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A revision of the late Eocene snakeflies (Raphidioptera) of the Florissant Formation, Colorado, with special reference to the wing venation of the Raphidiomorpha

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Abstract

The snakeflies (Raphidioptera) of the late Eocene Florissant Formation (Colorado, USA) are revised. Seven species of Raphidiidae are assigned to three genera, i.e., *Megaraphidia* Cockerell, 1907, *Archiraphidia* Handlirsch, 1910, and *Florissantoraphidia* **gen. nov.** *Dictyoraphidia* Handlirsch, 1910 is assigned to Baissopteridae, a first Cenozoic record of the family. *Archiraphidia tumulata* (Scudder, 1890), *A. tranquilla* (Scudder, 1890) and *A.? somnolenta* (Scudder, 1890), **stat. res.** are treated as distinct species, and *A. eventa* (Scudder, 1890) as a new synonym of *A. tranquilla*. The lectotype of *A.*

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eventa is designated. '*Raphidia' exhumata* Cockerell, 1909 is transferred to *Megaraphidia*. '*Raphidia' mortua* Rohwer, 1909 and '*R.' funerata* Engel, 2003 constitute *Florissantoraphidia* **gen. nov.** Our findings support the treatment of the single Florissant species of Inocelliidae as preliminary assigned to *Fibla* Navás, 1915. We examine venational synapomorphies of Raphidiomorpha and provide a new diagnosis for it based on these characters. We evaluate putative derived venational character states of 'Neoraphidioptera' (Inocelliidae and Raphidiidae), finding no clear synapomorphy supporting its validity; these families may nest separately within a paraphyletic Mesoraphidiidae (s.l.). We provide diagnoses for the families occurring at Florissant (Baissopteridae, Inocelliidae and Raphidiidae) based on wing venation.

Key words: Baissopteridae, Raphidiidae, Inocelliidae, Eocene, Florissant, wing venation

Introduction

Raphidioptera (snakeflies) today constitutes one of smallest holometabolous insect orders, comprising approximately 240 valid extant species in two families, Raphidiidae and Inocelliidae (Aspöck & Aspöck 2013). They are now restricted to the Northern Hemisphere (Aspöck *et al.* 1991); in the New World occurring only in western North America, from British Columbia and Alberta, Canada to the southern boundary of Mexico. These include the genera *Agulla* Navás, 1914 and *Alena* Navás, 1916 (27 species) in the Raphidiidae, and *Negha* Navás, 1916 and *Indianoinocellia* Aspöck *et* Aspöck, 1970 (5 species) in the Inocelliidae (Carpenter 1936, 1959; Aspöck & Aspöck 1970, 1978, 2013; Aspöck *et al.* 1992, 1994a,b; Penny *et al.* 1997; Aspöck & Contreras-Ramos 2004). The fossil record of Raphidioptera extends to the Early Jurassic (Whalley 1985). They often occur in Late Jurassic to Early Cretaceous localities, but are much rarer in the Cenozoic. Little more than 100 fossil species have been described (Perez-de la Fuente *et al.* 2012; Oswald 2013).

The order Raphidioptera is divided into two suborders: the extinct Priscaenigmatomorpha, whose raphidiopteran affinity is still disputed, and the fossil and extant Raphidiomorpha (Engel 2002; Aspöck & Aspöck 2004; Liu *et al.* 2013). Priscaenigmatomorpha consists of the family Priscaenigmatidae, known from the Early Jurassic of Europe, and a recently discovered new genus from the Early Cretaceous Yixian Formation of China that is unassigned to family (Liu *et al.* 2013). All other reported Raphidioptera belong to the Raphidiomorpha. Difficulties remain with the fossil family concepts of the suborder; here, we employ the family-level groupings of Bechly and Wolf-Schwenninger (2011) as an interim working measure: Metaraphidiidae Bechly *et* Wolf-Schwenninger, 2011 (Early Jurassic); Mesoraphidiidae (s.l.) Martynov, 1925 (Middle Jurassic to Late Cretaceous); Baissopteridae Martynova, 1961 (Cretaceous to Eocene); Raphidiidae Latreille, 1810 (Eocene to Present); and Inocelliidae Navás, 1913 (Eocene to Present). The oldest record of the order is in the Sinemurian (190.8 ± 1.0–199.3 ± 0.3 Ma) of Charmouth (England), where both suborders have been reported (Whalley 1985). Recently, minute insects of the family Nanosialidae—which is presumably ancestral to Raphidioptera—were described from the Permian of Russia (Shcherbakov 2013).

The Cenozoic fossil Raphidioptera of North America are known from the early Eocene of British Columbia (Horsefly River and the Allenby Formation: Handlirsch 1910, Wehr 1998, Greenwood *et al.* 2005), Republic, Washington (Wehr & Barksdale 1996) and the Green River Formation in Colorado (Dayvault *et al.* 1995; Engel 2011); the late Eocene of Florissant and late Oligocene of Creede, Colorado (Carpenter 1936; Engel 2003); and the middle Miocene of Stewart Valley, Nevada (Engel 2009).

The Priabonian (late Eocene) Florissant Formation (Florissant, Colorado, USA) has the most diverse known Cenozoic raphidiopteran assemblage, with eleven described species (Scudder 1890; Cockerell 1907, 1909a, 1912, 1914; Rohwer 1909; Handlirsch 1910; Cockerell & Custer 1925; Engel 2003) of which eight are currently considered valid, seven assigned to the Raphidiidae and one to the Inocelliidae (Carpenter 1936; Engel 2003). However, many of these original species descriptions were written around a century ago and are in dire need of revision with modern theoretical grounding, and so their taxonomic attributions are now unclear. All species of Florissant Raphidiidae are currently considered to belong to the extant *Raphidia* Linnaeus, 1758 (Ponomarenko 2002; Engel 2009, 2011), a genus that does not occur in the New World today (Haring *et al.* 2011).

Here, we examined all of the type material (specimens or high-resolution photographs) and revise their taxonomy, finding nine valid species. We propose that none of these belong to *Raphidia*, but that they belong to extinct genera, in general agreement with the original assignments of Handlirsch (1910). Besides the previously established presence of the extant families Raphidiidae and Inocelliidae, we find, surprisingly, that *Dictyoraphidia* Handlirsch, 1910 belongs to the Baissopteridae, previously only known from the Cretaceous. Although the status of the Baissopteridae is in some doubt, we associate this genus with those genera currently grouped under that name; it clearly does not belong to either of the extant families. We provide new diagnoses of these and for one new genus.

We take advantage of the rather homogeneous, specialized and stable venational morphology within the Raphidiomorpha since the Early Jurassic to determine unambiguous homologies in these characters across the suborder. We primarily apply this theoretical framework to understand the relationships between and within the two extant families Inocelliidae and Raphidiidae; but this may be more widely applied across the Raphidiomorpha. This is particularly useful in that wings may provide the only clearly preserved morphology in many fossils. The monophyly of Raphidiomorpha is well established (e.g., Bechly & Wolf-Schwenninger 2011), although its finer level phylogeny, and the relationships among fossil families remain unresolved. Those of Willmann (1994), Engel (2002) and Bechly & Wolf-Schwenninger (2011) are preliminary and mostly contradictory below this level; however, these provide robust support that most Mesoraphidiidae (s.l.) represent more basal lineages, and that Raphidiidae and Inocelliidae are the most derived. The monophyly of the latter families is confident (Haring *et al*. 2011; Aspöck *et al*. 2012b). With these relationships established, the polarity of many of their wing characters becomes clear.

We provide new diagnoses for the Raphidiomorpha and for the three families occurring in Florissant (i.e., Baissopteridae, Inocelliidae and Raphidiidae) based on wing venation; examine venational synapomorphies of Raphidiomorpha, and evaluate putative derived character states of 'Neoraphidioptera', proposed by some authors to comprise the two extant families.

Material and methods

We examined seven specimens loaned to us from the Museum of Comparative Zoology (Harvard University) and photographs of others housed in the United States National Museum (Smithsonian Institution, Washington) (one specimen), the Natural History Museum (London) (one), American Museum of Natural History (New York) (one counterpart of a part among the UCM specimens), and the University of Colorado (Boulder) (four).

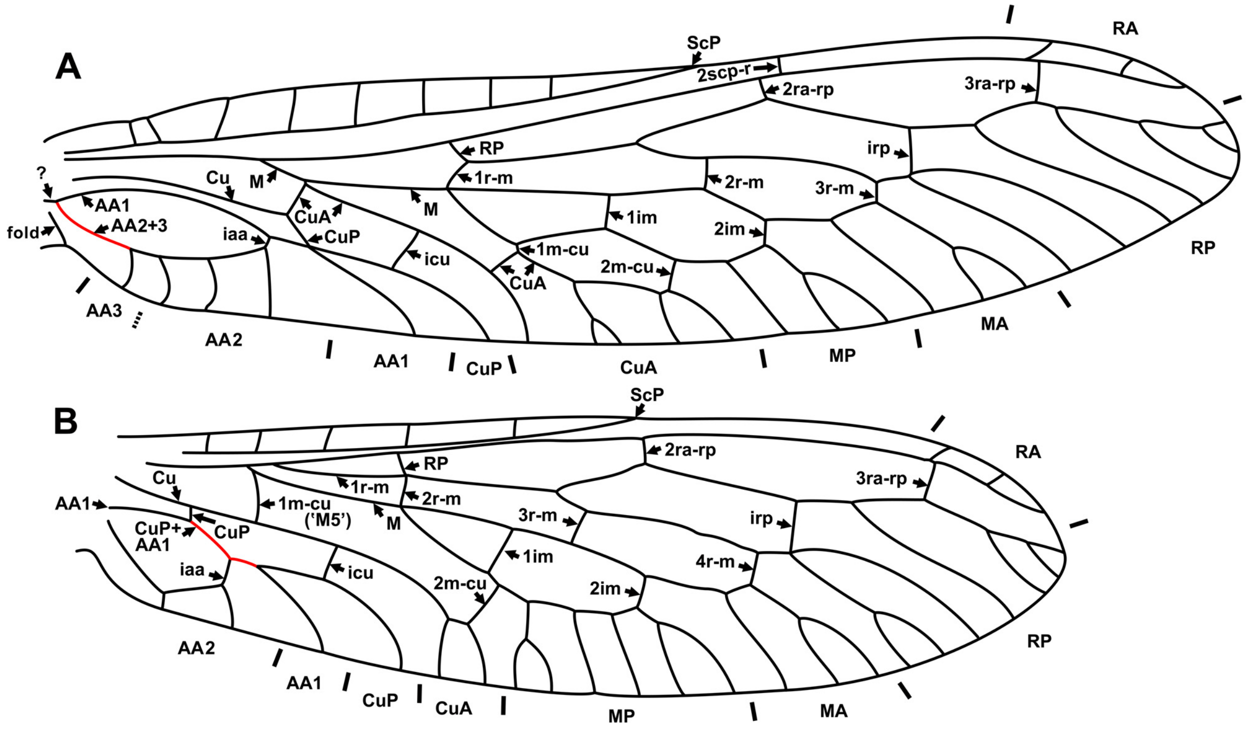

FIGURE 1. Wing venation of the Jurassic Mesoraphidiidae. A, *Mesoraphidia inaequalis* Martynov, 1925 (Late Jurassic of Karatau, Kazakhstan), forewing. B, same, hind wing. Re-drawn with slight simplification from Martynov 1925b. Fused veins are shown by red lines. Identity of the vein stub labeled "?" in basal-most part of forewing is unknown. Both wings are shown with apex to right. No scale provided or pterostigma shown in original figure.

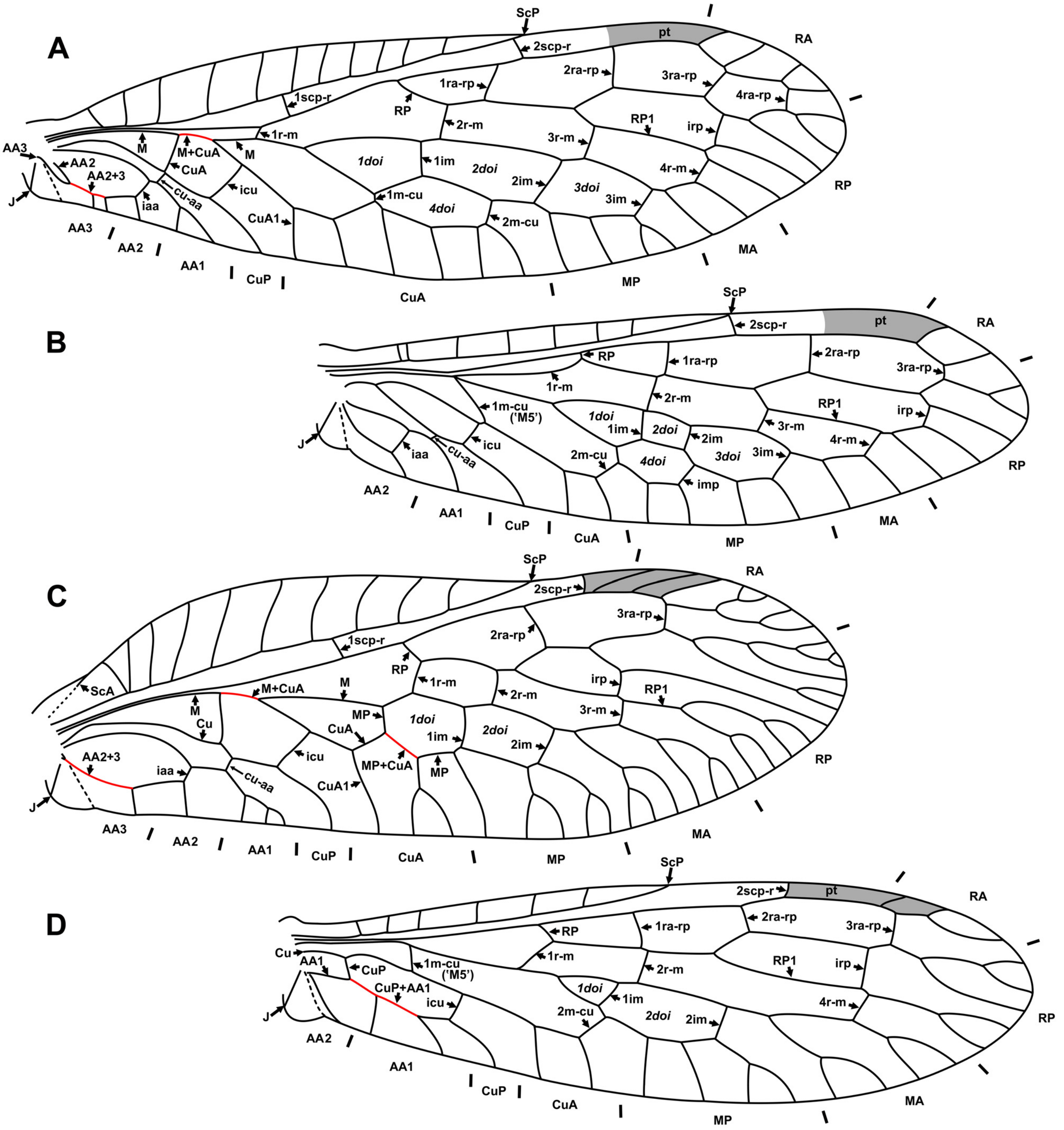

FIGURE 2. Wing venation of extant Inocelliidae (A, B) and Raphidiidae (C, D). A, *Sininocellia gigantos* Yang, 1985, forewing. B, *Fibla hesperica* Navás, 1915, hind wing. C, *Phaeostigma notatum* (Fabricius, 1781), forewing. D, *Ohmella casta* (Aspöck *et* Aspöck, 1968b), hind wing. Drawn from the photograph in Liu *et al*. 2012b (A), re-drawn with simplification from Aspöck *et al*. 1991 (B, D). Fused veins are shown by red lines. All wings are shown with apex to right and not to scale.

A number of these were covered with Canada balsam, a common practice in the early twentieth century. While this may have seemed to make good curatorial sense then, this substance now renders it difficult to determine certain details on some specimens due to refraction, yellowing, and in cases, clouding and cracking.

We follow the systematics of extant taxa (at the family, genus and species levels) of Aspöck *et al*. (1991), and of fossil taxa of Bechly & Wolf-Schwenninger (2011) at the family level and Engel (2002) at the suprafamily level. We broadly use the venational terminology of Kukalova-Peck & Lawrence (2004) as a basis, with the following modifications (Figs 1, 2): (1) the median vein is treated as by Yang *et al*. (2012), i.e., primitively having a common stem, and not fused with RP; (2) the subcosta anterior is treated as a vein (as by Kukalová-Peck 1991: Fig. 6.16) not a bulge (Kukalová-Peck & Lawrence 2004: Fig. 9); (3) the relationship between the M and Cu systems in the forewing of Raphidiidae is treated as discussed below and shown in Fig. 2C; in the interpretation of Kukalová-Peck & Lawrence (2004: Fig. 9), the posterior branch of MP originates at our 1im and is then fused with CuA; (4) in the hind wing, the basal part of CuA1 of Kukalová-Peck & Lawrence (2004) is treated as a crossvein (2m-cu); (5) all anal veins are treated as branches of the analis anterior. Crossveins are designated after the longitudinal veins with which they are connect and numbered in sequence from the wing base, e.g., 1ra-rp, first (proximal-most) crossvein connecting RA and RP; 2scp-r, second crossvein between ScP and RA; icu, crossvein between CuA and CuP; iaa, crossvein between AA1 and AA2. Additional crossveins which only occur in some families or genera are designated relative to the next distal crossvein, e.g., 2^bscp-r, located proximad 2scp-r (2scp-r bis). We have tried to homologize crossveins across the order (this system is, however, inapplicable to species of Baissopteridae, which possess numerous additional crossveins). Terminology of wing spaces and details of venation (e.g., traces, veinlets) follows Oswald (1993); and of male terminalia follows Aspöck & Aspöck (2008).

Abbreviations used for wing veins and spaces are: AA1 to AA3, first to third branches of analis anterior; C, costa; Cu, cubitus; CuA, cubitus anterior; CuA1, proximal-most branch of CuA; CuP, cubitus posterior; *doi*, discoidal cells; J, jugal vein; M, media; MA, media anterior; MP, media posterior; R, radius; RA, radius anterior; RP, radius posterior; RP1 (RP2, RP3), proximal-most branch (second, third) of radius posterior; ScA, subcosta anterior; ScP, subcosta posterior.

Institutional abbreviations are: AMNH, American Museum of Natural History (New York); NHM, Natural History Museum (London); MCZ, Museum of Comparative Zoology (Harvard University); UCM, University of Colorado Museum (Boulder); USNM, United States National Museum (Smithsonian Institution).

Systematic paleontology

Class Insecta Linnaeus, 1758

Order Raphidioptera Navás, 1916

Suborder Raphidiomorpha Engel, 2002

Diagnosis based on forewing venation. ScP short, terminating on C before pterostigma [ScP long, running within pterostigma, extending nearly to wing apex in Priscaenigmatomorpha]; origin of RP far from wing base [origin of RP near wing base in Priscaenigmatomorpha]; CuA appears proximally as long crossvein between Cu, M, therefore, Cu continuous with CuP [Cu continuous with CuA in Priscaenigmatomorpha]; AA2, AA3 fused basally for some distance [these free for entire length in Priscaenigmatomorpha]; broadly ovoid cell between AA1, AA2+3 [narrow cell in Priscaenigmatomorpha].

Description of wing venation. ***Forewing***. ScA vestigial, represented by short convex fold obliquely running from wing base near ScP to costal margin, where present very short vein-like structure lacking hairs, visible in at least some Raphidiidae and Mesoraphidiidae (s.l.). Pterostigma distinct, often dark. ScP relatively short, terminating on C before pterostigma. RA with one to several distal branches (veinlets); one to three branches incorporated in pterostigma in many taxa. RP originating far from wing base. M basally adjoining R for long distance, then fused usually with CuA for short distance, then divided into MA, MP. MA dichotomously branched. MP zigzagged, usually pectinately branched. Cu basally unclear, often almost reduced. CuA appears proximally as crossvein between Cu and M, then fused with M for short distance; distally strongly zigzagged, pectinately branched; sometimes fused with MP for some distance. CuP continuing Cu, simple or at most bifurcate. AA1 rather long, simple or few-branched; AA2, AA3 fused basally for long distance. AA1, AA2+3, crossvein (iaa) form broadly ovoid cell. Jugal lobe (area) well developed, with one jugal vein.

Hind wing. Structure of ScA unclear. ScP, RA, RP, pterostigma similarly configured as in forewing. M basally adjoining R for long distance, then divided into MA, MP. MA, MP usually similarly configured as in forewing; sometimes MP deeply dichotomous (e.g., Inocelliidae, Baissopteridae). Cu divided into CuA, CuP near wing base; CuA in general pectinate, with one to three branches; CuP usually simple, sometimes fused with AA1 for some distance. AA1 simple or bifurcate; AA2 simple. Jugal lobe (area) similar to that of forewing.

Comments on characters. ***Synapomorphies of Raphidiomorpha***. The phylogenetic analyses of Engel (2002) and Bechly & Wolf-Schwenninger (2011) agree in supporting a sister group relationships for Raphidiomorpha and Priscaenigmatomorpha, which we find reasonable. This implies that the following five character states are synapomorphies of Raphidiomorpha. Character states [1], [2], and [5] were previously indicated by Willmann (1994), and state [2] also by Aspöck & Aspöck (2004) and Bechly & Wolf-Schwenninger (2011).

[1] ScP is relatively short, terminating on C before the pterostigma;

[2] the origin of RP is very far from the wing base;

[3] CuA appears proximally as a crossvein between Cu and M, then is usually fused with M for a short distance. This character state is poorly detectable in specimens of both species of Metaraphidiidae from the Early Jurassic (oldest known Raphidiomorpha) due to poor preservation, but present in all other reported fossil (e.g., Fig. 1A) and extant species (Figs 2A, C). However, this character condition might in fact be plesiomorphic in Raphidioptera, as it occurs in Nanosialidae, which is presumably ancestral to Raphidioptera, and other Permian Neuropterida (Parasialidae from Megaloptera, Permithonidae from Neuroptera) (Martynov 1928: Pl. 15, Fig. 2; Shcherbakov 2013: Figs 1, 3);

[4] AA2 and AA3 are fused basally for some distance. In Metaraphidiidae, these veins are fused only basally (e.g., *Metaraphidia vhaldieki* Willmann, 1994: Fig. 4); in younger Raphidiomorpha AA2 and AA3 appear to be fused almost for their entire length (except for their branches) (e.g., Figs 1A, 2A, C);

[5] AA1, AA2+3, and the crossvein iaa form a broadly ovoid cell.

