 5 mm.

Range and age. Okanagan Highlands shale at Driftwood Canyon Provincial Park, British Columbia, Canada; mid-Ypresian.

Discussion. This damaged proximal half of a wing may be separated from those of other species of Dysagrioninae except *Primorilestes madseni* by infuscate membrane probably from the level of Ax1 (possibly proximal to this?) to the furthest preserved potion distal to the origin of IR1. The portion preserved is most easily distinguished from *P. madseni* by being narrower between the quadrangle and the posterior margin. Although it is distinct by these traits, we do not name this species by the very damaged and incomplete condition of its only known fossil. It is of particular interest as the only known odonate fossil of the Okanagan Highlands from Driftwood Canyon, indeed, the only one north of McAbee, some 600 kilometres to the southeast of Driftwood Canyon Provincial Park.

Cladistic analysis of the Dysagrionidae

Analysis 3, the phylogeny of Dysagrionidae, produced a single MPT (Fig. 65). We find high support for the supposition that the Paleocene *Thanetophilosina menatensis* and *Valerea multicellulata* and the Lutetian *cf.* Dysagrionidae Genus and species A (Petrulevičius *et al*. 2008) belong to the Dysagrionidae. The tree indicates minimal substructure among the genera, except for *Okanagrion* and *Valerea* as sister taxa, which has moderate support.

There is low support for any other relationships within the family, presumably due to low variation among characters scored and the incomplete nature of some of the fossils (Appendix B).

The genera *Petrolestes* and *Congqingia* were not recovered as sister taxa, suggesting that the Petrolestinae and, therefore, also the Dysagrioninae are invalid. However, support for their separation is low, and so we retain recognition of these subfamilies, pending higher resolution using more complete specimens in future analyses.

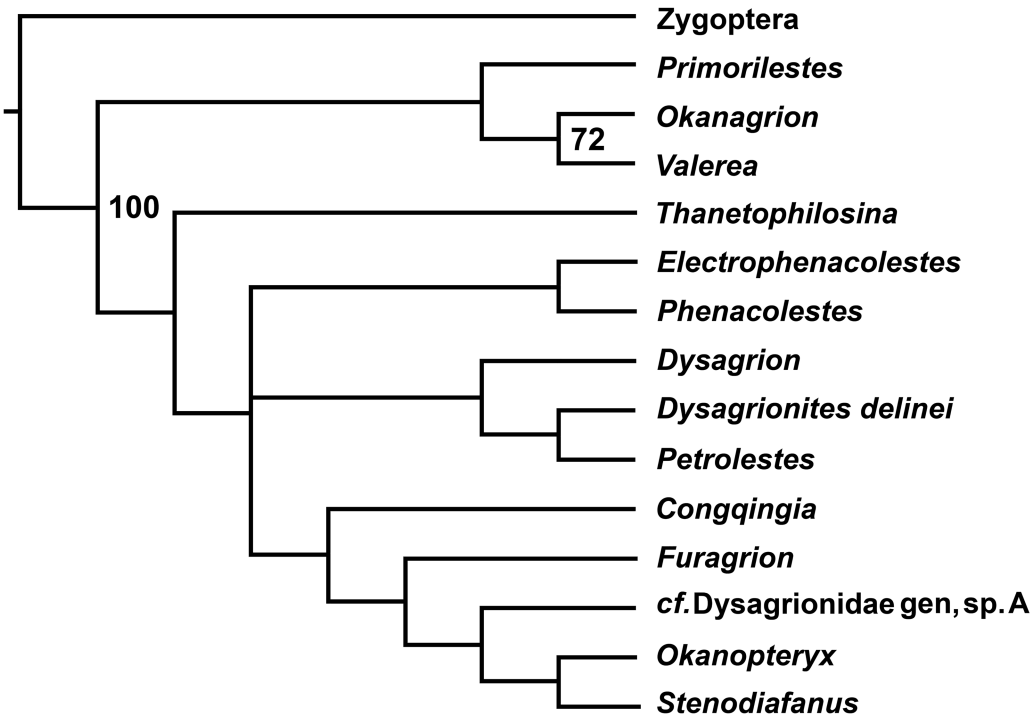

FIGURE 65. Tree resulting from parsimony-based analyses for Analysis 3 (phylogeny of Dysagrionidae). One single most-parsimonious tree (MPT) based on 23 continuous and 79 discrete characters. Symmetrical resampling values ≥70 are labelled at the nodes.

Cephalozygoptera *incertae sedis*
Fig. 71.

Material. GSC 141099 (collector number SBA-423) (Fig. 71A), collected at the McAbee Hoodoo Face beds, Geological Survey of Canada locality code V-016800, by SBA, 7.vii.2000, fragment of the apical region, figured by Archibald (2007) and listed by Archibald *et al*. (2010), in Geological Survey of Canada collections; SR 15-001-004.1 (Figs. 10J, 59E), collected at Republic A0307 by Liam Milliken, 25.iv.2015, a portion of the proximal posterior of a wing including the quadrangle, infuscate at least distally, probably throughout, in the Stonerose Interpretive Center collections; SRUI 09-96-91 (Fig. 71C), collected at Republic A0307 by Madilane Perry, 18.iv.2009, fragment of wing base, housed in the Stonerose Interpretive Center collections; SR 14-003-004, collected at Republic B4131 by Ed Prophet, 28.vi.2014, complete, but wings overlapping and impossible to separate, in the Stonerose Interpretive Center collections.

Description of SR 14-003-004. Probable female specimen (Figs. 10J, 59E), slender, rather well preserved in lateral aspect, head in dorsal aspect; abdomen distal to middle of segment 5 missing. Head (Figure 10J, Table 1) somewhat damaged, especially the left eye; in dorsal view estimated at about 4.1 mm across eyes at widest point; approximate length from anterior edge of antefrons to posterior of occiput about 2.0 mm; at level of hind ocelli distance between medial margins of eyes about 1.3 mm, width of eye about 1.4 mm, length 2.3 mm. Thorax: dorsally the pleura are strongly skewed posteriorly, not damaged or distorted, length of middorsal carina (medial margin of mesepisternum) 5.0 mm; prothorax laterally about 1.5 mm long. Wings hyaline (but apical portions not preserved). Legs slender, metafemur 6.2 mm long, metatibia 6.2 mm, metatarsus 2.3 (claw 0.5 mm long); leg setae relatively fine, at least some on femora and tibiae about 0.7-0.8 mm long and set about the same distance apart. Abdomen slender, no secondary male genitalia evident on venter of segment 2; segments 1 to 3 measure 1.7 mm, 2.8 mm, 6.0 mm long (the last about 1.7 mm wide).

Discussion. The head shape combined with the general wing shapes and gracile body place SR 14-003-004 in the Cephalozygoptera. It could be a species of *Okanopteryx* by its general wing shape, although if so, a new species by its hyaline wings lacking spots or fascia throughout their preserved portions. It could be *Stenodiafanus westersi-*

dei, or a new species of that genus. GSC 141099 is most likely a species of *Okanagrion* by the dense venation and by all main veins linear to their terminations on the margin. The shape of the quadrangle and the anterior anal vein joining CuP distal to the petiole in SR 15-001-004.1 agrees with the Cephalozygoptera. SRUI 09-96-91 is likely Cephalozygoptera by its agreement with species described here.

Possible Cephalozygoptera

Whetwhetaksidae Archibald & Cannings, new family

Figs. 66–70.

Diagnosis. Most easily separated from all other Cephalozygoptera and Zygoptera families by 1, distinctively long pterostigma: length about ten times width (roughly, where known), nodus to base of pterostigma 55–60% of nodus to apex; and from all Cephalozygoptera and all Zygoptera except the extant *Heliocharis amazona* (Dicteriadidae) and some Paleogene Euphaeidae by 2, arculus just distal to Ax1, closer to it than to Ax2. Differs further from Sieblosiidae by: 3, oblique vein O absent [present]; 4, nodal, subnodal crossveins oblique [usually nearly vertical, sometimes slightly oblique or reversed obliquity]; 5, base of RP2 close to nodus [more distal]; 6, CuA terminates at margin over half wing length [notably shorter, longest *Parastenolestes oligocenicus* Nel & Paicheler, under half wing length]; 7, MA close to, subparallel with RP3-4 to margin [subparallel with MP]; 8, MA, MP diverge to margin [remain close]; 9, MP, CuA remain subparallel to margin [widely diverge]; 10, base to nodus about 40% wing length, minimum about 38% [maximum about 35% where measurable]. Differs further from Dysagrionidae by: 4 [usually like Whetwhetaksidae, but *Dysagrion* subnodal crossvein reverse obliquity]; 7–9, [varies], 10, [*Dysagrion packardii*, about 42%, *Petrolestes hendersoni*, about 42%, the rest about 36–25%]; 11, origin of IR2 in middle third between arculus, nodus [at subnodus in Dysagrioninae, but as in Whetwhetaksidae, in Petrolestinae].

Type and included genera. *Whetwhetaksa*.

Description. As for its only genus, see below.

Etymology. The family name is formed from that of its type and only genus, *Whetwhetaksa*.

