



Early Eocene snakeflies (Raphidioptera) of western North America from the Okanagan Highlands and Green River Formation

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Abstract

Four new species of Raphidiidae are described from the early Eocene of western North America: *Megaraphidia antiquissima* **sp. nov.** from McAbee, *M. ootsa* **sp. nov.** from Driftwood Canyon, *M. hopkinsi* **sp. nov.** from the Allenby Formation (all from British Columbia, Canada), *M. klondika* **sp. nov.** from Republic (Washington, United States of America). *Archiinocellia* Handlirsch, 1910, *Archiinocellia oligoneura* Handlirsch, 1910 from Horsefly River (British Columbia, Canada), and *A. protomaculata* (Engel, 2011), **comb. nov.**, from the Green River Formation (Colorado, United States of America) are redescribed. *Archiinocellia* is assigned to Raphidiidae, **sit. nov.** The apparent absence of sclerotized gonocoxites 9 in the *Archiinocellia protomaculata* male is probably plesiomorphic at the family level. As some modern snakeflies do not require a cold interval to complete their development and Eocene Inocelliidae and Raphidiidae lived in regions of warm winters (especially *A. protomaculata*), adaptation to cold winters in many modern snakeflies is a post-Eocene phenomenon. Eocene Raphidiidae of Europe (Priabonian) differ greatly from those of North America (Ypresian and Priabonian). This pattern might reflect dispersal in either direction or ranges established prior to continental separation. Eocene Inocelliidae of Europe (Priabonian), however, are more similar to those of North America (Ypresian and Lutetian).

Key words: Raphidioptera, Raphidiidae, early Eocene, western North America

Introduction

The order Raphidioptera (snakeflies) is one of the smallest among holometabolous insects, with less than 250 extant species of two families, Inocelliidae and Raphidiidae of the suborder Raphidiomorpha (Haring *et al.*, 2011; Liu *et al.*, 2014). Thirty-one species occur in North America, five of two genera in the Inocelliidae, and 28 of two genera in the Raphidiidae (Aspöck and Aspöck, 1970, 1978, 2013; Aspöck, 1975, 1982, 1987, 1988; Aspöck *et al.*, 1992, 1994a, b; Aspöck & Contreras-Ramos, 2004). Their distribution in the United States and Canada is restricted to western regions.

Numerous fossil Raphidioptera have been reported from the Cenozoic of North America. Two have been described and named from Okanagan Highlands localities in south-central British Columbia, Canada: the raphidiid *Archiinocellia oligoneura* Handlirsch, 1910 from opposite Horsefly mine at the village of Horsefly, British Columbia, Canada (Handlirsch, 1910), and the inocelliid *Paraksenocellia borealis* Makarkin *et al.*, 2019 from Driftwood Canyon Provincial Park (Makarkin *et al.*, 2019). A specimen cited as a snakefly (Wilson, 1977a, 1977b: Fig. 2C) also from Horsefly, however, is a mecopteran (SBA, pers. obs.). Undescribed raphidiopterans have been figured or briefly mentioned from other Okanagan Highlands sites at Republic (Washington, United States of America), McAbee and the Allenby Formation at One Mile Creek (Canada) (Wehr & Barksdale, 1996; Archibald & Farrell, 2003; Greenwood *et al.*, 2005; Archibald *et al.*, 2013a). The Okanagan Highlands is a series of late Ypresian (second

half of the early Eocene) lake basins scattered across about a thousand kilometers from Driftwood Canyon in the north to the village of Republic in north-central Washington, United States of America (Archibald *et al.*, 2011).

Although Raphidioptera fossils are plentiful in the late Ypresian Green River Formation of Colorado, United States of America (Dayvault *et al.*, 1995; Aspöck, 1998; Pribyl *et al.*, 1998; Engel, 2011; pers. obs.), only one species has been described, '*Agulla protomaculata* Engel, 2011.

A well-preserved hind wing of the inocelliid *Paraksenocellia* Makarkin *et al.*, 2019 is known from the Lutetian (early middle Eocene) Kishenehn Formation of Montana, United States of America (Makarkin *et al.*, 2019).

Nine species of three families (the two extant families and the extinct Baissopteridae) have been described from the Priabonian (late Eocene) of Florissant, Colorado (Scudder, 1890; Cockerell, 1907, 1909a, b, 1912, 1914, 1917; Bather, 1909; Rohwer, 1909; Cockerell & Custer, 1925; Carpenter, 1936; Engel, 2003; Makarkin & Archibald, 2014).

Finally, *Agulla mineralensis* Engel, 2009 was described from the Miocene of Stewart Valley (USA, Nevada) based on a hind wing (Engel, 2009).

Here, we review, redescribe, and describe and name new species based on all known Raphidioptera fossils from the Okanagan Highlands, redescribe and revise the generic assignment of the Green River Formation snakefly '*Agulla protomaculata*, and discuss differences in North American and European Eocene snakeflies, the climatic implications of fossil snakeflies, biogeography, and the possible effect of the K/Pg extinction event on the order. The Okanagan Highlands has the oldest raphidiid, and the oldest Cenozoic inocelliid (its single possible Mesozoic specimen is undescribed, see below).

Materials and methods

We examined nine fossils in lacustrine shales from the following Okanagan Highlands localities and high-resolution photographs of fifty-one fossils from the Green River Formation (all accession numbers listed below). In line drawings of wing venation, all wings are depicted in standard view, with their apex to the right.

We use the venational terminology of Makarkin & Archibald (2014) as modified by Makarkin *et al.* (2019). Terminology of wing spaces and details of venation (*e.g.*, veinlets, traces) follows Oswald (1993).

Abbreviations: AA1–AA3, first to third branches of anterior anal vein; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; *Idoi-3doi*, first to third discoidal cells; MA and MP, anterior and posterior branches of media; *1r-3r*, first to third radial cells; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; ScP, posterior subcosta.

Institutions and their accession number suffixes: GSC, the Geological Survey of Canada, Department of Energy, Mines and Resources Canada, Ottawa, Canada; RBCM, the Royal British Columbia Museum, Victoria, British Columbia, Canada; SR and SRUI, the Stonerose Interpretive Center, Republic, Washington, U.S.A.; TRU, Thompson Rivers University, Kamloops, British Columbia, Canada (F-numbers); UCM, the Museum of Natural History of the University of Colorado, Boulder, United States of America; USNM, the National Museum of Natural History (Smithsonian Institution), Washington, D.C., United States of America; UWBM, the Burke Museum of Natural History and Culture, Seattle, Washington, United States of America.

Localities

Driftwood Canyon Provincial Park. The northern-most locality of the Okanagan Highlands. Lacustrine shale of the Ootsa Lake Group bearing abundant insects and other fossils outcrop in Driftwood Canyon Provincial Park near the town of Smithers in west-central British Columbia. It is dated as 51.77 ± 0.34 million years old (Moss *et al.*, 2005).

Horsefly River. Fossil-bearing shale of an unnamed formation is exposed along the Horsefly River near the village of Horsefly in the Cariboo region of south-central British Columbia. There has not been a radiometric age provided for these shales, but biostratigraphy of macro- and microfossils indicate that the Horsefly shales are contemporaneous with other sites of the Okanagan Highlands (Rouse *et al.*, 1970; Wilson, 1977b and references therein; Archibald, 2005) which are all dated through the second half of the Ypresian.

McAbee. McAbee fossils have three named exposures within a few kilometers of each other; Raphidioptera have been recovered from the Hoodoo Face beds exposure that faces Highway 1 about 13 kilometers east of the

village of Cache Creek in south-central British Columbia (the other two exposures are the Eastern beds immediately to the east, much of which was previously operated as a zeolite mine, and the Western beds between the Hoodoo beds and Cache Creek in the hills above a cattle ranch). It is dated as 52.90 ± 0.83 million years ago (Archibald *et al.*, 2010).

Allenby Formation. Fossiliferous lacustrine shale of the Vermilion Bluffs member outcrops in various locations in and surrounding the village of Princeton in southern British Columbia (Read, 2000). The One Mile Creek locality is about eight kilometres north of Princeton. The “Hospital Hill” exposure of the Vermilion Bluffs Shale in Princeton is estimated to be 52.08 ± 0.12 million years old (Archibald, 2005).

Republic. Fossils are found in the Tom Thumb Tuff Member of the Klondike Mountain Formation within and around the village of Republic, Washington. Republic is the southern-most and youngest deposit of the series, dated as 49.42 ± 0.54 million years old (Wolfe *et al.*, 2003). The locality code A0307 for the specific exposure where Raphidioptera have been recovered is a designation of the Burke Museum, also used by the Stonerose Interpretive Center.

Parachute Creek Member of the Green River Formation. The Green River Formation spans the latter half of the Ypresian from about 53.5 to 48.5 million years ago, with the Parachute Creek Member of the Piceance Basin in its approximately last 2.5 million years, *i.e.*, about 48.5 to 51 million years old (Smith *et al.*, 2003, 2008). The Piceance Basin is the eastern portion of Eocene Lake Uinta in northwestern Colorado. The majority of exposures where Raphidioptera have been recovered (listed below) are from so called from ‘B-Groove’ lying 45 meters below the Mahogany Bed (see Young, 1995: Fig. 4), and only one (*i.e.*, Douglass Pass/Radar Dome) lies approximately 45 m above this bed (Dayvault *et al.*, 1995; D. Kohls, pers. comm.). These sediments are approximately 49–49.5 Ma old, within the upper horizons of the Parachute Creek Member (Smith *et al.*, 2008). Green River Formation Raphidioptera are then contemporaneous with Republic and younger than other Okanagan Highlands localities for which an absolute age has been estimated.

Systematic paleontology

Order Raphidioptera Navás, 1916

Suborder Raphidiomorpha Engel, 2002

Family Raphidiidae Latreille, 1810

Genus *Megaraphidia* Cockerell, 1907

Emended diagnosis. Relatively large raphidiids (forewing up to 14 mm long), distinguished from other genera of the family by the following unique combination of character states: fore- and hind wings: (1) relatively long ScP (length from termination to pterostigma approximately equal to or less than that of pterostigma) [*Archiraphidia*, *Archiinocellia*: greater than that of pterostigma]; (2) relatively short pterostigma [long in *Florissantoraphidia*, *Archiinocellia*]; (3) crossvein 3ra-rp located within pterostigma [distad this in *Phaeostigma* Navás, 1909 and *Agulla* Navás, 1914a and the majority of other extant genera]; forewing: (4) costal space broad [relatively narrow in *Florissantoraphidia*]; (5) branches of CuA, M long [short in *Archiraphidia*]; hind wing: (6) basal crossvein 1r-m long, subparallel to R [crossvein-like in *Agulla*]; (7) two *doi* [one in *Archiraphidia*].

Type species. *Megaraphidia elegans* Cockerell, 1907, by monotypy.

Species included. *Megaraphidia antiquissima* sp. nov.; *M. ootsa* sp. nov.; *M. klondika* sp. nov.; *M. hopkinsi* sp. nov.; *M. elegans*, *M. exhumata* (Cockerell, 1909) and *Megaraphidia* sp. (Makarkin & Archibald, 2014).

Occurrence. The Ypresian to Priabonian of western North America.

Remarks. The venation of *Megaraphidia* is most similar to that of the extant European genus *Phaeostigma* (Makarkin & Archibald, 2014), but only superficially so. The Okanagan Highlands species are also rather similar to the extant North American *Agulla* by their long ScP and mostly (varies among species and individuals) simple branches of MP, whereas in Florissant species, these are mostly forked. However, the diagnostic character states are mostly plesiomorphic or their polarity is not clear, and therefore *Megaraphidia* might be paraphyletic.

***Megaraphidia antiquissima* sp. nov.**

Figs 1, 2, 10A, B

Type material. Holotype RBCM P1555, collected by John Leahy, unknown date, deposited in the RBCM collections. A nearly complete female specimen preserved in dorsal aspect.

Type locality and horizon. Hoodoo Face beds, McAbee, British Columbia, Canada; early Eocene (Ypresian).

Etymology. From the Latin *antiquissimus* [-a, -um], oldest, most ancient, as this is the oldest record of the genus.

Diagnosis. May be distinguished from other species of *Megaraphidia* by head broad, not cuneate [clearly cuneate, *i.e.*, narrowed posteriorly in *M. ootsa*]; ovipositor relatively short (0.28 body length) [0.34 in *M. ootsa*], relatively narrow costal space in forewing (2.3 times wider than subcostal space) [broader in *M. exhumata* (2.6), *M. klondika* (2.9), *M. klondika* (2.9), *M. elegans* (3.0); narrower in *M. hopkinsi*, *M. ootsa* (2.0)]; basal *doi* shorter than distal in hind wing [both approximately equal in length *M. klondika*].

Description. Female. Body length (without ovipositor) approximately 15 mm. Head broad, apparently not cuneate (incompletely preserved). Prothorax probably relatively long (poorly preserved), approximately 3.0–3.5 mm long (0.20–0.23 body length). Ovipositor relatively short, approximately 4.2 mm long. Details of body, legs not discernible by preservation.



FIGURE 1. *Megaraphidia antiquissima* sp. nov., holotype RBCM P1555, specimen as preserved. Scale bar = 5 mm.

Forewing approximately 12 mm long, approximately 3.5 mm wide (length/width: 3.43). Costal space broad, widest at proximal 1/5 of length; seven simple subcostal veinlets (right forewing: preserved, probably nine to ten total), all relatively closely spaced. ScP relatively long, terminating on costal margin opposite crossvein 2ra-rp; length from termination of ScP to pterostigma approximately equal to length of pterostigma. Subcostal space moderately broad, with basal crossvein located in middle between origin of RP, divergence of M, CuA; distal crossvein 2scp-r (forming basal margin of pterostigma) straight, slightly inclined toward base (*i.e.*, joins C slightly proximad joining RA). Pterostigma relatively short, rather strongly pigmented. Three RA branches: one incorporated in pterostigma medially well discernible; second forming distal margin of pterostigma; third distad pterostigma; none forked. RA entering margin about halfway between pterostigma, apex. RA space with two crossveins forming two radial cells: 2ra-rp long, located well proximad pterostigma, opposite termination of ScP; 3ra-rp long, joins distal part of pterostigma along RA. RP originates in proximal part of wing (approximately 0.39 wing length), with four (right wing) or six (left wing) pectinate branches: RP1 deeply forked; its anterior branch simple, posterior branch forked once (both wings). RP3 deeply forked (right wing), and RP4 shallowly forked (right wing); other branches simple. One long intraradial crossvein rp1-rp2 between stem of RP, RP1. Three crossveins between RP, MA: 1r-m, 2r-m connecting stem of RP, MA; 3r-m connecting RP1, anterior branch of MA. M fused with CuA for short distance; forked well proximad origin of RP. MA deeply dichotomously forked twice. MP zigzagged, with three simple branches.

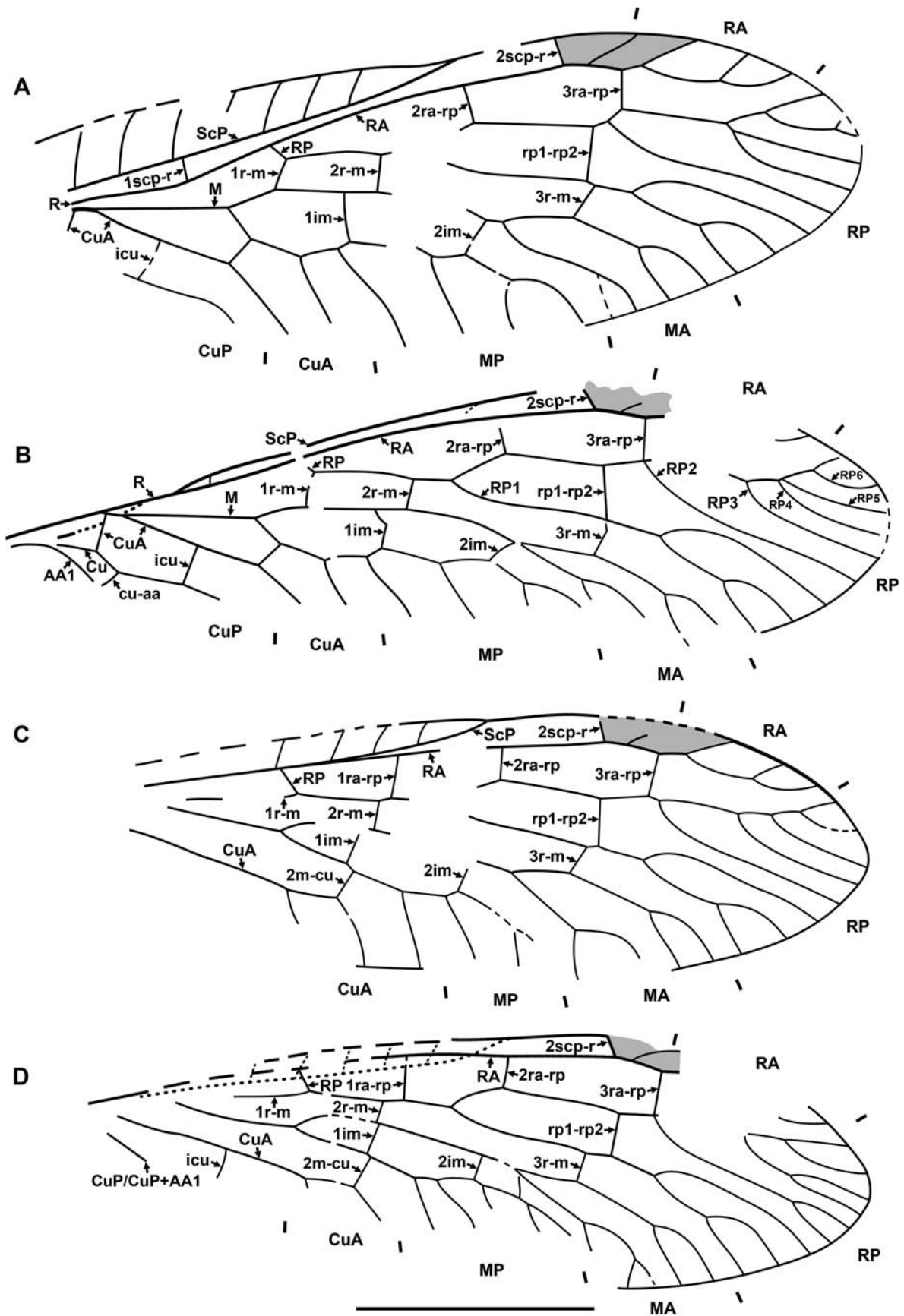


FIGURE 2. Wing venation of *Megaraphidia antiquissima* sp. nov., holotype RBCM P1555. A, right forewing; B, left forewing; C, right forewing; D, left hind wing. Scale bar = 3 mm (all to scale).