Bechly & Wolf-Schwenninger (2011) proposed two other synapomorphies of the suborder, which we consider invalid:

[6] "more distinct [ptero]stigma";

[7] "parallel course of CuA and CuP" (p. 229).

The pterostigma is very distinct in a new taxon of Priscaenigmatomorpha (Liu *et al.* 2013), and a more or less distinct pterostigma is a synapomorphy of all Raphidioptera (Bechly & Wolf-Schwenninger 2011; Liu *et al.* 2013). State [7] is too uncertain; in many Neuropterida CuA (and then CuA1) and CuP run parallel for most of their length; at least in some taxa of Neuroptera these veins run very similar to that found in Raphidiomorpha (e.g., the Permian Permithonidae *Palaemerobius proavitus* Martynov, 1928: Pl. 15, Fig. 2). Therefore, we cannot consider states [6] and [7] as synapomorphies of Raphidiomorpha.

Willmann (1994) proposed four other venational synapomorphies of Raphidiomorpha:

[8] the basal intramedian cell is shifted proximally;

[9] the free portion of M runs basad rather than apicad [=2r-m in Raphidiidae; Fig. 2C];

[10] elongation of the basal m-cu crossvein [=the length of M from M+CuA to its fork into MA and MP; Fig. 2C] and its position along wing length;

[11] distad elongation of the basal cell between M and Cu [=a cell formed by M, MP, and CuA].

However, state [8] is certainly not a synapomorphy of Raphidiomorpha; the basal intramedian cell is not shifted proximally compared with Priscaenigmatomorpha. Three other 'synapomorphies' [states 9–11] are consequences of Willmann's (1994) interpretation of the relationship between M and RP, with which we disagree (see Willmann 1994: Figs 8c–e, 9); their polarity is difficult to establish.

MP and CuA. The relationship between MP and CuA (especially in the forewing) is more difficult to interpret unambiguously. This question is rarely considered in detail; in particular, it was omitted in Aspöck *et al.*'s (1991) monograph of the order. Withycombe (1923) studied pupal venation of Raphidiidae and found that CuA is fused with MP for some distance in the forewing, and that these are free in the hind wing. Willmann (1994) considered these relationships as seen in the forewing of Raphidiidae to apply to the both fore- and hind wings in all families of Raphidiomorpha. However, this appears to us to be incorrect; we believe that the hind wind venation is quite easily homologized throughout the suborder, with MP not fused with CuA (Fig. 2B, D). This relationship is clearly visible in Mesozoic taxa (Fig. 1B) and is supported by pupal venation of the extant *Atlantoraphidia maculicollis* (Stephens, 1836) (Withycombe 1923). Also, similarities in the forewing venation between Raphidiidae and those species of Mesoraphidiidae (s.l.) that have two *doi* may be easily interpreted as CuA fused with MP for some distance, as shown by Withycombe (1923).

As to the forewing of Inocelliidae and most other Mesozoic taxa with similar venation, fossil evidence provides no unambiguous resolution of this question. Even the oldest known Raphidiomorpha (Early and Middle Jurassic) have venation that allows three interpretations: (1) the relationship between MP and CuA in the forewing is similar to the configuration found in the hind wing of Inocelliidae, i.e., MP is deeply dichotomously forked (as in Comstock 1918: Fig. 167); (2) MP is also deeply dichotomously forked, but its posterior branch is fused for some distance with CuA (as in Martynov 1925b: Fig. 2); (3) CuA is not fused with MP and connected with this by two crossveins (as in Carpenter 1968: Fig. 1; Willmann 1994: Fig. 4). We prefer interpretation (3) as most probable (Fig. 1A, 2A), recognizing that (1) and (2) are also possible.

Crossvein 2scp-r. Homology of 2scp-r in Raphidiidae and Inocelliidae is supported by the fact that the pterostigma in no species of Inocelliidae is closed by a crossvein, but all have a crossvein near the termination of ScP; contrasted with the pterostigma in all species of Raphidiidae being closed by a crossvein (a few species have a crossvein near the termination of ScP, which we treat as additional). Therefore, we treat 2scp-r in Raphidiidae as shifted distad.

Infraorder 'Neoraphidioptera' Perrichot *et* Engel, 2007

The two extant families (Raphidiidae and Inocelliidae) are currently considered as sisters, together forming the infraorder Neoraphidioptera (Perrichot & Engel 2007; Engel & Grimaldi 2008; Bechly & Wolf-Schwenninger 2011). However, we find that the characters proposed by Willmann (1994) and Bechly & Wolf-Schwenninger (2011) to define the 'Neoraphidioptera' may not in fact do so.

Willmann (1994) found three synapomorphies of the clade Raphidiidae + Inocelliidae (i.e., 'Neoraphidioptera'): [1] the origin of RP in the forewing is shifted to the midwing position; [2] "M and CuA touch each other"; [3] "the basal length of RP" [=1r-m] in the hind wing connects M and RP.

Bechly and Wolf-Schwenninger (2011) considered state [1] to be the single synapomorphy of 'Neoraphidioptera'; however, this appears too vague, as in most all Mesozoic species, the origin of RP is also shifted far distad the wing base, often only slightly proximal to the condition occurring in Raphidiidae and Inocelliidae. We understand putative state [2] as likely the same as state (6), below; if so, it is not a synapomorphy of 'Neoraphidioptera'. State [3], 1r-m connecting M and RP found in many 'Neoraphidioptera' and four Cretaceous genera is plesiomorphic (see below, state 5). 1r-m in the vast majority of other Mesozoic taxa connects R (near the apparent origin of M) and RP, and this condition appears to be apomorphic. We cannot explain this perplexing situation.

We find a number of derived character states of venation within groups of the extant Raphidioptera, but none that appear to define them as the proposed monophyletic unit 'Neoraphidioptera'. We suspect that the appearances of some of these in a few Mesozoic taxa may be homoplasious with regard to their presence within Raphidiidae and Inocelliidae, but some might also be homologous—this cannot be determined given current knowledge.

Derived states of (or predominantly within) Inocelliidae.

(1) ***3ra-rp in both wings is located distad the pterostigma, and therefore the distal part of RA becomes zigzagged***. This condition occurs in all Inocelliidae (fossil and extant) and most extant Raphidiidae. In the vast majority of Mesozoic taxa, 3ra-rp is located within the pterostigma, and the distal part of RA is smooth (plesiomorphic state; Fig. 1); only a few Cretaceous species of Mesoraphidiidae (s.l.) have an apomorphic condition, i.e., *Siboptera eurydictyon* Ponomarenko, 1993 and *Alloraphidia asiatica* Ponomarenko, 1993 (Baissa, Transbaikalia); *Nanoraphidia electroburmica* Engel, 2002 (Burmese amber); *Grimaldiraphidia luzzii* (Grimaldi, 2000) (New Jersey amber); *Amarantoraphidia ventolina* Pérez-de la Fuente *et al*., 2012 (Spanish amber). All known Eocene species of Raphidiidae (except two Baltic amber species) show the plesiomorphic state, but many fossil Oligocene and Neogene members of the family (mostly unnamed) possess the apomorphic condition. Among extant Raphidiidae, species of some genera have both conditions; this is noteworthy especially in the genus *Alena*, where it is associated with the presence of apomorphic character state (4): the species that have the apomorphic state (1) have apomorphic state (4) and vice-versa.

(2) ***The crossvein 1r-m ('MA' of various authors) in the forewing connects M and R***. This condition is only present in Inocelliidae (all) and in the Middle Jurassic *Styporaphidia magia* Engel *et* Ren (Engel & Ren 2008: Fig. 7), which we suspect may be homoplasious. In other Raphidiomorpha, this crossvein connects MA (or very rarely M) and RP (Fig. 1A).

(3) ***1ra-rp in the forewing is present***. In the vast majority of Mesoraphidiidae (s.l.) and Metaraphidiidae, the two crossveins between RA and RP are probably homologous with 2ra-rp and 3ra-rp in Raphidiidae based on

similar their location relative to the branches of RP and the pterostigma. In all Inocelliidae one or two additional such crossveins are present; 1ra-rp is present in all species, and 4ra-rp only in *Sininocellia.* The only fossil species with 1ra-rp (except multi-crossveined Baissopteridae) is *Styporaphidia magia* (Engel & Ren 2008: Fig. 7). We suspect that this may be homoplasious.

(4) ***1r-m in the hind wing is lost***. This is only characteristic of Inocelliidae, found in the majority of extant species (except of *Sininocellia* and *Fibla*) and in the Baltic amber *Electrinocellia peculiaris* (Carpenter, 1957). A strong reduction of 1r-m is documented in the extant *Fibla peyerimhoffi* (Navás, 1919) (see Aspöck *et al*. 1991: Figs 47–49).

Derived states of (or predominantly within) Raphidiidae.

(5) ***1r-m in the hind wing is crossvein-like***. This crossvein (brace) is considered the basal section of MA by authors that believe that MA is fused with RP for some distance. In the majority of Mesozoic taxa, 1r-m is configured similarly: long, longitudinal, connecting R near the wing base with RP so that 1r-m appears to be the proximal part of RP (Fig. 1B). However, the relocation of the proximal end of 1r-m from M to R in these taxa is most probably a derived condition. The plesiomorphic condition of 1r-m is a long, longitudinal brace connecting M near the wing base with RP. A similar structure of 1r-m occurs in other basal Neuropterida families (e.g., Permithonidae, Sialidae, Corydalidae), and is found in four Cretaceous Raphidioptera genera, i.e., *Baisoraphidia* Ponomarenko, 1993; *Austroraphidia* Willmann, 1994; *Nanoraphidia* Engel, 2002 (Mesoraphidiidae s.l.), and *Cretoraphidia* Ponomarenko, 1993 (Baissopteridae). This plesiomorphic condition is now retained in many genera of Raphidiidae (e.g., *Raphidia* Linnaeus, 1758, *Phaeostigma* Navás, 1909, *Dichrostigma* Navás, 1909) and two genera of Inocelliidae (*Sininocellia* and *Fibla*) (Fig. 2B). In other extant genera of Raphiididae, 1r-m is short and crossvein-like (Fig. 1D). This state is derived with regard to both conditions occurring in the Mesozoic, i.e., to a long, longitudinal brace connecting either M or R near the wing base with RP. Among fossil taxa this condition is present in two Miocene species of Raphidiidae: *A. mineralensis* Engel, 2009 (Stewart Valley, Nevada) and *Ohmella coffini* Nel, 1993 (Ardèche, France). This homology is clearly supported by occurrences of both conditions in species of the extant genus *Alena*.

(6) ***CuA in the forewing is fused with MP for some distance***. This condition is characteristic of all Raphidiidae. It is very probable that these veins are similarly fused in those species of Mesoraphidiidae (s.l.) and Inocelliidae that have two discoidal cells (see below). Most species of Mesoraphidiidae (s.l.) have three discoidal cells (Fig. 1A), and CuA and MP are connected by two crossveins (a plesiomorphic condition).

(7) ***CuP in the hind wing is medially fused with AA1 for some distance***. This apomorphic state is characteristic of all extant Raphidiidae and some Mesoraphidiidae (s.l.). In the latter, it appears to occur at least in the genera *Mesoraphidia* Martynov, 1925 and *Ororaphidia* Engel *et* Ren, 2008 (Fig. 1B; Engel & Ren 2008: Fig. 5). However, in both known species of Baltic amber Raphidiidae (‘*Raphidia*’ *baltica* Carpenter, 1957 and *Succinoraphidia exhibens* Aspöck *et* Aspöck, 2004), CuP and AA1 are not fused (a plesiomorphic state), whereas these veins are fused in two fossil Eocene and Oligocene species from North America (*Megaraphidia* sp. and ‘*Raphidia*’ *creedei* Carpenter, 1936) whose hind wing bases are well preserved (Fig. 8; Carpenter 1936: Fig. 12). Therefore, the occurrence of this apomorphic state in Raphidiidae and Mesoraphidiidae (s.l.) is most probably homoplasious.

(8) ***A free M in the forewing is absent (or strongly reduced).*** This state occurs in most Raphidiidae and a few Inocelliidae. In Raphidiidae, CuA is fused with M at approximately the point where M+CuA separates from the apparent fusion with R (Fig. 7). The entire M+CuA may occur adjoining R; R is not fused with M and M+CuA, but only adjoins them for an interval (Fig. 20). As a result, a free portion of M before the fusion with CuA occurs rarely; when it does, it is very short. In the majority of Inocelliidae species, the free portion of M is rather long; this is absent in a few species (e.g., *Inocellia striata* Aspöck *et al*., 2011), and the apparent fusion of R+M+CuA is present only in the genus *Indianoinocellia*. In Baissopteridae, the free portion of M is also always long, but the length of M+CuA varies, from very short (e.g., *Cretoraphidia macrocella* Ponomarenko, 1992) to long (e.g., *Baissoptera martinsoni* Martynova, 1961). A similar structure is characteristic of Mesoraphidiidae (s.l.) and probably Metaraphidiidae: the free portion of M is similarly always rather long (Fig. 1A), but M+CuA is usually very short, with the exception of *Nanoraphidia electroburmica* Engel, 2002 from the earliest Cenomanian of Burmese amber, in which it is long; very rarely, M and CuA are not fused (Fig. 1A).

None of these derived states are clear synapomorphies of ‘Neoraphidioptera’. Most probably, condition (5) evolved independently in Inocelliidae and Raphidiidae, as this remains in its plesiomorphic state in most Eocene species of both of these families, and first appear in the late Eocene and even later in some genera. We suspect that this might also be true for state (1), as in Eocene Raphidiidae, it occurs in only two Baltic amber species; and for state (8), as in Inocelliidae, it occurs in only a few species. States (2) and (3) are most probably autapomorphies of Inocelliidae, convergent in a few taxa of Metaraphidiidae and Mesoraphidiidae (s.l.). State (4) only appears within Inocelliidae at a later stage. State (6) appears to be an autapomorphy of Raphidiidae, paralleled in some Mesoraphidiidae (s.l.) with two discoidal cells, but it might also be a synapomorphy of all these taxa. State (7) probably appears within Raphidiidae at a later stage, paralleled in some Mesoraphidiidae (s.l.).

We find that the venation of Inocelliidae and Raphidiidae is dissimilar in many respects, and suspect that they may be more closely related to different taxa of Mesoraphidiidae (s.l.) than to each other, by similarities of head shape, prothorax, and wing venation; that is, they may be separately nested within a paraphyletic Mesoraphidiidae (s.l.).

Raphidiidae species are readily distinguished from those of Mesoraphidiidae (s.l.) whose CuP and AA1 are fused in the hind wing by the absence of an additional, third discoidal cell in the forewing (present in the vast majority of Mesoraphidiidae s.l.; Fig. 1A). Those few species of Mesoraphidiidae (s.l.) which have two discoidal cells as in Raphidiidae possess a long pterostigma which lacks the incorporated pterostigmal branches of RA, i.e., *Pararaphidia vitimica* (Martynova, 1961); *Amarantoraphidia ventolina* Pérez-de la Fuente *et al*., 2012; *Cantabroraphidia marcanoi* Pérez-de la Fuente *et al*., 2010; *Lebanoraphidia nana* Bechly *et* Wolf-Schwenninger, 2011. In this respect, these species of Mesoraphidiidae (s.l.) are rather similar to *Archiraphidia* Handlirsch, 1910 (see below), but these are readily distinguished by the latter's short pterostigma. These mesoraphidiid species share apomorphic condition (6) with Raphidiidae. The minute species *Allopraphidia petrosa* Ponomarenko, 1988 from the Early Cretaceous of Bon-Tsagaan (Mongolia) is hardly distinguished from Raphidiidae by forewing characters (but its posterior-proximal region is poorly preserved).

The venation of most Mesoraphidiidae (s.l.) is in general similar to that of Inocelliidae (cf. Fig. 1 and 2A, B), but the former always have the crossvein 1r-m connecting RP and MA in the forewing, not R and M (except one species, see above), and their pterostigma usually have at least one branch of RA within them, or is proximally closed by a crossvein.

Family Baissopteridae Martynova, 1961

Diagnostic character states of venation. Pterostigma usually with crossvein closing it proximally, with at least one incorporated branch of RA. Forewing: rich venation with 3–5 branches of RP, many crossveins: 3–5 ra-pr, 5–15 ir, 4–7 r-m, 3–5 im, 2–3 icu.

Hind wing: many crossveins: 4–5 ra-pr, 5–14 ir, 4–6 r-m, 2–4 m-cu.

Composition. Five genera from the Cretaceous and Eocene: *Cretoraphidiopsis* Engel, 2002 (monotypic) from Hauterivian/Aptian of Bon-Tsagaan, Mongolia; *Lugala* Willmann, 1994 (monotypic) from the Early Cretaceous of Bayan-Tsagaan, Mongolia; *Baissoptera* Martynova, 1961 (twelve species) from pre-Barremian/early Barremian of Baissa, Transbaikalian Russia; Barremian/Aptian of Huangbanjigou, Yixian Formation, China; late Albian of Spanish amber (Peñacerrada I); late Aptian of the Crato Formation of Brazil; *Cretoraphidia* (four species) from Baissa and Neocomian of Romanovka, Transbaikalian Russia; *Austroraphidia* Willmann, 1994 (monotypic) from the Crato Formation of Brazil; *Dictyoraphidia* (monotypic) from the late Eocene of Florissant.

Comments on characters. The venation of Baissopteridae is in general similar to that of those Mesoraphidiidae (s.l.) that have a similar structure of the pterostigma (e.g., the Cretaceous genus *Siboptera* Ponomarenko, 1993); it differs from these in possessing more branches of longitudinal veins and an enriched crossvenation. Therefore, the differences between this and other families are mainly numerical. The enriched venation of Baissopteridae is certainly secondary; Jurassic taxa of Raphidiomorpha (Metaraphidiidae and Mesoraphidiidae s.l.) have simpler venation.

Remarks. We base our comments on examination of a single (Cretaceous) specimen of a species assigned to this family and published descriptions and figures of the others. We agree with Bechly & Wolf-Schwenninger (2011) that some of these published descriptions and figures appear problematic, and therefore our conclusions (diagnosis and family composition) are preliminary pending extensive revision of these taxa.

The family is sometimes considered to be paraphyletic (e.g., Willmann 1994; Bechly & Wolf-Schwenninger 2011), as it is not defined by any distinct synapomorphies. We did not find these as well. It is unknown yet if this group of genera with enriched venation constitutes a monophyletic taxon or not, perhaps within a paraphyletic Mesoraphidiidae (s.l.). Both families are in strong need of detailed revision, but this is beyond of the scope of this paper.

Genus *Dictyoraphidia* Handlirsch, 1910

Dictyoraphidia Handlirsch, 1910: 103; Handlirsch 1920–1921 [1921]: 255; Martynov 1925a: 244; Cockerell & Custer 1925: 295; Carpenter 1936: 145; Metzger 1960: 41; Oswald 1990: 160 (as a synonym of *Raphidia*); Aspöck *et al*. 1991: 536, 537, 665; Engel 2002: 21 (as a tentative synonym of *Raphidia*).

Type and only species. *Inocellia veterana* Scudder, 1890, by monotypy.

Diagnosis. Unusual Cenozoic raphidiopteran with many additional crossveins; origin of RP shifted basad in both wings; CuP simple in hind wing. Differs from Cretaceous (i.e., all other) baissopterid genera by 1r-m crossvein-like.

Remarks. Handlirsch (1910) characterized this genus "by the much greater development and ramification of the sector radii [=RP], by the much more numerous cross-veins, and consequently by the far greater number of cells" (p. 103). Carpenter (1936) thought that the type of *Dictyoraphidia veterana* was lost, and did not consider this genus and species in detail in his revision, but remarked that "his [Handlirsch's] conclusions were based upon assumptions which are not valid, and his genera [*Dictyoraphidia* and *Archiraphidia*] based upon venational characteristics which appear in any series of specimens of Recent *Raphidia*" (p. 145). But even as the genus was defined in Carpenter's (1936) time, no species of *Raphidia* (i.e., in the broadest sense) had such dense venation as is found in *Dictyoraphidia veterana*.

We find that the venation of this genus most resembles that seen in the Baissopteridae. First, they share numerous crossveins, more than seen elsewhere in the Raphidiomorpha. Secondly, the simple CuA in the hind wing of *D. veternana* is a unique condition among Cenozoic fossil and extant Raphidioptera. This condition occurs in the hind wing of some Baissopteridae, e.g., *Austroraphidia brasiliensi*s (Nel *et al*., 1990) from the Aptian Crato Formation of Brazil and *Lugala longissima* (Ponomarenko, 1988) from the Early Cretaceous of Bayan-Tsagan, Mongolia (Ponomarenko 1988: Fig. 4; Nel *et al*. 1990: Fig. 3). Even in other Baissopteridae, which have the richest venation of the Raphidiomorpha, CuA is usually only forked once. A simple CuP, however, is also present in two species of small Mesoraphidiidae (s.l.) with rather reduced venation, i.e., *Archeraphidia yakowlewi* Ponomarenko, 1988 and *Nanoraphidia electroburmica*. Thirdly, the structure of the pterostigma in most Baissopteridae is similar to that of the Raphidiidae, i.e., with a crossvein closing the pterostigma proximally and an incorporated branch of RA present; both of these conditions are present in *Dictyoraphidia veterana*. Fourthly, the origin of RP is shifted proximally (i.e., located in the proximal half of wings), a characteristic feature of most Mesozoic Raphidiomorpha. Therefore, there is little doubt that this genus belong to the Baissopteridae. The single important difference between it and all known species of Baissopteridae is that 1r-m of the hind wing is crossvein-like (an apomorphic state), whereas this is long, longitudinal in the latter (a plesiomorphic state). But this state could be convergent with the general evolution of this character in Cenozoic Raphidioptera (see Inocelliidae and Raphidiidae, above).

Baissopteridae have been recorded hitherto only from the Cretaceous. Their youngest previously known occurrence is in the Turonian (VM, pers. obs.); the oldest is in the Early Cretaceous (Mongolian and Transbaikalian localities). This finding of a Mesozoic family in the late Eocene with at least a 55 Ma absence in the record has an analogue in Neuroptera. *Oligogetes relictus* Makarkin, 1998 was described from the late Eocene/early Oligocene locality at Bolshaya Svetlovodnaya River, Primorskii Krai (Makarkin 1998). It is the only Cenozoic Neuroptera genus which belongs to an extinct Mesozoic family with certainty (tentatively the Solenoptilidae).

Dictyoraphidia veterana (Scudder, 1890)
(Figs 3, 4)

Inocellia veterana Scudder, 1890: 156; Pl. 14, Fig. 1; Handlirsch 1906–1908 [1907]: 907; Cockerell & Custer 1925: 296, 297.