Range and age. Republic localities B4131 and A0307B of the Tom Thumb Tuff Member of the Klondike Mountain Formation; latest Ypresian.

Discussion. Such an extremely long pterostigma is never found in the Zygoptera to our knowledge, but is matched by some Petaluridae (Anisoptera).

The position of the arculus closer to, immediately distal to Ax1 is remarkable. This condition is found in the Anisozygoptera and Anisoptera, but in the Zygoptera only in the South American *H. amazona*, which otherwise differs strongly in many ways and a few Paleogene Euphaeidae (see above) which also strongly differ. In all other Zygoptera it is aligned with, slightly proximal to, or slightly to clearly distal to Ax2 (Bechly 1996; Fleck *et al*. 2004).

In SR 06-01-36, the subcosta appears to cross through the nodus, which is characteristic of the Sieblosiidae (see, *e.g*., Nel & Fleck 2012, their Fig. 3). This is not present in any other specimen of *Whetwhetaksa*, and it could be a crossvein adventitiously positioned between the costa and nodus in this specimen and not the subcosta.

We tentatively associate the Whetwhetaksidae with the Cephalozygoptera by the many similarities of their wings (see description of the suborder, above). The wings of Whetwhetaksidae are more like those of the Cephalozygoptera than any Zygoptera, but await confirmation of this relationship by the discovery of a more complete fossil that includes the head.

Whetwhetaksa Archibald & Cannings, new genus

Figs. 66–70.

Diagnosis. As for family.

Type species. *Whetwhetaksa millerae*.

Description. With the character states of its only species, below.

Etymology. The genus name is formed from the word in the language of the Colville Indian tribe xʷətxʷətaqs, meaning odonate, pronounced "*whetwhetaks*". The Republic site where the only known fossils of this family have

been found is on the traditional land of the Colville Indian Tribe, immediately north of the current Colville Reserve. Gender, feminine.

Range and age. Republic localities B4131 and A0307B of the Tom Thumb Tuff Member of the Klondike Mountain Formation; latest Ypresian.

Whetwhetaksa millerae Archibald & Cannings, new species

Fig. 66–70.

Diagnosis. As for genus and family.

Type and additional material. All are isolated wings. *Holotype*: SR 06-01-38 (Fig. 66): Republic B4131 collected by Gregg Wilson, 13.vi.2005; *paratype 1*: SR 10-36-10 (Fig. 67), Republic B4131, collected by Shannon Miller, June.vi.2010; *paratype 2*: SRUI 99-98-34 (Fig. 68), Republic B4131 collected by Shannon Miller, 6.x.2011. Additional material: SR 93-11-01 (Fig. 69), Republic A0307B collected by unknown person, 15.vii.1986; SR 06-01-36 (Fig. 69), collected at Republic B4131 by Gregg Wilson, 18.vi.2004; SR 05-11-01AB (Fig. 70), Republic A0307 collected by Peg Johnson, 11.vi.2005; SR 10-14-19 (Fig. 70), Republic B4131 collected by Stonerose staff, 23.iv.2010, a wing fragment of the anterior mid-wing. All specimens are housed in the collections of the Stonerose Interpretive Center.

Description. Holotype, SR 06-01-38, wing (Fig. 66). Mostly complete with small sections obscured, missing. Length 31.8 mm, arculus to apex: 27.9 mm, nodus to apex: 20.4 mm, origin of RP2 to apex: 17.5 mm, arculus to base of pterostigma: estimated 19.5 mm, nodus to base of pterostigma: estimated 11.8 mm, nodus at 44% wing length, width 8 mm. Infuscate in proximal half (in well-preserved portions), apical half hyaline (sex unknown). Pterostigma dark, estimated 5–5.5 mm long, eight–nine times longer than wide (distal end damaged), no oblique brace vein, subtending seven cells. Preserved crossveins in postnodal, postsubnodal spaces not aligned: 13 postnodal (or portions) preserved (likely five to six? more total); 17 postsubnodal preserved to pterostigma, likely few more total. Two cells wide distal to pterostigma in costal space. RA meets margin at apex. IR1 origin not preserved; RP2 origin 3.5 cells of RP1-2–IR2 space distal to subnodus; IR2 origin about 3/5 arculus to nodus; IR2 close to linear, only slightly zigzagged in preserved portions. RP3-4 origin >2/5 distance arculus to nodus. Arculus close to, just distal to Ax1. No accessory antenodal crossveins. Ax0 not detected. No crossvein O. Quadrangle about three times longer than wide, distal side twice length of proximal, anterior side about 5/6 length of posterior. Nodal, subnodal crossveins with normal obliquity. MA zigzags distal to about mid-wing (region poorly preserved); MP apparently linear from quadrangle to terminus (but distal portion poorly preserved), gently curved. CuA long, ends on margin just distal to mid-wing (about mid-way arculus to apex), well distal to base of RP2. CuA slightly zigzagged distal to level of quadrangle, more so at terminus (but much of distal half poorly or not preserved); CuA–A space partly missing, two cells wide preserved, at least three, perhaps four total.

Paratype 1, SR 10-36-10, wing (Fig. 67). Mostly whole, missing the proximal posterior region and a region of the posterior-mid region in the proximal part of the apical third. Length 30.5 mm (proximal-most part missing); arculus to apex: 26.8 mm; nodus to apex: 18.8 mm; origin of RP2 to apex: 16.5 mm; arculus to base of pterostigma: 18.1 mm; nodus to base of pterostigma: 10.1 mm; nodus at 40% wing length; width 8.0 mm. Colouration well-preserved (sex unknown): all preserved portions of proximal half (base to postnodal crossvein 6) darkly infuscate, apical half very lightly infuscate. Pterostigma dark, distal end oblique, 5.3 mm long, length about 11.5 times width, subtends 7.5 cells. No oblique brace vein; 13 crossveins preserved in postnodal space (probably one more), 17 in postsubnodal space to pterostigma (total), only one-two aligned. Two cells wide in costal space distal to pterostigma. RP1 meets margin at apex. RP1 space becomes two cells wide in level of pterostigma (region poorly preserved); IR1 origin slightly zigzagged, six cells distal to origin of RP2; IR1 two cells wide distal to level of base of pterostigma (region poorly preserved); RP2 origin 2.5 RP1-2–IR2 space cells distal to subnodus. IR2 origin about 3/5 distance arculus to subnodus; RP3-4 origin >2/5 distance arculus to nodus. Arculus close to, distal to Ax1. Ax0 not detected. No accessory antenodal crossvein detected (but region where one might be not preserved). No crossvein O. Quadrangle region not preserved. Nodal crossvein, subnodus angled as in holotype. MA linear in all preserved portions (some distal to mid-wing not preserved); MP preserved distal to between levels of origins of RP3-4, IR2: linear to terminus. CuA linear, deeply curved, wide; CuA–A space six cells wide not at widest (maybe one–two more total?).

Paratype 2, SR 99-98-34, wing (Fig. 68). Missing the posterior portion except in the apical quarter. Length 35.8 mm (proximal-most part missing), nodus to apex: 20.7 mm, origin of RP2 to apex: 19.5 mm, nodus to base of pterostigma: 12.4 mm; nodus at 43% wing length; width unknown by preservation. Colouration well-preserved (sex unknown): all preserved regions of proximal half (base to postnodal crossvein 6) darkly infuscate, apical half lightly infuscate. Pterostigma anterior, posterior margins oblique, posterior more so, length 5.4 mm, length about 9.5 times width, subtends eight cells. No oblique brace vein; nodal crossvein, subnodus oblique as in holotype, 18 crossveins in postnodal space (total), 19 postsubnodal space (probably one more), one-two aligned. Two cells wide in most of costal space distal to pterostigma. RA meets margin at apex. RP1–IR1 space becomes two cells wide at level of mid-pterostigma. IR1 origin not preserved, slightly zigzagged until near margin, then breaks up in strong zigzag. IR1–RP2 space becomes two cells wide same level as RP1–IR1 space. RP2 origin close to subnodus, about one cell distant. IR2 origin not preserved, but far proximal to subnodus (could be as in holotype); origin, most of RP3-4 not preserved); arculus, quadrangle not preserved; Ax0 not detected; one accessory antenodal crossvein; region where crossvein O might be not preserved; nothing proximal to fragments of RP3-4 preserved.

Additional material.

SR 93-11-01, wing (Fig. 69). Anterior mid-portion. Length: nodus to base of pterostigma: 11.3 mm. Colouration difficult to assess by preservation, possibly like holotype (sex unknown); 16 crossveins preserved in postnodal space (probably one more total), 17 in postsubnodal space (total), only one–two aligned. IR1 origin seven cells RP1–RP2 space distal to origin of RP2; RP2 origin 2.5 cells RP1-2–IR2 space distal to subnodus; arculus not preserved, but IR2, RP3-4 origins appear the same position proximal to subnodus as in holotype, paratypes 1, 2; no crossvein O (in region preserved); MA, MP, CuA linear in all portions preserved; little of CuA–A space preserved, at least three cells wide.