Two intramedian crossveins form two *doi*, basal cell somewhat shorter than apical. Anterior trace of CuA strongly zigzagged, simple, fused with MP for short distance forming part of posterior margin of basal *doi*; posterior trace of CuA simple. CuP probably simple (distal portion not visible). Crossvein *icu* between CuA, CuP long. Crossvein *cu-aa* between CuP, AA1 closer to origin of CuA than to *icu*. Only basal AA1 discernible, AA2, AA3 not.

Hind wing approximately 11 mm long, approximately 3.05 mm wide (length/width: 3.61). Costal space moderately broad; four to five simple subcostal veinlets preserved, rather closely spaced. ScP relatively long; length from termination of ScP to pterostigma approximately equal to its length. In subcostal space, one crossvein detected (2scp-r, forming basal margin of pterostigma), straight, distinctly inclined toward base. Pterostigma elongate, slightly longer than in forewing. RA with three branches: first, within pterostigma, easily visible; second, forming distal margin of pterostigma, straight, oblique to margin; third, simple. RA terminating on margin about mid-way between pterostigma, apex. Three crossveins between RA, RP: 1ra-rp slightly distad 2r-m; 2ra-rp approximately opposite termination of ScP; 3ra-rp located in distal half of pterostigma along RA. RP originating at approximately 0.36 wing length. Anterior trace of RP simple apically, with four (left wing) to five (right wing) branches, in both wings one proximad 3ra-rp, three to four at beginning or distad 3ra-rp. RP1 deeply forked, its anterior branch simple, posterior forked once; RP2, RP3 in left wing forked; other branches simple. One intraradial crossvein (rp1-rp2), between stem of RP, RP1. Three crossveins between R, M: 1r-m long, running subparallel to R; 2r-m connects stem of RP, MA; 3r-m connecting RP1, anterior branch of MA. M forked approximately at level of origin of RP. MA deeply dichotomously forked twice. MP pectinately branched, with probably three branches (right wing; poorly preserved), four probably simple branches (left wing). Two intramedian crossveins form two *doi*; basal *doi* markedly shorter than distal; one indistinct crossvein distad 2im (this may be artefact). One crossvein 2m-cu between M, Cu detected, connecting MP, CuA. Anterior trace of CuA simple distally, with one simple (but incompletely preserved) branch. CuP or CuP+AA1 partially preserved; anal veins not preserved.

***Megaraphidia ootsa* sp. nov.**

Figs 3, 4, 10C, D

Type material. Holotype RBCM P1556, found by unknown person on an unknown date, deposited in the RBCM collections. A complete female in lateral aspect with four overlapping wings.

Type locality and horizon. Driftwood Canyon Provincial Park, near Smithers, British Columbia, Canada; early Eocene (Ypresian).

Etymology. From the Ootsa Lake Group shale within which the holotype is preserved (specific epithet is a noun).



FIGURE 3. *Megaraphidia ootsa* sp. nov., holotype RBCM P1556, specimen as preserved. Scale bars = 5 mm.

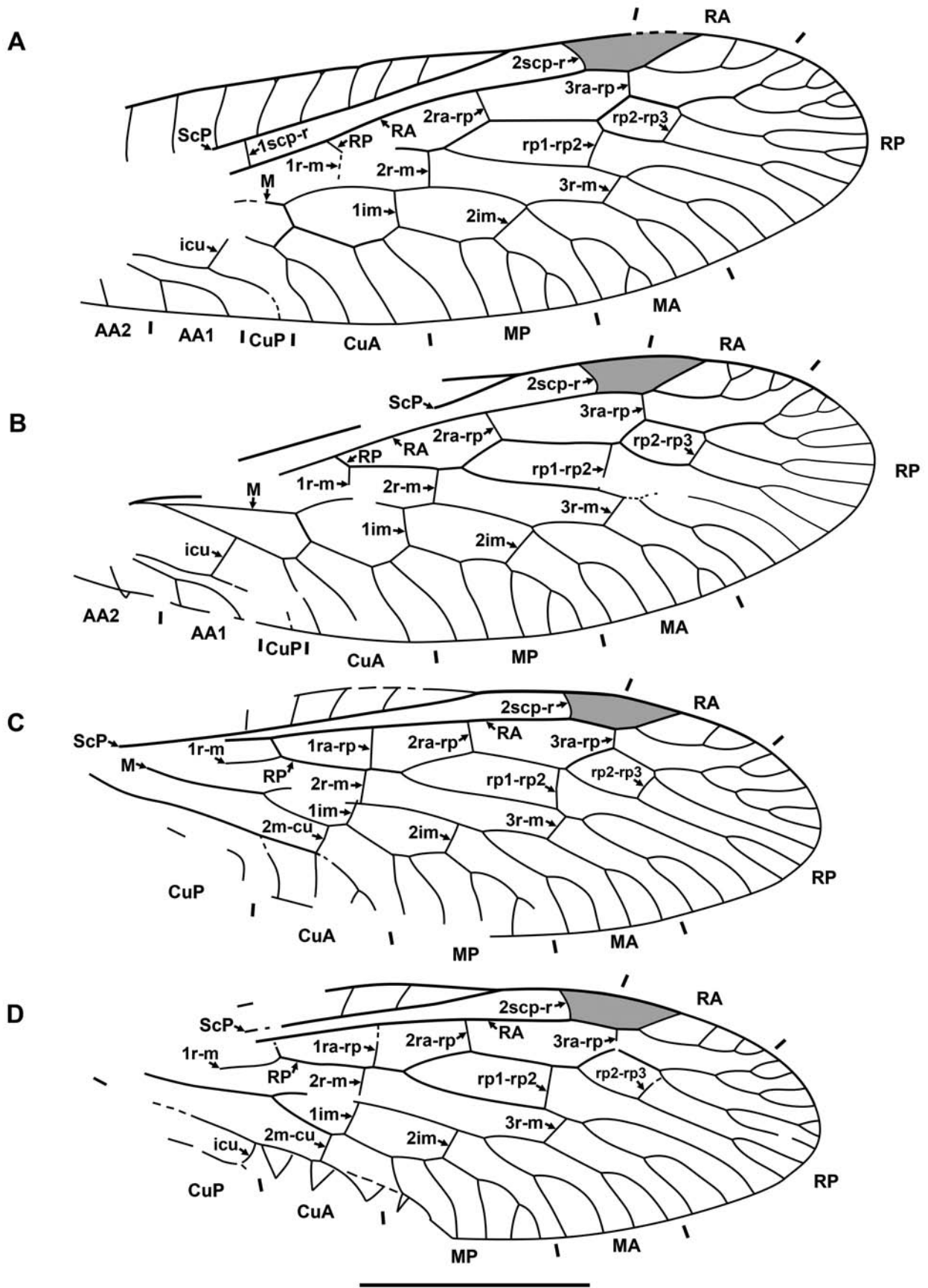


FIGURE 4. Wing venation of *Megaraphidia ootsa* sp. nov., holotype RBCM P1556. A, right forewing, B, left forewing; C, right hind wing; D, left hind wing. Scale bar = 3 mm (all to scale).

Diagnosis. May be distinguished from other species of *Megaraphidia* by head clearly narrowed posteriorly (cuneate) [broad, not cuneate in *M. hopkinsi*, *M. antiquissima*]; ovipositor relatively long (0.34 body length) [0.28 in *M. antiquissima*]; two intraradial crossveins in both wings [one in other species].

Description. Female. Body length (without ovipositor) approximately 15 mm. Head blackish, clearly narrowed posteriorly; antennae with ≥ 38 flagellomeres. Prothorax blackish, narrow, relatively short, approximately 2.5 mm long (0.17 body length). Mesothorax, metathorax poorly preserved, blackish. Legs pale, covered with dense, rather short setae; third tarsomeres strongly bifurcate. Abdomen with blackish tergites, sternites; 8th, 9th tergites extend laterally for relative short distance; ectoproct relatively large. Ovipositor relatively long, approximately 5.1 mm (0.34 body length).

Forewing approximately 12 mm long, 3.5 mm wide (length/width: 3.43). Costal space relatively narrow (two times wider than subcostal space), widest at 1/5 length (basal-most portion obscured); eight preserved subcostal veinlets (probably ≥ 10), all simple, relatively closely spaced. ScP long, terminating on costal margin notably distad crossvein 2ra-rp; length from termination of ScP to pterostigma approximately half length of pterostigma (measured along C). Subcostal space broad, with basal crossvein 1scp-r slightly proximad fork of M; distal crossvein 2scp-r (basal margin of pterostigma) markedly incurved (joins C proximad basad joining RA). Pterostigma rhombic (distal margin oblique, angled opposite to basal), relatively short, strongly pigmented. Two RA branches detected (branch presumed within pterostigma not discernible): one forming distal margin of pterostigma; other distad this (simple in right wing, forked in left wing). Stem of RA simple in right wing, forked in left wing, entering margin well before wing apex. RA space with two crossveins forming two radial cells: 2ra-rp located well proximad termination of ScP; 3ra-rp located in distal part of pterostigma along RA (at approximately 2.45 wing length), with five pectinate branches: RP1 deeply forked, its anterior branch simple, posterior forked once; other branches once or twice forked. Two intraradial crossveins: rp1-rp2 in right wing between RP2, RP1, in left wing between anterior trace of RP, RP1; other between RP2, RP3. Three crossveins between RP, MA: 1r-m, 2r-m connecting stem of RP, stem of MA; 3r-m connecting RP1, anterior branch of MA. M joined with CuA for short distance (seen on left wing, obscured on right wing); forked well proximad origin of RP. MA deeply dichotomously forked twice (one branch in each right and left wings further shallowly forked). MP zigzagged with four simple, pectinate branches. Two intramedian crossveins forming two *doi*; basal *doi* slightly shorter than distal. Basal parts of Cu not visible. Anterior trace of CuA strongly zigzagged, fused with MP for short distance (forming part of posterior side of basal *doi*), with two pectinate long simple branches (left wing) or one deeply forked branch (right wing). CuP simple. Crossvein icu between CuA, CuP long. AA1 rather deeply forked; small portion of AA2 visible.

Hind wing approximately 11 mm long, approximately 3.4 mm wide (length/width: 3.24). Costal space relatively broad (incompletely preserved); four preserved subcostal veinlets (right wing) simple, widely spaced. ScP long; length from termination of ScP to pterostigma shorter than length of pterostigma. One crossvein detected in subcostal space (2scp-r, forming basal margin of pterostigma), slightly incurved. Pterostigma nearly equal in length with that in forewing. RA with two to three branches detected (branch presumed within pterostigma not discernible), branch forming distal margin of pterostigma straight; one (right wing) to two (left wing) simple, slightly curved branches distad pterostigma. Three crossveins between RA, RP: 1ra-rp located slightly distad 2r-m; 2ra-rp located notably proximad termination of ScP (left wing, but only slightly proximad in right wing); 3ra-rp located in distal half of pterostigma along RA. RP originating at approximately 0.36 wing length. Anterior trace of RP forked apically, with four branches, two proximad 3ra-rp, two distad. RP1 deeply forked, its anterior branch simple, posterior forked once; most other branches rather deeply forked. Two intraradial crossveins: one connecting stem of RP, RP1; other between RP2, RP3. Three crossveins between R, M: 1r-m very long, subparallel to R (basal portion obscured); 2r-m connecting stems of RP, MA slightly proximad 1ra-rp; 3r-m connecting RP1, anterior branch of MA. M forked close to or slight basad level of origin of RP. MA deeply dichotomously forked twice. MP: anterior trace zigzagged, with four simple pectinate branches (basal-most branch in left wing forked). Two intramedian crossveins forming two *doi*; basal *doi* markedly shorter than distal. One crossvein (2m-cu) detected between M, Cu straight, proximad 1im. CuA with two (left wing) to three (right wing) simple branches. Small portions of CuP preserved.

Remarks. In this specimen, light areas of the head, thorax, and abdomen (Fig. 3) surely do not represent colouration of the living insect, but were most likely caused by post-mortem damage.

***Megaraphidia klondika* sp. nov.**

Figs 5–7, 10E, F

Type material. Holotype SR 03-01-01 (part), UWBM 97073 (counterpart), collected by Wes Wehr, 13.v.2003, deposited in the SR collections (SR 03-01-01) and UWBM collections (UWBM 97073). An overlapping forewing and hind wing, both almost complete, slightly damaged.

Other material. SR 16-004-001.01 (only part), collected by Joanne West, 13.vi.1998, locality the same as holotype, deposited in the SR collections. An apical well-preserved portion of a wing.

SRUI 99-71-63 (part and counterpart), 28.iv.2017, collected by Gregg Wilson at the same exposure, 28.iv.2017, deposited in the SR collections. A well-preserved middle portion of a hind wing.

Type locality and horizon. Tom Thumb Tuff Member of the Klondike Mountain Formation, exposure A0307, Republic, Washington, U.S.A.; early Eocene (Ypresian).

Etymology. The specific epithet is an adjective referring to the Klondike Mountain Formation shale within which its specimens are preserved.

Diagnosis. May be distinguished from other species of *Megaraphidia* by branch of RA within pterostigma very poorly or not visible [clearly visible in *M. elegans*, *M. exhumata*]; costal space strongly dilated in forewing (2.9 times wider than subcostal space) [2.3 in *M. antiquissima*, 2.0 in *M. hopkinsi*, *M. ootsa*]; two *doi* approximately equal in length in hind wing [proximal *doi* shorter than distal in *M. antiquissima*, *M. ootsa*, *M. hopkinsi*]; two pectinate branches of CuP in hind wing [one in *M. hopkinsi*, *M. antiquissima*].

Description. *Holotype.* Forewing 12.4 mm long, approximately 3.9 mm wide (length/width: 3.2). Costal space broad, strongly dilated at proximal 1/4 length; eight preserved subcostal veinlets simple (probably nine to ten total), three basal veinlets more closely spaced. ScP relatively long, terminating on costal margin slightly distad crossvein 2ra-rp; length from termination of ScP to pterostigma approximately equal to length of pterostigma. Subcostal space broad, with basal crossvein located in middle between origin of RP, divergence of M, CuA; distal crossvein (2scp-r, forming basal margin of pterostigma) slightly incurved. Pterostigma relatively short, strongly pigmented. Two RA branches (none detected within pterostigma); one forming distal margin of pterostigma; other distad pterostigma; none forked. RA joining margin well before apex. RA space with two crossveins forming two radial cells: 2ra-rp located well proximad pterostigma, slightly proximad termination of ScP; 3ra-rp located in middle of pterostigma along RA. RP originates at nearly half (0.44) wing length, with five pectinate branches: RP1 deeply dichotomously forked twice; other branches forked once. One long intraradial crossvein rp1-rp2 between stem of RP, RP1. Three crossveins between RP, MA: 1r-m, 2r-m connecting stem of RP, MA; 3r-m connecting RP1, anterior branch of MA. M close to R (appears fused) for considerable distance, and then fused with CuA for short distance; forked well proximad origin of RP. MA deeply dichotomously forked twice. MP zigzagged, anterior trace with three simple branches (proximal-most branch fused basally for long distance with CuA). Two intramedian crossveins form two *doi*, approximately equal in length. Cu basally not visible; dividing to CuA, CuP relatively close to wing base. Anterior trace CuA strongly zigzagged, fused with MP for long distance to form part of posterior margin of basal *doi*, and then with proximal-most branch of MP; two pectinate long simple branches, their bases close). CuP simple, aligned with Cu. Crossvein icu between CuA, CuP long. AA1 with shallow fork near margin; AA2, AA3 simple. One short crossvein iaa in anal space, between AA1, AA2.

Hind wing 11.6 mm long, approximately 3.5 mm wide (length/width: 3.3). Costal space relatively broad (incompletely preserved); four preserved simple subcostal veinlets, widely spaced. ScP relatively long; length from termination of ScP to pterostigma slightly shorter than length of pterostigma. One crossvein detected in subcostal space (2scp-r, forming basal margin of pterostigma), slightly incurved. Pterostigma elongate, slightly longer than in forewing. RA with two branches (one presumably within pterostigma not detected); branch forming distal margin of pterostigma slightly curved; one simple branch distad pterostigma; portion of RA distad pterostigma relatively short. Three crossveins between RA, RP: 1ra-rp located slightly distad 2r-m; 2ra-rp located clearly proximad termination of ScP; 3ra-rp terminating within pterostigma, just proximad its middle along RA. RP originating 0.39 wing length, with five pectinate branches, two proximad 3ra-rp, three distad. RP1 deeply dichotomously forked twice; other branches rather deeply forked once each. One intraradial crossvein rp1-rp2 between RP1, RP2. Three crossveins between R, M: 1r-m very long, subparallel to R connecting to RP near its origin (its base unclear); 2r-m connecting stems of RP, MA; 3r-m connecting RP1, anterior branch of MA. M forked proximad origin of RP. MA deeply dichotomously forked twice. MP: anterior trace zigzagged, simple, with three simple, pectinate branches.