Dictyoraphidia veterana: Handlirsch 1910: 104; Cockerell & Custer 1925: 295; Aspöck *et al.* 1991: 537, 665, Fig. 3047.
[*Raphidia*] *veterana*: Carpenter 1936: 143–145.
Raphidia veterana: Oswald 1990: 161; Engel 2003: 125; Engel 2009: 213 (Tabl. 1); Engel 2011: 79 (Tabl. 2).
"Raphidia veterana": Engel 2002: 22.

Revised description. Forewing narrow, basal part not preserved; 6 mm long (as preserved; estimated complete length ca. 9 mm), 2.6 mm wide (as preserved; estimated complete length ca. 2.7 mm). Costal space not preserved. ScP relatively long; length from its termination to pterostigma probably less than pterostigma length. One poorly preserved crossvein between ScP, RA at termination of ScP; another crossvein closes pterostigma proximally. Pterostigma rather long; incorporated pterostigmal branches of RA not detected. Posterior trace of RA distad pterostigma zigzagged, with two branches: one closed pterostigma distally, other distad pterostigma. RA space nearly equal in width for most length, with five crossveins (two distad pterostigma). RP with three branches; RP1 dichotomously branched. RP2, RP3 simple. Nine intraradial crossveins irregularly arranged. Five radio-medial crossveins connect RP1, MA. MA dichotomously branched; one intra-MA crossvein. MP pectinately branched, with two branches; proximal branch deeply forked (alternatively, latter represents anterior trace of CuA). Three intramedian crossveins. Cu, anal veins not preserved. All longitudinal veins (except ScP, proximal RA) strongly zigzagged.

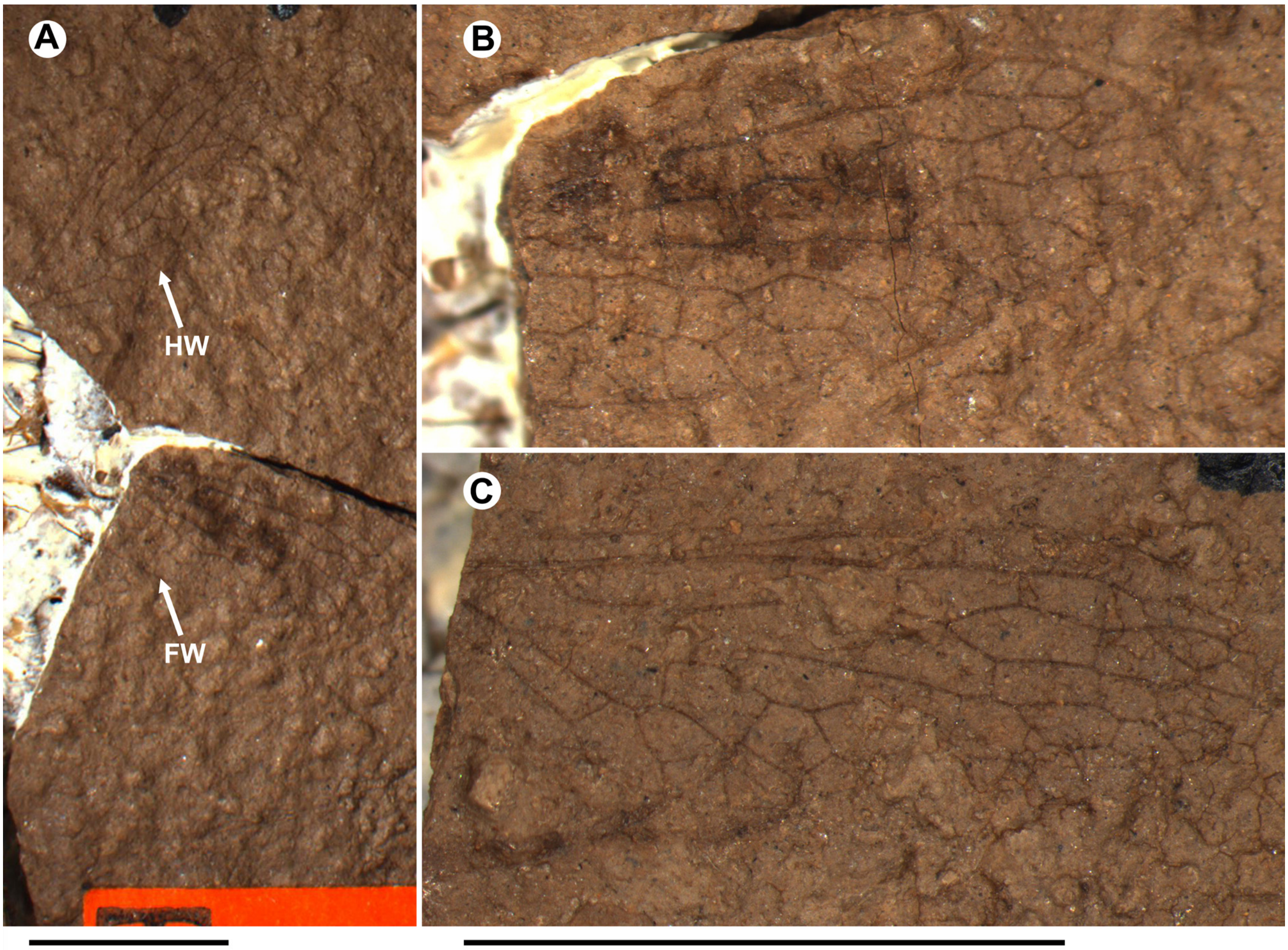

FIGURE 3. *Dictyoraphidia veterana* (Scudder, 1890). Holotype PU 6385, EM 1.385. A, the specimen as preserved today. B, forewing. C, hind wing. FW, forewing; HW, hind wing. Scale bars = 4 mm (B, C to scale).

Hind wing 7.3 mm long (as preserved; estimated complete length ca. 8.5 mm), 2.4 mm wide. Costal space narrow. ScP relatively long; length from its termination to pterostigma much less than pterostigma length. Subcostal veinlets simple widely spaced. In subcostal space, two crossveins detected; one near distal termination of ScP; another curved, closes pterostigma proximally. Pterostigma rather long. RA distally zigzagged, with four preserved branches: one incorporated branch not clearly visible; one closed pterostigma distally, other two short, distad pterostigma. Four crossveins between RA, RP; one in middle of pterostigma, two proximad, one distad. Anterior trace of RP shallowly forked distally, with three branches; RP1 dichotomously branched; RP2, RP3 simple. Seven intraradial crossvein detected. Five crossveins between RP, MA; 1r-m short, crossvein-like, slightly curved; connecting RP, MA relatively far distad origin of RP. M forked slightly proximad RP origin. MA deeply forked, at least anterior branch forked (posterior branch not completely preserved). MP pectinately branched, with two simple branches, simple stem. Three intramedian crossveins; one crossvein between branches of MP. Two crossveins between M and Cu/CuA. 1m-cu ('M5') short, only slightly oblique; 2m-cu connects M before branching, CuA. CuA simple. CuP, anal veins not preserved. All longitudinal veins (except ScP, proximal RA, CuA) strongly zigzagged.

Type material. PU 6385, EM 1.385, collected by the Princeton Scientific Expedition in 1877, deposited in USNM. A poorly preserved male specimen, consisting today of two isolated parts: (1) an abdomen and incomplete forewing, and (1) a hind wing with hardly visible fragments of another wing which is impossible to identify. Verbatim label data: (1) [typed] "PU 6385 EM 1.385 TYPE / Inocellia veterana Scudder / Florissant Fm., M. Olig. / Florissant, Teller Co, Color. / Princeton Sci. Exped. 1877 / Scudder S. H. 1890, Tertiary / Insects of North America, p. / 156–157, pl. 14 fig. 1 / Princeton University Department of Geology"; (2) [hand written] "EM 1.385 is the type of / Inocellia veterana Scud. / fide Carpenter ['s] letter. / D. Baird 22.iii.1993". The specimen has black ink writing on the rock that says "PU / 6385", "E M / 1.385.", and a red label glued to the rock that says "Type".

Type locality. Florissant (precise collecting locality unknown).

Remarks. The holotype was more complete when Scudder (1890: Pl. 14, Fig. 1) described the species. It has been damaged since then, with a rather large potion now missing (Fig. 3A).

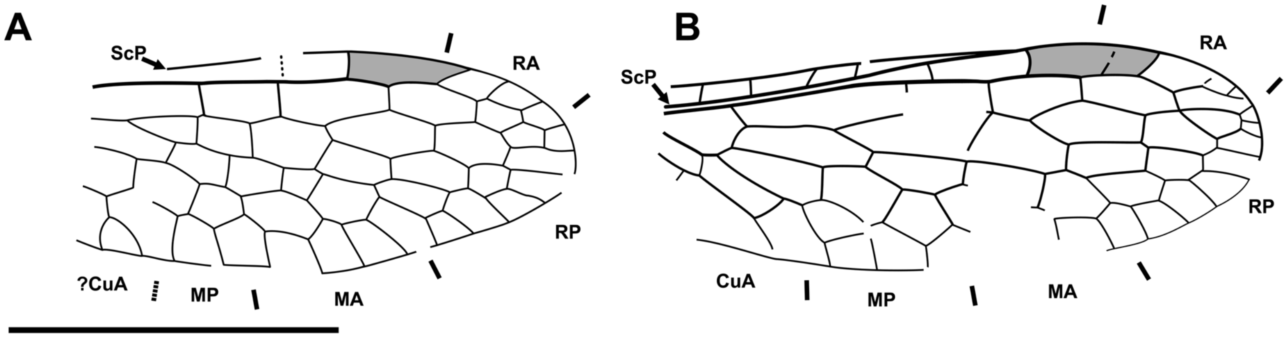

FIGURE 4. *Dictyoraphidia veterana* (Scudder, 1890). Wing venation of the holotype PU 6385, EM 1.385. A, forewing. B, hind wing. Scale bar = 4 mm.

Family Raphidiidae Latreille, 1810

Diagnostic character states of venation. Forewing: In subcostal space, two crossveins: one connecting ScP, RA; other closing pterostigma proximally. At least one branch of RA incorporating in pterostigma. In RA spaces, two crossveins between RA, RP (three crossveins in *Mongoloraphidia abnormis* Liu *et al.*, 2010a: Fig. 1). M, CuA appear to originate from R either separately or at same point (rarely stem M+CuA present). 1r-m connects RP and MA. In medial space, only two crossveins between MA, MP forming two *doi*. CuA fused with MP for short distance. AA2, AA3 basally almost entirely fused.

Hind wing: In subcostal space, one crossvein closing pterostigma proximally; at least one branch of RA incorporating in pterostigma; two *doi* (except normally one in few species); CuP, AA1 medially fused (except two Baltic amber species).

Composition. Twenty six extant genera (ca. 200 species) distributed in the Northern Hemisphere (Aspöck *et al*. 2012a) and four fossil genera from the late Eocene of Baltic amber (*Succinoraphidia* Aspöck *et* Aspöck, 2004) and Florissant (*Megaraphidia* Cockerell, 1907; *Archiraphidia*; *Florissantoraphidia* gen. nov.).

Besides seven from Florissant, the following six named species have been described: '*Agulla*' *protomaculata* Engel, 2011 (late Ypresian of the Green River Formation, Parachute Creek Member of Colorado); '*Raphidia*' *baltica* and *Succinoraphidia exhibens* (late Eocene of Baltic amber); '*Raphidia*' *creedei* (late Oligocene of Creede, Colorado); *Agulla mineralensis* (middle Miocene of Stewart Valley, Nevada); and '*Ohmella*' *coffini* (late Miocene of Ardèche (Mt. Andance), France). Also, six specimens have been figured, but not named, from the early Oligocene of the Anna potash mine in Haut-Rhin department, France (Nel 1993: Fig. 10); the late Oligocene of Enspel, Germany (Wedmann 2000: Fig. 13); the early Miocene of Rubielos de Mora, Spain (Peñalver & Seilacher 1995: Fig. 8), and the late Miocene of Murat, France (Nel 1993: Figs 6–9).

Comments on characters. ***The additional distal crossvein between C/ScP and RA (2^{b}scp-r).*** This crossvein is absent in extant Raphidiidae, except in the three species (both in fore- and hind wings) of the subgenus *Harraphidia* Steinmann, 1963 of the genus *Harraphidia,* distributed in Morocco and extreme south of Spain (Monserrat & Papenberg 2006: Fig. 1). 2^{b}scp-r is present in at least one Florissant species, *Archiraphidia tumulata* (Scudder, 1890). Carpenter (1936) identified this crossvein in one forewing of the '*Raphidia' creedei* holotype, but found it certainly absent in the other.

Discoidal cells (doi). Some specimens of species which normally have two *doi* may adventitiously possess other numbers of these. Figured examples of such aberrant individuals include an instance of one *doi* in *Mongoloraphidia kaszabi* Aspöck *et* Aspöck, 1968 (Aspöck & Aspöck 1968a: Fig. 1), *Alena infundibulata* Aspöck *et al*., 1994: Fig. 18, and *Raphidia ophiopsis* Linnaeus, 1758 (Aspöck *et al*. 1977: Fig. 1e); three in *Turcoraphidia acerba* (Aspöck & Aspöck, 1966) (Aspock *et al*. 1991: Fig. 18); and four in *Raphidia ophiopsis* (Aspöck *et al*. 1977: Fig. 1h). One *doi* is characteristic of all species of the genus *Harraphidia* (Monserrat & Papenberg 2006) (see below).

Remarks. No raphidiopteran specimens with the full combination of the raphidiid diagnostic character states in their venation are known before the Eocene, except probably one mesoraphidiid forewing (see above; but this is incompletely preserved). The two genera described from the Middle Jurassic of Daohugou (Engel & Ren 2008) were placed in Raphidiidae (Ren *et al*. 2010). However, they cannot be assigned to this family, as both genera lack a crossvein closing the pterostigma proximally, and the third *doi* is present.

No venational autapomorphies of Raphidiidae were identified by Aspöck and Aspöck (2004); however, we find that MP fused for a short distance with CuA in the forewing may be considered one. The CuA fused for some distance with AA1 in the hind wing is an apomorphy characterisizing all extant raphidiids. However, this condition probably appeared at later stage; it is absent in the two Baltic amber species (above).

Generic attribution of Florissant raphidiid species. Extant genera and species of Raphidioptera are based on genitalic characters, as eidonomic characters (external, visible without dissection) have been widely considered too conservative to be useful at those levels (e.g., Aspöck 1986). This has rendered the fossil history of the order obscured below the family level.

Florissant species are currently assigned to the extant genus *Raphidia*, a situation that most recent authors recognize as a problematic lumping (e.g., Aspöck *et al*. 1991; Engel 2002). Alternatively, Engel (2002) suggested that all North American fossil Raphidiidae might be assigned to *Agulla*, citing lack of reliable wing characters with which to confidently separate them further.

We examined wing venation within the order, and found broad patterns that covary with genera or generic groups that are congruent with those that have been independently based on genetalic characters, and so appear useful in distinguishing the generic relationships of extinct species known only or primarily by their wings. Based on these characters, described in the genus diagnoses provided here, we found three distinct species groups of Florissant raphidiid species which we recognize as the genera *Megaraphidia*, *Archiraphidia*, and *Florissantoraphidia* gen. nov.

All three of these genera share a combination of the proximal location of 3ra-rp (located within the pterostigma) in both their fore- and hind wings and the presence of the long basal 1r-m in the hind wing. Both conditions are plesiomorphic in the order, which precludes their usefulness in assessing its internal relationships. In extant snakeflies, this combination is present in some species of the raphidiid genera *Alena*, *Agulla, Dichrostigma*, and *Phaeostigma*. In these cases, however, their venation differs from the Florissant species in other aspects, suggesting that the Florissant species cannot be confidently attributed to these or other extant genera; they might be closely related. This placement of 3ra-rp excludes these fossil species from *Raphidia*, where, in all species this crossvein is almost invariably located distad the pterostigma, rendering the distal portion of RA zigzagged. We know of only a single specimen of *Raphidia ophiopsis* where 3ra-rp is aberrantly located within the pterostigma (Steinmann 1964: Fig. 26; as *Raphidia helvetica* Steinmann, 1964); all others that we are aware of have 3ra-rp located distad the pterostigma (see e.g., Aspöck *et al*. 1977: Figs 1a–h). Venational character states indicate the following possible close relationships between Florissant and extant genera: *Megaraphidia* and *Phaeostigma*, *Archiraphidia* and *Harraphidia*, and *Florissantoraphidia* gen. nov. and *Agulla* or *Alena*.

We recognize that at least two of these three Florissant genera are preliminary; however, this status has more confidence than leaving them in *Raphidia* where they clearly do not belong, and which would render that genus paraphyletic.

Genus *Megaraphidia* Cockerell, 1907

Megaraphidia Cockerell, 1907: 606; Cockerell 1908: 342 (as a possible subgenus of *Raphidia*); Cockerell 1909a: 73; Cockerell 1909b: 78; Cockerell 1912: 216 (as a possible subgenus of *Raphidia*); Handlirsch 1913: 812; Handlirsch 1920–1921 [1921]: 255; Cockerell & Custer 1925: 295; Martynov 1925a: 244, 245; Carpenter 1936: 145, 146; Metzger 1960: 41; Oswald 1990: 160 (as a synonym of *Raphidia*); Aspöck *et al*. 1991: 536, 537, 665; Engel 2002: 21 (as a tentative synonym of *Raphidia*).

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

Diagnosis. Relatively large raphidiids (forewing up to 14 mm long). Both wings: relatively long ScP [short in *Archiraphidia*, *Florissantoraphidia* gen. nov.]; short, rather pale pterostigma [long in *Florissantoraphidia* gen. nov.] in which incorporated branch of RA clearly visible [incorporated branch of RA poorly visible in *Archiraphidia*]. Forewing: costal space broad [relatively narrow in *Florissantoraphidia* gen. nov.]; branches of CuA, M long [short in *Archiraphidia*], mainly forked [mainly simple in *Archiraphidia*, *Florissantoraphidia* gen. nov.].

Species included. Two species from Florissant, *Megaraphidia elegans* and *M. exhumata* (Cockerell, 1909), comb. nov.

Remarks. Two species included in this genus have very similar venation, distinguished as indicated in their diagnoses. However, they may represent one variable species.

The venation of this genus is most similar to that of the extant Palearctic genus *Phaeostigma* (41 species) distributed mainly in the eastern Mediterranean. In particular, they share a strongly broadened costal space; branches of CuA to RP mainly forked; and a long ScP. However, the majority of *Phaeostigma* species possess two or more branches of RA incorporated in the pterostigma, and/or 3ra-rp is located distad the pterostigma. The venation of a few *Phaeostigma* species differs from that of *Megaraphidia* species only in small details. Nevertheless, the possible synonymization of two these genera is premature. Further, among other considerations, the body of *Megaraphidia* (the senior name) is unknown.

Megaraphidia elegans Cockerell, 1907
(Fig. 5)

Megaraphidia elegans Cockerell, 1907: 607, Fig. 3; Cockerell 1909b: 78; Rohwer 1909: 534; Handlirsch 1910: 103, 104; Cockerell 1912: 216; Handlirsch 1913: 812; Cockerell & Custer 1925: 295; Rodeck 1938: 290; Aspöck *et al.* 1991: 535, 665, Fig. 3046.

Raphidia elegans: Carpenter 1936: 145, 146; Oswald 1990: 160; Engel 2003: 125; Engel 2009: 213 (Tabl. 1); Engel 2011: 79 (Tabl. 2).

"*Raphidia" elegans*: Engel 2002: 22.

Diagnosis. May be distinguished from *M. exhumata* by AA1 touching AA2 [these connecting by crossvein in *M. exhumata*]; by two branches of CuA before fusion with MP [one in *M. exhumata*].

Revised description. Forewing 14.0 mm long, 4.5 mm wide (length/width ratio 3.1). Costal space broad, strongly dilated at proximal 1/4 of length; eight preserved subcostal veinlets simple, widely spaced. ScP relatively long, terminating on costal margin at ca. 1/3 of wing length, slightly distad crossvein 2ra-rp; length from termination of ScP to pterostigma shorter than length of pterostigma. Subcostal space broad, with one crossvein located in middle between origin of RP, divergence of M, CuA; crossvein closing pterostigma proximally straight, slightly inclined to wing base. Pterostigma rather long, weakly pigmented. Four RA branches: one incorporated in pterostigma proximally clearly visible; other at distal end of pterostigma; two distad pterostigma, one long, other short, very shallowly forked. Posterior trace of RA after pterostigma long, smoothly incurved; entering margin before wing 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 distal part of pterostigma. RP originates at nearly half wing length, with six pectinate branches: RP1, RP2 deeply forked; RP3, RP4, RP6 shallowly forked; RP5 simple. One crossvein in radial space, between RP1, RP2. Three crossvein between RP, MA. M appears fused with R for considerable distance, and then fused with CuA for short distance; forked well proximad origin of RP. MA deeply dichotomously forked. MP zigzagged, anterior trace deeply forked distally; with three long pectinate branches: two deeply forked, one simple. Two intramedian crossveins form two *doi*. Cu basally not visible; dividing into CuA, CuP far from wing base. CuA crossvein-like before fusion with M and perpendicular to Cu; after fusion running parallel to CuP, then its anterior trace strongly zigzagged, shallowly forked, with two pectinate long simple branches. CuP simple, continuing Cu. Crossvein between CuA, CuP long. Crossvein cu-aa short. AA1 to AA3 simple. AA1, AA2 touching slightly proximad origin of CuP.