SR 06-01-36, wing (Fig. 69). Much of the basal half (unknown if fore- or hind) missing proximal-most portion. Colouration difficult to determine by preservation (sex unknown). Few crossveins preserved in postnodal, postsubnodal spaces, none aligned. Subcosta may cross nodus (but could be adventitious crossvein between costa, nodus?). IR2, RP3-4 origins as in holotype, paratypes, roughly mid-way between arculus, subnodus. Nodal, subnodal crossveins of normal obliquity. Arculus far-proximal to Ax2 as in holotype, paratypes (Ax1 not preserved). Quadrangle similar to holotype. All main vein portions preserved (proximal portions of RP1-2, IR2, RP3-4, MA, MP, CuA) linear. CuA–A space with four cells wide preserved (one or more further complete?).

SR 05-11-01AB, wing (Fig. 70). Mostly complete, very crushed, torn, apical region bent. Length: arculus to base of pterostigma: 23? mm, nodus to base of pterostigma: 11.3 mm. Colouration (sex unknown): proximal half apparently darkly infuscate throughout as preserved, apical half apparently very lightly infuscate as preserved. Pterostigma little-preserved; 20 crossveins preserved in postnodal space (likely one–two? more), 15 in postsubnodal space, likely many more?, one–two aligned. Arculus closer to, just distal to Ax1. Ax0 detected at wing base. One accessory antenodal crossvein detected. Crossvein O not detected. Major veins very broken up, crimpled; all preserved portions linear. CuA–A space with four cells at widest (level of nodus), perhaps similar to SR 06-01-36.

SR 10-14-19, wing (Fig. 70). Small anterior mid-portion. Proximal portion darkly infuscate as in paratypes 1, 2, apical portion hyaline as preserved (sex unknown). Nodus, subnodus angled as in other specimens. Origins of RP2, IR2, crossvenation in postnodal, subnodal spaces as in holotype.

Etymology. The specific epithet is a patronymic formed from the surname of Shannon Miller, who found paratypes 1 and 2.

Range and age. Republic localities B4131 and A0307B of the Tom Thumb Tuff Member of the Klondike Mountain Formation; latest Ypresian.

Discussion. There is notable variation among these specimens in the length of the antenodal space, the presence of an accessory antenodal crossvein, and the width of the CuA–A space. SR 99-98-34 has a longer antenodal

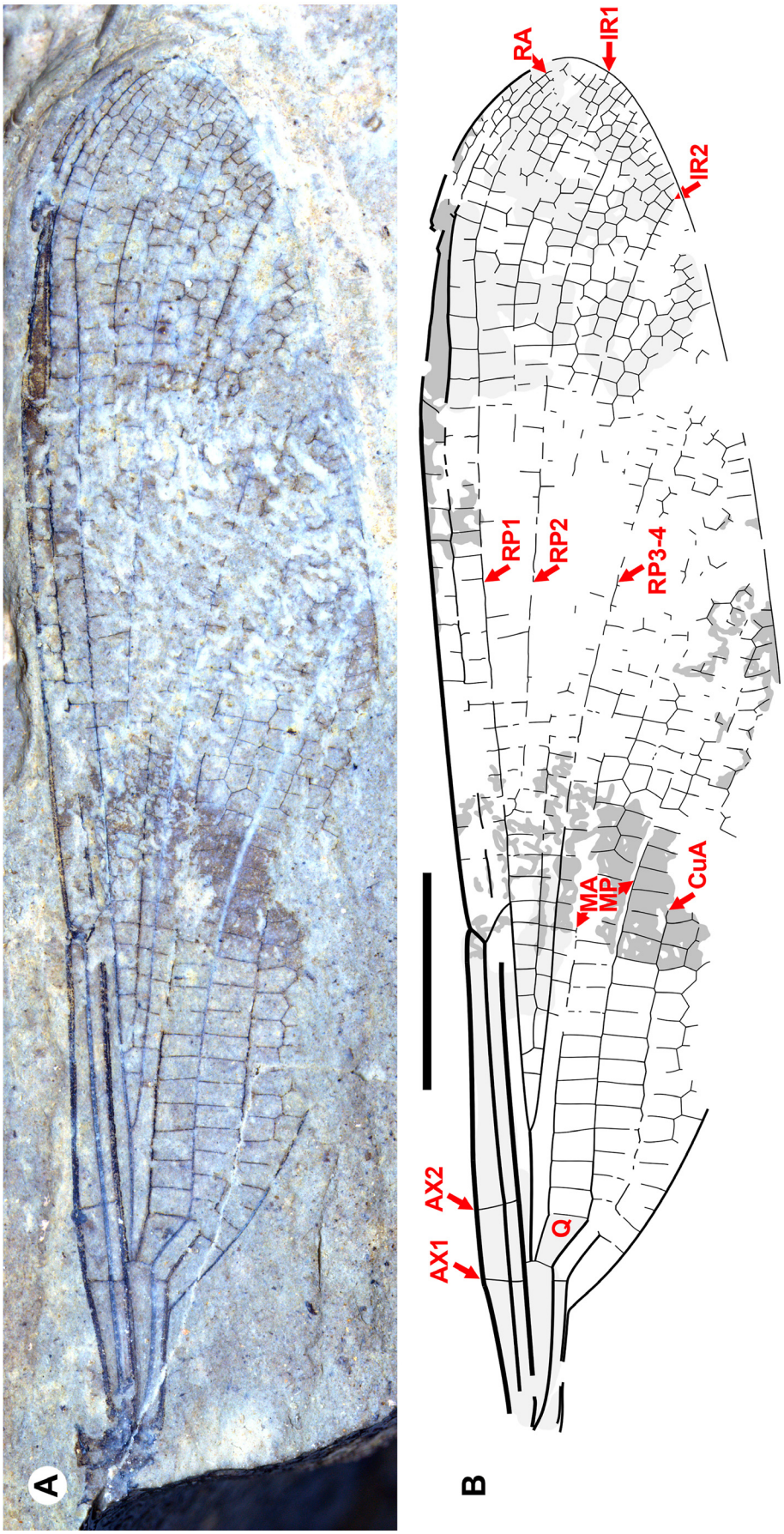

FIGURE 66. *Whetwhetaksa millerae* holotype, SR 06-01-38. A, photograph; B, drawing. Both to scale, 5 mm.

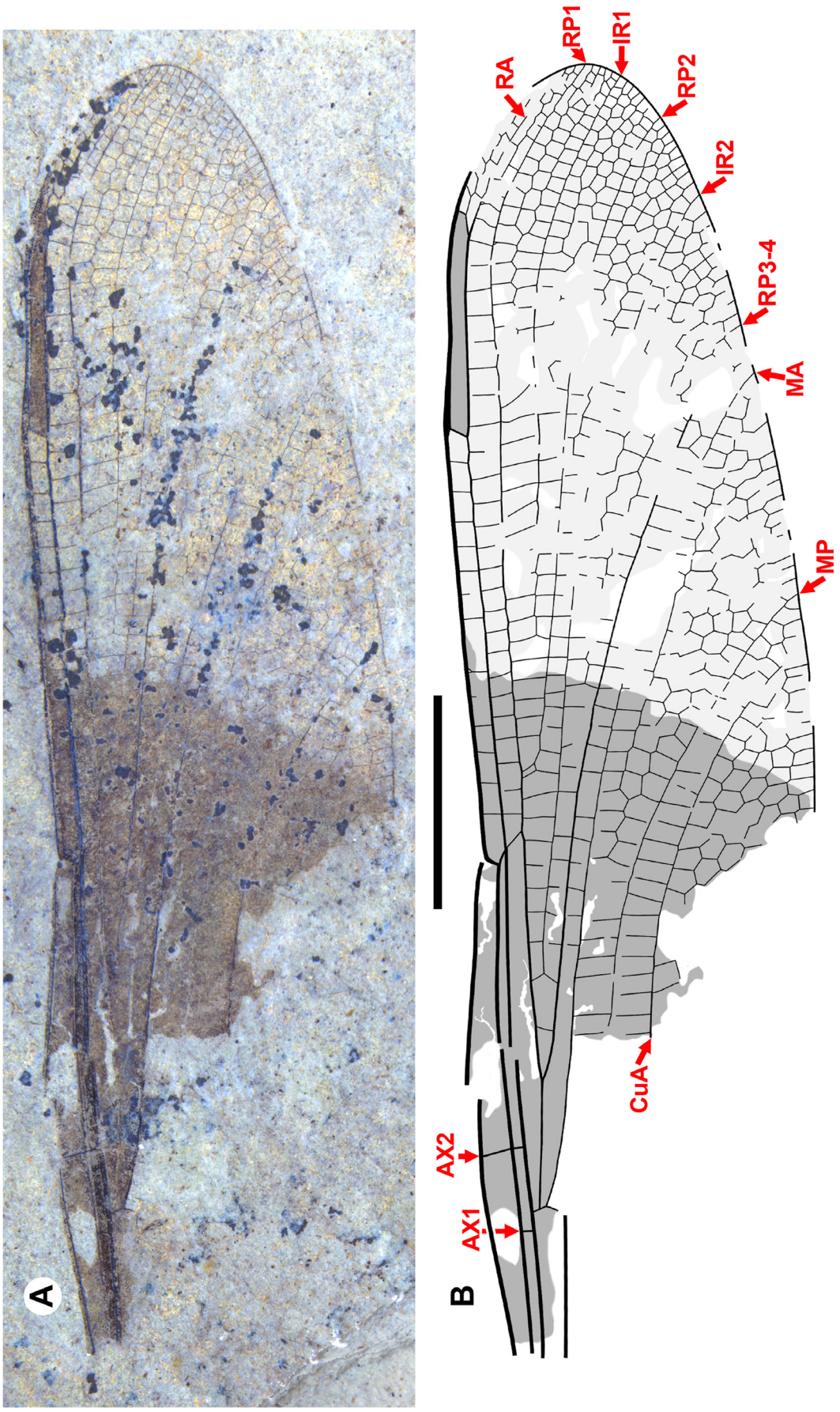

FIGURE 67. *Whetwhetaksa millerae* paratype 1, SR 10-36-10. A, photograph; B, drawing. Both to scale.