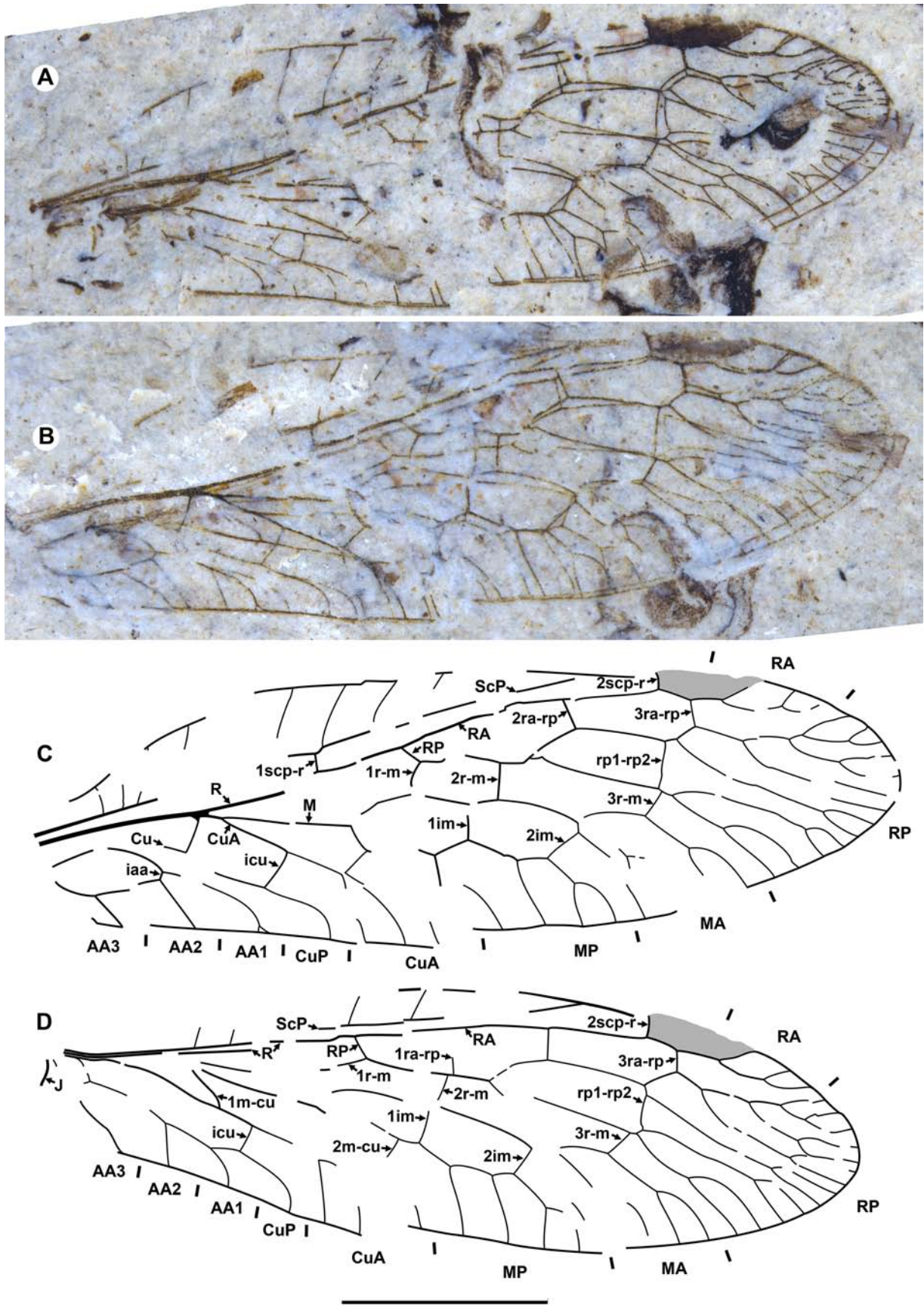


FIGURE 5. *Megaraphidia klondika* sp. nov., holotype. A, counterpart UWBM 97073; B, part SR03-01-01; C, forewing venation; D, hind wing venation. Scale bar = 3 mm (all to scale).

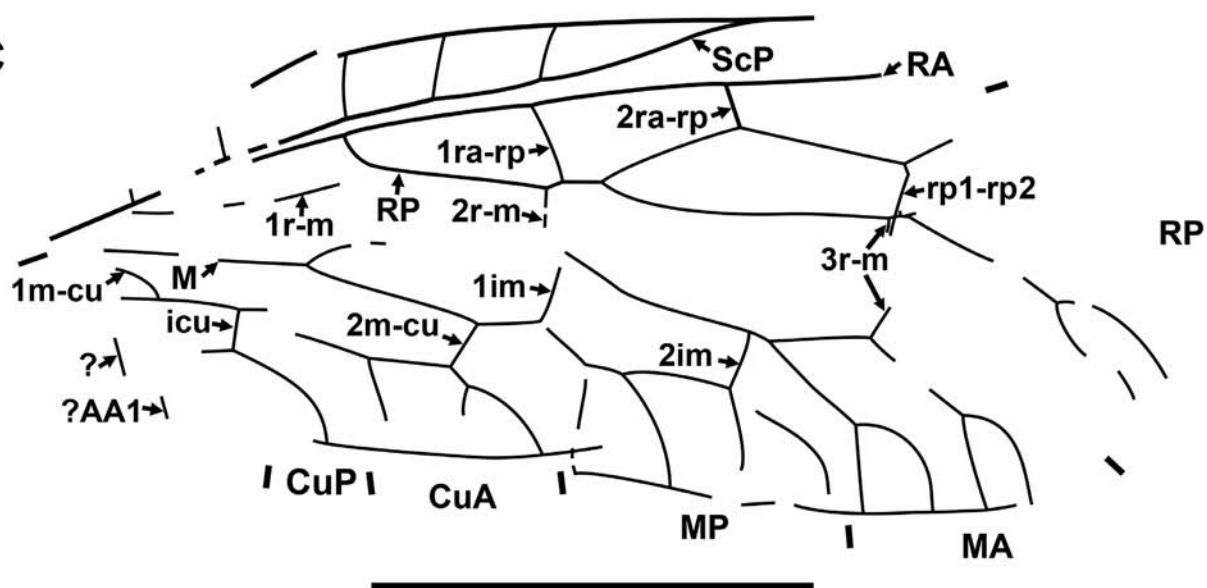
A**B****C**

FIGURE 6. *Megaraphidia klondika* sp. nov., specimen SRUI99-71-63. A, part; B, counterpart; C, drawing of the hind wing venation. Scale bar = 3 mm (all to scale).

Two intramedian crossveins forming two *doi*, approximately equal in length. Two crossveins between M and Cu: basal 1m-cu long, very oblique, connecting M, CuA; 2m-cu straight, perpendicular to MP, connecting it, CuA. Anterior trace of CuA probably simple distally, with two simple branches (incompletely preserved). One crossvein (icu) between CuA, CuP long. CuP originating very closely to wing base; fused with AA1+2, then AA1 for long distance. AA1 basally fused with AA2 for long distance. AA3 simple. Jugal vein stout.

SRUI99-71-63 (Fig. 6). Hind wing 7.7 mm long as preserved (11 mm estimated length), 3.5 mm wide as preserved (approximately identical to estimated width). Costal space relatively broad (incompletely preserved); five preserved subcostal veinlets (three distal-most simple), widely spaced. Subcostal space narrow proximally, broadened distally; no crossveins, pterostigma preserved. Distal part of RA not preserved. Two crossveins between RA, RP preserved: 1ra-rp located slightly distad 2r-m; 2ra-rp located clearly proximad termination of ScP. RP originates far from wing base, with only RP1 partially preserved. One intraradial crossvein (rp1-rp2) detected, between RP1, RP2 near its origin. Three crossveins between R, M: 1r-m very long, subparallel to R connecting to RP near its origin (its base unclear); 2r-m connecting stems of RP, MA; 3r-m connecting RP1, anterior branch of MA. M forked proximad origin of RP. MA deeply dichotomously forked twice. MP: anterior trace zigzagged, simple, with three simple, pectinate branches. Two intramedian crossveins forming two *doi*, approximately equal in length. Two crossveins between M and Cu: basal 1m-cu long, very oblique, connecting M, CuA; 2m-cu straight, connecting it, CuA. Anterior trace of CuA simple distally, with two probably simple branches (incompletely preserved). Small distal portions of CuP, AA1 preserved.

SR 16-004-001-01.01 (Fig. 7, 10F). Distal part of wing preserved, 5.7 mm long, 3.4 mm wide. Pterostigma elongate, 1.72 mm long (along costal margin), 0.47 mm wide (length/width: 3.66). RA with three branches: one within pterostigma indistinct; branch forming distal margin of pterostigma slightly curved; one simple branch distad pterostigma. Portion of RA distad pterostigma relatively short (along costal margin), 0.63 length of pterostigma. Two crossveins between RA, RP preserved; 3ra-rp located in distal part of pterostigma. RP with five pectinate branches, two proximad 3ra-rp, three distad. RP1 rather deeply forked; its anterior branch simple, posterior forked. Other branches forked once each. One intraradial crossvein rp1-rp2 between origin of RP1, RP2. Two crossveins between R, M detected: 2r-m connecting stems of RP, probably MA; 3r-m connecting RP1, anterior branch of MA. MA deeply dichotomously forked twice.

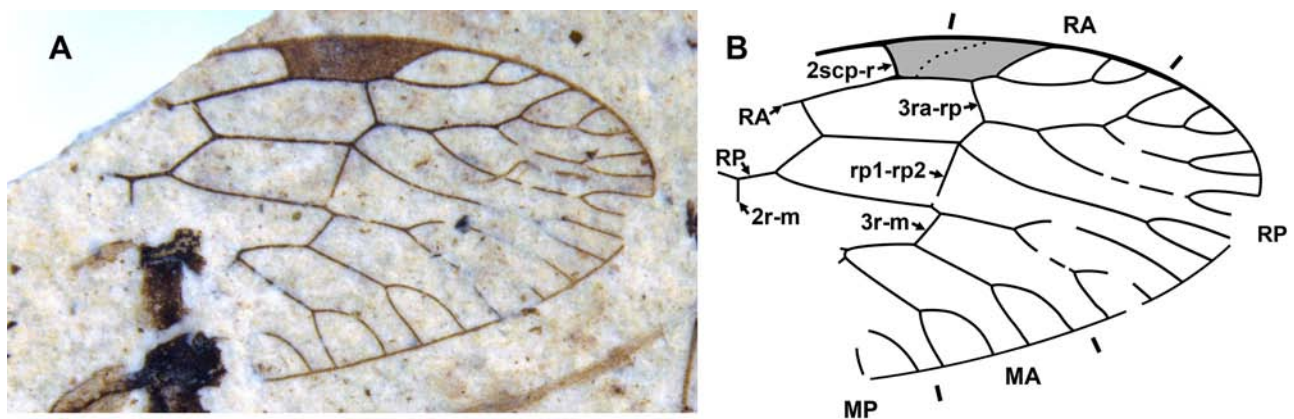


FIGURE 7. *Megaraphidia klondika* sp. nov., specimen SR16-004-001-01.01. A, specimen as preserved; B, drawing. Scale bar = 3 mm (both to scale).

Remarks. The preserved hind wing venation of SRUI-99-71-63 is almost identical to that of the hind wing of the holotype.

It is not determinable if specimen SR 16-004-001.01, the distal part of a wing, is a forewing or hind wing. Its venation differs from that of the holotype by its slightly more distal position of crossvein 3ra-rp, more distal forking of RP1, the anterior branch of RP1 being simple, and as a branch of RA within the pterostigma is visible, although indistinct (Fig. 10F). We preliminarily consider these differences as intraspecific variability.

Megaraphidia hopkinsi sp. nov.

Figs 8, 9

Raphidioptera: Greenwood *et al.*, 2005: 180, Fig. 4.

Type material. Holotype UWBM77544, collected by Donald Hopkins in 1990; deposited in the UWBM collections. A nearly complete female specimen preserved in lateral aspect, except the head in ventral aspect.

Type locality and horizon. The One Mile Creek exposure of the Allenby Formation north of Princeton, British Columbia, Canada (part of the Okanagan Highlands series); early Eocene (Ypresian).

Etymology. The specific epithet is a patronym formed from the surname of Don Hopkins, collector of the holotype.

Diagnosis. May be distinguished from other species of *Megaraphidia* by broad head [cuneate in *M. ootsa*]; forewing costal space narrow (2 times wider than subcostal space) [2.3 in *M. antiquissima*, 2.6 in *M. exhumata*, 2.9 in *M. klondika*, 3.0 in *M. elegans*]; subcostal veinlets more strongly inclined than in other species.

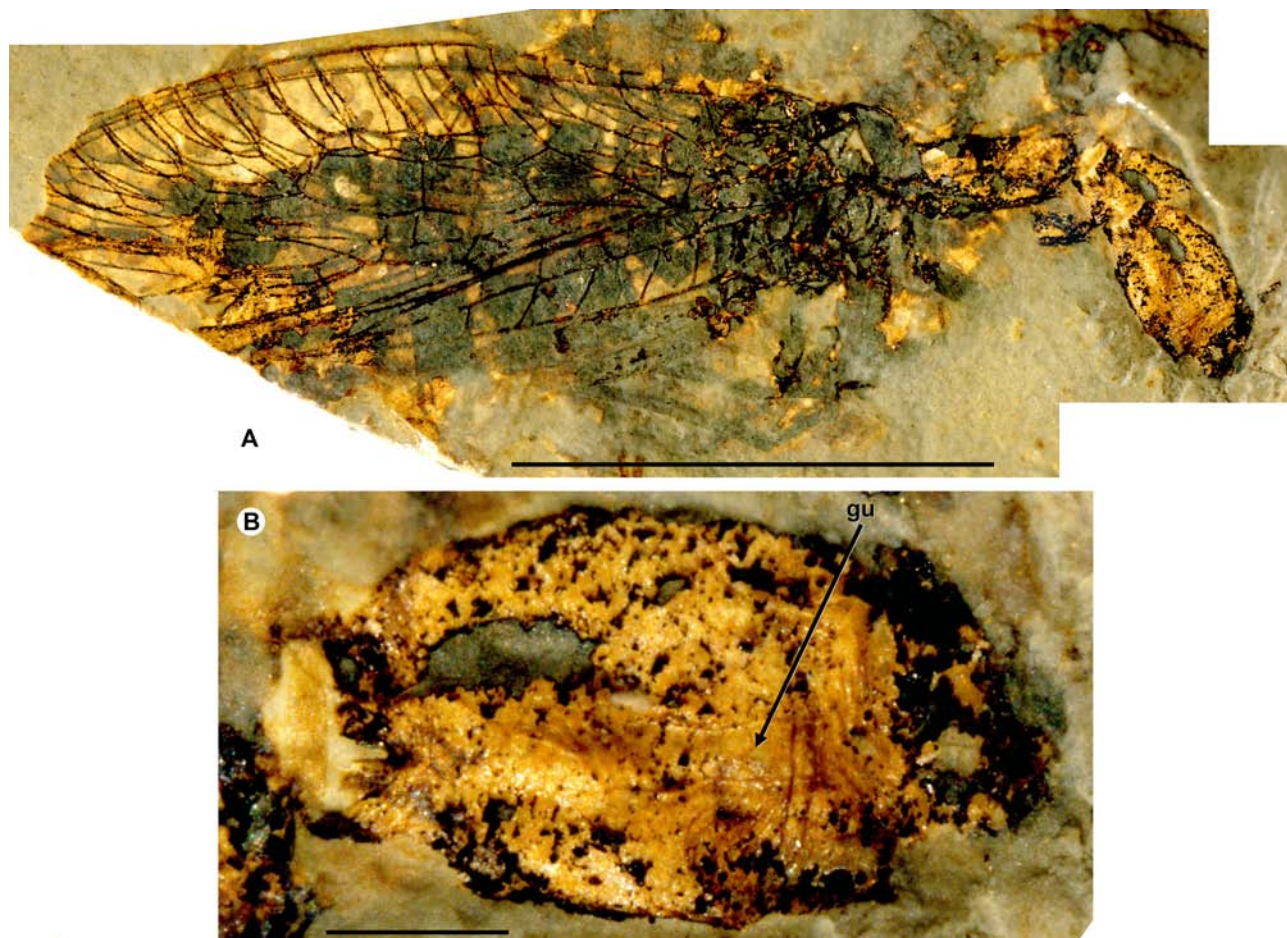


FIGURE 8. *Megaraphidia hopkinsi* sp. nov., holotype UWBM77544. A, specimen as preserved; B, head. gu, gula. Scale bars = 5 mm (A), 1 mm (B).

Description. Female. Body length (without ovipositor) approximately 11.3 mm. Head disarticulated, exposed ventrally, yellowish-brown; broad, not narrowed posteriorly except for posterior-most short portion; gula well discernible, narrow. Mouthparts very poorly preserved, incomplete. Prothorax broad in lateral view, relatively short, approximately 2 mm long (0.18 body length); mainly yellowish-brown. Meso-, metathorax, legs appear very dark, blackish; details poorly discernible. Abdominal tergites, sternites very dark, poorly preserved; 9th tergite narrow; ectoproct appears large; ovipositor incompletely preserved.