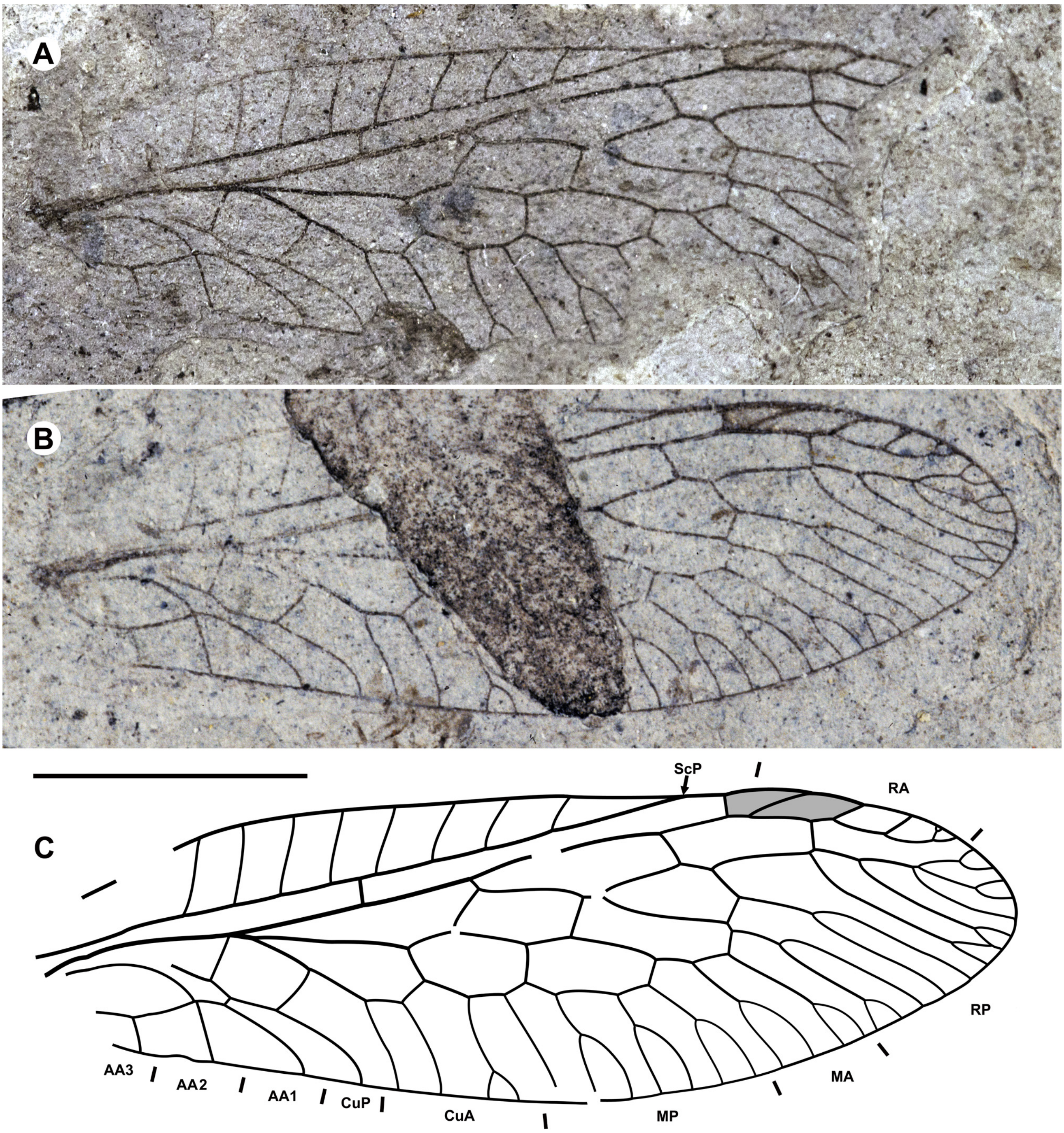

FIGURE 5. *Megaraphidia elegans* Cockerell, 1907, holotype. A, part UCM 8602. B, counterpart AMNH 35861 (converted to right). C, forewing venation. Scale bar = 4 mm.

Type material. Holotype: Specimen No. 35861, deposited in AMNH (part), No. 8602, deposited in UCM (counterpart), collected by W.P. Cockerell in 1906. A well-preserved nearly complete forewing. The counterpart 8602: Verbatim label data [typed and hand written]: "R / B / UCM Paleontology TYPE Collection / Neuroptera: Raphidiidae / UCM#: 8602 / Locality #: 83013 Description: wing / ID: Megaraphidia elegans Cockerell / Age: Late Eocene Collector: WP Cockerell 1906 / Fm: FLFO [Florissant Formation] Citation: Toohey 55210". The specimen has black ink writing on the rock that says "Megaraphidia / elegans / Ckll / Reverse [counterpart] / TYPE / UCM 8602", and "N 13".

Type locality. Florissant: Station 13 (UCM locality No. 83013).

Remarks. The species was described only from the part, in which the central portion of the forewing is missing. Our description and drawing are based on both the part and counterpart, allowing reconstruction of the complete forewing venation, with which we provide our revised genus diagnosis and species description.

Megaraphidia exhumata (Cockerell, 1909), comb. nov.

(Figs 6, 7)

Raphidia exhumata Cockerell, 1909a: 73; Rohwer 1909: 534; Cockerell 1912: 215, 216; Cockerell 1914: 715; Cockerell & Custer 1925: 296; Martynov 1925a: 245; Rodeck 1938: 290; Carpenter 1936: 143, 146–148, Fig. 9; Nel *et al*. 1990: 34; Oswald 1990: 160; Engel 2003: 125; Engel 2009: 213 (Tabl. 1); Engel 2011: 79 (Tabl. 2), 80.

Raphidia exhumata var. a: Cockerell 1912: 215, Fig.

"Raphidia" exhumata: Aspöck *et al*. 1991: 539, 665, Fig. 3052; Engel 2002: 22.

Raphidia pulveris Cockerell, 1914: 714; Carpenter 1936: 143, 146–148 (as a synonym of *Raphidia exhumata*); Oswald 1990: 160 (as a synonym of *R. exhumata*); Engel 2002: 22 (as a synonym of *R. exhumata*); Engel 2003: 125 (as a synonym of *R. exhumata*).

"Raphidia" pulveris: Aspöck *et al*. 1991: 540, 665.

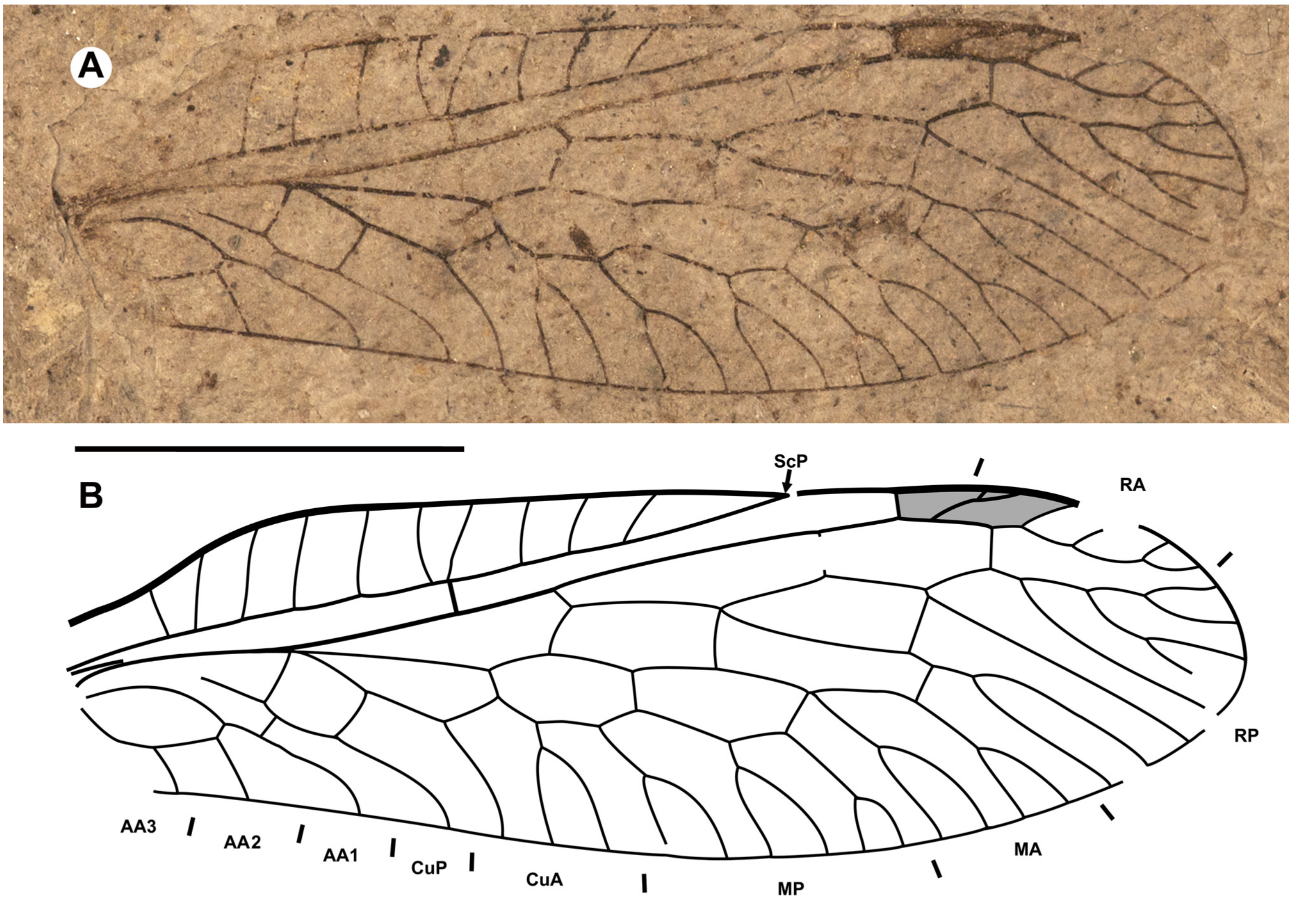

FIGURE 6. *Megaraphidia exhumata* (Cockerell, 1909). Holotype UCM 4513. A, the specimen as preserved. B, forewing venation. Scale bar = 4 mm (both to scale).

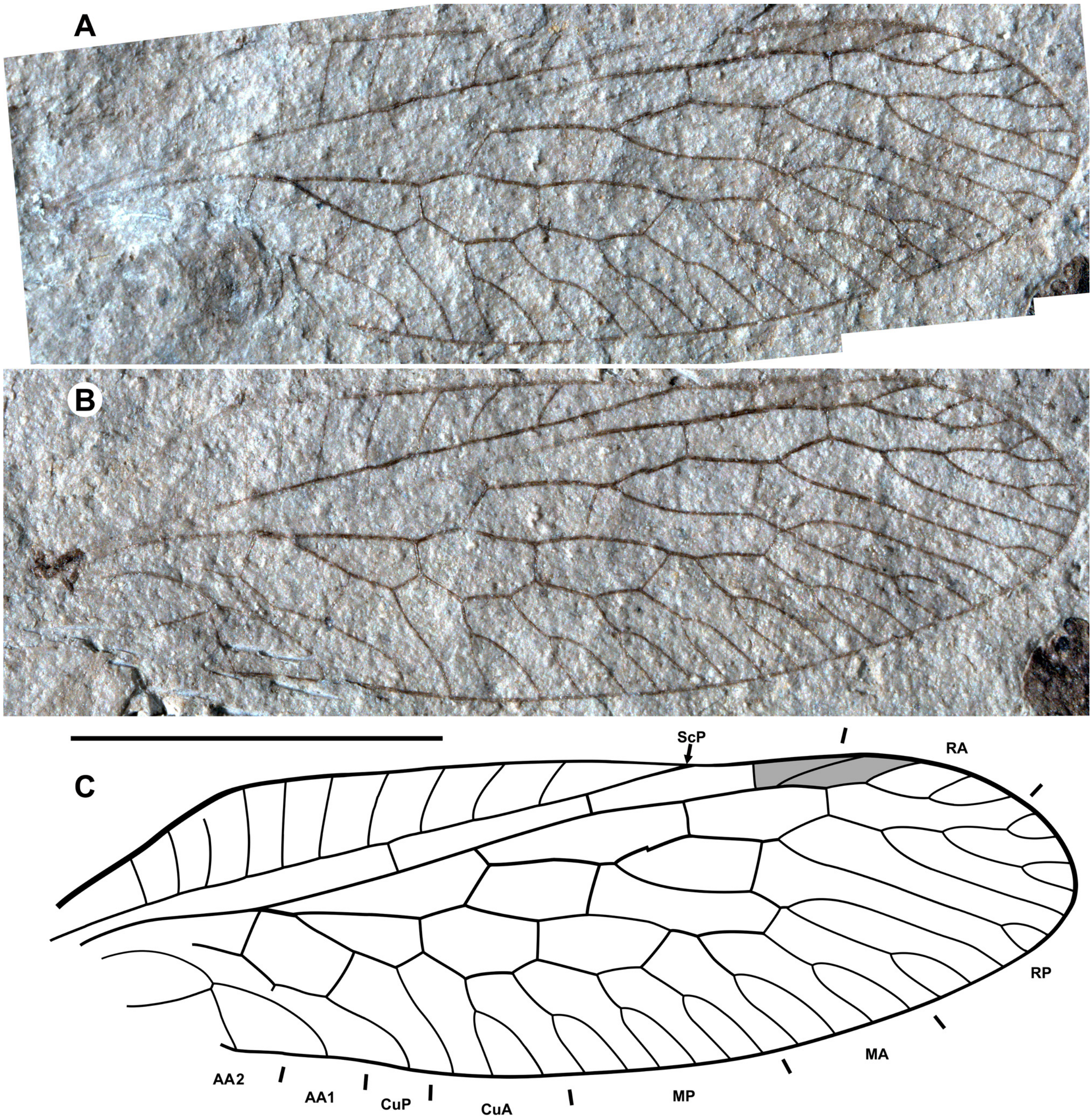

FIGURE 7. *Megaraphidia exhumata* (Cockerell, 1909). Holotype MCZ 3640. A, part (converted to right). B, counterpart. C, forewing venation. Scale bar = 4 mm (all to scale).

Diagnosis. May be distinguished from *M. elegans* by crossvein between AA1, AA2 [these touching in *M. elegans*]; by one branch of CuA before fusion with MP [two in *M. elegans*].

Revised description. *Specimen UCM 4513* (Fig. 6). Forewing relatively broad, 12.1 mm long, 3.7 mm wide (length/width ratio 3.3). Costa in proximal portion and apically very stout. Costal space broad, strongly dilated at proximal 1/3. Ten subcostal veinlets (branches of ScP) simple, relatively closely spaced. Length from termination of ScP to pterostigma less than length of pterostigma. In subcostal space, one crossvein between ScP, RA located slightly distad middle between origin of RP, divergence of M, CuA; other crossvein closes pterostigma proximally. Pterostigma moderately long, darkish. RA with four branches, three long: one forked within pterostigma, second closing pterostigma distally, two other distad pterostigma; posterior trace of RA distad pterostigma long. Two crossveins between RA, RP; 2ra-rp located opposite termination of ScP; 3ra-rp located within pterostigma, in distal portion. Anterior trace of RP forked apically, with two branches proximad 3ra-rp, two distad. RP1 deeply forked, both branches simple; RP2, RP3 simple; PR4 forked. One intraradial crossvein, between stem of RP, RP1 at origin. Three crossveins between RP, MA; 1rp-m close to origin of RP. M appears fused with R for considerable distance (near wing base these separate), then forked well proximad origin of RP. MA dichotomously branched; MP pectinately branched; anterior trace, both branches deeply forked. Two long intramedian crossveins. M, CuA fused basally for very short distance, then running parallel to CuP, then its anterior trace strongly zigzagged, deeply forked, with one long simple branch. CuP simple. One long intracubital crossvein. Crossvein between CuP, AA1 rather long, located much closer to origin of CuA than to intracubital crossvein. AA1 to AA3 simple; crossvein iaa moderately long.

Specimen MCZ 3640, holotype of Raphidia pulveris (Fig. 7). Forewing 11.0 mm long, 3.3 mm wide (length/width ratio 3.3). Venation very similar to that of the holotype, except: 3ra-rp located distantly to ending of pterostigma; RA with three branches: one simple within pterostigma, second closed pterostigma distally, third distad pterostigma; one branches of RP1, and RP2 forked; crossvein between CuP, AA1 incompletely preserved, positioned mid-way between origin of CuA, intracubital crossvein; crossvein between AA1, AA2 much shorter.

Type material. Holotype of *Raphidia exhumata*: Specimen No. 4513 (collected by S.A. Rohwer in 1908), deposited in UCM. A forewing. Verbatim label data [typed and hand written]: "F / UCM Paleontology TYPE Collection / Neuroptera: Raphidiidae / UCM#: 4513 Locality #: 83013 Description: wing / ID: Raphidia exhumata Cockerell / Age: Late Eocene Collector: SA Rohwer 1908 / Fm: FLFO Citation: Toohey 55263". The specimen has a blue hand written label glued to the rock that says "TYPE / Raphidia / exhumata / Ckll/ Florissant", and red / black ink writing on the rock that say "TYPE / R 139 ['9' unclear]" and red / black ink writing on a circular paper glued to the rock that says "TYPE / 4513".

Holotype of *Raphidia pulveris*: No. 3640 a, b (part, counterpart) (collected by H. F. Wickham), deposited in MCZ. A well preserved forewing. Verbatim label data associated with the part 3640A: [1] "Mus. Comp. Zoöl., Cambridge, Mass. / No. 3640 ab / Raphidia / pulveris Cock. / Holotype / H.F.W. Coll. Florissant"; [2] "3640-a / type / Raphidia / pulveris Cock. / Florissant / Neuroptera: Raphididae [sic]". The part has a red label glued to the rock that says "Holotype.", and black ink writing on the rock that says "3640.-a" and on the back "Raphidia / pulveris / Ckll / type". Labels associated with the counterpart 3640B: [3] "Mus. Comp. Zoöl., Cambridge, Mass. / No. 3640 b / Raphidia pulveris / Cock. / holotype/ Scudder Collection Florissant, Colo[rado]"; [4] same text as in the label [2], except "3640-b". The counterpart has a red label glued to the rock that says "Holotype.", and black ink writings on the rock that say "3640-b" and on the back "Raphidia / pulveris / Ckll / type".

Type locality. Florissant: Station 13B (UCM locality No. 83013) (holotype of *R. exhumata*); Wilson Ranch (holotype of *R. pulveris*).

Remarks. T.D.A. Cockerell (1912) reported a well-preserved forewing that was collected by his wife at Station 23, *Raphidia exhumata* var. a. It was only partially figured, and the current location of this specimen is unknown. Judging from the original description, this specimen is very similar to MCZ 3640.

***Megaraphidia* sp.**

(Fig. 8)

Raphidia pulveris Cockerell, 1914: 714 (*partim*; only hind wing); Carpenter 1936: 146, Fig. 9 (*partim*, only hind wing; as a synonym of *Raphidia exhumata*).

Redescription. Hind wing 8.8 mm long as preserved (complete estimated length ca. 9.5 mm), 3.1 mm wide (length/width ratio 3.1). Costal space relatively broad. ScP relatively long; length from termination of ScP to pterostigma shorter than length of pterostigma. In subcostal space, two crossvein detected between ScP, RA; crossvein closing pterostigma proximally incurved. Pterostigma long. RA with three branches: incorporated branch very long and oblique; branch closing pterostigma distally smoothly curved; one branch distad pterostigma; portion of RA distad pterostigma long. Three crossveins between RA, RP; 2ra-rp located at level of termination of ScP; 3ra-rp within pterostigma, just distad its middle. Anterior trace of RP forked apically, with two branches proximad 3ra-rp, two distad. RP1 deeply forked; anterior branch simple, posterior branch rather deeply forked; RP2, RP4 simple; RP3 with deep narrow fork. One intraradial crossvein, between stem of RP, RP1. Four crossveins between R, M: 1r-m very long, running nearly parallel to R connecting RP, M near its separating from R; 2r-m connects stem of RP, M; 3r-m connects RP1, MA; 4r-m connects RP1, anterior branch of MA. M forked slightly proximad origin of RP. MA deeply dichotomously (twice) forked. MP pectinately branched; anterior trace weakly zigzagged, simple; three pectinate branches deeply forked. Two intramedian crossveins. Anterior trace of CuA forked distally, with one simple branch. CuP simple, basally fused with AA1. AA1 with two simple branches.

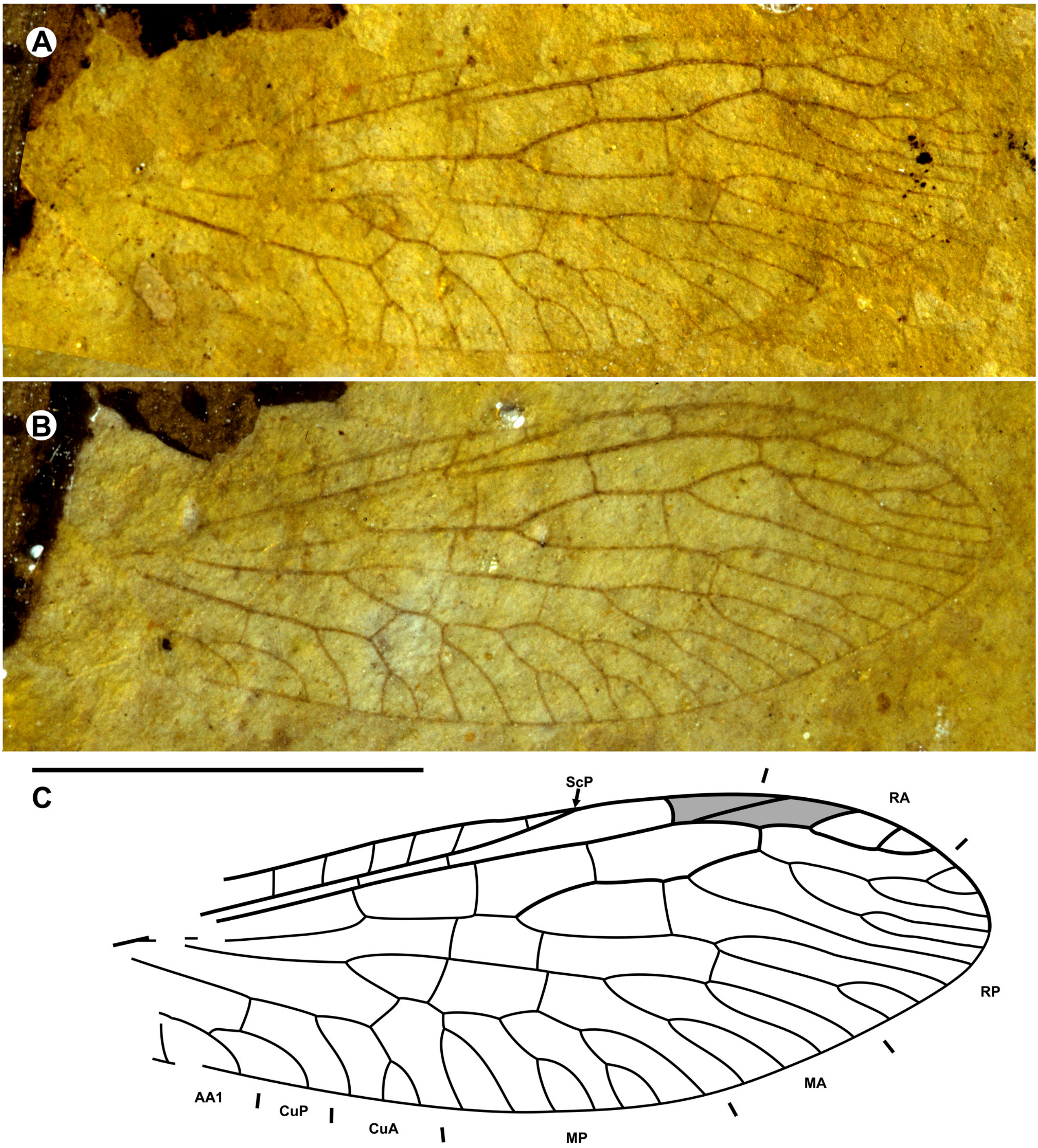

FIGURE 8. *Megaraphidia* sp. Specimen MCZ 3641. A, part (converted to right). B, counterpart. C, hind wing venation. Scale bar = 4 mm (all to scale).