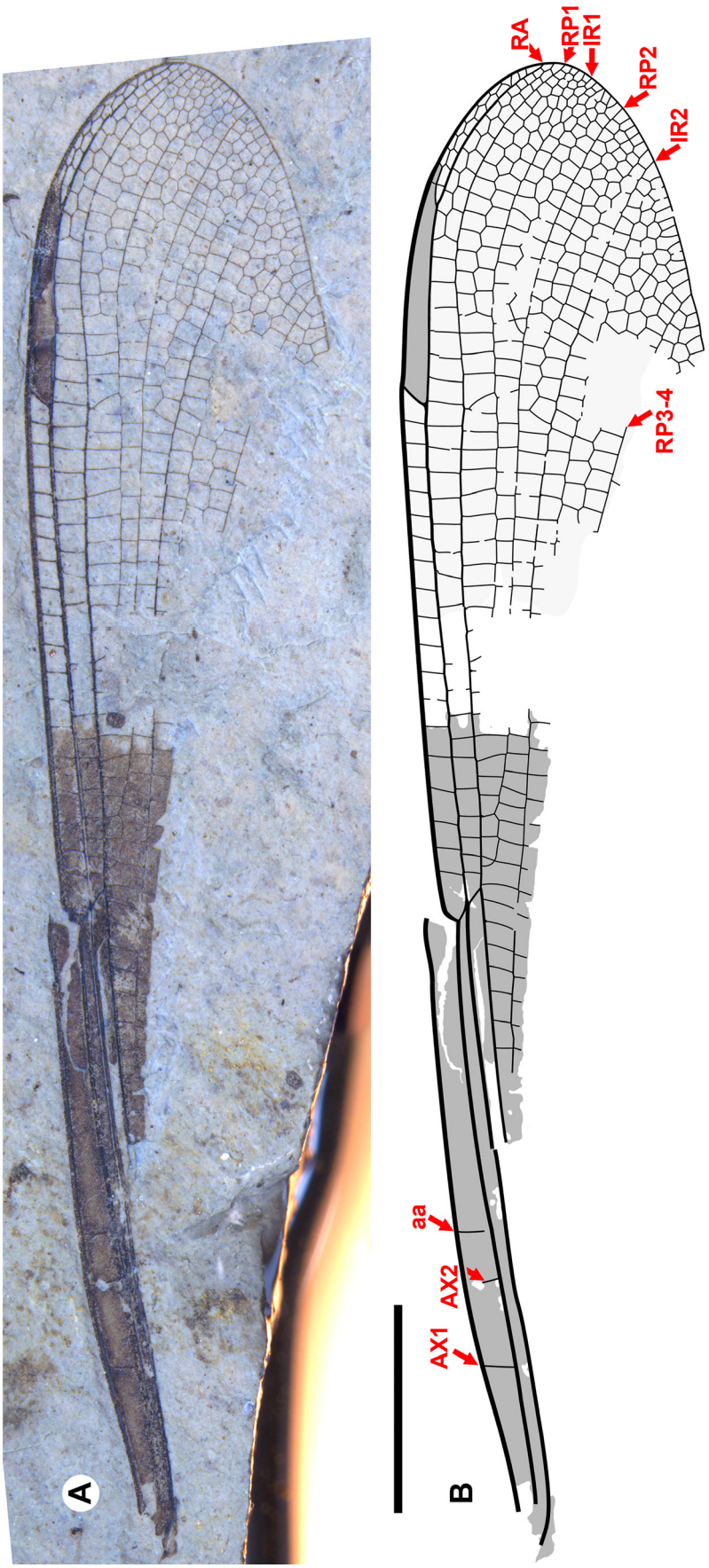

FIGURE 68. *Whetwhetaksa millerae* paratype 2, SRUI 99-98-34. A, photograph; B, drawing. Both to scale; aa, accessory antenodal crossvein.

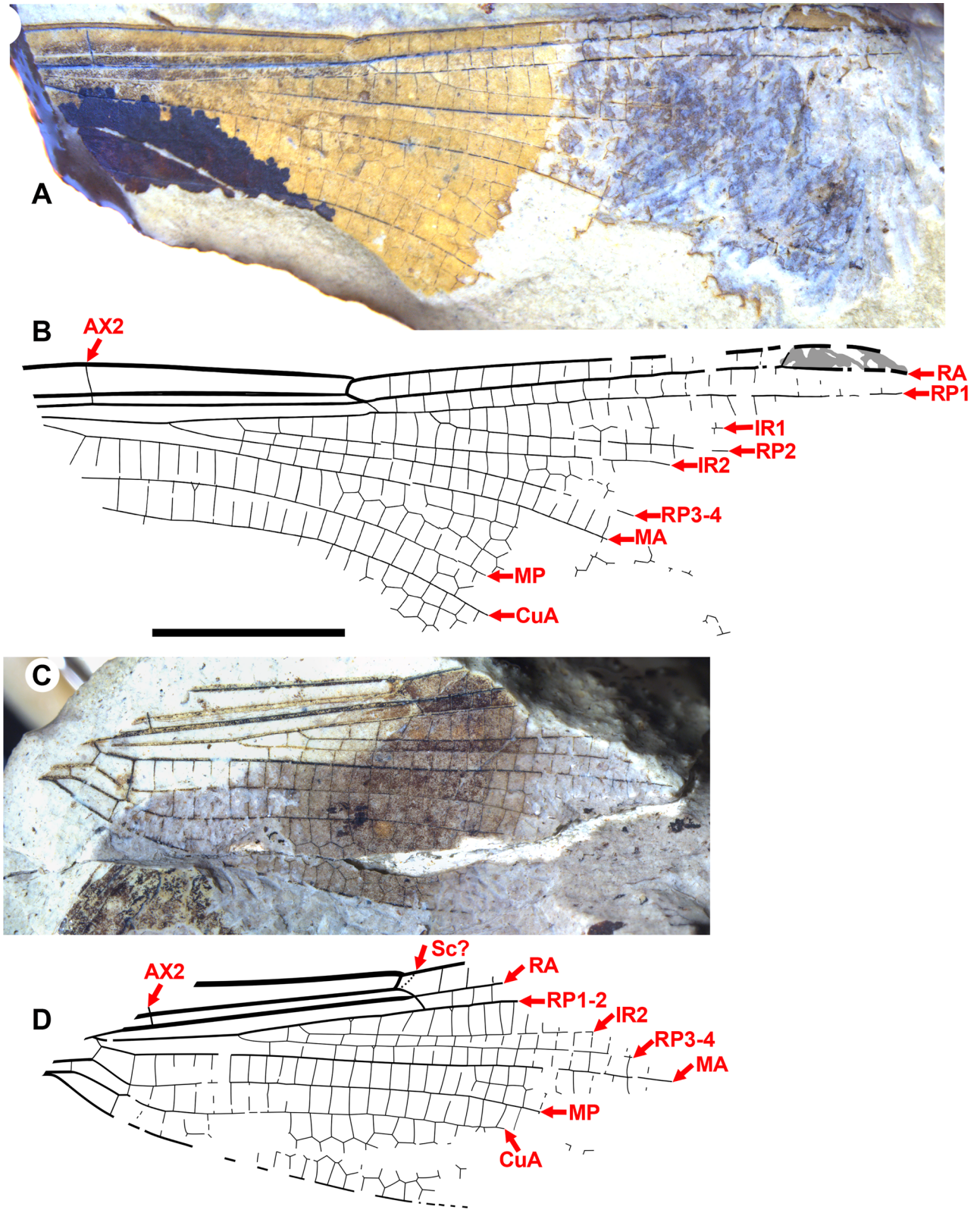

FIGURE 69. *Whetwhetaksa millerae* additional material. SR 93-11-01: A, photograph; B, drawing; SR 06-01-36: C, photograph; D, drawing. All to scale, 5 mm.