Forewing: 8.0 mm long as preserved (approximately 9.4 mm estimated length), 2.95 mm wide (estimated length/width: 3.19). Costal space moderately broad, dilated at proximal 1/4 length; nine subcostal veinlets simple, distally widely spaced, proximally more closely spaced. ScP relatively long, terminating on costal margin slightly distad

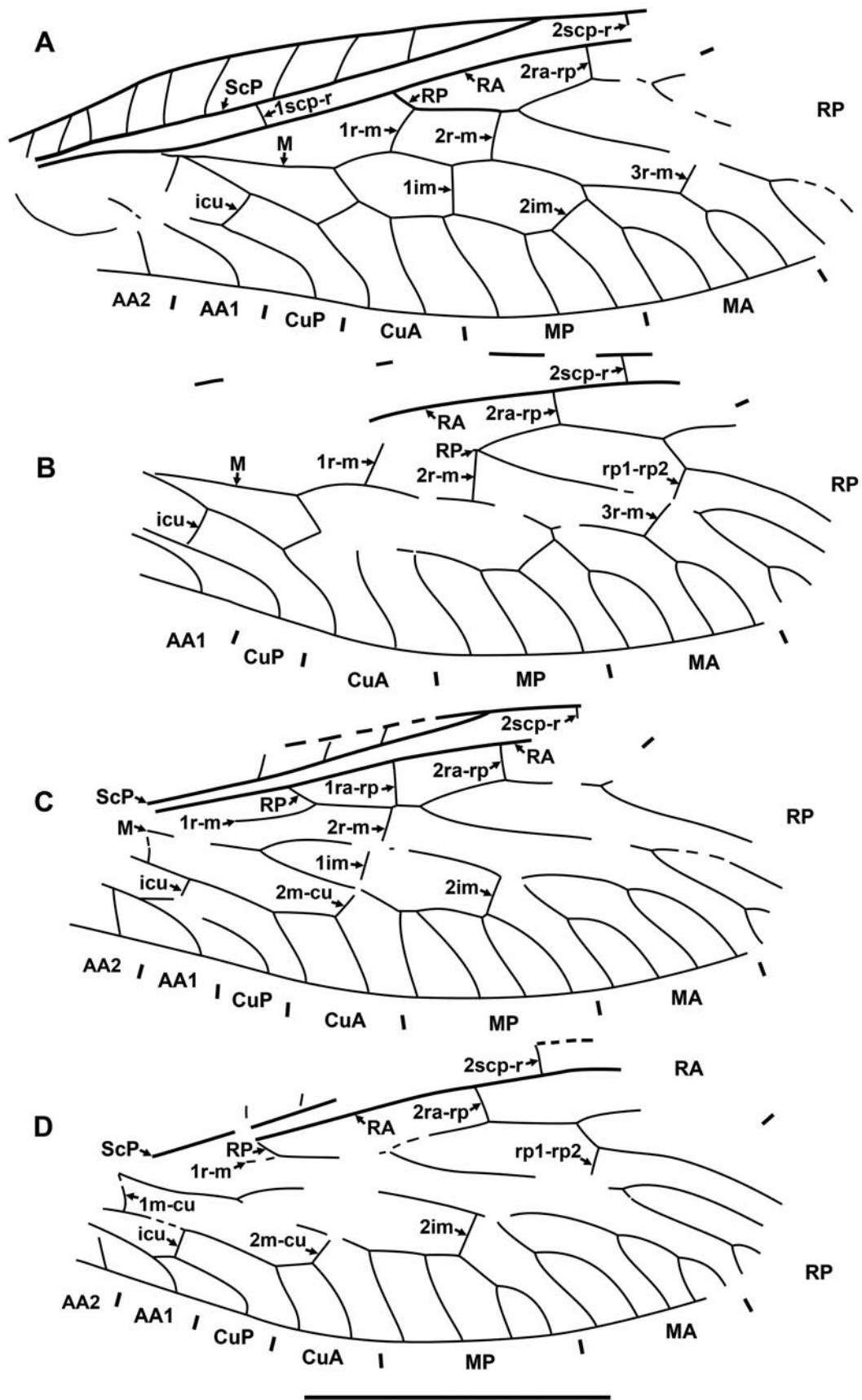


FIGURE 9. Wing venation of *Megaraphidia hopkinsi* sp. nov., holotype UWBM77544. A, right forewing; B, left hind wing; C, right forewing; D, left hind wing. Scale bar = 3 mm (all to scale).

crossvein 2ra-rp. Subcostal space very broad, with basal crossvein located farther to origin of RP than to divergence of M, CuA; distal crossvein (2scp-r, forming basal margin of pterostigma) straight. Only poorly preserved proximal-most part of pterostigma discernible. RA space with one preserved crossvein (2ra-rp) well proximad pterostigma. RP originating 0.46 estimated wing length, with two preserved proximal branches: RP1 deeply, dichotomously forked, with anterior branch simple, posterior branch shallowly forked (right wing); relatively shallowly forked once (left wing). RP2 incompletely preserved. One intraradial crossvein rp1-pr2 between stem of RP1, RP2. Three crossveins between RP, MA: 1r-m, 2r-m connecting stem of RP, MA; 3r-m connecting RP1, anterior branch of MA. M fused with CuA for very short distance; forked well proximad origin of RP. MA deeply, dichotomously forked twice. MP slightly zigzagged, anterior trace with two simple long branches. Two long intramedian crossveins form two *doi*; basal *doi* slightly shorter than distal. Anterior trace of CuA strongly zigzagged, fused with MP for short distance to form part of posterior margin of basal *doi*; one long simple branch. CuP simple distally. Crossvein icu between CuA, CuP long. AA1 simple; AA2+AA3 then AA2 strongly incurved, simple distally; AA3 not preserved.

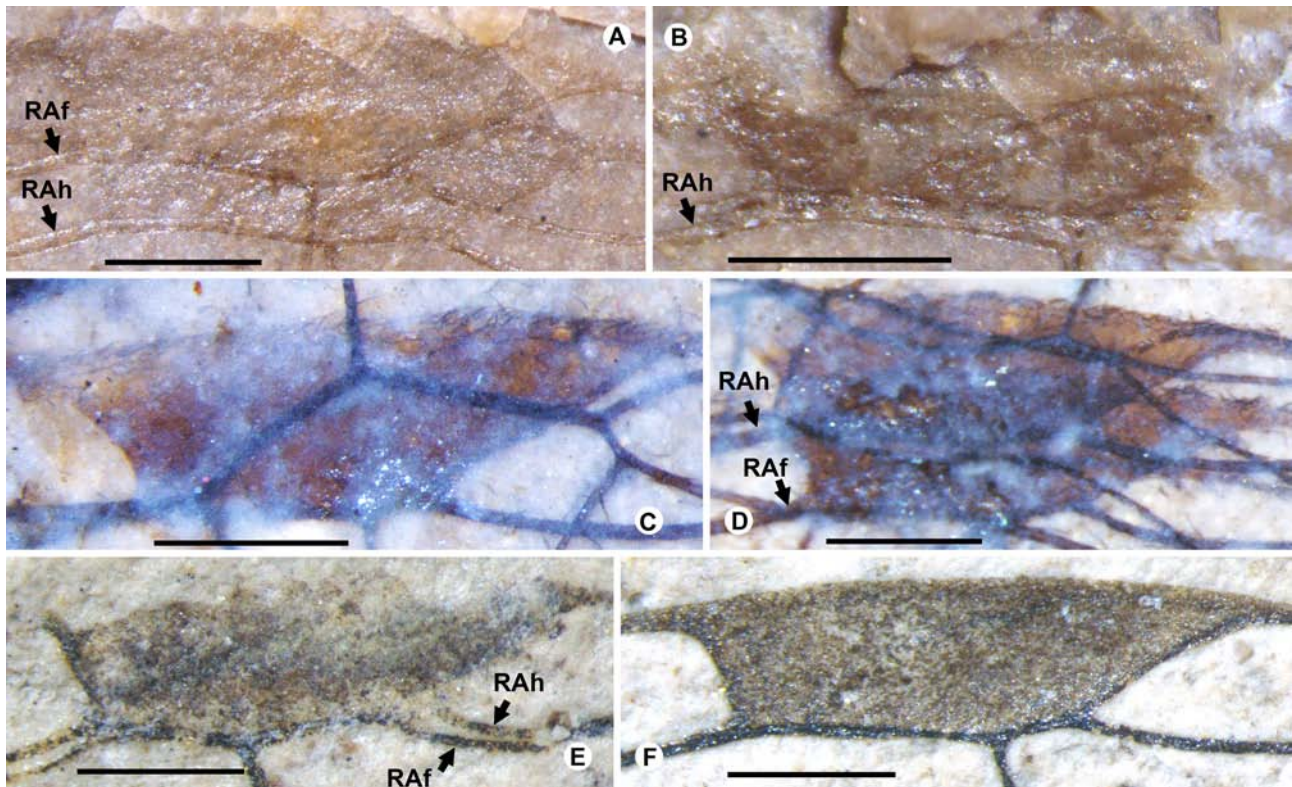


FIGURE 10. Pterostigmata of *Megaraphidia*. A, *M. antiquissima* sp. nov., right wings of the holotype RBCM P1555; B, *M. antiquissima* sp. nov., left wings of same specimen; C, *M. ootsa* sp. nov., right hind wing of the holotype RBCM P1556; D, *M. ootsa* sp. nov., left wings of same specimen; E, *M. klondika* sp. nov., holotype, an overlapping forewing and hind wing SR03-01-01; F, *M. klondika* sp. nov., specimen SR-16-004-001-1. RAf, RA of forewing; RAh, RA of hind wing. Scale bars = 0.5 mm.

Hind wing: 6.9 mm long as preserved (approximately 8.6 mm estimated length), 2.75 mm wide (estimated length/width: 3.12). Costal space relatively narrow (incompletely preserved); three preserved simple subcostal veinlets, widely spaced. ScP relatively long. One crossvein detected in subcostal space (2scp-r, forming basal margin of pterostigma), straight. Only proximal part of pterostigma, poorly preserved. Two crossveins between RA, RP preserved: 1ra-rp located slightly distad 2r-m; 2ra-rp located slightly distad termination of ScP. RP originating 0.32 estimated wing length, with two preserved pectinate branches. RP1 deeply dichotomously forked, with anterior branch simple, posterior branch shallowly forked; RP2 incompletely preserved. One intraradial crossvein rp1-rp2 between RP1, RP2. Two preserved crossveins between R, M: 1r-m very long, subparallel to R connecting to RP near its origin (its base not preserved); 2r-m connecting stems of RP, MA. M forked proximad origin of RP. MA deeply, dichotomously forked twice. MP: anterior trace slightly zigzagged, simple, with three simple pectinate branches, all long (right wing), two long, one short (left wing). Two intramedian crossveins forming two *doi*; basal *doi* markedly shorter than distal. Two crossveins between M and Cu: basal 1m-cu long, curved, somewhat oblique (with its ante-

rior end inclined to wing base), connecting M, CuA; 2m-cu straight, with its anterior end inclined toward apex, connecting MP, CuA. Anterior trace of CuA simple distally, with one simple branch. One crossvein (icu) between CuA, CuP long. CuP fused with AA1+2, then AA1 for long distance. AA1 basally fused with AA2. AA3 not preserved.

Remarks. The broad head of this species is rather similar to that of *e.g.*, species of *Phaeostigma* and *Agulla arizonica* (Banks, 1911), but its shape is not characteristic of most other Raphidiidae, in which the head is clearly narrowed posteriorly (cuneate) (*e.g.*, *Megaraphidia ootsa*: Fig. 3A). Some species of Raphidiidae (including *A. arizonica*), however, show striking variation in head shape (see *e.g.*, Carpenter, 1936: Fig. 5).

The variation of venation seen in the left and right wings of the holotype shows a remarkable example of fluctuating asymmetry (*i.e.*, non-directional deviation from bilateral symmetry: Palmer & Strobeck, 1986). RP1 is forked only once in the right wing (1), but twice in the left; and the anterior branch of MP is forked once in the right wing, but twice in the left (2) (see Fig. 9). Condition (1) occurs very rarely in fossil Raphidiidae in North America (and this is its first record in the early Eocene), and condition (2) is not detected in any other of these specimens.

Genus *Archiinocellia* Handlirsch, 1910, *sit. nov.*

Diagnosis. Relatively small raphidiids (forewing up to 8 mm long), distinguished from other genera of the family by the following combination of character states. Fore- and hind wings: (1) ScP short (length from termination to pterostigma greater than that of pterostigma) [relatively long ScP (length from termination to pterostigma approximately equal to or less than that of short pterostigma) in *Megaraphidia*]; (2) pterostigma elongate (4.5–5.1 times longer than width measured along to costal margin) [short in *Megaraphidia*, *Archiraphidia*]; (3) 3ra-rp located within the pterostigma; (4) RP1 twice forked, proximal fork proximad level of 3ra-rp. Hind wing: (5) two *doi* [one in *Archiraphidia*]; (6) CuA with one branch [three in *Florissantoraphidia*].

Type species. *Archiinocellia oligoneura*, by monotypy.

Species included. *A. oligoneura*, *A. protomaculata* (Engel, 2011), **comb. nov.**

Occurrence. Ypresian of the Okanagan Highlands at Horsefly, British Columbia, Canada, Canada; the late Ypresian Green River Formation, Colorado, United States of America.

Remarks. The genus was originally considered to be of unknown family (Handlirsch, 1910; Martynov, 1925; Carpenter, 1936). Aspöck *et al.* (1991) assigned it to the Inocelliidae, but more recent authors have treated it again as Raphidioptera *incertae sedis* (*e.g.*, Oswald, 1990; Carpenter, 1992; Nel, 1993; Engel, 2002, 2009). Here, we assign it to the Raphidiidae by venation characteristic of the family, including the placement of crossvein 2ra-scp at the proximal end of the pterostigma.

Archiinocellia protomaculata from the Green River Formation was originally assigned to *Agulla* (Engel, 2011: Figs 1–9). We believe that this is incorrect by its wing venation, which possesses at least three important character states not present in that genus. First, the basal 1r-m in the hind wing of this species is long and subparallel to R (clearly visible in Fig. 17D and the paratype USNM 31752), but it is crossvein-like in all known species of *Agulla* (see *e.g.*, Carpenter, 1936: Fig. 1). Secondly, the crossvein 3ra-rp in both wings is located within the pterostigma in this species, whereas it is normally located distad the pterostigma in all known species of *Agulla* (*e.g.*, see Carpenter, 1936: Fig. 1); very rarely, adventitiously at the distal end of pterostigma (*e.g.*, Wognum, 1959: Figs 20, 35; Aspöck, 1987: Fig. 1); and only abnormally within the pterostigma in one of the wings (*e.g.*, Wognum, 1959: Fig. 21). Thirdly, ScP is very short in this species, whereas it is long in all species of *Agulla* (from its termination to the pterostigma is nearly equal to the length of pterostigma or slightly shorter in the species of *Agulla*).

We assigned *Archiinocellia protomaculata* to this genus as its venation is very similar to the preserved venation of *A. oligoneura*, agreeing with all character states of the genus diagnosis.

Of extant genera, the venation of *Archiinocellia protomaculata* is most similar to that of *Alena* Navás, 1916, the southern-most genus of Raphidiidae in the Western Hemisphere, occurring in south-western United States of America and Mexico (south to Chiapas) with ten species (Aspöck, 1975; Aspöck & Aspöck, 2013). A combination of the following features is characteristic of only five species of this genus among extant Raphidiidae: (A) the basal crossvein 1r-m in the hind wing is long, subparallel to R; (B) very short ScP (from its termination to pterostigma is much longer than the length of pterostigma), and (C) the proximal position of the crossvein 3ra-rp (*i.e.*, located within the pterostigma) in both wings. The venation of *A. protomaculata* shares all of these character states. It is most similar to that of some species of the Mexican genus *Alena* (*e.g.*, *Alena americana* Carpenter, 1958, *A. caudata*

(Navás, 1914b); see Carpenter, 1958: Fig. 1; Aspöck & Aspöck, 1970: Fig. 3). The only venational feature clearly distinguishing *A. protomaculata* from extant species of *Alena* is the branching of RP1. It is forked twice, with the proximal fork located very deeply, proximad the level of 3ra-rp, while RP1 is forked once in most species of *Alena*, and in the few other species of *Alena* it is forked twice (*i.e.*, *A. americana*, *A. tenochtitlana* Aspöck & Aspöck, 1978), the proximal fork is relatively shallow (distad the level of 3ra-rp). However, the shape of the male terminal segments of *Archiinocellia protomaculata* fundamentally differs from those of all species of *Alena*. In *A. protomaculata*, the ninth tergite extends laterally to the ventral margin, and is probably fused with the ninth sternite to form a ring, a plesiomorphic condition at the family level, characteristic of all Raphidiidae except *Alena*, in which these are widely separated (Haring *et al.*, 2010). The apparent absence of sclerotized gonocoxites 9 in *A. protomaculata* is also noteworthy and probably plesiomorphic at the family level. But we do not know if these terminal characters are also shared by other two species of the genus.

In all extant genera, these are the largest sclerites of the terminalia and are strongly sclerotized (Aspöck & Aspöck, 2008). Gonocoxites 9 are also well developed in the Baltic amber *Succinoraphidia exhibens* Aspöck & Aspöck (Aspöck & Aspöck, 2004: Fig. 6).

Makarkin & Archibald (2014) referred *Archiraphidia? somnolenta* (Scudder, 1890) from Florissant to that genus only provisionally. It is similar to *Archiinocellia* in some ways, sharing with *Archiinocellia oligoneura* the following character states: (1) *Archiraphidia? somnolenta* has a long pterostigma, 4.5 to 5 times longer than wide (*A. oligoneura*, 4.6–4.7), while those of *Archiraphidia* species are much shorter, 2.3 to 3.2 times longer than wide, and (2) both have two *doi* in the hind wing (one in species of *Archiraphidia*). However, the ScP of *Archiraphidia? somnolenta* is slightly longer than in *Archiinocellia oligoneura* and *A. protomaculata*, somewhat differing from character state (1) of the *Archiinocellia* diagnosis, and the proximal-most branching of RP1 is clearly distad the level of 3ra-rp, contradicting diagnostic character state (4). The taxonomic placement of *Archiraphidia? somnolenta* will be clarified by the discovery of more complete specimens; the species does not belong to *Archiinocellia* and probably does not belong to *Archiraphidia*.

Of fossil genera, the venation of *Archiinocellia* is most similar to that of *Archiraphidia* and *Florissantoraphidia*, which share character states A–C. However, *Archiinocellia* clearly differs from these genera as stated in its diagnosis.

***Archiinocellia oligoneura* Handlirsch, 1910**

Fig. 11

Type material. Holotype GSC 7250, collected by L[awrence]. M. L[ambe], 21.vii.1906, deposited in the collections of the GSC, Ottawa. Portions of overlapped fore- and hind wings covered with Canada balsam.

Type locality and horizon. “Opposite Horsefly mine”, Horsefly, British Columbia, Canada; early Eocene (Ypresian).

Diagnosis. May be distinguished from *A. protomaculata* by clearly wider wings (forewing length/width 2.69–3.08 in *A. oligoneura*; 3.63–4.15 in *A. protomaculata*).