Material examined. Specimen No. 3641a, b (part, counterpart) (collected by H. F. Wickham), deposited in MCZ. A well-preserved nearly complete hind wing. Verbatim label data associated with the part 3641a: [1] "Mus. Comp. Zoöl., Cambridge, Mass. / No. 3641 a b / Raphidia/ pulveris Cock. / H. F. W. coll. Florissant"; [2] "3641 / type / Raphidia / pulveris Cock. / Florissant / Neuroptera: Raphididae [sic]". The part has black ink writing on the rock that says "3641-a" and on the back "hind wing. / Raphidia / pulveris / Ckll". Verbatim label data associated with the counterpart 3641b [3] “Mus. Comp. Zoöl., Cambridge, Mass. / No. 3641-b / Raphidia pulveris / Cock. / Scudder Collection Florissant, Colorado”; [4] same text as in the label [2], except “3641-b”. The counterpart has black ink writing on the rock that says “3641-b” and on the back “Raphidia / pulveris / Ckll”.

Locality. Florissant: Wilson Ranch.

Remarks. Cockerell (1914) described *Raphidia pulveris* from two specimens: a forewing (MCZ 3040) and this hind wing (MCZ 3041). The hind wing is designated in one label as the [holo]type of *Raphidia pulveris*, although neither the part nor the counterpart has a red holotype label. However, Cockerell (1914) clearly indicated that “the upper wing is the type” of this species (p. 715), i.e., MCZ 3040. This hind wing may, however, belong to either *Megaraphidia exhumata* or *M. elegans*, or to some other new species.

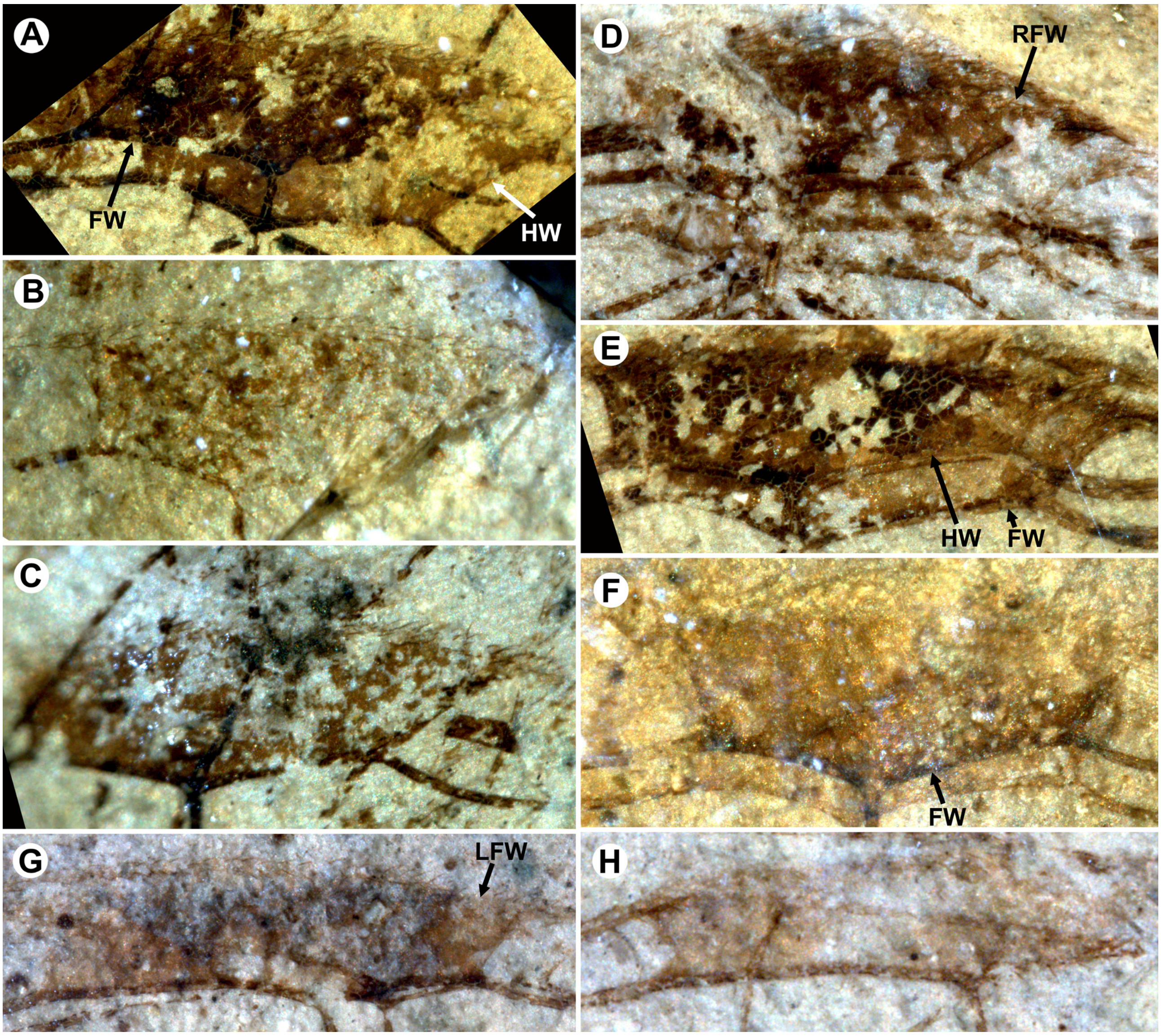

FIGURE 9. Pterostigma of *Archiraphidia* species. A–C, *A. tumulata* (Scudder, 1890): A, left wings. B, right forewing. C, right hind wing. D–F, *A. tranquilla* (Scudder, 1890): D, four wings of the holotype MCZ 446. E, four wings of MCZ 4137 (lectotype of *A. eventa* (Scudder, 1890)); F, left wings of MCZ 253 (paralectotype of *A. eventa*). G, three wings of *A.? somnolenta* (Scudder, 1890). H, right forewing of *A.? somnolenta*. HW, hind wing; LFW, left forewing; RFW, right forewing. All wings are shown with apex to right and not to scale.

Genus *Archiraphidia* Handlirsch, 1910

Archiraphidia Handlirsch, 1910: 103; Handlirsch 1920–1921 [1921]: 255; Cockerell & Custer 1925: 295; Martynov 1925a: 244; Carpenter 1936: 145; Metzger 1960: 41; Oswald 1990: 160 (as a synonym of *Raphidia*); Aspöck *et al.* 1991: 536, 538, 665; Engel 2002: 21 (as a tentative synonym of *Raphidia*).

Type species. *Inocellia tumulata* Scudder, 1890, by monotypy (Oswald 1990).

Diagnosis. Very small raphidiids (forewing <10 mm long). Both wings: relatively short ScP [long in *Megaraphidia*]; short, dark pterostigma in which incorporated branch of RA not or poorly visible [incorporated branch of RA clearly visible in *Megaraphidia*, *Florissantoraphidia* gen. nov.]. Forewing: additional crossvein 2^bscp-r sometimes present [not detected in *Megaraphidia*, *Florissantoraphidia* gen. nov.]; MP strongly zigzagged [moderately zigzagged in *Megaraphidia*, *Florissantoraphidia* gen. nov.]; branches of CuA, MP short, not longer then width of *2doi* [distinctly longer than width of *2doi* in *Megaraphidia*, *Florissantoraphidia* gen. nov.]. Hind wing: *doi* single [two in *Megaraphidia*, *Florissantoraphidia* gen. nov.].

Species included. Three species from Florissant, *Archiraphidia tumulata*, *A. tranquilla* (Scudder, 1890) and *A.? somnolenta* (Scudder, 1890). The latter assignment is preliminary.

Remarks. This genus is characterized by its pterostigma appearing very dark (Fig. 9), and the incorporated pterostigmal RA branch being hardly detectable. The paler pterostigma in some wings, however, is probably due to poor preservation of pigmentation (Figs 9B, F). A branch of RA incorporated within the pterostigma is only detected in one wing—and then only poorly visible—however, we assume that is likely present in all of these, although await future specimens to strengthen this supposition.

The minute size and venation of this genus are most similar to those of the genus *Harraphidia* (forewing 5.5–8.5 mm long; see Monserrat & Papenberg 2006). They share in particular a relatively short ScP; short pterostigma; 3ra-rp located within pterostigma; the same configuration of RA distad pterostigma in both wings; the presence of additional crossvein 2^bscp-r; short branches of CuA and MP in the forewing; one *doi* in the hind wing. In extant Raphidiidae, the single *doi* is a generic feature only of *Harraphidia*, although this condition is known, rarely, in a few other species, where it is considered anomalous (see above). The additional crossvein 2^bscp-r is also characteristic of only this genus (in extant Raphiididae). *Archiraphidia* may only be distinguished from *Harraphidia* in that MP+CuA never has the long stem characteristic of the latter. These genera are undoubtedly closely related, but the occurrence of this condition (i.e., MP+CuA) and the poorly preserved male terminalia in specimens of *Archiraphidia* (the senior name) prevent their synonymization. Moreover, although the male terminalia in these genera are rather similar in their general appearance, the ectoproct of all *Harraphidia* species is clearly caudally elongate, whereas that of *Archiraphidia* clearly not (Fig. 15). Also, 1r-m in the hind wing of *Harraphidia* is crossvein-like, but this is not detected in *Archiraphidia* due to poor preservation.

Archiraphidia tumulata (Scudder, 1890)

(Figs 10, 11)

Inocellia tumulata Scudder, 1890: 158, 160, 161; Pl. 14, Fig.15; Handlirsch 1906–1908 [1907]: 907; Bather 1909: 161; Rohwer 1909: 534; Cockerell 1917: 391; Cockerell & Custer 1925: 296, 297.

Archiraphidia tumulata: Handlirsch 1910: 104; Cockerell 1914: 715; Cockerell & Custer 1925: 295; Aspöck *et al.* 1991: 538, 665, Figs 3048, 3049.

Raphidia tumulata: Carpenter 1936: 149, Fig. 11; Oswald, 1990: 161; Engel 2003: 125; Engel 2009: 213 (Tabl. 1); Engel 2011: 79 (Tabl. 2), 80.

"Raphidia" tumulata: Engel 2002: 22.

Diagnosis. May be distinguished from other species by CuA1 in forewing simple [forked in *A. tranquilla*]; by short pterostigma [elongate in *A.? somnolenta*].

Revised description. *Holotype 244*. Male. Body poorly preserved. Head strongly narrowed caudally (dorso-ventral view). Prothorax probably slightly less than 2 mm long; pterothorax, legs poorly preserved. Abdomen rather well preserved; with dark segments separated by broad pale intersegmental membrane between second/third to seventh/eighth segments. Apex of abdomen unclear, but surely male.

Forewing approximately 9.2 mm long, 2.6 mm wide (length/width ratio 3.5). Costal space incompletely preserved, broad. ScP relatively short; length from termination of ScP to pterostigma much longer than length of pterostigma. Four preserved subcostal veinlets (branches of ScP) distad M+CuA fusion simple, widely spaced. In subcostal pace, two crossveins between ScP, RA (additional long oblique crossvein 2^bscp-r proximad termination of ScP); third crossvein closing pterostigma proximally nearly straight. Pterostigma short, dark. RA with one branch, closing pterostigma distally; no branches within pterostigma detected (Figs 9A–C); portion of RA distad pterostigma short, deeply curved. RP forked apically, with two branches proximad 3ra-rp, one distad. Two crossveins between RA, RP; 2ra-rp located slightly distad termination of ScP; 3ra-rp located within pterostigma, in its middle. Three (right wing) intraradial crossveins, between branches of RP, forming short gradate series. RP1 forked, one branch simple, other rather deeply forked (right wing); both branches shallowly forked (left wing). RP2, RP3 simple. Three crossveins between RP, MA; 1r-m rather close to origin of RP; 3r-m connecting RP1, MA oblique. MA dichotomously forked; MP strongly zigzagged, pectinately branched; anterior trace, all three branches

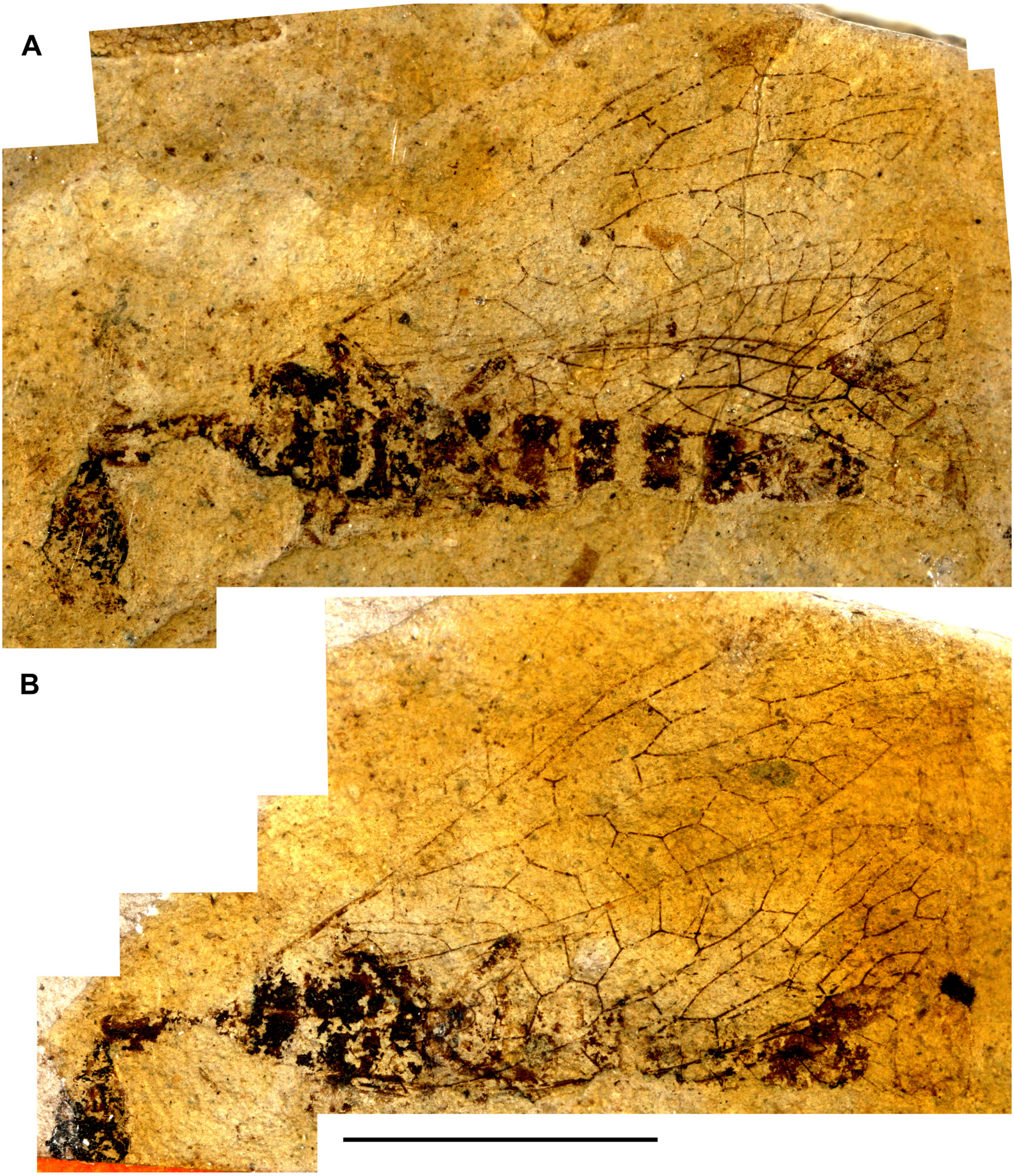

FIGURE 10. *Archiraphidia tumulata* (Scudder, 1890). Holotype MCZ 244. A, counterpart. B, part (converted to right). Scale bar = 4 mm (both to scale).

rather short, simple. Two long intramedian crossveins; 2im connects posterior branch of MA, MP. M, CuA fused basally for short distance; free stem of M+CuA (after apparent separation from R) very short. CuA strongly zigzagged distally; anterior trace simple, with one simple branch. CuP simple. One long intracubital crossvein. AA1 simple; AA2 incompletely preserved; crossvein between these moderately short.

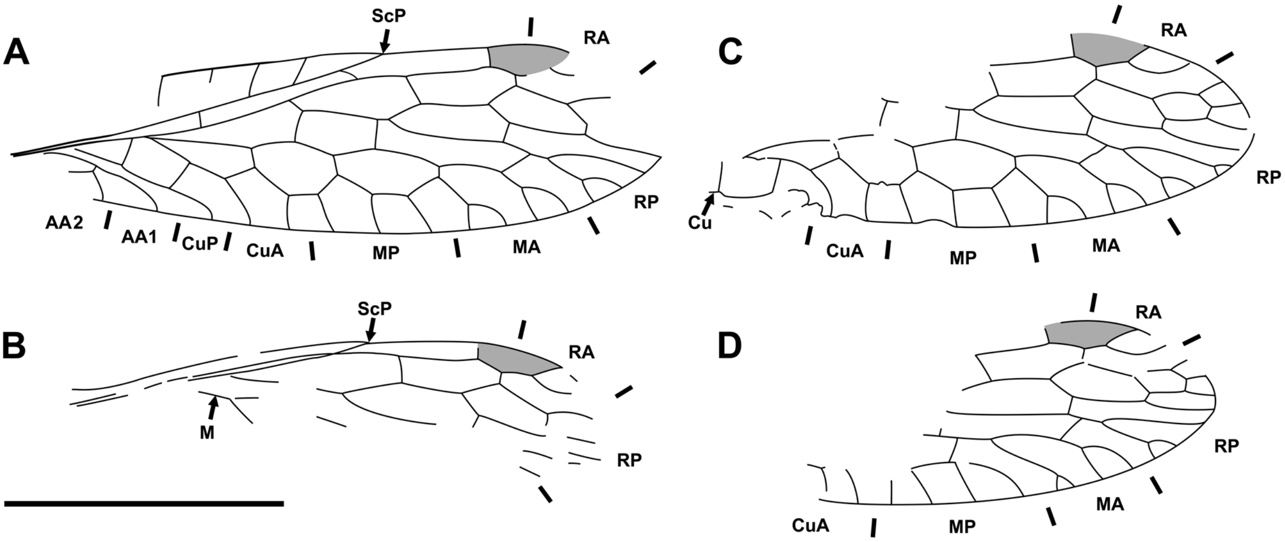

FIGURE 11. *Archiraphidia tumulata* (Scudder, 1890). Wing venation of the holotype MCZ 244. A, right forewing. B, right hind wing. C, left forewing. D, left hind wing. Scale bar = 4 mm (all to scale).

Hind wing approximately 8 mm long, 2.3–2.4 mm wide (estimated) (3.4–3.5). Costal space, ScP poorly preserved. ScP short; length from termination of ScP to pterostigma much longer than length of pterostigma. In subcostal space, one crossvein detected, closing pterostigma proximally. Pterostigma longer than in forewing. RA with one preserved rather short branch, which closes pterostigma distally; incorporated branch not detected; portion of RA distad pterostigma short, deeply curved. Two crossvein between RA, RP preserved; 2ra-rp located distad termination of ScP; 3ra-rp within pterostigma, in middle portion. Anterior trace of RP forked apically, with two branches proximad 3ra-rp, one distad. RP1 deeply forked; anterior branch simple, posterior branch shallowly forked; RP2, RP3 simple. Three intraradial crossveins forming short gradate series, all between branches of RP. Two crossveins between RP, M/MA detected; 4r-m connecting RP1, anterior branch of MA long, oblique. MA dichotomously (twice) forked. MP pectinately branched; anterior trace, all three branches simple. One (2im) intramedian crossvein preserved. CuA incompletely preserved; anterior trace, one branch simple. Basal portion of wing, CuP, anal veins not preserved.

Type material. Holotype: Specimen No. 244a, b (part, counterpart; Scudder's numbers 956 and 4330), deposited in MCZ. A rather poorly preserved, crumpled male specimen. Verbatim label data: [1] "Mus. Comparative Zoölogy, Cambridge, / No. 244 / Inocellia tumulata Scud. / Florissant Miocene"; [2] 244 / type / Inocellia / tumulata Scud. / Florissant / Neuroptera: Inocelliidae". The part (244a) has a red label glued to the rock that says "Type.", and black ink writing on the rock that says "244-a" and red ink writing that says "956"; the counterpart (244b) has analogous red label, and writing "244-b" and "4330".

Locality. Florissant (precise collecting locality unknown).

Remarks. Two other specimens have been assigned to this species by Bather (1909) and Cockerell (1917) but these were neither described nor illustrated. The first is housed in NHM (specimen I.8416); the other is reported to be in USNM (the number is unknown).

Archiraphidia tranquilla (Scudder, 1890)

(Figs 12–16)

Raphidia (?) tranquilla Scudder, 1890: 154, 155; Pl. 14, Fig. 2; Scudder 1891: 369; Handlirsch 1906–1908 [1907]: 907; Rohwer 1909: 534; Cockerell & Custer 1925: 296.

?Archiraphidia tranquilla: Handlirsch 1910: 104.
Archiraphidia? tranquilla: Aspöck *et al*. 1991: 538, 665, Fig. 3050.
"Raphidia" tranquilla: Engel 2002: 22.
Raphidia tranquilla: Carpenter 1936: 143, 146, 150, Fig. 12; Oswald 1990: 160; Engel 2003: 125; Engel 2009: 213 (Tabl. 1); Engel 2011: 79 (Tabl. 2).
Inocellia eventa Scudder, 1890: 160; Handlirsch 1906–1908 [1907]: 907; Cockerell & Custer 1925: 297; Carpenter 1936: 143, 145, 146, 149 (as a synonym of *Inocellia tumulata*); Oswald 1990: 161 (as a synonym of *I. tumulata*); Engel 2002: 22 (as a synonym of "*Raphidia" tumulata*); Engel 2003: 125 (as a synonym of *R. tumulata*), **syn. nov.**
?Archiraphidia eventa: Handlirsch 1910: 104.
Archiraphidia? eventa: Aspöck *et al.* 1991: 538, 665.

Diagnosis. May be distinguished from other species by forewing CuA1 forked [simple in *A. tumulata*]; by short pterostigma [elongate in *A.? somnolenta*].