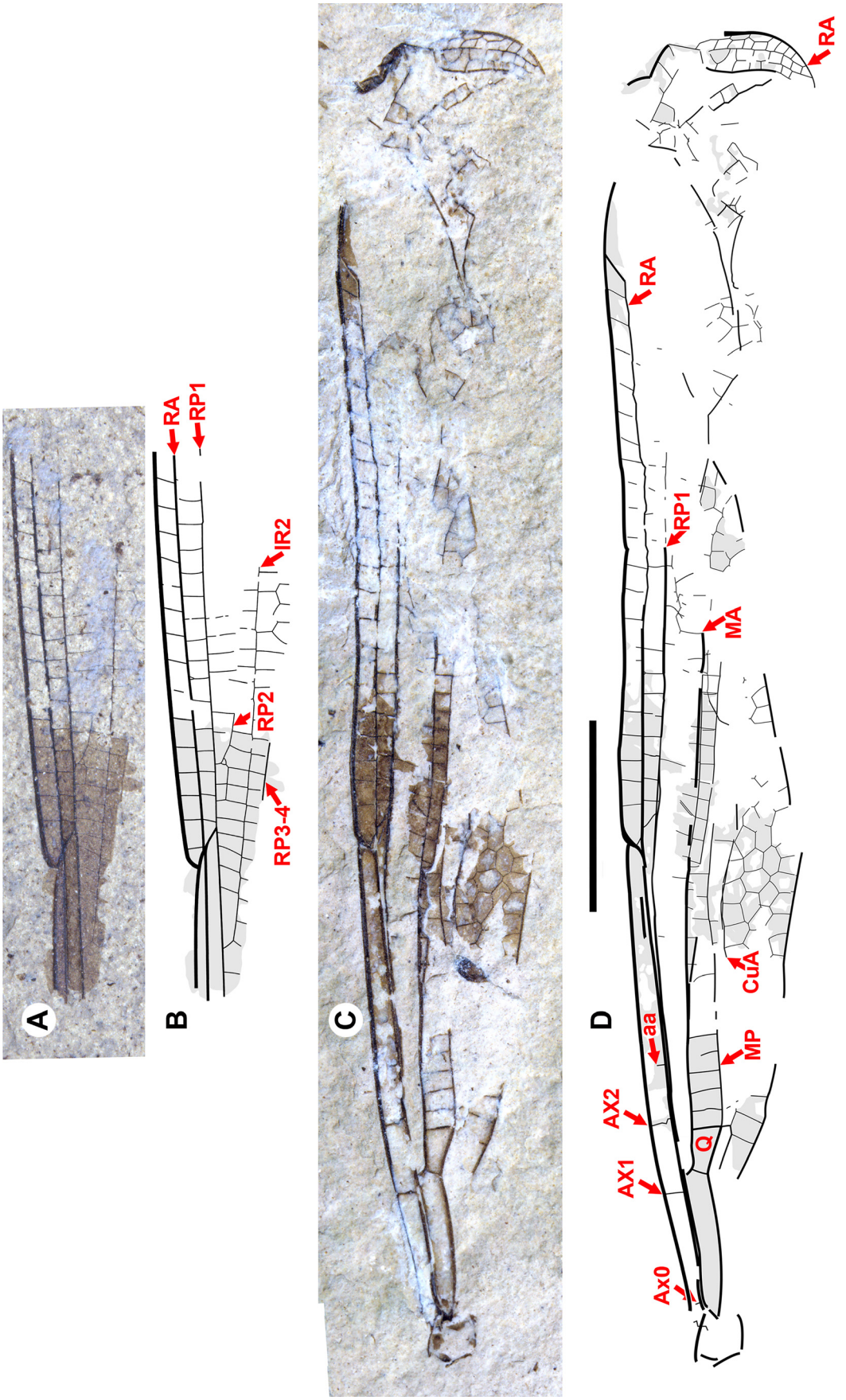

FIGURE 70. *Whetwhetaksa millerae*, additional material. SR 10-14-19: A, photograph; B, drawing; SR 05-11-01: C, photograph; D, drawing. All to scale, 5 mm.

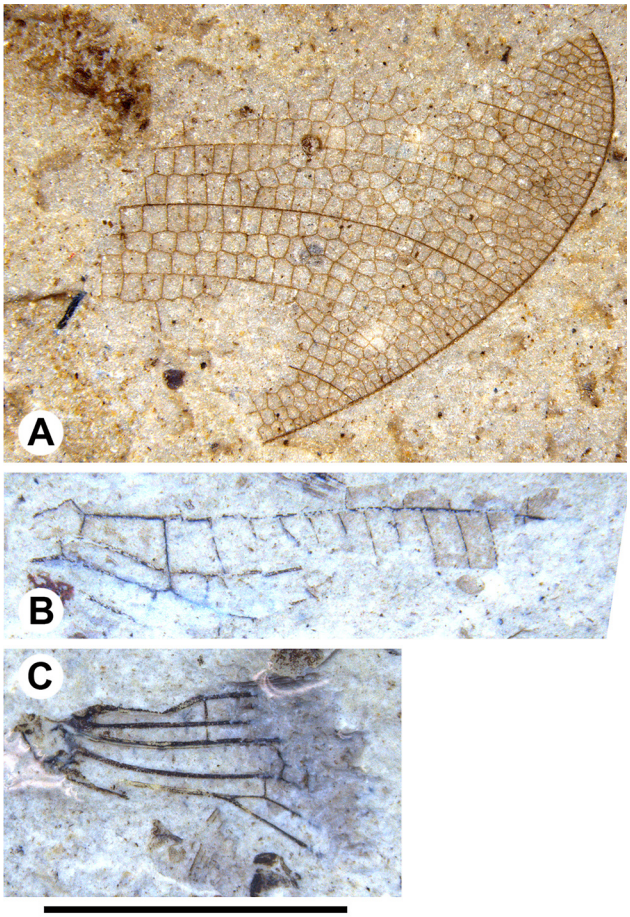

FIGURE 71. Cephalozygoptera *incertae sedis*. A, GSC 141099; B, SR 15-001-004.1; C, SRUI 09-96-91. All to scale, 5 mm. space measured Ax1 to nodus of 11 mm. In SR 10-36-10 this is 8.8 mm; in SR 06-01-38, 8.0 mm; and in SR 05-11-01, 9.0 mm. SR 05-11-01, SR 99-98-34 each possess a single accessory antenodal crossvein. In SR 10-36-10 and SR 10-14-19, this is not determinable by preservation, whereas SR 06-01-38, SR 06-01-36, and SR 93-11-01 definitely do not have this crossvein. SR 10-36-10 has a much wider CuA–A space (at least six cells deep; probably more: the widest part is not preserved), whereas SR 06-01-38, SR 06-01-36 and SR 05-11-01 apparently have a maximum of four cells deep (others not known by preservation). Forewing/hind wing differences and sexual dimorphism might explain some or all of this variation; more complete specimens are needed to evaluate these possibilities and so at present we refrain from assuming more than one species here.

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APPENDIX A. Character descriptions. (F), forewing; (H), hind wing; cv, crossvein. Characters with references are as defined in those sources and character states confirmed from illustrations in them; all others were scored from specimens.

Continuous characters

1 (F) Number of Ax in C–ScP space.
2 (H) Number of Ax in C–ScP space.
3 (F) Number of Ax in ScP–RA space.
4 (F) Angle of nodal cv between costa and ScP compared to costa towards base of wing.
5 (H) Angle of nodal cv between costa and ScP compared to costa towards base of wing.
6 (F) Angle of nodal cv between ScP and RA compared to costa towards base of wing.
7 (H) Angle of nodal cv between ScP and RA compared to costa towards base of wing.
8 (F) Angle of subnodus to RA towards base of wing.
9 (H) Angle of subnodus to RA towards base of wing.
10 (F) Number of postnodal crossveins (in C–RA space between nodus and pterostigma).
11 (H) Number of para-anal cells.
12 (F) Number of cells in C–RA space pterostigma to termination of RA.
13 (H) Number of cells in C–RA space pterostigma to termination of RA.
14 (F) Number of cells between RP3-4 and MA at wing margin.
15 (H) Number of cells between RP3-4 and MA at wing margin.
16 (F) Ratio of pterostigma length vs. width.
17 (H) Ratio of pterostigma length vs. width.
18 (F) Number of cells wide in costal space at distal end of pterostigma.
19 (H) Number of cells wide in costal space at distal end of pterostigma.
20 (F) Maximum number of cells wide in CuA–A space.
21 (H) Maximum number of cells wide in CuA–A space.
22 (F) Number of cells subtending pterostigma.
23 (H) Number of cells subtending pterostigma.