Redescription. Forewing 7–8 mm long (estimated), 2.6 mm wide. Costal space not preserved. ScP very short, terminating on costal margin strongly distad crossvein 2ra-rp; length from termination of ScP to pterostigma slightly greater than length of pterostigma. Distal part of subcostal space broad, with distal crossvein 2scp-r nearly straight. Pterostigma elongate (4.6 times longer than width measured along to costal margin), lightly pigmented. At least two branches of RA: one within pterostigma, strongly inclined, in middle of pterostigma; other forming distal margin of pterostigma; no branch distad pterostigma discernible. RA space with two crossveins forming two radial cells nearly equal in length: 2ra-rp located about mid-way between pterostigma, termination of ScP; 3ra-rp located in distal part of pterostigma along RA. RP originating at obtuse angle, with three pectinate branches: RP1 deeply forked, with anterior branch simple, posterior forked; other branches (RP2, RP3) simple. One long intraradial crossvein rp1-rp2 between stems of RP, RP1. Two preserved between RP, MA (1r-m, 2r-m) connecting stem of RP, MA. M forked well proximad origin of RP, probably fused with CuA for short distance. MA deeply, dichotomously forked twice. MP strongly zigzagged, anterior trace with two simple branches. Two intramedian crossveins form two *doi* (distal *doi* markedly longer): 2im very long, joins posterior branch of MA. Anterior trace CuA strongly zigzagged, fused with MP for long distance to form part of posterior margin of basal *doi*. Crossvein icu between CuA, CuP long. Basal portion, CuP, anal veins not preserved or not clearly understandable.

Hind wing about 6.5–7 mm long (estimated), 2.25 mm wide. Costal space and ScP not preserved. One crossvein detected in subcostal space, 2scp-r, forming basal margin of pterostigma. Distal part of subcostal space broad, with distal crossvein 2scp-r nearly straight. Pterostigma elongate (4.7 times longer than width measured along to costal margin), lightly pigmented. At least two branches of RA: one within pterostigma, strongly inclined, in middle of pterostigma; other forming distal margin of pterostigma; no branches distad pterostigma discernible. RA space with two preserved crossveins: 2ra-rp distad termination of ScP; 3ra-rp located in distal part of pterostigma along RA. RP with three pectinate branches: RP1 deeply forked, with anterior branch simple, posterior forked; other branches (RP2, RP3) simple. One long intraradial crossvein rp1-rp2 between stems of RP, RP1. Two preserved between RP, MA: 2r-m connects stem of RP, MA; 3r-m connects stem of RP1, MA. M probably forked proximad origin of RP. MA deeply dichotomously forked twice. MP: anterior trace zigzagged, simple, with three simple, pectinate branches (alternatively: anterior trace forked, with two simple, pectinate branches). Two intramedian crossveins form two *doi*, proximal much shorter than distal. One preserved crossvein between M, Cu (2m-cu) connecting MP, CuA. Anterior trace of CuA simple distally, with one preserved simple branch. Basal portion, CuP, anal veins not preserved or not clearly understandable.

Remarks. Handlirsch (1910) incorrectly believed that his Fig. 4 depicted the forewing and his Fig. 5 the hind wing, however, the opposite is true.

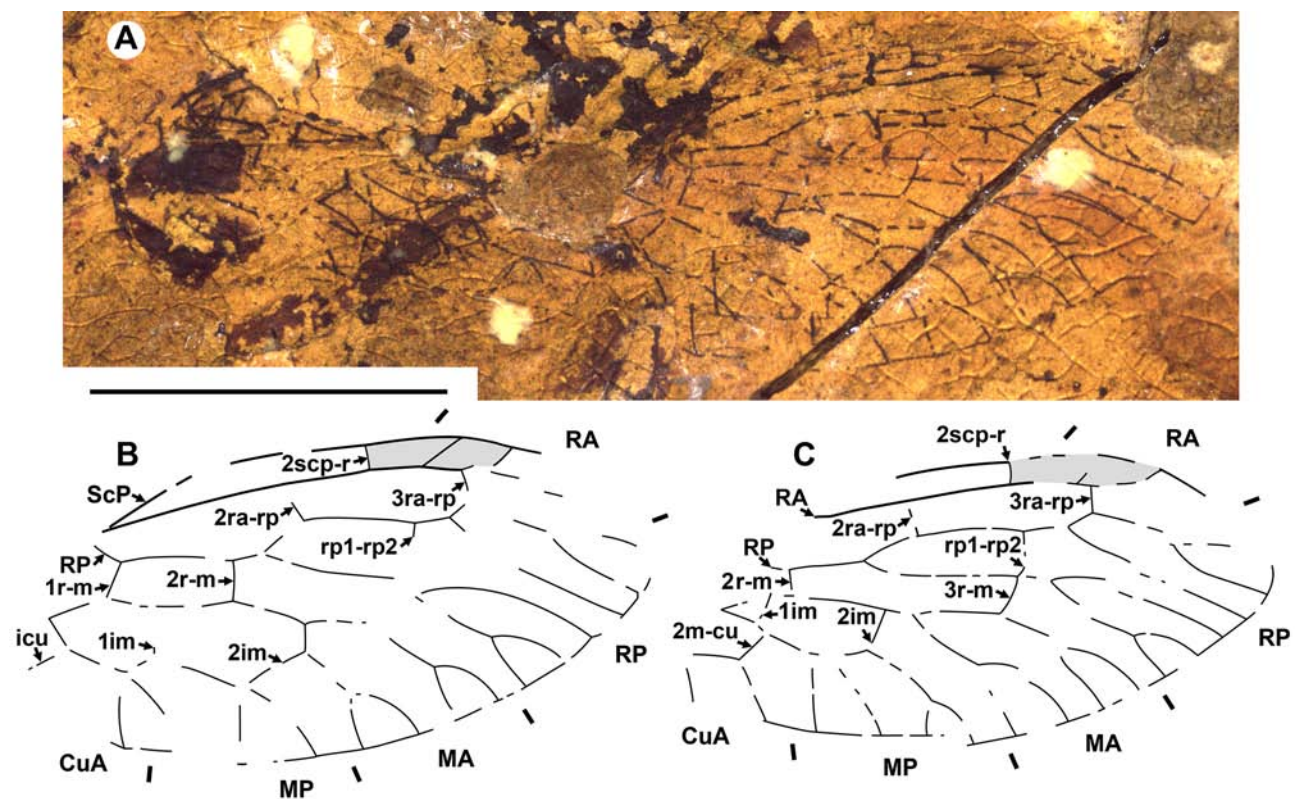


FIGURE 11. *Archiinoceilia oligoneura* Handlirsch, 1910. A, holotype GSC 7250; B, forewing venation; C, hind wing venation. Venation drawn in B and C overlap on the right half of the photograph, venation on the left side could be of either wing. Scale bars = 3 mm.

***Archiinoceilia protomaculata* (Engel, 2011), comb. nov.**

Figs 12–17

Material examined. Thirty-six specimens collected by David D. Kohls in 2004 to 2009 at three localities in Garfield County (Colorado, U.S.A.): (1) UCM locality 2005026 (Labandeira Site): specimens UCM 35717 (female); UCM 40659 (male); UCM 58068 (sex unknown); UCM 59090 (female); UCM 59509 (male); UCM 60297 (female); UCM 61231a (female); UCM 61231b (male); UCM 61231c (sex unknown); UCM 62026 (male); UCM 62523 (sex unknown); UCM 62525 (three specimens: male, female, and sex unknown); UCM 62687 (female); UCM 64319

(sex unknown); UCM 64727 (female); UCM 65146 (sex unknown); UCM 66134 (sex unknown); UCM 67986 (female); UCM 72989 (female); UCM 73247 (female); (2) UCM locality 2006032 (Donnell Site): UCM 40057 (male); UCM 42684 (male); UCM 42744 (female); UCM 45968 (female); UCM 45969 (female); UCM 45970 (female); UCM 53268 (female); (3) UCM locality 2007238 (Denson Site): UCM 41697 (male); UCM 42105 (female); UCM 42107 (female); UCM 42122 (sex unknown); UCM 54806 (male); UCM 55329 (female); UCM 56552 (female); the Parachute Creek Member of the Green River Formation; all are deposited in UCM collections.

Type locality and horizon. Probably Labandeira Site in the Parachute Creek Member of the Green River Formation, Garfield County, Colorado, U.S.A.; early Eocene (Ypresian).

Diagnosis. May be distinguished from *A. oligoneura* by markedly narrower fore- and hind wings (see above).

Redescription (based on the holotype and material from UCM listed above): body length of male 8.1–9.2 mm (five specimens), female (without ovipositor) 8.7–9.1 mm (seven specimens). Head broadly oval, somewhat narrowed posteriorly (in dorsal view); dorsal maculation very distinct with extensive pale areas (Fig. 15), especially beyond and around eyes, broad medial stripe (sometimes divided by a thin brown medial line: Fig. 15F), and most areas before the eyes. Palpi brownish. Antennae: scapus brown to dark brown; flagellum distinctly paler, with slightly more than 40 segments. Ocelli not detected.



FIGURE 12. *Archiinocecellia protomaculata* (Engel, 2011), females. A, holotype USNM 31487 (counterpart); B, UCM 42107. Scale bars = 5 mm.

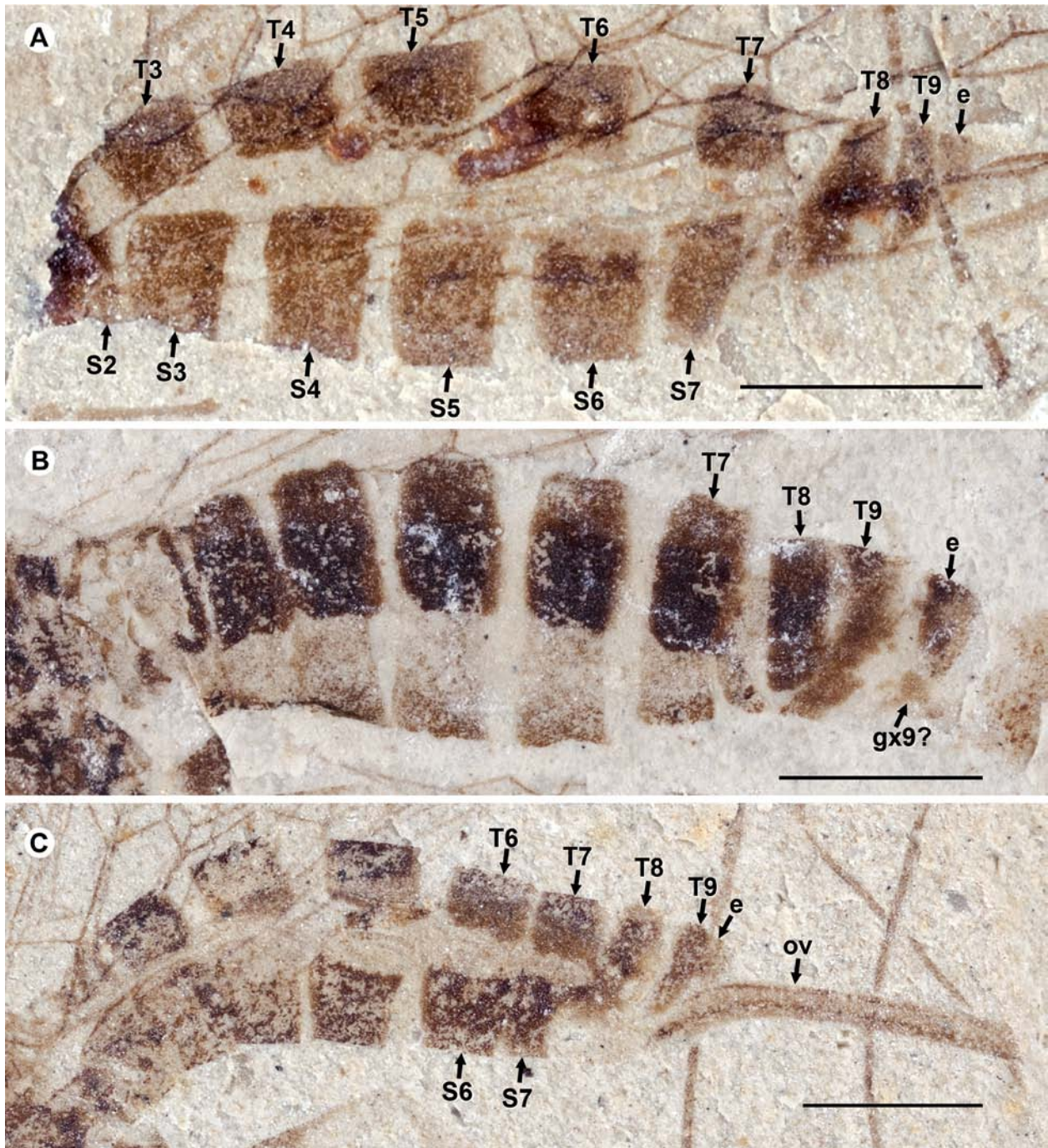


FIGURE 13. *Archiinoceilia protomaculata* (Engel, 2011), abdomen. A, UCM 61231b, male (lateral/slightly dorsal view); B, UCM 42684, male (lateral view); C, UCM 45968, female. e, ectoproct; gx9?, possible gonocoxites 9; ov, ovipositor; S2 to S7, second to seventh sternites; T3 to T9, third to ninth tergites. Scale bars = 1 mm.

Pronotum dark brown, relatively short, 1.20–1.50 mm long; maximum width 0.57 mm in dorsal view, 0.65 mm in lateral view. Meso- and metathorax dark brown.

Legs pale except brown in proximal half of femora and in coxae (Fig. 12).

Abdomen of male (Fig. 13): Tergites, sternites dark, easily distinguished; T3 to T7, and S3 to S7 nearly equal, moderately long; T8 slightly shorter than T3 to T7, extending laterally notably more than these tergites; T9 short, extending laterally to ventral margin; ectoproct short, elongate in lateral view, ventrally appears narrowed; gonocoxites 9 not discernible (as in Fig. 2A) or apparently weakly sclerotized (see Fig. 13B). Abdomen of female (Fig. 13C): Tergites, sternites dark, easily distinguished; T8, T9 relatively short; ectoproct small, elongate in lateral view; ovipositor moderately long, 3.25–3.80 mm (0.27–0.30 body length).



FIGURE 14. *Archiinocecellia protomaculata* (Engel, 2011). A, UCM 61231, rock with four specimens of *A. protomaculata* (a–c) and one undeterminable Raphidioptera (d); B, UCM 62523. Scale bars = 1 mm.

Forewing relatively narrow, 7.4–8.0 mm long, 1.8–2.2 mm wide (length/width: 3.63–4.15, measured in five females). Costal space narrow, most dilated at proximal 1/6 wing length; at maximum four subcostal veinlets simple preserved (basal regions not preserved, probably six total), widely spaced. ScP very short, terminating on costal margin approximately at just basad mid-wing, strongly distad crossvein 2ra-rp; from termination of ScP to pterostigma approximately double length of pterostigma. Subcostal space: basal crossvein 1scp-r closer to divergence of M, CuA than to origin of RP; distal crossvein (2scp-r, forming basal margin of pterostigma) straight to incurved. Pterostigma elongate (4.9–5.1 times longer than width measured along to costal margin), lightly pigmented (from very pale to slightly brownish as preserved). Two branches of RA: one within pterostigma usually easily visible, strongly inclined, in middle of pterostigma; branch forming distal margin of pterostigma usually straight; no branch distad pterostigma; portion of RA distad pterostigma short. RA space with two crossveins forming two radial cells nearly equal in length: 2ra-rp usually relatively short, located about mid-way between pterostigma, termination of ScP; 3ra-rp located in distal part of pterostigma along RA. RP originating at nearly half (0.43–0.48) wing length, usually with four pectinate branches (rarely three): RP1 deeply forked (at about half or somewhat less its length),

with anterior branch simple, posterior forked; other branches (RP2 to RP4) simple. One long intraradial crossvein rp1-rp2 between stems of RP, RP1. Three crossveins between RP, MA: 1r-m, 2r-m connecting stem of RP, MA; 3r-m connecting RP1, anterior branch of MA. M close to R (appears fused) for considerable distance, and then fused with CuA for short distance; forked well proximad origin of RP. MA deeply dichotomously forked twice. MP strongly zigzagged, anterior trace with two (rarely one) simple branches. Two intramedian crossveins form two *doi*, approximately equal in length (sometimes distal *doi* longer): 2im very long, joining posterior branch of MA near origin or at forking of MA. CuA fused with M for short distance; anterior trace CuA strongly zigzagged, fused with MP for long distance to form part of posterior margin of basal *doi*, with one long simple branch. CuP simple, aligned with Cu. Crossvein icu between CuA, CuP long. Crossveins between CuP, AA1, between AA1, AA2 short. AA1, AA2 simple; region of AA3 poorly discernible.