Redescription. *Specimen MCZ 246, holotype of Raphidia tranquilla* (Figs 12, 13). Pterothorax poorly preserved; details not visible. Legs not preserved. Abdomen rather well preserved; with eight dark segments separated by broad pale intersegmental membrane between fourth to eighth segments. Apex of abdomen unclear, but surely male.

Forewing long approximately 8.5 mm (estimated), 2.6 mm wide (length/width ratio 3.2). Costal space incompletely preserved, moderately broad. Distal part of ScP not preserved. Three preserved subcostal veinlets (branches of ScP) distad M+CuA fusion simple, widely spaced. In subcostal space, one preserved crossvein between ScP, RA well proximad origin of RP; other crossvein closes pterostigma proximally. Pterostigma short, dark. RA with one branch, closing pterostigma distally; no branches within pterostigma detected (Fig. 9D); portion of RA distad pterostigma short, deeply curved. Two crossveins between RA, RP; 3ra-rp located within pterostigma, in its proximal half. Anterior trace of RP forked apically, with two branches proximad 3ra-rp, one distad. RP1 forked, one branch simple, other rather shallowly forked; RP2 simple; RP3 simple (left wing), shallowly forked (right wing). Two intraradial crossveins, between branches of RP1, PR2 at its origin, and RP2, RP3. Three crossveins between RP, MA; 1r-m rather close to origin of RP; 3r-m connecting RP1, anterior branch of MA oblique. MA dichotomously forked; MP strongly zigzagged, pectinately branched; anterior trace, all two branches rather short, simple. Two long intramedian crossveins; 2im connects posterior branch of MA near its origin, MP. Proximal part of M, CuA mostly not preserved. Anterior trace of CuA simple, with one rather deeply forked branch. CuP, anal veins not preserved.

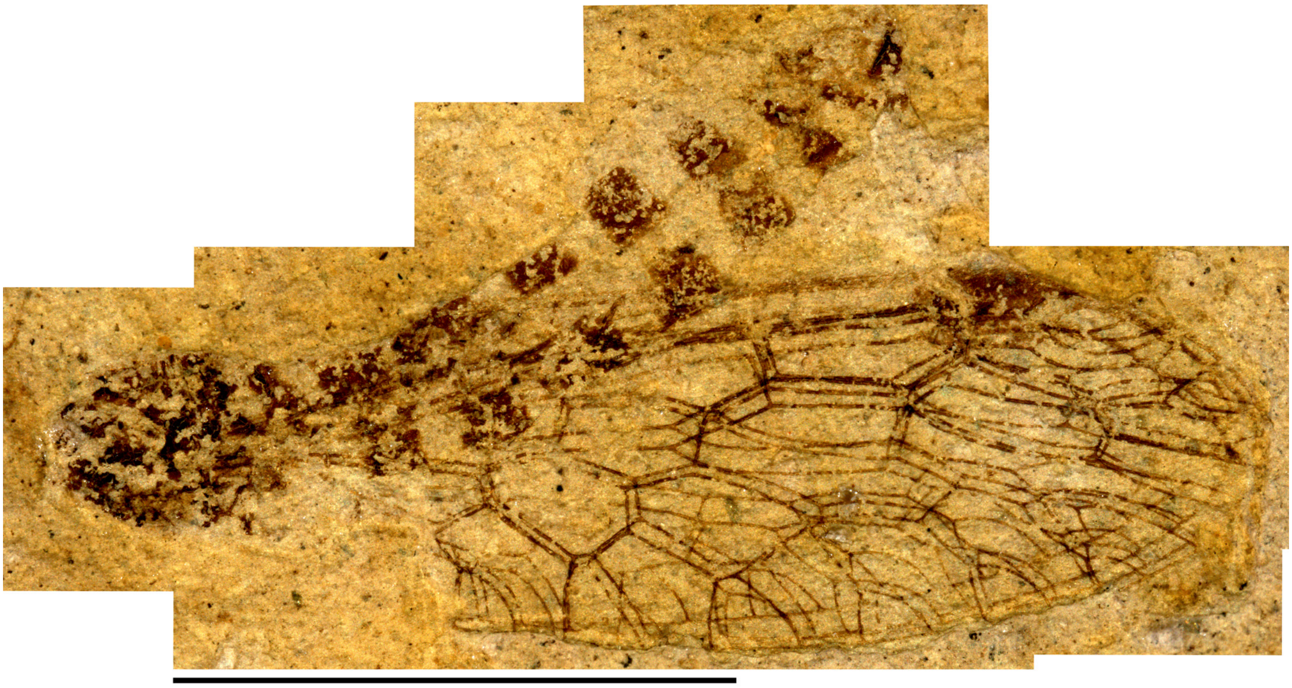

FIGURE 12. *Archiraphidia tranquilla* (Scudder, 1890). Holotype MCZ 246, the specimen as preserved. Scale bar = 4 mm.

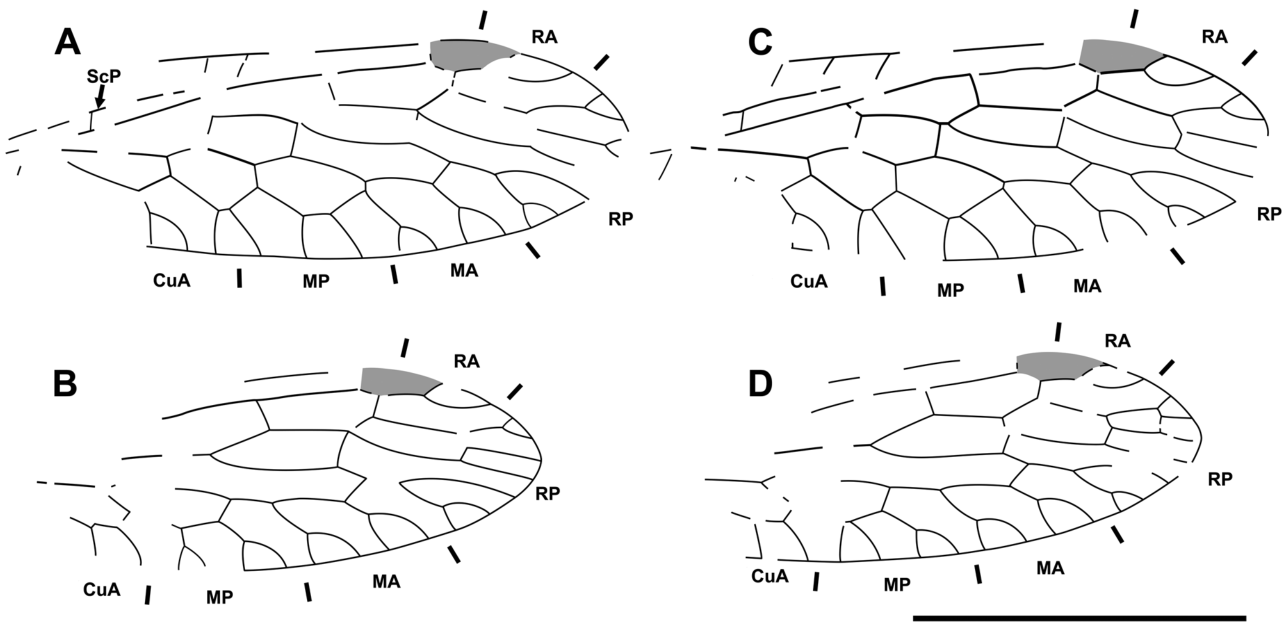

FIGURE 13. *Archiraphidia tranquilla* (Scudder, 1890). Wing venation of the holotype MCZ 246. A, right forewing. B, right hind wing. C, left forewing. D, left hind wing. Scale bar = 4 mm (all to scale).

Hind wing approximately 7.5 mm (estimated), 2.3 mm wide (length/width ratio 3.2). Costal space not preserved. ScP poorly preserved. In subcostal space, one crossvein detected, closing pterostigma proximally. Pterostigma slightly longer and narrower than in forewing. RA with one branch, which closes pterostigma distally; incorporated branch not detected; portion of RA distad pterostigma short, deeply curved. Two crossvein between RA, RP preserved; 3ra-rp within pterostigma, in its proximal half. Anterior trace of RP forked apically, with two branches proximad 3ra-rp, one distad. RP1 deeply forked; anterior branch simple, posterior branch shallowly forked; RP2, RP3 simple. Three intraradial crossveins forming short gradate series, all between branches of RP (left wing); two intraradial crossveins between RP1, origin of RP2, and RP2, RP3 (right wing). Only one oblique distal crossvein between R, M detected (4r-m), connecting RP1, anterior branch of MA. MA dichotomously (twice) forked. MP zigzagged, pectinately branched; anterior trace rather deeply forked; two branches simple, with their bases rather closely spaced (left wing), or one branch rather shallowly forked (right wing). One (2im) intramedian crossvein preserved. CuA incompletely preserved; anterior branch, one branch simple. 2m-cu connects MP, CuA. Basal portion of wing, CuP, anal veins not preserved.

Specimen MCZ 4137, lectotype of Inocellia eventa (Fig. 14). Male. Head long, details not clear. Prothorax relatively long, ca. 2.2 mm, 0.7 mm maximum width (caudally, in lateral view). Pterothorax, legs poorly preserved. Abdomen well preserved; with eight dark segments separated by broad pale intersegmental membrane between fifth to eighth segments. Apex of abdomen: Tergite 9 long (in lateral view); sternite 9 short; tergite 9, sternite 9 appear to form a ring; gonocoxites of segment 9 forms a large plate, its shape not entirely clear, probably somewhat elongate rectangular; gonapophyses of segment 9 (hypovalva) narrow anteriorly, appears broadened caudally. Segment 10 (ectoproct) appears nearly quadrate, without caudal elongation; gonostyli of gonocoxites 9 strongly curved apically upwards (Fig. 15).

Forewing approximately 9.5 mm long (estimated), 3.0 mm wide (length/width ratio 3.2). Costal space incompletely preserved, moderately broad. ScP relatively short; length from termination of ScP to pterostigma longer than length of pterostigma. Four preserved subcostal veinlets (branches of ScP) distad M+CuA fusion simple, widely spaced. In subcostal space, no crossvein between ScP, RA detected; crossvein closing pterostigma proximally straight. Pterostigma short, dark. RA with one branch, closing pterostigma distally; no branches within pterostigma detected (Fig. 9E); portion of RA distad pterostigma short, deeply curved. Two crossveins between RA, RP; 2ra-rp located slightly distad termination of ScP; 3ra-rp short (very short in left wing), located within pterostigma, in its proximal half. Anterior trace of RP deeply forked apically, with posterior branch shallowly forked; two branches proximad 3ra-rp, one distad. RP1 deeply forked, anterior branch simple, posterior shallowly forked. RP2, RP3 simple. Three (left wing), two (right wing) intraradial crossveins, between branches of RP. Three crossveins between RP, MA; 1rp-m rather close to origin of RP; 3rp-m connecting RP1, anterior branch of MA oblique. MA dichotomously (twice) forked. Anterior trace of MP strongly zigzagged, simple, pectinately branched; two short branches, one simple, other fused for long distance with anterior trace of CuA. Two long intramedian crossveins; 2im connects posterior branch of MA near its origin, MP. Proximal part of M, CuA mostly not preserved. Anterior trace of CuA simple, fused for long distance with basal-most branch of MP; with one forked branch. CuP simple. AA1 simple (left wing), very shallowly forked (right wing). AA2 incompletely preserved. Crossvein between AA1, AA2 (iaa) moderately long.

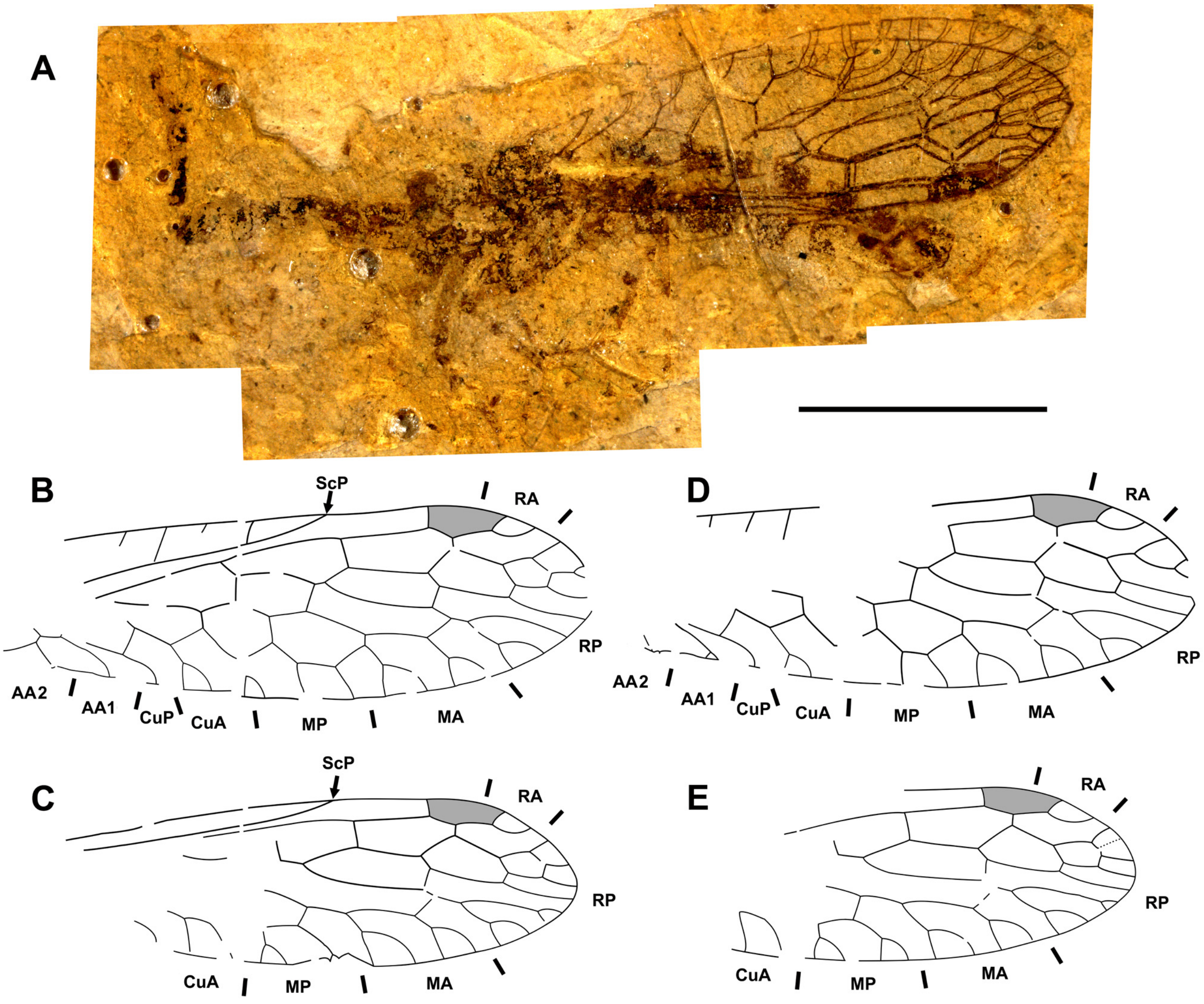

FIGURE 14. *Archiraphidia tranquilla* (Scudder, 1890) (lectotype of *A. eventa* (Scudder, 1890), MCZ 4137). A, the specimen as preserved (covered by Canada balsam). B, left forewing. C, left hind wing. D, right forewing. E, right hind wing. Scale bar = 4 mm (all to scale).

Hind wing approximately 8.8 mm (estimated), 2.7 mm wide (length/width ratio 3.3). Costal space narrow; subcostal veinlets not preserved. ScP relatively short; length from termination of ScP to pterostigma longer than length of pterostigma. In subcostal space, one crossvein detected, closing pterostigma proximally. Pterostigma slightly longer and narrower than in forewing. RA with one preserved branch, which closes pterostigma distally; incorporated branch not detected; portion of RA distad pterostigma short, deeply curved. Three crossveins between RA, RP preserved; 2ra-rp somewhat distad termination of ScP; 3ra-rp within pterostigma, in its middle. Anterior trace of RP rather deeply forked apically (additional vein probably divided fork in right wing); with two branches proximad 3ra-rp, one distad. RP1 deeply forked, each branch shallowly forked; RP2, RP3 simple. Three intraradial crossveins forming short gradate series, all between branches of RP. Only one oblique distal crossvein between R, M detected, connecting RP1, anterior branch of MA. MA dichotomously (twice) forked. MP zigzagged; anterior trace rather deeply (right wing) or shallowly (left wing) forked; one rather deeply forked branch. One (distal) intramedian crossvein preserved (2im). CuA incompletely preserved; anterior trace, one branch simple. Basal and anal portion of wing not preserved.

Specimen MCZ 253, *paralectotype of Inocellia eventa* (Fig. 16). Male. Head relatively short (ca. 1.8 mm including mouthparts), strongly narrowed caudally (in dorso-ventral view); antennae, palpi not preserved. Prothorax relatively long, slender, 2.0 mm long, ca. 0.4 mm (in anterior portion), ca. 0.5–0.6 mm maximum width (caudally). Abdomen poorly preserved, but surely male.

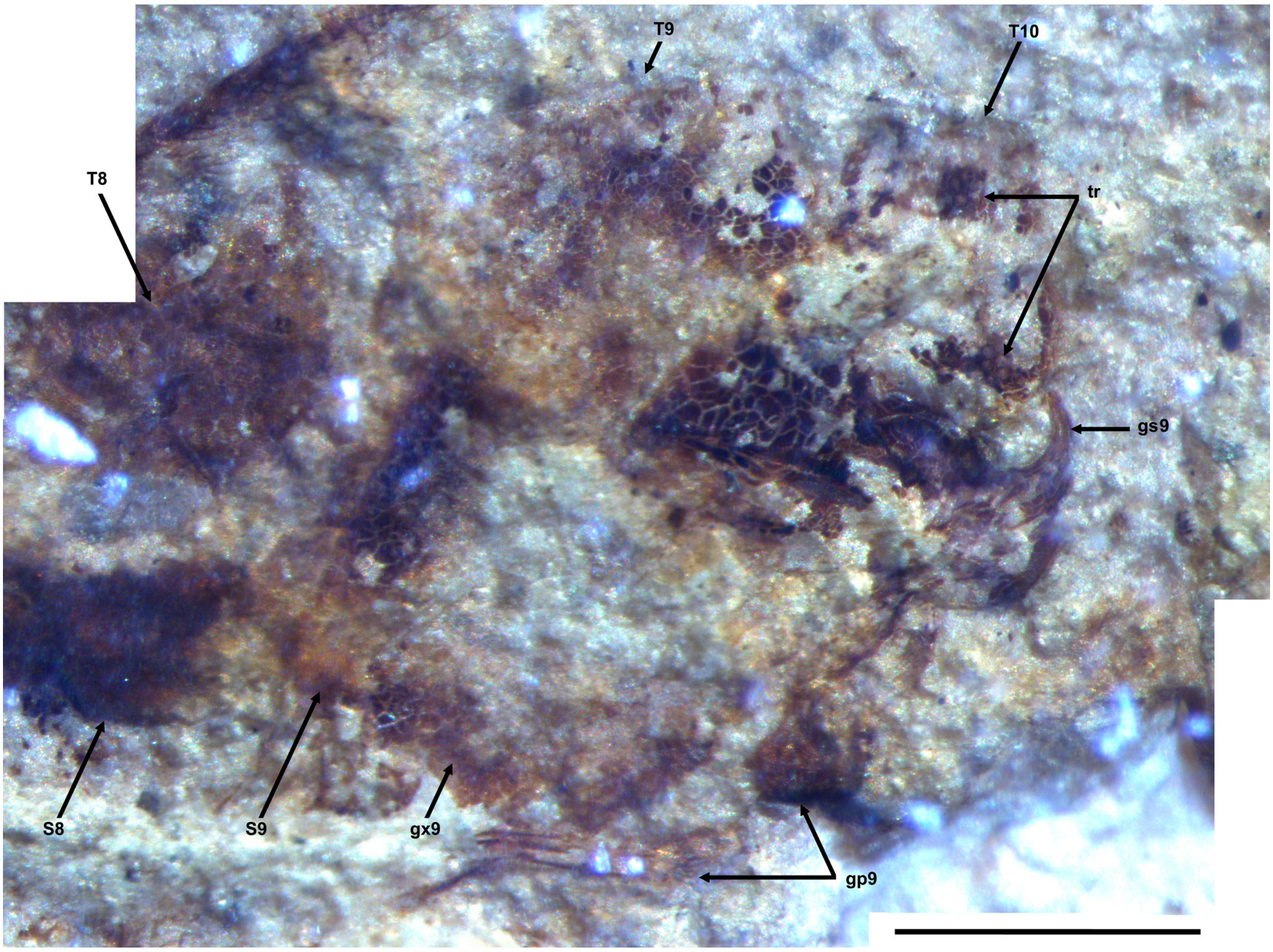

FIGURE 15. *Archiraphidia tranquilla* (Scudder, 1890) (lectotype of *A. eventa* (Scudder, 1890), MCZ 4137). Apex of abdomen (lateral view). gp9, gonapophyses of segment 9 (hypovalva); gs9, gonostyli of gonocoxites 9; gx9, gonocoxites of segment 9; S8, S9, sternites 8 and 9; T8, T9, T10, tergites 8 to 10. Scale bar = 400 μm.

Forewing approximately 8.8 mm long (estimated), 2.8 mm wide (3.1). Costal space incompletely preserved, relatively broad. ScP relatively short; length from termination of ScP to pterostigma much longer than length of pterostigma. Five preserved subcostal veinlets (branches of ScP) distad fusion of M+CuA simple, widely spaced, except two which abnormally convergent towards ScP. In subcostal pace, one crossvein between ScP, RA; other crossvein closing pterostigma proximally nearly straight. Pterostigma short, dark. RA with two branches: one long, incorporated in pterostigma, other closing pterostigma distally (Fig. 9F); portion of RA distad pterostigma short, deeply curved. Anterior trace of RP forked apically: branches of fork divergent at right angle forming very broad, shallow forking; with two branches proximad 3ra-rp, one distad (wing apex poorly preserved). RP1 forked, anterior branch simple, posterior rather deeply forked. RP2 simple. RP3 shallowly forked at least in right wing. Two crossveins between RA, RP; 3ra-rp located within pterostigma, in its middle. Three intraradial crossveins between branches of RP; distal-most crossvein long. Three crossveins between RP, MA; 1r-m rather close to origin of RP; 3r-m connecting RP1, MA oblique. MA dichotomously forked; MP strongly zigzagged, pectinately branched; anterior trace, all two branches rather short, simple. Two long intramedian crossveins; 2im connects posterior branch of MA and MP. M, CuA diverge at apparent R (free stem of M+CuA absent). Anterior trace of CuA with one shallowly forked branch. CuP simple. One long intracubital crossvein (incompletely preserved). AA1 simple; AA2 incompletely preserved; crossvein between these (iaa) moderately short.