Discrete characters

Head characters

24 Shape of frons: (0) smoothly rounded in profile; (1) angulate; (2) flattened; (3) grossly enlarged, forming most of the head anterior to the eyes (Rehn 2003).
25 Shape of vertex: (0) transverse protuberance; (1) small protuberance; (2) large transverse oriented plate; (3) flat; (4) two protuberances or horn-like structures; (5) conical (Blanke *et al*. 2013).
26 Ocelli: (0) forming a close equilateral triangle on the same plane; (1) not in equilateral triangle, or if so, not close, not on the same plane (modified from Fleck *et al*. 2004).
27 Antero-dorsal surface of the occiput distinctly bulged and with two posterior tubercles: (0) present; (1) absent (Nel *et al*. 1998).
28 Eyes: (0) separated; (1) touching (Kalkman 2006).
29 Distance between eyes: (0) less than their width; (1) greater than their width; (2) none, touching (Rehn 2003).
30 Shape of head from the front: (0) globular; (1) transversely elongate (Rehn 2003).
31 Head width: (0) not very wide, about twice as wide as long; (1) very wide, about three times wide as long (Kalkman 2006).

Thoracic characters

32 Interpleural suture: (0) complete; (1) broken in the middle with distinct upper and lower halves; (2) upper portion of suture absent, and only a vestigial remainder below the metathoracic spiracle (Rehn 2003).
33 Thorax: (0) not oblique; (1) oblique (Rehn 2003).

Abdominal characters

34 Paraproct: (0) vestigial; (1) well developed (Pessacq 2008).

35 Epiproct: (0) present; (1) absent (Rehn 2003).

Wing characters

36 (F) Ax0 is prolonged by a cross-vein between ScP and RA: (0) present; (1) absent (Bechly 1996).

37 (F) Ax2: (0) as strong as Ax1; (1) weaker than Ax1 (Fleck & Nel 2003).

38 (H) Ax2: (0) as strong as Ax1; (1) weaker than Ax1 (Fleck & Nel 2003).

39 (F) Secondary (accessory) antenodal crossveins: (0) all distinctly thinner than primary antenodal crossveins; (1) more than half are as thick as primary crossveins; (2) all as thick as the primary crossveins (Jarzembowski & Nel 1996).

40 (H) Secondary (accessory) antenodal crossveins: (0) all distinctly thinner than primary antenodal crossveins; (1) more than half are as thick as primary crossveins; (2) all as thick as the primary crossveins (Jarzembowski & Nel 1996).

41 (F) Antenodal crossveins (Ax): (0) many (at least five, but usually ten or more) present in C–Sc space and Sc–R space; (1) many present in C–Sc space only; (2) only two in C–Sc space and Sc-R space (Rehn 2003).

42 (H) Antenodal crossveins (Ax): (0) many (at least five, but usually ten or more) present in C–Sc space and Sc–R space; (1) many present in C–Sc space only; (2) only two in each C–Sc space and Sc–R space (Rehn 2003).

43 (H) Crossveins in the C–RA space between AX1 and AX2 present and: (0) complete; (1) incomplete (Nel *et al*. 1996).

44 Antenodal crossveins: (0) more in forewing than hind wing (by two or more); (1) or almost as numerous in forewing as hind wing (one more or less); (2) more in the hind wing than forewing (by two or more) (Jarzembowski & Nel 1996).

45 (F) Antenodal crossveins (Ax): (0) unaligned; (1) aligned (Rehn 2003).

46 (F) Secondary (accessory) antenodal and antesubnodal crossveins: (0) not aligned (0%); (1) more or less aligned (1–50%); (2) nearly all aligned (50–99%); (3) all aligned (100%) (Bechly *et al*. 1998).

47 (F) Rows of cells between Ax2 and nodus (in C–ScP space): (0) one; (1) two; (2) three (Fleck & Nel 2003).

48 (F) Antenodal area: (0) not shorter than postnodal area (+100%); (1) slightly shorter (80-99%); (2) distinctly shorter (<80%) (Bechly *et al*. 1998).

49 (H) Antenodal area: (0) not shorter than postnodal area (+100%); (1) slightly shorter (80-99%); (2) distinctly shorter (<80%) (Bechly *et al*. 1998).

50 (F) Junction of costa and ScP: (0) clearly acute; (1) ScP turned forward to meet costa; (2) ScP turned sharply forward to meet costa at nearly a right angle (Rehn 2003).

51 (F) Angle of nodal cv between costa and ScP compared to costa towards base of wing: (0) <40°; (1) 40°–60°; (2) 60°–85°; (3) 85°–95°; (4) >95° (Fleck *et al*. 2003).

52 (H) Angle of nodal cv between costa and ScP compared to costa towards base of wing: (0) <40°; (1) 40°–60°; (2) 60°–85°; (3) 85°–95°; (4) >95° (Fleck *et al*. 2003).

53 (F) Angle of nodal cv between ScP and RA compared to costa towards base of wing: (0) <85°; (1) 85°–95°; (2) 95°–120°; (3) 120°–140°; (4) >140° (Fleck *et al*. 2003).

54 (F) Postnodal crossveins between RA–RP1: (0) present; (1) absent (Fleck & Nel 2003).

55 (F) Number of postnodal Ax between C-RA until pterostigma: (0) <5; (1) 5–9; (2) 10–14; (3) 15–19; (4) >19.

56 (F) Postnodal crossveins: (0) aligned in C-RA and RA–RP spaces only; (1) aligned in a transverse series (running across; at right angles to longitudinal axis) to beyond IR2 (Rehn 2003).

57 (F) Proportion of aligned postnodal crossveins in C–RA and RA–RP spaces: (0) 0%; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%.

58 (F) Distal side of pterostigma: (0) well-defined and strong; (1) not well-defined or absent (Fleck & Nel 2003).

59 (F) Pterostigma brace: (0) straight; (1) curved and arched (Fleck & Nel 2003).

60 (F) Discoidal cells: (0) trapezoidal; (1) rectangular (Kalkman 2006).

61 (F) Anterior border of discoidal cell: (0) less than twice length of distal border; (1) twice; (2) three times (Kalkman 2006).

62 (H) Distal portion of AA in cubito-anal area: (0) well defined, as long as longitudinal vein; (1) not well defined, strongly zigzagged; (2) appears as a cross-vein (Huguet *et al*. 2002).

63 (F) AA at contact with CuP: (0) angled; (1) linear (Nel *et al*. 1993).

64 (H) AA at contact with CuP: (0) angled; (1) linear (Nel *et al*. 1993).

65 (H) Para-anal cells: (0) two; (1) three; (2) four.

66 (F) CuP crosses submedian space: (0) at or proximal to Ax1; (1) distal to Ax1 (Nel *et al*. 1996).

67 (F) CuA and CuP: (0) closely parallel; (1) not closely parallel (Nel *et al*. 2001).

68 (F) Row(s) of cells between CuA and CuP: (0) one; (1) two or more (Nel *et al*. 2001).

69 (F) CuA direction: (0) zigzagged; (1) linear (Nel *et al*. 2001).

70 (H) CuA direction: (0) zigzagged; (1) linear (Nel *et al*. 2001).
71 (F) MA: (0) zigzagged; (1) linear (Fleck & Nel 2003).
72 (H) MA: (0) zigzagged; (1) linear (Fleck & Nel 2003).
73 (F) If MA zigzagged, zigzag beginning: (0) beyond origin of RP2; (1) from opposite or proximal to origin of RP2 (Jarzembowski *et al*. 1998).
74 (F) MA near termination on margin: (0) linear with a distinct curve; (1) linear, not distinctly curved; (2) zigzagged (Lin *et al*. 2002).
75 (H) MA near termination on margin: (0) linear with a distinct curve; (1) linear, not distinctly curved; (2) zigzagged (Lin *et al*. 2002).
76 (F) MA at wing margin: (0) at right angle or nearly so; (1) oblique. (Lin *et al*. 2002)
77 (F) MA ends: (0) beyond origin of IR1; (1) at level of origin of IR1; (2) prior to origin of IR1 (Jarzembowski *et al*. 1998).
78 (F) IR2: (0) linear; (1) zigzagged in its distal part; (2) zigzagged beyond its distal part (Bechly *et al*. 1998, Nel & Jarzembowski 1998).
79 (F) Cells in C–RA space distal to pterostigma: (0) greater than 12; (1) 12 or less (Nel *et al*. 1998).
80 (H) Cells in C–RA space distal to pterostigma: (0) greater than 12; (1) 12 or less (Nel *et al*. 1998).
81 (F) Rows of cells in C–RA space distal to pterostigma: (0) one; (1) two; (2) more than two (Fleck & Nel 2003).
82 (F) RA terminating on wing margin: (0) anterior to apex; (1) posterior apex (Rehn 2003).
83 (F) RP1 terminating on margin: (0) anterior to apex; (1) posterior apex (Rehn 2003).
84 (F) Proximal concave 'supplementary vein' between RP1 and RP2: (0) present; (1) absent (Fleck & Nel 2003).
85 (F) Distal concave 'supplementary vein' between RP1 and RP2: (0) present; (1) absent (Fleck & Nel 2003).
86 (F) Rows of cells subtending pterostigma (*i.e*., between RA and RP1): (0) one; (1) two; (2) more than two (Fleck & Nel 2003).
87 (F) IR1 at wing margin: (0) closer to RP1 than to RP2; (1) equidistant from RP1 and RP2; (2) closer to RP2 than to RP1 (Rehn 2003).
88 (H) IR1 at wing margin: (0) closer to RP1 than to RP2; (1) equidistant from RP1 and RP2; (2) closer to RP2 than to RP1 (Rehn 2003).
89 (F) MA and MP close near posterior wing margin: (0) present; (1) absent (Nel *et al*. 2001).
90 (H) MA and MP close near posterior wing margin: (0) present; (1) absent (Nel *et al*. 2001).
91 (F) MA–MP field, intercalated sectors: (0) present; (1) absent (Rehn 2003).
92 (F) MA–MP field, number of cells separating at termination on margin: (0) one; (1) two; (2) three; (3) four; (4) five; (5) six; (6) seven or more (Rehn 2003).
93 (H) MA–MP field, number of cells separating at termination on margin: (0) one; (1) two; (2) three; (3) four; (4) five; (5) six; (6) seven or more (Rehn 2003).
94 (H) Widest part of the wing: (0) distal of midpoint; (1) proximal of midpoint.
95 (F) Wing colour: (0) present; (1) absent (hyaline).
96 (F) Apical wing colour: (0) present; (1) absent (hyaline).
97 (F) Proximal end of pterostigma meets C at: (0) acute angle; (1) about 90°; (2) obtuse angle.
98 (H) Proximal end of pterostigma meets C at: (0) acute angle; (1) about 90°; (2) obtuse angle.
99 (F) CuA zigzagged at about level of nodus: (0) present; (1) absent.
100 (F) RP3-4 originate: (0) in proximal third between the arculus and subnodus; (1) in middle third; (2) in the distal third.
101 (F) IR2 origin: (0) in the middle third between the arculus and subnodus; (1) very near or at subnodus.
102 (H) IR2 origin: (0) in middle third between the arculus and subnodus; (1) very near or at subnodus.