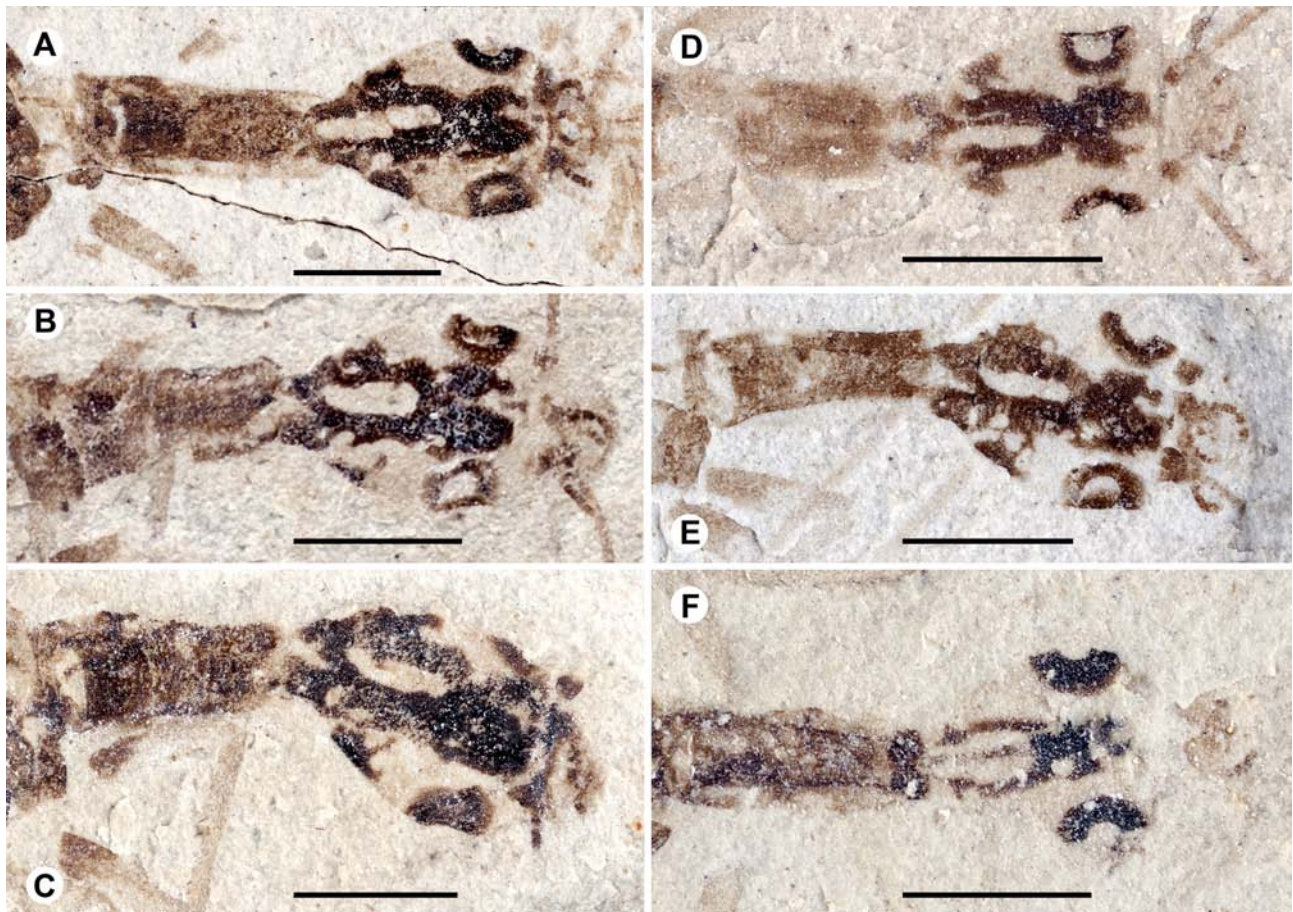


FIGURE 15. *Archinoceilia protomaculata* (Engel, 2011), head and prothorax (dorsal view). A, UCM 64727; B, UCM 62525; C, UCM 35717; D, UCM 45969; E, UCM 42122; F, UCM 62687. Scale bars = 1 mm.

Hind wing 6.5–7.1 mm long, 1.7 mm wide (length/width: 3.82). Costal space narrow; at maximum three discernible simple subcostal veinlets, very widely spaced (slightly wider than in forewing). ScP very short, terminating at approximately mid-wing; from termination of ScP to pterostigma approximately twice length of pterostigma. One crossvein detected in subcostal space, 2scp-r, forming basal margin of pterostigma, straight to incurved. Pterostigma elongate (4.5–5.1 times longer than width measured along to costal margin). RA with two branches: one within pterostigma usually clearly visible, strongly inclined, located medially in pterostigma; branch forming distal margin of pterostigma usually straight; no branches distad pterostigma; portion of RA distad pterostigma short. Three crossveins between RA, RP: 1ra-rp located slightly proximad 2r-m (rarer probably distad: Fig. 17B); 2ra-rp located far distad termination of ScP; 3ra-rp located just distad middle of pterostigma along RA. RP originating 0.33 wing length, with three to four pectinate branches, two proximad 3ra-rp, one to two distad. RP1 deeply forked, anterior branch simple, posterior forked; other branches (RP2 to RP4) simple. One intraradial crossvein rp1-rp2 between stems of RP, RP1. Three crossveins between R, M: 1r-m long, subparallel to R connecting to RP near its origin (its base unclear); 2r-m connecting stems of RP, MA; 3r-m connecting RP1, anterior branch of MA. M forked distad

origin of RP. MA deeply dichotomously forked twice. MP: anterior trace zigzagged, simple, with three simple, pectinate branches. Two intramedian crossveins form two *doi*, proximal much shorter than distal. Two crossveins between M, Cu: basal 1m-cu relatively short, oblique, connecting M, CuA; 2m-cu connecting MP, CuA. Anterior trace of CuA simple distally, with one simple branch. CuP fused with AA1 (incompletely preserved).

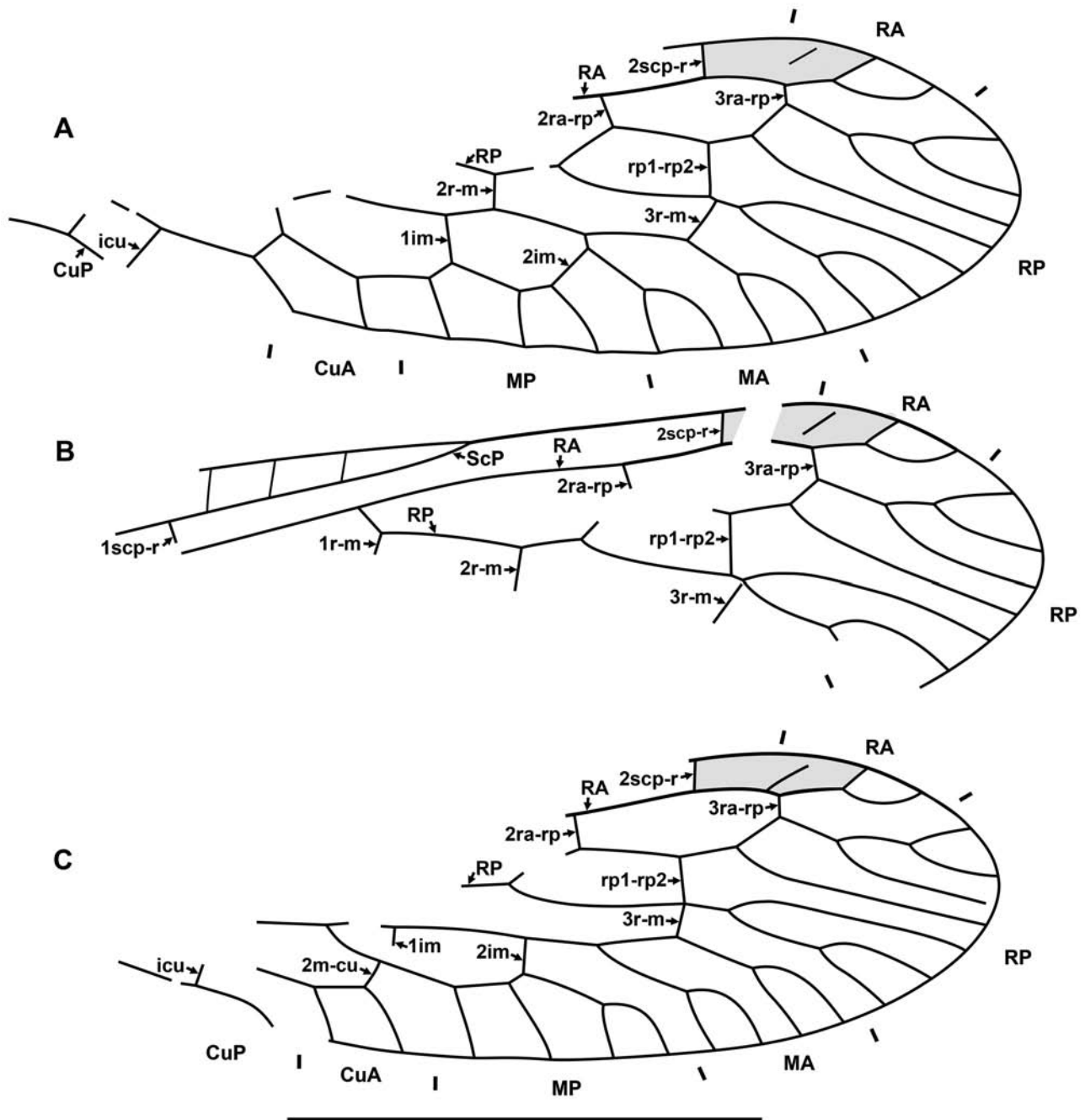


FIGURE 16. Venation of *Archiinocelesia protomaculata* (Engel, 2011), holotype USNM 31487. A, right forewing; B, left forewing; C, right hind wing. Scale bar = 3 mm (all to scale).

Remarks. This species was described based on 19 specimens from the National Museum of Natural History (Engel, 2011). The specimen mentioned and figured by Dayvault *et al.* (1995: Fig. 35) belongs to this species (Engel, 2011), as does Aspöck's (1998: Fig. 7) specimen (determination here by head maculation). We examined high-quality photographs of 51 specimens in the UCM collections. Most are only partially visible pending preparation, as the rock in these beds does not split along fine, thin laminae bearing the fossil as is usually the case in Okanagan Highlands fossils, and portions often protrude into the matrix. We confidently assign 36 of these to *A. protomaculata* by their characteristic head maculation and/or wing venation. Five further fossils possibly belong to this species,

but cannot be assigned with certainty by preservation: three females from the Labandeira Site (UCM 60298; UCM 62430; UCM 65597), a probable male (UCM 42748) from the Donnell Site, and a female (UCM 75788) from the UCM locality 2009063 (Claudia's Place in Garfield County). Characters present on the remaining ten more poorly preserved specimens suggest that at least some of them might also belong to the species, including four from the Labandeira Site: UCM 61231d (sex unknown); UCM 61320 (male), UCM 62686 (sex unknown), UCM 62689 (sex unknown), UCM 68352 (sex unknown); two from the Donnell Site: UCM 39661 (sex unknown) and UCM 39662 (female); two from Claudia's Place: UCM 75468 (sex unknown) and UCM 75790 (male); and one from the Denson Site: UCM 56842 (sex unknown).

The maculation of the head in *Archiinocellia protomaculata* is distinctive (Fig. 14). Paler areas occupy most of the lateral part of its head, whereas there are paler streaks in some extant genera of both families; others are mostly dark, lacking reddish regions (see *e.g.*, Albarda 1891). While the life colour of these pale regions of the head of *A. protomaculata* is unknown, lighter regions in the heads of extant species are reddish. Carpenter (1936) stated that the size of the reddish patches varies freely within Raphidiidae species (p. 9), but the colour patterning of the heads of *A. protomaculata* is strongly consistent among individuals, and so we consider it to be a good diagnostic character state of the species.

The maculation of the holotype head is typical of the species, but its wings are overlapping and many portions are obscured by the abdomen (Fig. 12A; Engel, 2011: Figs 1, 2). The venation of both the fore- and hind wings (Figs. 16A, B), is generally similar to that of other examined specimens (*e.g.*, Figs. 16C–D; 17A–D).

Wing venation shows little variation among the specimens examined. There are usually two branches of RP distad 3ra-rp, but in one specimen there is only one (Figs. 17C–D) in both the forewing and hind wing. The length of 3ra-rp varies from long (*e.g.*, Fig. 17B–C) to short (*e.g.*, Figs. 16A, C), also in both wings. In forewings, crossvein 2im usually joins the posterior branch of MA (*e.g.*, Fig. 17C), but may rarely be at its forking (*e.g.*, Fig. 17A), and while MP usually has two branches, it may rarely have one (Engel, 2011: Figs 4, 7). In hind wings, the size of the basal *doi* varies from relatively long (Fig. 17D) to short (Fig. 17B), and crossvein 2r-m may be placed relatively distally (distad 2ra-rp: Fig. 17D; Engel, 2011: Fig. 7) to proximally (proximad 2ra-rp: Fig. 17B). These variations are normal for the suborder, and in some species are greater (see *e.g.*, Zelený, 1969).

Raphidiidae genus and species A

Fig. 18

Material. UWBM74306, collected by Wesley Wehr in 2003, deposited in the UWBM collections. An incomplete folded forewing.

Locality and horizon. Tom Thumb Tuff Member of the Klondike Mountain Formation, exposure B4131, Republic, Washington, U.S.A.; early Eocene (Ypresian).

Description. Forewing 9.3 mm as preserved (estimated complete length approximately 11 mm). Costal, subcostal spaces not preserved. Pterostigma partially preserved, well pigmented. Two RA branches (none detected within pterostigma); one long forming distal margin of pterostigma; other short distad pterostigma; neither forked. Portion of RA distad pterostigma relatively long, terminates halfway between pterostigma, apex. RA space with two crossveins forming two radial cells (distal slightly shorter than proximal); 3ra-rp located in distal part of pterostigma along RA. RP with four pectinate branches: anterior trace shallowly forked; RP1 deeply forked, its anterior branch incompletely preserved, posterior branch forked again; RP2 about basal half preserved; RP3, RP4, each forked once. One long intraradial crossvein rp1-rp2 between stems of RP, RP1. Two crossveins between RP, MA detected (1r-m, 2r-m) connecting stem of RP, MA. M forked well proximad origin of RP. MA deeply dichotomously forked twice. MP zigzagged, anterior trace simple terminally with two simple branches; proximal branch originating from terminal point of MP+CuA. Two intramedian crossveins form two *doi*, equal in length. Anterior trace CuA strongly zigzagged, fused with MP for relatively long distance to form part of posterior margin of basal *doi*, with one long simple branch. CuP simple. Crossvein icu between CuA, CuP long. Crossvein between CuP, AA1 fragmentary preserved.

Remarks. The specimen has typical venation for Raphidiidae (see Makarkin & Archibald, 2014). Its forewing venation differs from that of all other species from the Okanagan Highlands by relatively short branches of MP, however we decline to name it as its venation lacks such important character as ScP and the costal space, and the pterostigma is incomplete.

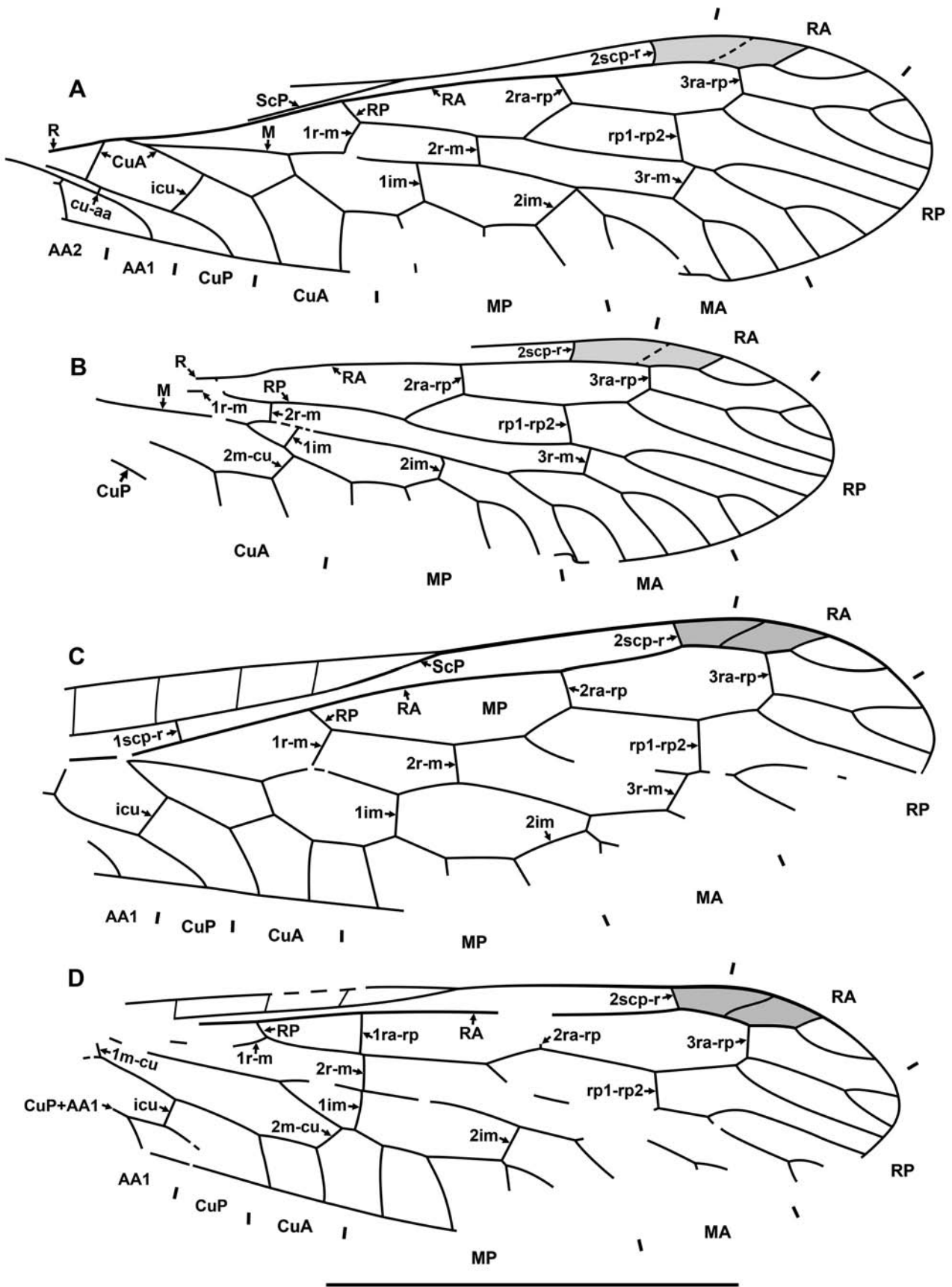


FIGURE 17. Venation of *Archiinocelesia protomaculata* (Engel, 2011). A, right forewing of UCM 61231a (female); B, right hind wing of the same specimen; C, right forewing of UCM 62523; D, right hind wing of the same specimen. Scale bar = 3 mm (all to scale).