Hind wing approximately 7.5 mm long, 2.5 mm wide (estimated 3.0 mm). Costal space, ScP poorly preserved. ScP short; length from termination of ScP to pterostigma much longer than length of pterostigma. In subcostal space, one crossvein detected, closing pterostigma proximally. Pterostigma narrower than in forewing. RA with two branches; one probably long, incorporated in pterostigma (only its basal part visible), other closing pterostigma distally (Fig. 9F); portion of RA distad pterostigma short, deeply curved. Two crossveins between RA, RP preserved; 2ra-rp located distad termination of ScP; 3ra-rp relatively short, within pterostigma (in middle portion). Anterior trace of RP forked apically: branches of fork divergent at right angle forming very broad, shallow fork; with two branches proximad 3ra-rp, one distad. RP1 deeply forked; both branches rather deeply forked; RP2, RP3 incompletely preserved. Three-four intraradial crossveins between RP1 to stem of RP (crossvein between RP2, RP3 abnormally doubled in left wing). M forked distad origin of RP; mode of branching not visible. One (distal) intramedian crossvein (2im) preserved. Cu, anal veins not preserved.

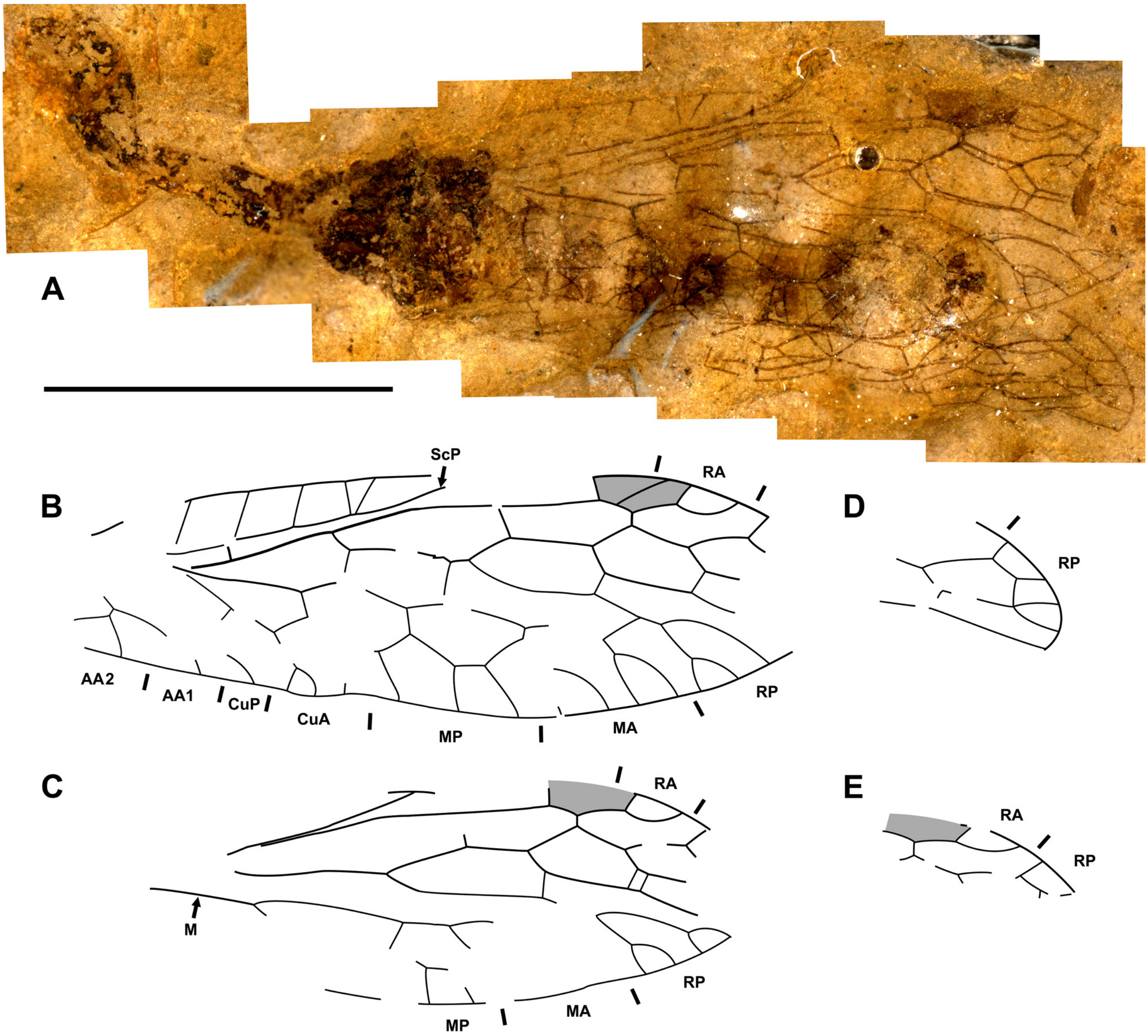

FIGURE 16. *Archiraphidia tranquilla* (Scudder, 1890) (paralectotype of *A. eventa* (Scudder, 1890), MCZ 253). A, the specimen as preserved (covered by Canada balsam). B, right forewing, C, right hind wing. D, left forewing. E, left hind wing. Scale bar = 4 mm (all to scale).

Type material. Holotype of *A. tranquilla*: MCZ 246 (Scudder's number 4383), deposited in MCZ. A rather poorly preserved, incomplete male specimen in lateral aspect; all wings overlapping; head, prothorax and legs missing. Verbatim label data: [1] "Mus. Comparative Zoölogy, Cambridge, / No. 246 / Raphidia (?) tranquilla / Scud. / Florissant Miocene"; [2] 246 / type / Raphidia (?) / tranquilla Scud. / Florissant / Neuroptera: Raphididae [sic]". The specimen has a red label glued to the rock that says "Type.", and black ink writing on the rock that says "246".

Types of *A. eventa*: lectotype (designated here) MCZ 4137 (Scudder's number 9391), deposited in MCZ. An almost complete male specimen in lateral aspect; head poorly preserved. Verbatim label data: [1] "Mus. Comp. Zoöl. Cambridge, Mass. / No. 4137 / Inocellia eventa / Scud. / Florissant"; [2] 4137 / type / Inocellia / eventa Scud. / Florissant / Neuroptera: Inocellidae [sic]". The specimen has a red label glued to the rock that says "Type. / 4137", and red ink writing on the rock that says "9391".

Paralectotype (designated here) MCZ 253 (Scudder's number 8319), deposited in MCZ. An almost complete male specimen in dorso-lateral aspect; legs not preserved, right wings crumpled. Verbatim label data: [1] "Mus. Comp. Zoöl. Cambridge, Mass. / No. 253 / Inocellia eventa Scud. / Florissant Miocene"; [2] 253 / type / Inocellia / eventa Scud. / Florissant / Neuroptera: Inocelliidae". The specimen has a red label glued to the rock that says "TYPE"; black ink writing on the rock that says "253", and red ink writing on the rock that says "8319".

Type locality. Florissant (precise collecting localities unknown).

Remarks. The venation of these two specimens assigned to *Archiraphidia eventa* is so similar to that of the holotype of *A. tranquilla* that we do not doubt in their conspecifity. *Archiraphidia tumulata* and *A. tranquilla* are also very similar; the minor differences in morphologies noted in their diagnoses may be intraspecific variation.

Archiraphidia tranquilla has only been figured by Scudder, once, with errors (1890), and neither specimens of *A. eventa* have been illustrated. Scudder (1890) described the latter species based on two these specimens (i.e., syntypes), both of which are designated in MCZ as the type. We designate here a better preserved specimen (MCZ 4137) as the lectotype, and other (MCZ 253) as the paralectotype.

Archiraphidia? somnolenta **(Scudder, 1890), stat. res.**

(Figs 17, 18)

Inocellia somnolenta Scudder, 1890: 157, Pl. 14, Fig. 12; Handlirsch 1906–1908 [1907]: 908; Cockerell & Custer 1925: 297; Carpenter 1936: 143, 145, 150 (as a synonym of *Raphidia tranquilla*); Oswald 1990: 160 (as a synonym of *R. tranquilla*); Engel 2002: 22 (as a synonym of *R. tranquilla*); Engel 2003: 125 (as a synonym of *R. tranquilla*).

?Inocellia somnolenta: Handlirsch 1910: 104.

"Raphidia" somnolenta: Aspöck *et al*. 1991: 539, 665, Fig. 3051.

Diagnosis. May be easily distinguished from other species of genus (and other Florissant genera) by long pterostigma (short in other *Archiraphidia* species) in which incorporated RA branch hardly detectable (clearly visible in species of *Megaraphidia*, *Florissantoraphidia* gen. nov.); two *doi* in hind wing (one in other *Archiraphidia* species).

Redescription. Head appears short (length slightly less than 2 mm), but possibly an artefact of preservation. Prothorax appears strongly narrowed caudally (in ventral view), ca. 2.0–2.3 mm long, ca. 1 mm maximum wide. Pterothorax, legs, abdomen poorly preserved, but surely male.

Forewing ca. 7.0 mm long as preserved (estimated complete length ca. 9 mm), 2.6 mm wide. Costal space incompletely preserved, relatively broad. ScP relatively short; length from termination of ScP to pterostigma slightly less than length of pterostigma. Four preserved subcostal veinlets (branches of ScP) distad fusion of M+CuA simple, widely spaced. In subcostal space, two crossveins preserved, one well proximad origin of RP; second closes pterostigma proximally. Pterostigma rather long, dark, but lighter than in congeners. RA with two branches preserved: one closing pterostigma distally, other distad pterostigma; no branches within pterostigma detected. Portion of RA distad pterostigma rather long. Anterior trace of RP deeply forked apically; with one branch proximad 3ra-rp, two distad (alternatively, anterior trace of RP simple; with one branch proximad 3ra-rp, three distad). RP1 forked once, relatively shallowly. RP2 simple. RP3 shallowly forked in right wing, simple in left. Two crossveins between RA, RP; 2ra-rp distad termination of ScP; 3ra-rp located within pterostigma, in its distal half. One intraradial crossvein, between anterior trace of RP, RP1. Three crossveins between RP, MA; 1r-m close to origin of RP; 3r-m connecting RP1, MA located near intraradial crossvein. MA dichotomously forked; MP zigzagged, pectinately branched; anterior trace, both branches simple (proximal-most branch fused for short distance with anterior trance of CuA in left wing). Two long intramedian crossveins; 2im connects anterior trace of MA, MP. Free stem of M+CuA very short. Anterior trace of CuA, its single branch simple. CuP simple. One long intracubital crossvein. Crossvein cu-aa rather long. AA1 simple; AA2 incompletely preserved; crossvein between these (iaa) very long.

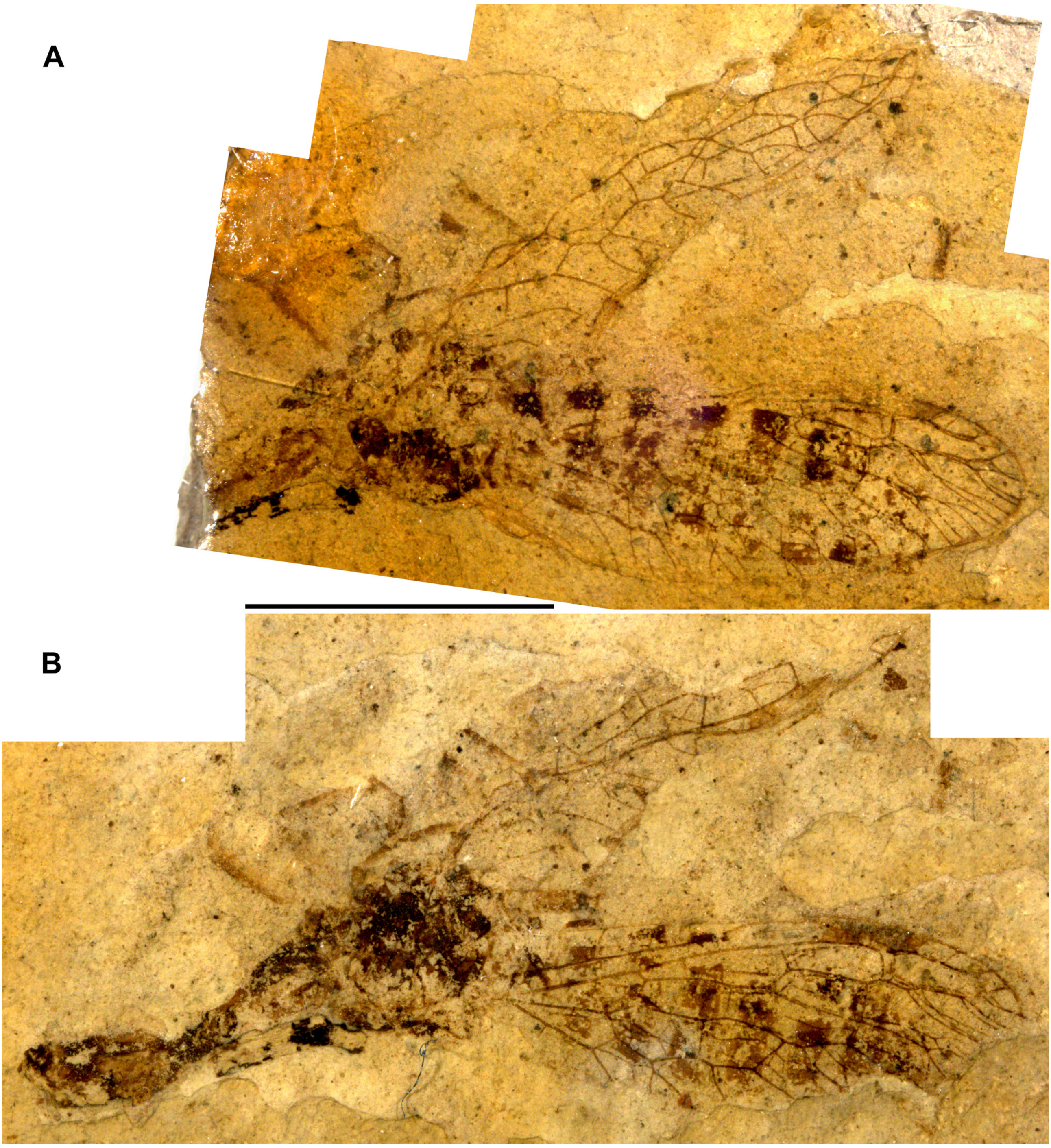

FIGURE 17. *Archiraphidia? somnolenta* (Scudder, 1890). Holotype MCZ 488. A, part (converted to right). B, counterpart. Scale bar = 4 mm (both to scale).

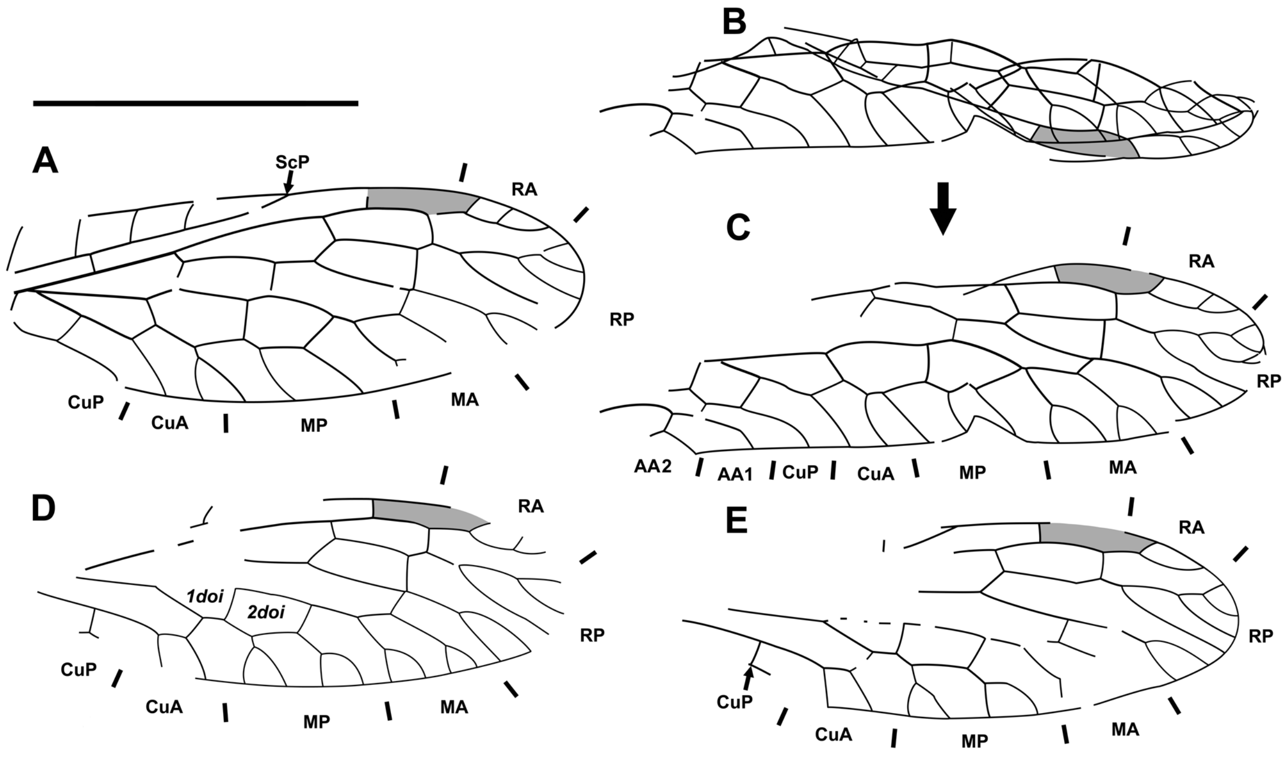

FIGURE 18. *Archiraphidia? somnolenta* (Scudder, 1890). Wing venation of the holotype MCZ 488. A, left forewing. B, right forewing as preserved. C, right forewing, reconstruction. D, left hind wing. E, right hind wing. Scale bar = 4 mm (all to scale).

Hind wing ca. 6.5 mm long as preserved (estimated complete length ca. 8 mm), 2.35 mm wide. Costal space poorly preserved. ScP fragmentarily preserved; length from termination of ScP to pterostigma slightly less than length of pterostigma. In subcostal space, one crossvein preserved, closing pterostigma proximally. Pterostigma rather long, slightly narrower than in forewing. RA with one branch (left wing), two branches (right wing); no branches detected within pterostigma; one branch closes pterostigma distally; other (right wing) distad pterostigma. Portion of RA distad pterostigma short, deeply curved in right wing; longer in left wing. Two crossveins between RA, RP preserved; 2ra-rp located well distad termination of ScP; 3ra-rp relatively short, within pterostigma (in distal half). Anterior trace of RP deeply forked apically in right wing, simple in left; with one branch proximad 3ra-rp, two distad (alternatively, anterior trace of RP simple in right wing, with one branch proximad 3ra-rp, three distad). RP1 forked once; other branches simple. One intraradial crossvein, between anterior trace of RP, RP1. MA dichotomously forked; MP pectinately branched; anterior trace, one branch rather deeply forked. Two *doi*; two intramedian crossveins. Anterior branch of CuA, one branch simple. 2m-cu connects MP well proximad 1im, CuA. Basal portion of wing, CuP, anal veins not preserved. CuP fragmentarily preserved. Anal veins not preserved.

Type material. Holotype MCZ 488a, b (part, counterpart; Scudder's numbers 9373 and 10389), deposited in MCZ. An incomplete, strongly crumpled male specimen; right forewing preserved separately from other wings, which are overlapping. Verbatim label data associated with the part 488a: [1] "Mus. Comparative Zoölogy, Cambridge, / No. 488 / Inocellia somnolenta / Scud. / Florissant Miocene"; [2] 488 a / type / Inocellia / somnolenta Scud. / Florissant / Neuroptera: Inocelliidae". The part has a red label glued to the rock that says "Type. / 488 a", and red ink writing on the rock that says "9373". Label data associated with the counterpart 488b: [3] "Mus. Comp. Zoöl. Cambridge, Mass. / No. 488-b / Inocellia somnolenta Scud. / Scudder Collection Florissant, Colo.". The counterpart has a red label glued to the rock that says "Type / 488 b", and red ink writing on the rock that says "10389".

Type locality. Florissant (precise collecting locality unknown).

Remarks. This species was considered as a synonym of *A. tranquilla* by Carpenter (1936, p. 50: "there is no reason for regarding these two species [*tranquilla* and *somnolenta*] as distinct"), which subsequent authors have followed, although it was only very schematically figured by Scudder (1890). We find that this species is clearly distinguished from *tranquilla* by a much longer pterostigma and two *doi* in the hind wing (one in *tranquilla*). We preliminarily assign the species to this genus. Its pterostigma is longer and slightly paler than in other specimens assigned to *Archiraphidia*, but an incorporated RA branch is not visible (see Fig. 9G, H). Also, it has two *doi* in the hind wing (one in other specimens of *Archiraphidia*); its MP in the forewing is not so zigzagged. It is then probable that this species belongs to a fourth genus of Florissant Raphidiidae, but we find no distinct diagnostic characters, which prevents us from creating a new genus for it.

Scudder (1890) provisionally assigned the specimen No. 2603 to this species, "the apical half of two overlapping fore wings" (p. 158). The present depository of this specimen is unknown.

Genus *Florissantoraphidia* gen. nov.

Type species. *Raphidia funerata* Engel, 2003.

Diagnosis. Moderate-sized raphidiids (forewing ca. 11 mm long); pterostigma long, rather pale, with incorporated branch of RA distinct; distal crossvein 3ra-rp located within pterostigma, far proximad its distal ending. In hind wing, 1r-m long, parallel to R; two *doi* [one in *Archiraphidia*]; CuA pectinate, three-branched [one-branched in *Archiraphidia*, *Megaraphidia*].

Species included. Two species from Florissant, *Florissantoraphidia mortua* (Rohwer, 1909) and *F. funerata*.

Etymology. From Florissant, type locality of the type species, and *Raphidia*, a genus-group name.

Remarks. The three-branched pectinate CuA in the hind wing is the most distinctive feature of *Florissantoraphidia* gen. nov. Within the family, this condition occurs only in single species of the North America genus *Agulla*; to our knowledge, most other species in this genus normally possess a two-branched CuA as do some species of the Palearctic genera *Phaeostigma*, *Dichrostigma*, *Harraphidia*, and *Mongoloraphidia* H. Aspöck & U. Aspöck, 1968c. CuA is one-branched in other extant Raphiididae.