APPENDIX B. Taxa included in analyses with counts of missing ("?") and inapplicable ("-") characters. Extant taxa in bold font.

Suborder	Family	Genus	species	"?"	"-"	**Total unkn.**	**% unkn.**
	Tarsophlebiidae	*Tarsophlebia*	*T. eximia*	31	2	33	32.4
Zygoptera	?	*Burmadysagrion*	*B. zhangi*	8	5	13	12.7
Zygoptera	?	*Electrodysagrion*	*E. lini*	56	3	59	57.8
Zygoptera	?	*Palaeodysagrion*	*P. cretacicus, P. youlini*	46	2	48	47.1
Anisoptera	list below*			26	3	29	28.4
Anisozygoptera	Burmaphlebiidae, Epiophlebiidae	*Burmaphlebia*, ***Epiophlebia***	*B. reifi*, ***E. superstes***	30	3	33	32.4
Zygoptera	list below†			0	3	3	2.9
Cephalozygoptera	list below‡			1	1	2	2.0
Cephalozygoptera	Dysagrionidae	*Congqingia*	*C. rhora*	10	7	17	16.7
Cephalozygoptera	Dysagrionidae	*Dysagrion*	*D. fredericii, D. lakesii, D. packardii*	21	6	27	26.5
Cephalozygoptera	Dysagrionidae	*Dysagrionites*	*D. delinei*	69	1	70	68.6
Cephalozygoptera	Dysagrionidae	*Electrophenacolestes*	*E. serafini*	61	3	64	62.7
Cephalozygoptera	Dysagrionidae	*Furagrion*	*F. jutlandicus*	44	2	46	45.1
Cephalozygoptera	Dysagrionidae	*Okanagrion*	list below‖**	6	7	13	12.7
Cephalozygoptera	Dysagrionidae	*Okanopteryx*	list below††	28	4	32	31.4
Cephalozygoptera	Dysagrionidae	*Petrolestes*	*P. hendersoni, P. messelensis*	26	5	31	30.4
Cephalozygoptera	Dysagrionidae	*Phenacolestes*	*P. mirandus, P. parallelus*	10	4	14	13.7
Cephalozygoptera	Dysagrionidae	*Primorilestes*	*P. madseni, P. violetae*	48	4	52	51.0
Cephalozygoptera	Dysagrionidae	*Stenodiafanus*	*S. westersidei*	68	1	69	67.6
Cephalozygoptera	Dysagrionidae	list below§		1	1	2	2.0
Cephalozygoptera	Dysagrionidae?	*cf.* Dsyagrioninae gen.	species A	64	0	64	62.7
Cephalozygoptera	Dysagrionidae?	*Thanetophilosina*	*T. menatensis*	59	2	61	59.8
Cephalozygoptera	Dysagrionidae?	*Valerea*	*V. multicellulata*	78	2	80	78.4
Cephalozygoptera	Sieblosiidae	*Germanostenolestes*	*G. lutzi*	42	5	47	46.1
Cephalozygoptera	Sieblosiidae	*Miostenolestes*	*M. zherikhini*	24	5	29	28.4
Cephalozygoptera	Sieblosiidae	*Paraoligolestes*	*P. miocenicus, P. stavropolensis*	23	5	28	27.5
Cephalozygoptera	Sieblosiidae	*Parastenolestes*	*P. oligocenicus*	48	3	51	50.0

.....contiuned on the next page

APPENDIX B. (Continued)

Suborder	Family	Genus	species	"?"	"-"	**Total unkn.**	**% unkn.**
Cephalozygoptera	Sieblosiidae	*Sieblosia*	*S. jucunda*	26	6	32	31.4
Cephalozygoptera	Sieblosiidae	*Stenolestes*	list below‡‡	9	6	15	14.7
Cephalozygoptera	Sieblosiidae	List below[ll]		8	6	14	13.7
Cephalozygoptera	Whetwhetaksidae	*Whetwhetaksa*	*W. millerae*	46	2	48	47.1
Totals				1121	114	1235	44.8

*Anisoptera families: **Aeshnidae**, Aktassiidae, Araripechlorogomphidae, Araripegomphidae, Araripelibellulidae, Araripephlebiidae, **Austropetaliidae**, Bolcacorduliidae, Burmaeshnidae, Burmagomphidae, **Chlorogomphidae**, **Cordulegastridae**, **Corduliidae**, Cratopetaliidae, Cretapetaluridae, Cymatophlebiidae, Daohugoulibellulidae, Enigmaeshnidae, Eocorduliidae, Eumorbaeschnidae, Gallophlebiidae, Gomphaeschnidae, Gomphidae, Hageniidae, Henrotayiidae, Juracorduliidae, Juragomphidae, Juralibellulidae, **Libellulidae**, Liupanshaniidae, **Macromiidae**, Magnathemidae, Megaphlebiidae, Mesochlorogomphidae, Nannogomphidae, **Neopetaliidae**, Nodalulaidae, Palaeomacromiidae, Paracymatophlebiidae, **Petaluridae**, Progobiaeshnidae, Prohemeroscopidae, Proterogomphidae, Protolindeniidae, Rudiaeschnidae, **Synthemistidae**, Urolibellulidae, Valdicorduliidae.

†Zygoptera families: unknown family ("?"), **Amphipterygidae**, **Argiolestidae**, **Austroperilestidae**, Burmacoenagrionidae, **Calopterygidae**, **Chlorocyphidae**, **Coenagrionidae**, Cretacoenagrionidae, **Devadattidae**, **Dicteridadidae**, **Epallagidae**, **Euphaeidae**, **Hemiphlebiidae**, **Heteragrionidae**, **Hypolestidae**, **Isostictidae**, Latibasaliidae, **Lestidae**, **Lestoideidae**, **Megapodagrionidae**, Mesomegaloprepidae, **Pentaphlebiidae**, **Perilestidae**, **Philogangidae**, **Philogeniidae**, **Philosinidae**, **Platycnemididae**, **Platystictidae**, **Polythoridae**, Priscalestidae, Protoneuridae, **Protostictidae**, **Pseudolestidae**, **Synlestidae**, **Thaumatoneuridae**.

‡Unknown family ("?"), Dysagrionidae, Sieblosiidae, Whetwhetaksidae.

§*Congqingia*, *Dysagrion*, *Dysagrionites*, *Electrophenacolestes*, *Furagrion*, *Okanagrion*, *Okanopteryx*, *Petrolestes*, *Phenacolestes*, *Primorilestes*, *Stenodiafanus.*

[ll]*Germanostenolestes, Miostenolestes, Paraoligolestes, Parastenolestes, Sieblosia, Stenolestes.*

***Okanagrion threadgillae, O. beardi, O. lochmum, O. hobani, O. angustus, O. dorrellae, O. liquetoalatum, O. worleyae*.

††*Okanopteryx jeppesenorum, O. fraseri, O. macabeensis*.

‡‡*Stenolestes* species: *S. adygeianensis, S. andancensis, S. belligaudi, S. camoinsi, S. cerestensis, S. coulleti, S. dauphinensis, S. falloti, S. fasciata, S. fischeri, S. hispanicus, S. iris, S. rhodopensis, S. ronzonense*.

APPENDIX C. Data matrix for 27 terminal taxa and 102 characters used in analyses. See Appendix B for listings of species scored for each terminal taxon. Unknown character states are coded as missing ("?") and inapplicable data as ("-"). Multistate characters are indicated by characters: A=[01]; B=[012]; C=[0123]; D=[01234]; E=[01345]; F=[012346]; G=[02]; H=[023]; I=[0234]; J=[056]; K=[06]; L=[12]; M=[123]; N=[124]; O=[1234]; P=[23]; Q=[234]; R=[34].