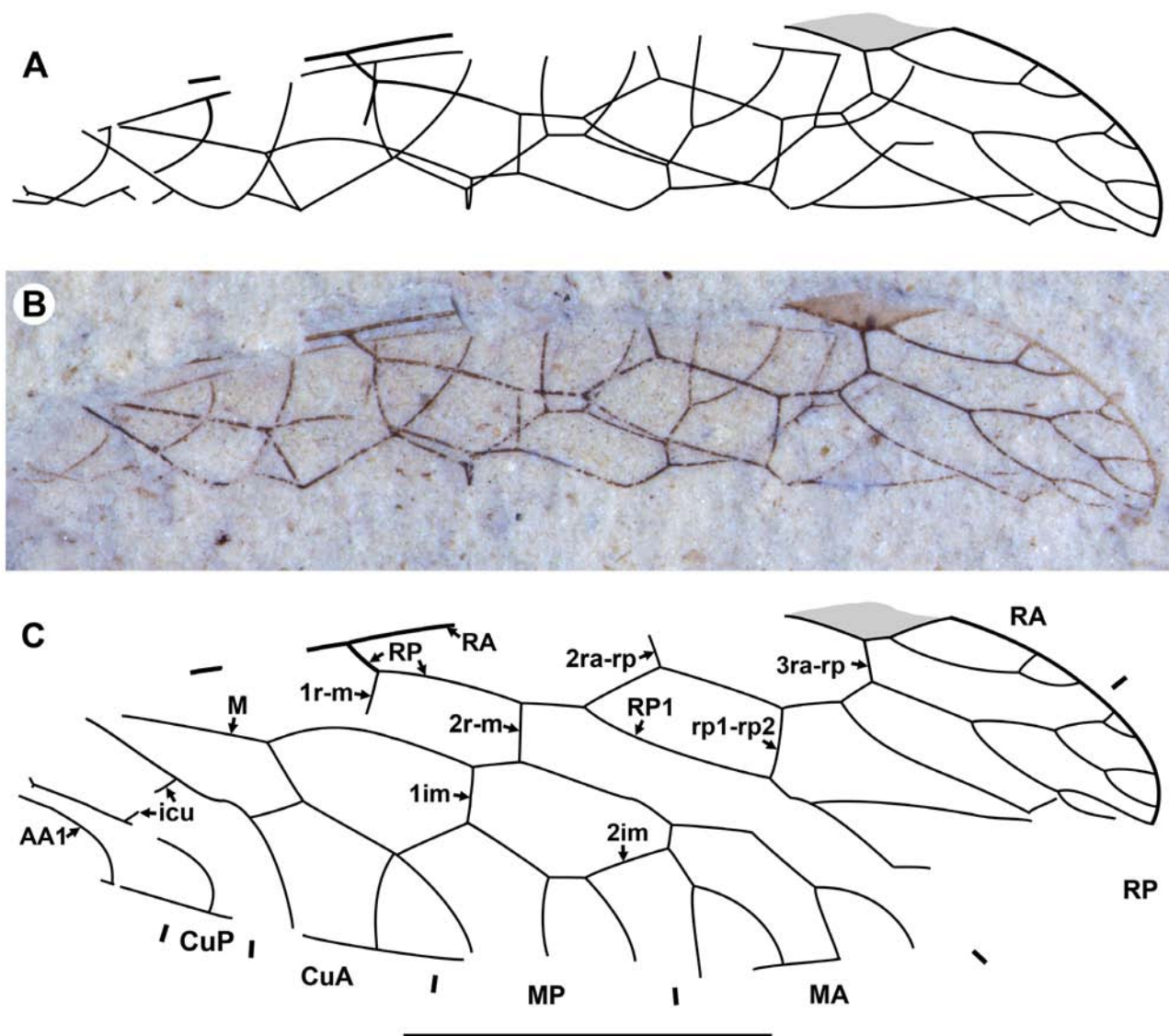


FIGURE 18. Raphidiidae genus and species A, UWBM 74306. A, forewing venation; B, specimen as preserved; C, venation of 'graphically unfolded' forewing. Scale bar = 3 mm (all to scale).

Raphidiidae genus and species indet.

Fig. 19

Material. F-982, collected by unknown person, unknown date, deposited in the TRU collections. A nearly complete body mostly preserved in dorso-lateral aspect and head in dorsal aspect, with very poorly preserved and fragmentary wings.

Type locality and horizon. Hoodoo Face beds, McAbee, British Columbia, Canada; early Eocene (Ypresian).

Description. Body approximately 17–18 mm long. Head clearly narrowed posteriorly, 4.2 mm long (including mandibles), 1.9 mm maximum width (dorsal view); mostly appearing black with pale patches (probably post-mortem artefact), anterior part (clypeus, labrum, mandibles) paler, brownish. Mandibles with long sub-apical tooth. Ocelli not detected. Antennae approximately 4 mm long. Prothorax dark brown, relatively short, approximately 3 mm long (0.17–0.18 body length), 0.9 mm maximum width (lateral view); pterothorax dark-brown to black (details not discernible). All legs pale-brownish or dark yellowish, covered with short setae. Most segments of abdomen dark, easily distinguished; genital segments very poorly preserved, not allowing sex determination.

Wings only fragmentarily preserved, venation indistinct.

Remarks. The specimen is assigned to Raphidiidae by its head clearly narrowed posteriorly, while those of

Inocelliidae are always broad with mostly parallel sides. It is difficult to determine its generic and species affinity; however, it is probably not conspecific with the other species known from McAbee, *Megaraphidia antiquissima*, whose prothorax is relatively longer (0.20–0.23 body length). Prothorax length does not, however, separate it from *M. ootsa* from Driftwood Canyon, which has similar colouration and head shape, but these often occur in extant species of various genera, and so are not especially informative. They do, however, clearly differ in *M. hopkinsi* from One Mile Creek.

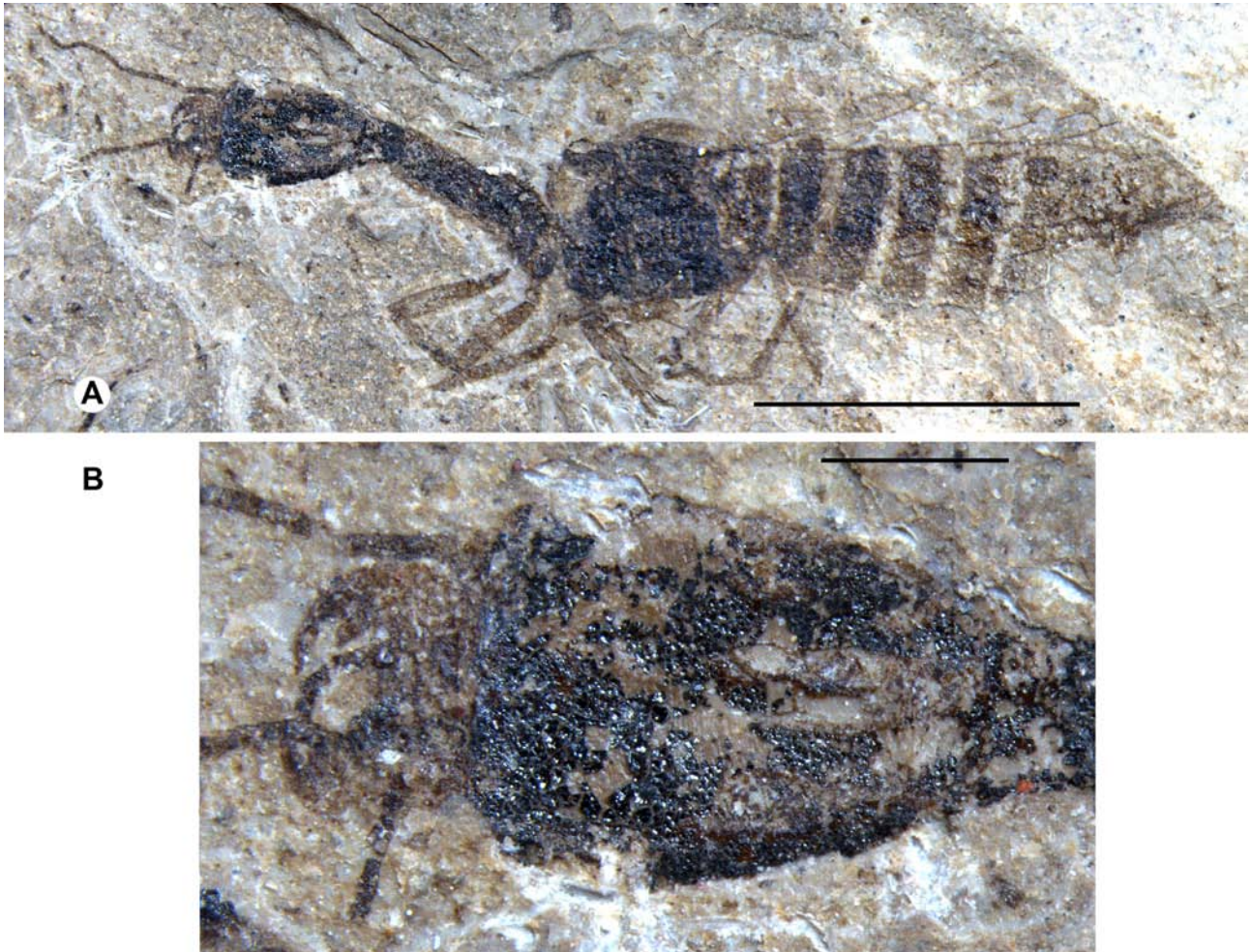


FIGURE 19. Raphidiidae genus and species indet., F-982. A, specimen as preserved; B, head. Scale bars = 5 mm (A), 1 mm (B).

Family Inocelliidae Navás, 1913

Paraksenocellia borealis Makarkin, Archibald & Jepson, 2019

Type material. Holotype RBCM.EH2018.129.1, collected by SBA, 12.vi.2012, deposited in the collections of the RBCM. A well-preserved, complete forewing.

Type locality and horizon. Driftwood Canyon Provincial Park, near Smithers, British Columbia, Canada; early Eocene (Ypresian).

Remarks. This holotype is the single known specimen of Inocelliidae from Okanagan Highlands (see Makarkin *et al.*, 2019 for more details).

Discussion

North American vs European Eocene Raphidioptera: taxonomic and morphological differences

Eocene Raphidioptera are only known from North America and Europe. The single specimen reported by Zherikhin (1978) as “a fragmentary remnant” from the Tadushi Formation in the southern Russian Far East was not figured and has not been located in the collections of Paleontological Institute, Moscow (A. Khramov, pers. comm.).

North America. Six species are known from the Okanagan Highlands, four of which are described here. Five are species of *Megaraphidia* and *Archiinocellia* (Raphidiidae, their oldest record), and one belongs to *Paraksenocellia* (Inocelliidae, their oldest Cenozoic record: see the sole probable Mesozoic member of the family, below) (Table 1).

Raphidioptera are amazingly abundant in the Green River Formation, found only in the later Ypresian Parachute Creek Member of the Piceance Creek Basin, Colorado. It appears likely that all specimens that can be identified belong to *Archiinocellia protomaculata*, although several are not determinable. The twenty-three specimens housed in the USNM (0.17% of 13151 insect specimens) were collected at the Labandeira Site (Pribyl *et al.*, 1998). Other known material includes an undescribed specimen in the collection of Horst and Ulrike Aspöck (Aspöck, 1998: Fig. 7), ‘several’ from Dayvault’s ‘Site A’ (near Rifle, Garfield County, Colorado) and ‘Site C’ (Douglas Pass, Garfield County, Colorado) (Dayvault *et al.*, 1995), and one from ‘Site B’ (Rio Blanco County, Colorado, also known as Gus’ Pit) (Codington, 1995; Antell & Kathirithamby, 2016). Thirty-six of the 51 UCM collections specimens are confidently assigned to *A. protomaculata*, five possibly so, and the remaining ten might be or are indeterminate by preservation (see above).

The taxonomic compositions and relative abundances of Ypresian Raphidioptera fossils in the Okanagan Highlands and the Green River Formation then have little in common. These deposits are roughly coeval, but differ by elevation, climate, and continental position, and so their assemblages could reflect real community differences, although differing taphonomic processes may play a role.

Two specimens are known from the Coal Creek Member of the Kishenehn Formation (Montana, USA): one is a well-preserved hind wing of the inocelliid *Paraksenocellia* species (Makarkin *et al.*, 2019); the other is an incomplete forewing of an undescribed raphidiid species (VNM, pers. obs.). The Coal Creek Member is Lutetian, with radiometric ages of 46.2 ± 0.4 Ma and 43.5 ± 4.9 Ma (Constenius, 1996).

Seven species (13 known specimens) of Raphidiidae, and one species each of Baissopteridae and Inocelliidae (both with a single specimen) have been described from the Priabonian of Florissant, Colorado (Scudder, 1890; Cockerell, 1907, 1909a, b, 1912, 1914; Bather, 1909; Rohwer, 1909; Cockerell & Custer, 1925; Engel, 2003; Makarkin & Archibald, 2014). Raphidiidae are represented by three genera (*Megaraphidia*, *Archiraphidia*, and *Florisantoraphidia*), one of which is known from early Eocene Okanagan Highlands localities, and Inocelliidae by *Fibla* (provisionally, as it is known from a hind wing). The generic placement of *Archiraphidia? somnolenta* remains unclear (see above). It is noteworthy that Raphidiidae have both greater taxonomic diversity and numbers of specimens than Inocelliidae at Florissant and the Okanagan Highlands. This is characteristic also of the modern world, but not of Baltic amber (see below).

Europe. Raphidioptera have not been found in the rich insect bearing earliest Ypresian Fur Formation of northern Denmark. It was previously believed that the order is represented there by a single forewing of the enigmatic *Raphia paleocenica* (here considered *nomen nudum*), which has venation somewhat like that of the Mesozoic family Priscaenigmatidae (suborder Priscaenigmatomorpha) (Rust, 1999: Fig. 79; *cf.* Whalley, 1985; Willmann, 1994). Since then, two new families of Raphidioptera with similar venation have been described from the Mesozoic of China (Liu *et al.*, 2013, 2014). However, we now believe that the Fur Formation species likely belongs to the megalopteran family Corydasialidae by the stronger similarity of its venation to that of species of *Corydasialis* Wichard from Baltic amber (Wichard *et al.*, 2005). The absence of Raphidioptera from the Fur Formation might be explained by taphonomic reasons, as it is composed of marine sediments, and transporting these weak fliers (see below) offshore may have been difficult.

Inocelliidae in Priabonian Baltic amber are represented by four species of three genera: *Electrinocellia*, *Succinofibla*, and *Fibla* (Carpenter, 1957; Engel, 1998; Aspöck & Aspöck, 2004). Some undescribed specimens of Inocelliidae have been reported (*e.g.*, Weitschat & Wichard, 1998: Pl. 52a; Janzen, 2002: Figs 54, 547; Gröhn, 2015: Fig. on p. 251). We know of nine specimens, including unreported. Raphidiidae are rarer in Baltic amber, with two

described species of the genus *Succinoraphidia*, which have similar wings (Carpenter, 1957; Aspöck & Aspöck, 2004; Perkovsky & Makarkin, 2019). We know of four specimens, including unreported. The dominance of Inocelliidae over Raphidiidae in both taxonomic diversity and numbers of specimens is noteworthy.

TABLE 1. Eocene Raphidioptera

Species	Family/Age	Locality
	Baissopteridae	
<i>Dictyoraphidia veterana</i> (Scudder, 1890)	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A.
	Raphidiidae	
<i>Megaraphidia antiquissima</i> sp. nov.	Ypresian (52.90 ± 0.83 Ma) ²	McAbee, Canada, Okanagan Highlands
<i>Megaraphidia hopkinsi</i> sp. nov.	Ypresian (52.08 ± 0.12 Ma) ³	Allenby Fm., Canada, Okanagan Highlands
<i>Megaraphidia ootsa</i> sp. nov.	Ypresian (51.77 ± 0.34 Ma) ⁴	Driftwood Canyon, Canada, Okanagan Highlands
<i>Megaraphidia klondika</i> sp. nov.	Ypresian (49.4 ± 0.5 Ma) ⁵	Republic, U.S.A., Okanagan Highlands
<i>Archiinocellia oligoneura</i> Handlirsch, 1910	Ypresian (no radiometric age) ⁶	Horsefly River, Canada, Okanagan Highlands
<i>Archiinocellia protomaculata</i> (Engel, 2011), comb. nov.	Ypresian (51.3 to about 48.5 Ma) ⁷	Parachute Creek Member, Green River Fm, U.S.A.
<i>Megaraphidia elegans</i> Cockerell, 1907	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A
<i>Megaraphidia exhumata</i> (Cockerell, 1909)	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A
<i>Megaraphidia</i> sp.: Makarkin & Archibald, 2014	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A
<i>Archiraphidia tumulata</i> (Scudder, 1890)	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A
<i>Archiraphidia tranquilla</i> (Scudder, 1890)	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A
<i>Archiraphidia? somnolenta</i> (Scudder, 1890)	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A
<i>Florissantoraphidia mortua</i> (Rohwer, 1909)	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A
<i>Florissantoraphidia funerata</i> (Engel, 2003)	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A
<i>Succinoraphidia baltica</i> (Carpenter, 1957)	Priabonian ⁸	Baltic amber
<i>Succinoraphidia exhibens</i> Aspöck & Aspöck, 2004	Priabonian ⁸	Baltic amber
<i>Succinoraphidia radioni</i> Perkovsky & Makarkin, 2019	Priabonian ⁸	Rovno amber, Ukraine
	Inocelliidae	
<i>Paraksenocellia borealis</i> Makarkin <i>et al.</i> , 2019	Ypresian (51.77 ± 0.34 Ma) ⁴	Driftwood Canyon, Canada, Okanagan Highlands
<i>Paraksenocellia</i> sp.: Makarkin <i>et al.</i> , 2019	Lutetian (46.2 ± 0.4 Ma by ⁴⁰ Ar/ ³⁹ Ar) ⁹	Kishenehn Fm, U.S.A.
<i>Fibla? exusta</i> (Cockerell & Custe, 1925)	Priabonian (34.07 ± 0.10 Ma) ¹	Florissant, U.S.A.
<i>Fibla erigena</i> (Menge in Pictet-Baraban & Hagen, 1856)	Priabonian ⁸	Baltic amber
<i>Fibla carpenteri</i> Engel, 1998	Priabonian ⁸	Baltic amber
<i>Electrinocellia peculiaris</i> (Carpenter, 1957)	Priabonian ⁸	Baltic amber
<i>Succinofibla aperta</i> Aspöck & Aspöck, 2004	Priabonian ⁸	Baltic amber

1, Evanoff *et al.* (2001); 2, Archibald *et al.* (2010); 3, Allenby Fm., Vermilion Bluff Member at the One Mile Creek exposure, value given is for the Vermilion Bluff Member at the Hospital Hill exposure, Archibald (2005); 4, Mortensen & Archibald, work in progress cited in Moss *et al.* (2005); 5, Wolf *et al.* (2003); 6, summary by Barton & Wilson (2005); 7, Smith *et al.* (2008); 8, summary by Perkovsky *et al.* (2007); 9, Constenius (1996): or 43.5 ± 4.9 Ma by fission-track analysis.

One species of the raphidiid genus *Succinoraphidia* is described from Ukrainian Rivno [=Rovno] amber based on a single specimen (Perkovsky & Makarkin, 2019). This species is not known from contemporaneous Baltic amber (Aspöck & Aspöck, 2004).

Morphologically, the oldest known Raphidiidae (described here) are typical members of the family, more similar to extant taxa than are those from Eocene Baltic amber. Two plesiomorphic character states of venation occur in all Eocene Raphidiidae from North America: (1) 3ra-rp is located within the pterostigma in both wings, and (2) 1r-m is long, sub-parallel to R in the hind wing. In extant raphidiids, these only occur together in some species of the North American genus *Alena*. In all other extant raphidiids, one or the other of these character states are absent (*i.e.*, they possess the derived state), but they may adventitiously co-occur in individuals. In contrast, in European Eocene Raphidiidae (and most extant taxa) 3ra-rp is located distad the pterostigma, although state (2) is the same.

The European Priabonian *Succinoraphidia* is distantly related to all extant and North American Eocene (Ypresian and Priabonian) taxa. It is the only member of the basal subfamily Succinoraphidinae, based on its male genitalia (Aspöck & Aspöck, 2004). Its wing venation differs from that of all other Raphidiidae by: (1) the anterior trace of RP distad the crossvein 3ra-rp is not forked in both wings, (2) the hind wing CuP and AA1 are fully separated, and (3) the crossvein between AA1+2 and AA3 in the hind wing is present (Perkovsky & Makarkin, 2019). Plesiomorphic state (2) is especially informative as it is found in Mesoraphidiidae (see Perkovsky & Makarkin, 2019). It is interesting that the oldest known Raphidiidae (Ypresian, North America) possess the derived state of CuP fused with AA1 from some distance.

Therefore, snakefly assemblages of Priabonian northern Central Europe differ greatly from all those of the North American Eocene (Ypresian European snakeflies are unknown). There are no shared genera of Raphidiidae, and only *Fibla* is shared in the Inocelliidae (although the sole North American species *F. exusta* from Florissant is referred to this genus only provisionally by the presence of the plesiomorphic long basal 1r-m in the hind wing).

The molecular phylogeny of Haring *et al.* (2011) recovered all Palearctic genera as sister to the Nearctic *Alena* and these as sister to the Nearctic *Agulla*. This is consistent with the presence of the plesiomorphic position of crossvein 3ra-rp in all North American Eocene Raphidiidae and its derived state in most extant and all Eocene Palearctic taxa (see above). Its basal subfamily Succinoraphidinae, however, occurs only in the European Priabonian.

Haring *et al.* (2011) hypothesised that the Palearctic and Nearctic Raphidiidae diverged prior to the loss of land connections between North America and Europe. These provided episodic dispersal corridors in the Late Cretaceous through early Ypresian prior to Okanagan Highlands and Green River time; there was also a land connection between North America and East Asia across Beringia at least in the Paleocene and perhaps early Ypresian (Brikiatis, 2014). Dispersal could have been through any of these routes, in any direction, perhaps multiple times. The Raphidiidae could have originated during the long Late Cretaceous interval lacking fossil Raphidioptera, with the major events of their evolution obscured.

In contrast, the Eocene (Ypresian and Lutetian) Inocelliidae of North America (*Paraksenocellia*) are morphologically more similar to those of the Priabonian of Europe (*Electrinocellia*) than they are to the vast majority of extant taxa (see Makarkin *et al.*, 2019). The inocelliid genus *Fibla* was distributed in both continents in the Priabonian (however, its presence in North America is tentative, see above; if they are not congeners, still, they bear great similarities). Intercontinental dispersal of Inocelliidae might have been easier for an unknown reason, might have been facilitated by contingencies that the Raphidiidae were not subject to, might have dispersed more recent to the Eocene and so had less time to differentiate, or perhaps remained stable in place over the long interval from when they may have ranged throughout Europe and North America preceding their separation.

The absence of Raphidioptera in eastern North America is unexplained. Its climate appears suitable, and there are no known limiting competitors or predators unique to the region or sufficient geographic barriers. It may have been extirpated from the region, or never have occupied it. The reason for their absence in the tropics and Southern Hemisphere is also unknown.

Raphidioptera and the necessity of cold winter

It has been generally thought that extant snakeflies (Inocelliidae and Raphidiidae) require a cold interval to mature, explaining their restriction to mid- and higher latitudes of the Northern Hemisphere, reportedly in high, cooler elevations in the southern portions of their range (Aspöck, 1998, 2000, 2002; Aspöck & Aspöck, 2009, 2014; Abbt *et al.*, 2018). Aspöck (2000) stated that the cold interval is necessary to induce pupation and develop the imago,

which must be 0° C or below. Abbt *et al.* (2018) later found that at least some can mature in the laboratory with a cold interval of 4°C.

This would account for their exclusion from the tropics. In North America, they are found west of the Rocky Mountains from about 53° N in southern British Columbia with some known from as far south as the Mexico-Guatemala border. In the Eastern Hemisphere, they range from Norway at 70° N as far south as parts of Mediterranean North Africa, with scattered records eastward through Asia to the Pacific, southward to the Himalayas, northern Thailand and Taiwan (Aspöck, 1998; Aspöck *et al.*, 2011, 2012a, b; Aspöck & Aspöck, 2014; Blades, 2019).

The fossil record of Raphidioptera before the Oligocene, especially of the extant families, would then present a biogeographic puzzle. The Eocene/Oligocene boundary represents the end of the globally warm “greenhouse world” climates of the Cretaceous through the Paleocene and Eocene, with higher mean annual temperatures (MAT), a low pole to equator MAT gradient, and lowered temperature seasonality with mild winters. The post-Eocene onset of the modern “icehouse world” regime saw extra-tropical climates with colder MAT, lacking Arctic ice sheets until the later Neogene and Antarctic ice sheets beginning to form at the end of the Eocene, an increased latitudinal MAT gradient, and more severe extra-tropical winters (Zachos *et al.*, 2008). Raphidioptera of the Paleocene and Eocene did not then experience cold winters, and in the Mesozoic lived under even warmer conditions, some in low latitudes, *e.g.*, Brazil (*e.g.*, Oswald, 1990) and Myanmar (*e.g.*, Engel, 2002; Liu *et al.*, 2016).

Agulla bicolor (Albarda, 1891) from Texas was successfully raised in laboratory conditions at a constant temperature of 23 ± 3°C (Kovarik *et al.*, 1991). Raphidiidae of the North American genus *Alena* and Mexican inocelliid species apparently also don't require a cold interval to mature, as these pupate in summer and the imago emerges in late summer (Aspöck, 2002). At least two species of *Harraphidia* Steinmann in the Iberian Peninsula inhabit low elevation regions without cold winters, some at locations on the Mediterranean coast such as Tarifa, Spain, which has a coldest month mean temperature of 13.0°C and minimum temperature of 8°C (Montserrat and Papenberg, 2006; AEMET, 2020). A cold interval is then not required for all modern snakeflies.

Inocelliidae and Raphidiidae of the Okanagan Highlands and Green River Formation are from the latter portion of the Ypresian, which had the hottest sustained global MAT values of the Cenozoic, the Early Eocene Climatic Optimum (Zachos *et al.*, 2008). While nearby coastal climates had hot MATs, the interior Okanagan Highlands localities bearing Raphidioptera were at some elevation, and had cooler, upper microthermal MAT values (microthermal = MAT ≤ 13°C), similar to that of south-coastal British Columbia today (Rouse *et al.*, 1970; Greenwood *et al.*, 2005; Tribe, 2005; Archibald *et al.*, 2011). These values would usually be associated with cold winters in the modern seasonal Northern Hemisphere, however, winters there appeared to be mild, without frost days; its forests included plants such as palms and their obligate palm feeding bruchids (Coleoptera, Chrysomelidae, Pachymerina: Archibald *et al.* 2014), as well as other insects restricted to frost-free regions today, *e.g.*, *Megymenum* Guérin-Méneville (Hemiptera, Dinidoridae), Mastotermitidae (Isoptera), Myrmeciinae (Hymenoptera, Formicidae), and Diplopterinae (Blattodea, Blaberidae) (*e.g.*, Archibald *et al.*, 2014, 2018).

The regional tectonic uplift in the Ypresian that raised the Okanagan Highlands created a landscape of great topographic relief, with high mountains and deeply incised valleys in which the fossil-bearing lacustrine depositional basins formed (Ewing, 1980; Tribe, 2005). Its snakefly fossils are in good general condition, having not suffered the extensive mechanical damage that would be consistent with post-mortem downslope transport from cooler elevations in streams feeding the depositional lakes. Nor can their presence be easily explained by occasional transport of living adults by winds from local higher elevations. The larvae of modern Raphidioptera live from one to six years, usually under bark, but some in litter below trees or bushes (Aspöck, 2002). Most adults live for a very short while, often a few days, and are weak fliers with low vagility, remaining close to their resident tree or bush (Aspöck, 1998). We believe that Okanagan Highlands snakeflies lived in close proximity to their depositional lakes.

The Okanagan Highlands communities also included a suite of other insects that today inhabit cooler boreal regions, higher elevations in lower latitudes, or mostly so. These include aphids (Hemiptera, Aphidoidea), scorpionflies (Mecoptera, Panorpidae, species of *Panorpa* Linnaeus: Archibald *et al.*, 2013b) and sawflies and wood wasps (Hymenoptera, Symphyta: Tenthredinidae, Siricidae, Pamphiliidae, Cephidae: Archibald & Rasnitsyn, 2015; Archibald *et al.*, 2018).

The Okanagan Highlands green lacewings (Neuroptera, Chrysopidae) consist of at least nine species of Nothochrysininae and one of the predominantly Mesozoic Limaiiinae, it's youngest occurrence. Today, Nothochrysininae mostly prefer Mediterranean climates of milder winters (Archibald *et al.*, 2014). Green lacewings of the Chrysopinae thrive in a wide range of climates, including regions of very cold winters. They appear in the fossil record

after Okanagan Highlands time at the end of the Eocene, subsequently diversifying to vastly dominate the family today across most of the globe from the equator to northern Siberia in our post-Eocene icehouse world as the Nothochrysininae became relictual. Nymphinae (Neuroptera, Nymphidae), found at two Okanagan Highlands localities (Archibald *et al.*, 2009; Archibald & Makarkin, 2020) is today restricted to Australia, where it is less seasonal than at equivalent northern latitudes.

At the same time, snakeflies to the east of the Okanagan Highlands from the Green River Formation of Colorado inhabited much warmer lowland climates, with high mesothermal (mesothermal = MAT >13°, <20° C) to megathermal (MAT ≥20° C) MAT value estimates ranging from 19.6°C to 23.0°C (Wilf, 2000; Archibald *et al.*, 2011 and references therein). Its forests also included frost-intolerant palms. Green River Raphidioptera probably inhabited similar or warmer temperatures than *Harraphidia* at Tarifa, Spain, where MAT is 17.2° C and had mild coldest months as above (Monserrat & Papenberg, 2006; AEMET, 2020). Although the Green River Formation was deposited in a lowland intermontane basin, the abundance of snakefly fossils indicates that they were part of the local community, as river transport from a distant mountain source would have been a rare event. There are numerous rocks with more than one specimen, in one case, four (Fig. 14A). Further, almost all specimens in the UCM collection examined have a body with wings, *i.e.*, are complete or at least relatively so. The wings may be folded in some, but in general, these do not appear to have suffered mechanical degradation characteristic of long-distance river transport. We believe that these also lived near their depositional lake.

A generalised climatic profile has been estimated for the Kishenehn formation by a nearest living relative analysis of mollusks (Pierce & Constenius, 2001). These include taxa associated with both megathermal and microthermal climates. Pierce and Constenius rejected the notion that these coexisted, assuming the mixing of populations from different elevations. Such a mixed community is, however, consistent with a temperate climate with mild winters as in the Okanagan Highlands (above).

Global MAT declined through the remainder of the Eocene (Zachos *et al.*, 2008), but by the late Priabonian, close to the end of the greenhouse world, MAT estimates for upland Florissant, indicate an upper microthermal climate (Allen *et al.*, 2020) like those for the Okanagan Highlands, apparently also with no frost days by the presence of *e.g.*, palms and *Pachymerina* (Manchester, 2001; Archibald *et al.*, 2014). The youngest occurrence of the otherwise Cretaceous raphidiopteran family Baissopteridae is at Florissant.

Therefore, all known Raphidioptera before the Oligocene, including Inocelliidae and Raphidiidae, inhabited regions of mild winters without cold intervals whether in hot or temperate climates. An adaptation to winter cold must have evolved independently in both extant families sometime after the Eocene/Oligocene boundary in the modern icehouse world climatic regime, with some members retaining or subsequently reverting to the plesiomorphic adaptation to warm winters.

After the onset of cold extra-tropical icehouse world winters, biota of latitudes outside of the tropics either went extinct (perhaps accounting for the extinctions of, *e.g.*, the Limaiinae and Baissopteridae), moved to or restrict their ranges to lower latitudes and Southern Hemisphere regions of mild winters (*e.g.*, Nymphidae, palm bruchids, Dinidoridae, Mastotermitidae, Mymeciinae, and Diplopterinae), or remained and adapted to more severe winters (*e.g.*, aphids, *Panorpa*, Tenthredinidae, Siricidae, Pamphiliidae, Cephidae, Panorpidae, shift to dominance of the Chrysopinae within Chrysopidae). Raphidioptera appears to have mostly followed the latter path.

The effect of the K/Pg extinction event on Raphidioptera

The end-Cretaceous extinction event is thought to have had a profound effect on Raphidioptera, reducing a large, diverse Mesozoic order to a small, relictual one in the Cenozoic (Aspöck, 1998, 2000, 2002, 2004). However, a precise characterisation of Raphidioptera diversity in the Mesozoic—particularly at the genus and species levels—would require extensive revisions, and so is currently unresolved. It seems clear on the broad level, however, that there were three major lineages in the evolution of the order: Priscaenigmatomorpha (Priscaenigmatidae, Chrysoraphidiidae), Juroraphidiidae, and Raphidiomorpha (Metaraphidiidae, Mesoraphidiidae, Baissopteridae, Raphidiidae, and Inocelliidae) (Liu *et al.*, 2014). Priscaenigmatomorpha and Juroraphidiidae strongly differ from Raphidiomorpha, and are extinct, ranging from the Early Jurassic (Sinemurian) to the Early Cretaceous (Barremian/Aptian) (Willmann, 1994; Liu *et al.*, 2014). Raphidiomorpha were represented by two families in the Jurassic (Metaraphidiidae, Mesoraphidiidae), and two at least for the first half of the Cretaceous (Mesoraphidiidae, Baissopteridae). However, the family Mesoraphidiidae lacks clear synapomorphies and is probably paraphyletic. The venation of some Cretaceous genera is very similar to that of Raphidiidae, especially to Succinoraphidinae; *e.g.*,

Dolichoraphidia Liu *et al.* from Burmese amber (see Liu *et al.*, 2016: Fig. 4) (which might belong to a probable stem group leading to Raphidiidae: Perkovsky & Makarkin, 2019). An undescribed male from Burmese amber is probably an inocelliid, if so, it would be the oldest occurrence of the family. Its venation is most similar to that of the *Inocellia fulvostigmata* group from southeastern Asia (see Aspöck *et al.*, 2011; Liu *et al.*, 2012), except the basal crossvein 1r-m in the hind wing is in a plesiomorphic condition (VNM, pers. obs.). The Late Jurassic *Sinoiocellia liaoxiensis* Wang, 1987 was assigned to the Inocelliidae, but it was inadequately described (Wang, 1987), and probably belongs to the Mesoraphidiidae.

The Late Cretaceous is depauperate of insect shale localities and no Raphidioptera have been recovered in them (Aspöck, 1998, and see overviews by Rasnitsyn, 2002 and Grimaldi & Engel, 2005). There are, however, some well-studied Late Cretaceous amber sites, but the only snakefly reported in them is a poorly preserved partial head from Campanian Canadian amber from Grassy Lake, Alberta (Engel & Grimaldi, 2008: Fig. 52), reported to belong to the Mesoraphidiidae, but which appears to present too few characters to allow a firm family-level identification. Paleocene Raphidioptera are unknown. The order is found again in the second half of the Ypresian with both extant families (but the Baissopteridae ranging through this time, and so three), three families in the Priabonian (including the last record of the Baissopteridae), and two thereafter.

Family level representation of Raphidiomorpha, therefore, varies little through its history, with two families (as currently defined) in the Jurassic and known portion of the Cretaceous (three in the mid-Cretaceous if the undescribed Burmese amber specimen belongs to the Inocelliidae), three in the Eocene, and two after.

Given current limitations of knowledge, it appears that fossil genus and species numbers peaked in the Early Cretaceous, however, its history is unknown for a roughly 50-million-year gap that includes the K/Pg boundary. Therefore, we cannot evaluate any possible effect of the K/Pg extinction event on its diversity.

While ichnofossil evidence indicates a temporary loss of insect leaf-feeding diversity following the K/Pg extinction event with unbalanced food webs persisting perhaps 1–2 million years (Wilf *et al.*, 2006), the extinction event appears to have had little or no impact on insects at the family level (Jarzembowski, 1989; Labandeira & Sepkoski, 1993; Labandeira *et al.*, 2002; Condamine *et al.*, 2016; Rasnitsyn *et al.* 2016). Any effect of the event on carnivorous insects such as the Raphidioptera has not been evaluated.

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