	1	2	3	4	5	6	7	8	9	10	11	12
Tarsophlebiidae	17	13	16	86	69	127	128	135	150	16	5	6
Burmadysagrion zhangi	3	?	3	99	74	148	122	117	106	5	2	4
Electrodysagrion	3	?	3	68	?	149	?	143	?	8	?	?
Palaeodysagrion	2	?	2	93	?	150	?	140	?	?	?	5
Anisoptera	4-36	3-34	4-54	47-102	52-109	79-147	75-154	87-170	109-157	3-26	2-11	3-27
Anisozygoptera	5-16	10	5-18	93-99	65	119-127	130	134-224	127	8-14	3	9
Zygoptera	2-49	2-48	2-42	45-103	39-102	68-203	95-173	91-246	71-163	4-84	2-30	2-20
Cephalozygoptera	2-4	2-4	2-3	40-96	18-116	99-153	88-137	70-137	78-138	17-40	2	4-17
Congqingia	2	2	2	78	77	129	116	128	112	12	2	6
Dysagrion	?	?	?	41	51	133	131	70	?	18	?	9
Dysagrionites delinei	2	?	2	79	?	147	?	137	?	?	?	?
Electrophenacolestes	4	4	2	?	110	?	104	?	120	?	?	?
Furagrion	2	?	2	54	?	142	?	108	?	20	?	5
Okanagrion	2	2	2	68	65	133	137	126	138	40	?	17
Okanopteryx	2	2	2	50	?	136	?	113	?	20	?	15
Petrolestes	2	3	2	72	61	144	135	112	107	18	?	7
Phenacolestes	5	5	2	49	79	132	121	118	106	18	?	4
Primorilestes	3	?	3	80	?	141	?	128	?	25	?	7
Stenodiafanus	?	?	?	58	?	153	?	135	?	18	?	11
Dysagrionidae	2-4	2-4	2-3	41-80	51-110	129-153	104-137	70-137	106-138	12-40	2	4-17
cf. Dysagrionidae gen, sp. A	?	?	?	147	?	?	?	133	?	23	?	10
Thanetophilosina	2	?	2	78	?	137	?	136	?	29	?	6
Valerea	?	?	?	52	?	101	?	127	?	36	?	15
Sieblosiidae	2	2	2	51-96	18-116	99-120	88-104	80-105	78-113	19-25	?	9-14
Whetwhetaksidae	2	?	2	42	?	147	?	136	?	18	?	11

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APPENDIX C. (Continued)

	13	14	15	16	17	18	19	20	21	22	23
Tarsophlebiidae	9	15	20	?	?	?	?	?	?	?	?
Burmadysagrion zhangi	3	4	3	2	2.1	1	1	1	1	1	1
Electrodysagrion	?	?	?	?	?	1	?	?	?	?	?
Palaeodysagrion	?	3	?	1.5	?	1	?	1	?	1	?
Anisoptera	2-18	1-8	1-15	?	?	?	?	?	?	?	?
Anisozygoptera	7	3-6	5	?	?	?	?	?	?	?	?
Zygoptera	2-17	2-26	1-33	3.6-4.8	4.5	2-3	3	13	17	9.5	9
Cephalozygoptera	4-20	6-18	11-16	2-10.8	2.2-8.5	1-3	1-3	2-6	1-7	2-13	2-16
Congqingia	5	11	8	2.4	2.3	1	1	2	2	2	2
Dysagrion	8	13	15	3-4.5	5.6	1	1	4	4	2-3	?
Dysagrionites delinei	?	?	?	?	?	?	?	3	?	?	?
Electrophenacolestes	?	?	?	?	?	?	?	?	4	?	?
Furagrion	?	7	?	2	?	1	?	2	?	2.5	?
Okanagrion	20	11	12	2.4-3.3	2.5-3	3	3	4-6	6-7	4-7	6-6.5
Okanopteryx	?	?	?	2-2.5	2-2.5	2	?	2-4	?	2.5	?
Petrolestes	?	?	?	4.9	?	1	?	5	5	6	?
Phenacolestes	4	6	?	4.1-4.8	4.4	1	1	4	4	4.5-5	4-4.5
Primorilestes	?	9	?	3.1	?	2	?	3-5	?	3.5	?
Stenodiafanus	?	17	?	3.5	?	1-2	?	?	?	3.5	?
Dysagrionidae	4-20	6-17	8-15	2-4.9	2.2-5.6	1-3	1-3	2-6	2-7	2-7	2-6.5
cf. Dysagrionidae gen, sp. A	?	6	?	1.9	?	2	?	2	?	3	?
Thanetophilosina	?	?	?	4.9	?	1	?	?	?	7	?
Valerea	?	?	?	2.7	?	4	?	?	?	?	?
Sieblosiidae	9-18	17-18	11-16	4.2-7.2	4.6-8.5	1	1	2-4	1-3	9-13	9-16
Whetwhetaksidae	?	2	?	8.8-10.8	?	2	?	4-6	?	7-8	?

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APPENDIX C. (Continued)

	2	3	4	5	6	7	8	9	10
	456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012
Tarsophlebiidae	041000	0001110002	2000001000	2323030210	--1102011?	??????????1	100011000?	????1?????	???
Burmadysagrion zhangi	?3?-01	11?1???00-	-22-?02022	0424011100	0021100000	0001221211	1000110111	114301-220	122
Electrodysagrion	03?-01	11?1??000-	?22??130??	02?4011400	00?1??100?	??????????	????1?0???	?????1-2??	22?
Palaeodysagrion	??????	??????00?-	?22??130??	03?40?1?00	1L?A??1000	?0?02?1211	?000110?1	?15??1-2?1	22?
Anisoptera	REAAAB	0A2000AAAB	BAAAAAM0BB	G00D0DACAA	10AAA2A1A?	??????????A	A000AAABB?	?---AAA???	???
Anisozygoptera	321?00	002000-000	00010010G0	GR2P0L-0A0	012A01AAA?	??????????1	100010000?	????11-???	???
Zygoptera	C30-01	1ABAA1000G	GBBABAM0BB	0DDD0DADAA	ABLAABAAA1	111-00000A	ABAAAABBB1	1066AAAG0-	G22
Cephalozygoptera	?4010A	00AA110002	2LL-LAM0LL	00DI0QAM00	002AA0AA1A	AAAAA110AA	ABAAAAAAAA	AAFJ0AABBA	BBB
Congqingia	??0-01	00?1???00-	-22-113022	022302110-	0021101010	011-111001	1000110000	0-??0??210	100
Dysagrion	??????	??01??000-	-22-???022	0113031100	00211-1110	000A111001	1000000000	0-0001-2?0	12?
Dysagrionites delinei	??????	??????00?-	?2???130??	02?40?1???	00?0??1110	?0?0???0??	??????????	?????1??2A	12?
Electrophenacolestes	??????	???1???002	211-1020??	0?4???????	00200-1111	1?1??1????	??????????	1??60??22-	??1
Furagrion	??????	????????0?-	?2???1302?	01?4041200	00?1??1110	?0?10?1001	?001100?1	?06??1-2?1	12?
Okanagrion	????01	00?111000-	-22-113022	-22304110-	00211-1111	111-111000	0200111001	116600022-	122
Okanopteryx	?4??01	00?111000-	-22-11302?	01?3041200	00?1?-1110	?0?02?0010	011111100??	?1???01211	12?
Petrolestes	???100	0010??000-	-22-21301?	-22403010-	00200-1110	00010?0001	?0??00000?	???????1?0	100
Phenacolestes	????00	00????-002	211-101022	-12303110-	00211-1110	0000101001	1001110001	1065001210	222
Primorilestes	??????	??????0??-	?22??130??	02?404110-	??????1111	?1?-1?0001	?001101111	?16?????2?-	12?
Stenodiafanus	??????	??????????	??????????	01?4031200	?????????0	?0?02?1011	?1??110???	?1???1-???	?2?
Dysagrionidae	?4010A	00AA110002	2LL-LAM0L2	0LNR0QAL00	002AA01A1A	AAAABAA0AA	ABAAAAAAAA	AAKJ0AALLA	LGB
cf. Dysagrionidae gen, sp. A	??????	??????????	??????????	04??041200	?????????0	?0?00?1001	?111000?1	?06??01??1	???
Thanetophilosina	??????	???????0?-	?2???1302?	02?304?10-	00?0??1??0	?????????1	?000100???	?????002?0	21?
Valerea	??????	??????????	??????????	01?204110-	??????????	?????????0	?201??20??	?????1-???	???
Sieblosiidae	???-01	00?1??000-	-22-11302L	00IH0R1M00	002AA-111A	AAAAA110AA	A0AAAA00?A	AAD001-BBA	A1L
Whetwhetaksidae	??????	??????00?-	?2???1302?	01?403110-	00?1??0110	????1?10?1	?101100?1	?16??011?0	10?