Florissantoraphidia gen. nov. may be distinguished from *Agulla* by the following character states: the costal space is narrower; the pterostigma is longer; 3ra-rp is located within the pterostigma [usually just distad pterostigma (very rarely in distal part of pterostigma) in *Agulla*]; the basal 1r-m in the hind wing is long, running nearly parallel to RA [short, crossvein-like, inclined to RA at some angle in *Agulla*]. The only known fossil species of *Agulla* is *A. mineralensis* known from a single hind wing, whose characters agree well with *Agulla*. We consider it likely that '*Agulla*' *protomaculata* from the Early Eocene Green River Formation does not belong to this genus, however (Archibald & Makarkin, ongoing research).

Some doubt remains as to the distinctiveness of the two species included here in the new genus, as differences present in their known fossils might possibly be intraspecific. We prefer to leave these separate, however, until future fossils may clarify this question.

Florissantoraphidia mortua (Rohwer, 1909), comb. nov.

(Figs 19, 20)

Raphidia mortua Rohwer, 1909: 533, 534; Cockerell 1912: 215, 216 [as a probable variety of *Raphidia exhumata*]; Cockerell 1914: 715; Martynov 1925a: 245; Carpenter 1936: 143, 146, 148, Fig. 10; Rodeck 1938: 290; Oswald 1990: 160; Engel 2003: 124, 125; Engel 2009: 211, 213 (Tabl. 1); Engel 2011: 79 (Tabl. 2), 80.

Raphidia moriua [sic]: Carpenter 1953: Fig. 6.

"Raphidia" mortua: Aspöck *et al*. 1991: 540, 665, Fig. 3053; Engel 2002: 22.

Diagnosis. Distinguished from *F. funerata* by distal position of 2ra-rp in forewing, absence of branch of RA distad pterostigma in both wings; by forked branches of MP in hind wing.

Redescription. Meso-, metathorax preserved; abdomen possibly present, region poorly preserved. Details not visible.

Forewing narrow, ca. 11 mm long, 2.9 mm wide. Costal space relatively narrow, strongly dilated at proximal 1/3. Length from termination of ScP to pterostigma slightly less than length of pterostigma. Subcostal veinlets simple, widely spaced. One crossvein between ScP, RA; other crossvein closes pterostigma proximally. Pterostigma long, rather pale. RA with two branches: one long oblique within pterostigma, another closing pterostigma distally; portion of RA distad pterostigma rather long, lacks branches. RP with two branches proximad

3ra-rp, probably two distad; RP1 deeply forked, RP2 simple. Two crossveins between RA, RP; 2ra-rp somewhat distad termination of ScP; 3ra-rp located within pterostigma, near its ending. Two radial cells, nearly equal in length. One intraradial crossvein, between RP1, RP2. Three crossveins between RP, MA; proximal crossvein 1rp-m rather far from origin of RP. MA dichotomously branched; MP weakly zigzagged, pectinately branched; anterior trace, two branches all simple. Two long intramedian crossveins. M, CuA diverge at apparent R (free stem of M+CuA absent or very short). Anterior trace of CuA, one branch simple. CuP simple. Intracubital crossvein long. Crossvein between CuP, AA1 not detected. AA1 simple; AA2 incompletely preserved; crossvein between (iaa) these rather short.

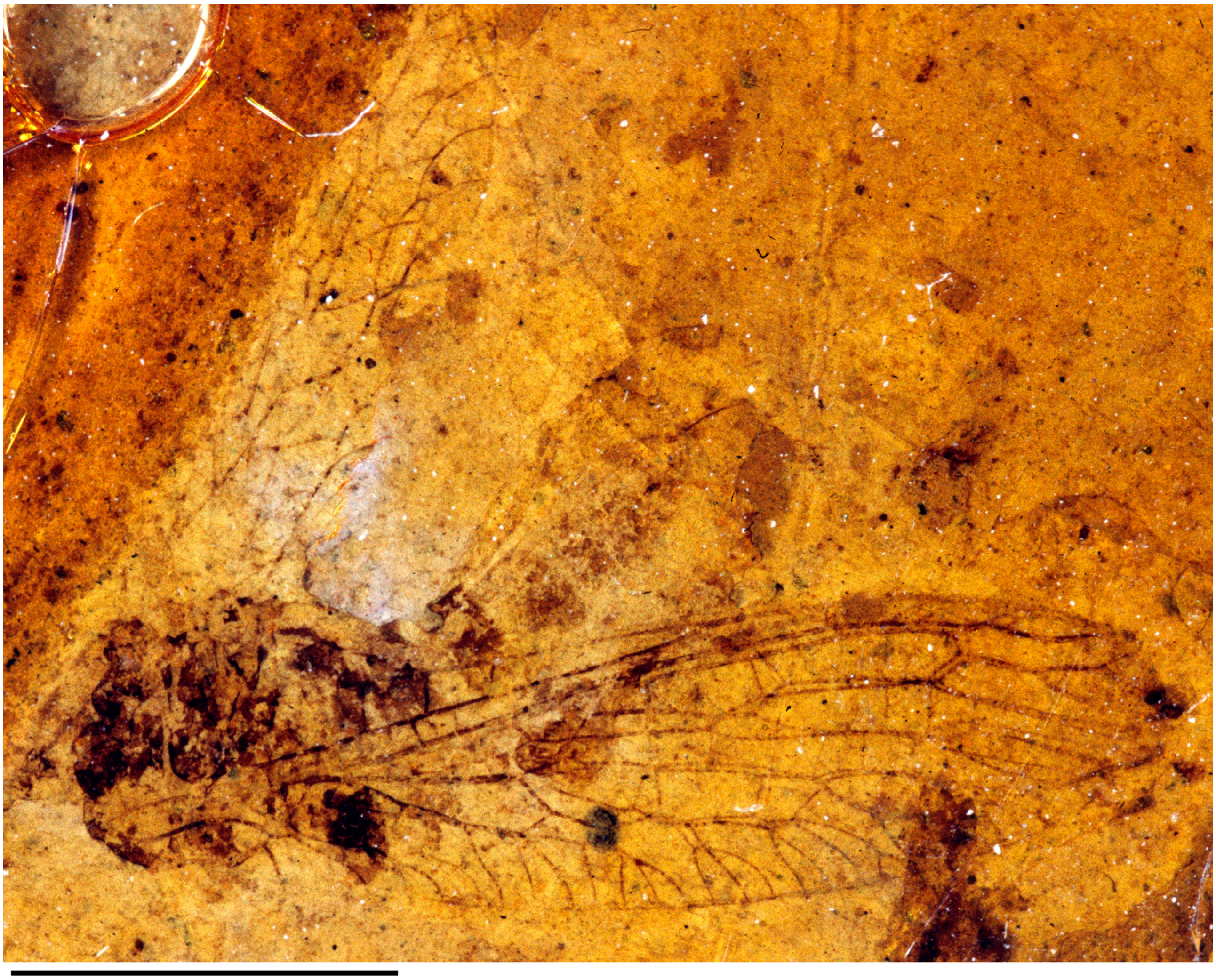

FIGURE 19. *Florissantoraphidia mortua* (Rohwer, 1909). Holotype UCM 4512 as preserved (covered by Canada balsam). Scale bar = 4 mm.

Hind wing approximately 9–9.5 mm long, 2.7 mm wide (estimated). Costal space, ScP not preserved. In subcostal space, one crossvein detected, closed pterostigma proximally. Pterostigma long. RA with one preserved rather short branch, which closes pterostigma distally; incorporated branch not detected. Three crossvein between RA, RP; 3ra-rp located within pterostigma, in distal portion. RP with two branches proximad 3ra-rp. RP1 deeply forked. Two intraradial crossvein detected, both between RP1, RP2. Three crossveins between RP, M/MA detected; 1r-m long, running parallel to R; connecting RP, M relatively far distad wing base. M forked distad origin of RP. MA deeply forked, each branch forked. MP pectinately branched, anterior trace shallowly forked with one deeply forked, one simple branch (right wing); simple with two deeply forked and one simple branch (left wing). Two intramedian crossveins. CuA pectinate, with three simple branches (right wing), probably with two branches (left wing). Long intracubital crossvein (icu) partially preserved. CuP, anal veins fragmentarily preserved; their pattern implies that CuP simple.

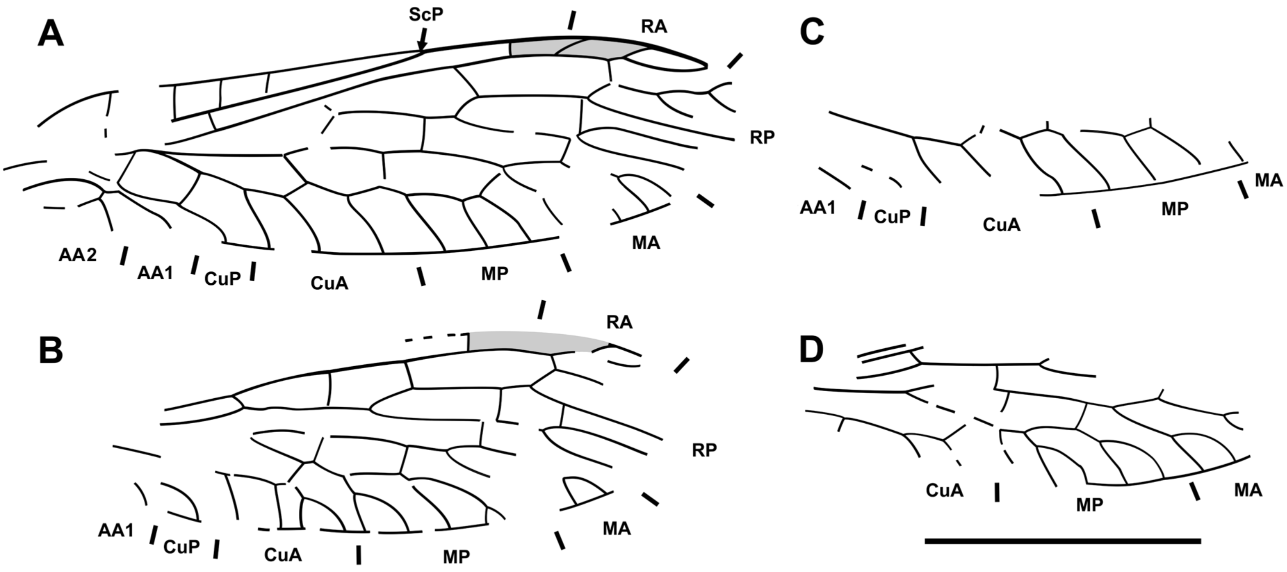

FIGURE 20. *Florissantoraphidia mortua* (Rohwer, 1909). Wing venation of the holotype UCM 4512. A, right forewing. B, right hind wing. C, left forewing. D, left hind wing. Scale bar = 4 mm (all to scale).

Type material. Holotype: No. 4512 (collected by G.N. Rohwer in 1908), deposited in UCM. An incomplete and crumpled specimen. Verbatim label data [typed and hand written]: "F / UCM Paleontology TYPE Collection / Neuroptera: Raphidiidae / UCM#: 4512 Acc#: / Locality #: 83014 Description: lateral / ID: Raphidia mortua Rohwer / Age: Late Eocene Collector: GN Rohwer 1908 / Fm: Florissant Citation: Toohey #52984". The specimen has black ink writings on the rock that say " Raphidia / motrua / Roh. / TYPE" and "N 14"; red ink writing that says "TYPE"; and red / black ink writing on a circular paper glued to the rock that says "TYPE / 4512".

Type locality. Florissant: Station 14 (UCM locality No. 83014).

Florissantoraphidia funerata (Engel, 2003), comb. nov.

(Figs 21, 22)

"Raphidia" sp.: Aspöck *et al.* 1991: 541, Fig. 3065.

Raphidia funerata Engel, 2003: 124–127, Figs 1, 2; Grimardi & Engel 2005: 339, Fig. 9.10; Engel 2009: 211, 213 (Tabl. 1); Engel 2011: 79 (Tabl. 2).

Diagnosis. Distinguished from *F. mortua* by more proximal position of 2ra-rp in forewing, presence of one branch of RA distad pterostigma in both wings; by simple branches of MP in hind wing.

Redescription. Head elongate, ca. 2.6 mm long (including mouthparts); antennae and palpi preserved, but details poorly discernible. Prothorax quite short, broad (ca. 2.3 mm), slightly dilated caudally (in lateral view), maximum width ca. 1 mm. Legs covered with fine dense hairs; tibia also with scarce longer bristles. Abdomen with six long dark segments well discernible, separated by broad pale intersegmental membrane between latter five; with relative short ovipositor, length ca. 4.5 mm as preserved.

Forewing narrow: 10.7 mm long, 2.8 mm wide. Costal space relatively narrow, strongly dilated at proximal 1/3. ScP relatively short; length from its termination to pterostigma equal pterostigma length. Subcostal veinlets simple widely spaced. One crossvein between ScP, RA; other crossvein closes pterostigma proximally. Pterostigma long, rather pale. RA with three branches: long, oblique distinct within pterostigma; two shorter, one closing pterostigma distally, other distad pterostigma. RP with two branches proximad 3ra-rp; RP1 forked well distad intraradial crossvein, posterior branch rather shallowly forked; RP2 simple. Two crossveins between RA, RP; 2ra-rp well distad termination of ScP; 3ra-rp located within pterostigma, far proximad its ending. Two radial cells nearly equal length. Proximal crossvein 1rp-m located near origin of RP. One intraradial crossvein; three crossveins between RP, MA. MA dichotomously branched; MP pectinately branched; stem and three branches simple. Two long intramedian crossveins. M, CuA fused basally for short distance. CuA deeply forked. CuP simple. Intracubital crossvein (icu) long. Crossvein between CuP, AA1 not detected. AA1 simple; AA2 incompletely preserved; crossvein between these (iaa) rather long.

Hind wing approximately 9–9.5 mm long (estimated), 2.5 mm wide. Costal space narrow. ScP relatively short; length from its termination to pterostigma slightly less than pterostigma length. Subcostal veinlets simple widely spaced. In subcostal space, one crossvein, which closes pterostigma proximally. Pterostigma long, narrower than in forewing. RA with two preserved rather short branches: one closed pterostigma distally, other distad pterostigma; incorporated branch not detected. Three crossveins between RA, RP; 3ra-rp located within pterostigma, far proximad its ending. RP with two branches proximad 3ra-rp; RP1 dichotomously branched. One intraradial crossvein detected. Three crossveins between RP, M/MA; basal 1r-m long, running parallel to R; connecting RP, M relatively far distad wing base. M forked distad RP origin. MA deeply forked, each branch forked. Anterior trace of MP simple, pectinately branched, with three simple branches (alternately, anterior trace deeply forked and with two simple branches). Two long intramedian crossveins. CuA pectinate, with three simple branches. Intracubital crossvein (icu) long. CuP, anal veins fragmentarily preserved; their pattern implies that CuP simple, AA1 two-branched.

Type material. Holotype: In. 26922, deposited in NHM (Department of Palaeontology). A complete rather well preserved female specimen in lateral aspect with all four wings overlapping; one forewing, one hind wing relatively complete, distinctly preserved.

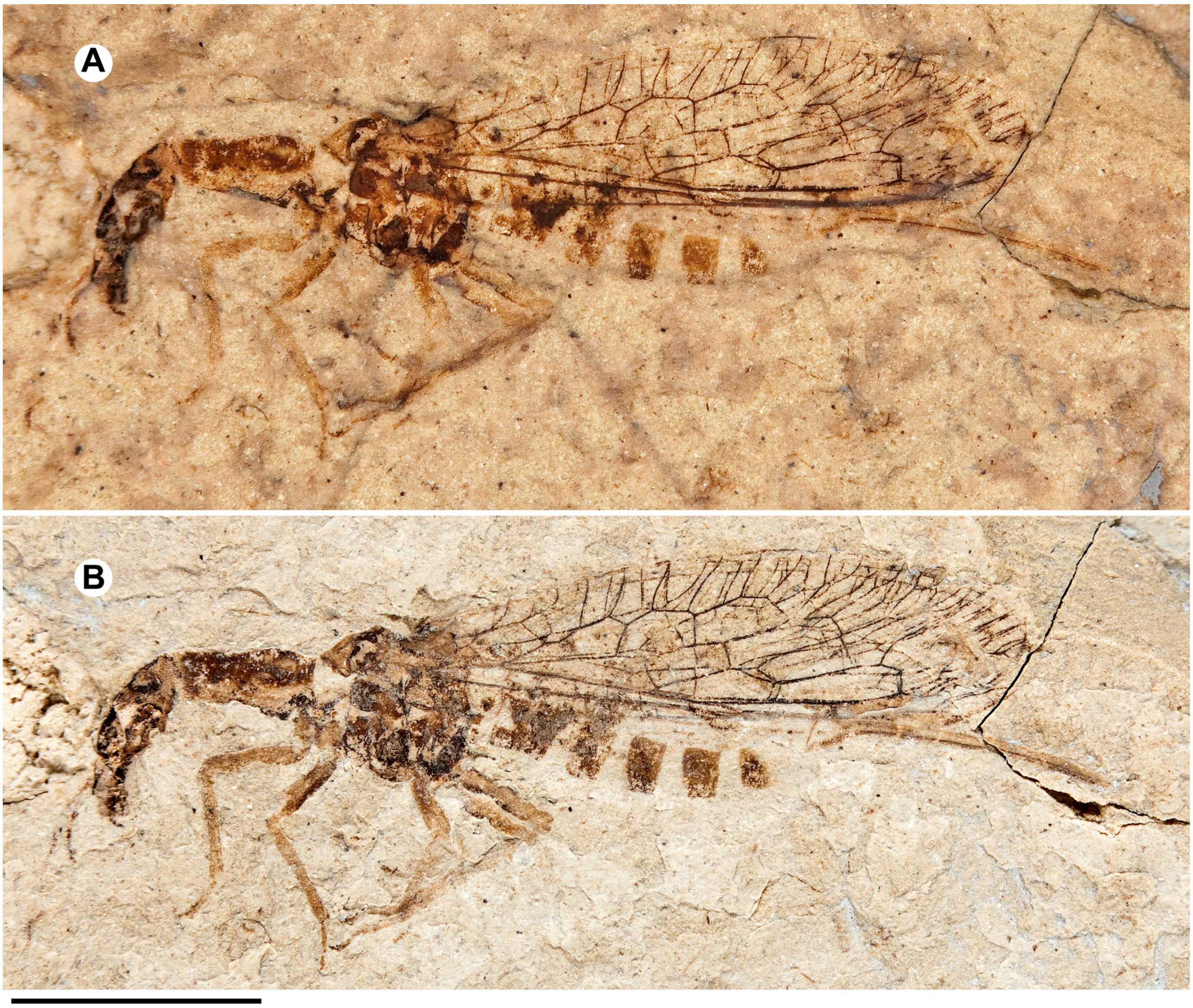

FIGURE 21. *Florissantoraphidia funerata* (Engel, 2003). Holotype NHM In. 26922. A, the specimen as preserved (wetted with ethanol). B, the same (dry). Scale bar = 4 mm (both to scale).

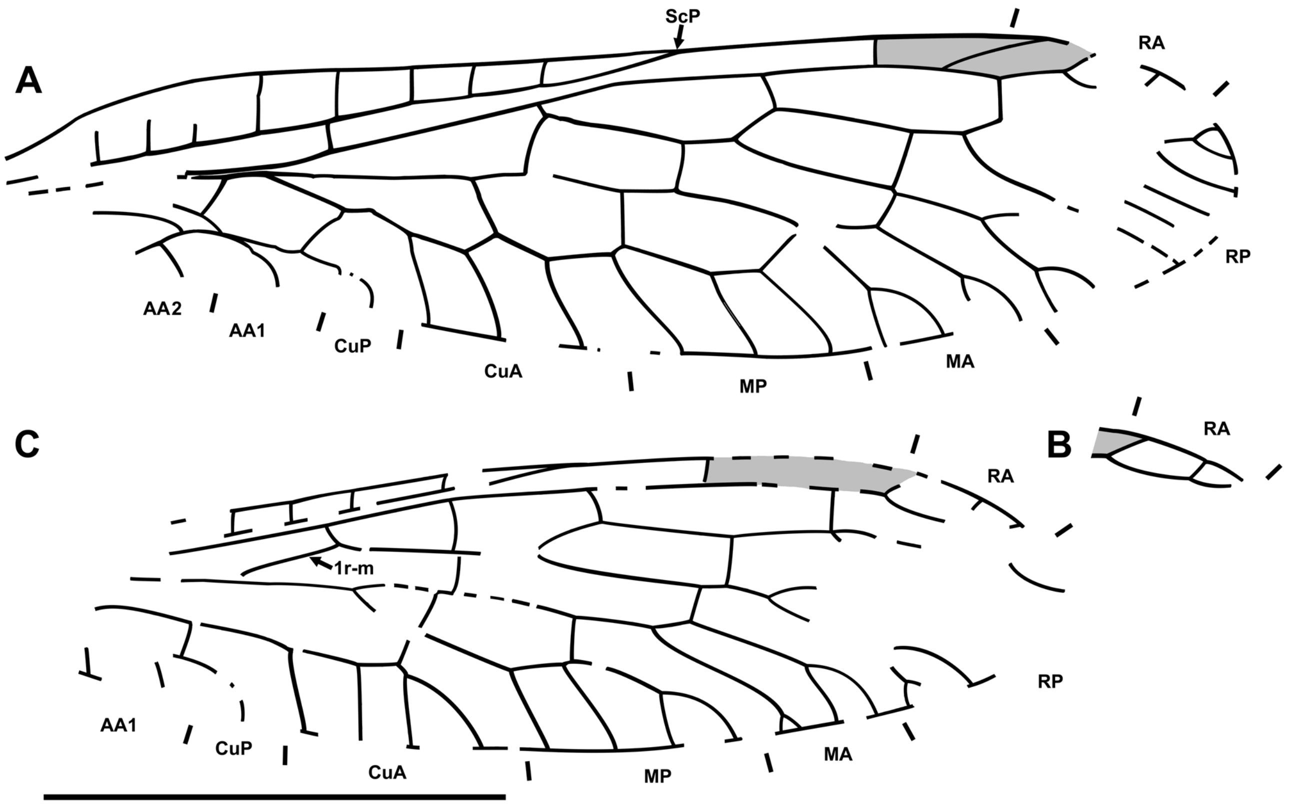

FIGURE 22. *Florissantoraphidia funerata* (Engel, 2003). Wing venation of the holotype NHM In. 26922. A, left forewing. B, apical portion of right forewing. C, left hind wing. Scale bar = 4 mm (all to scale).

The specimen was recently returned to the NHM from the MCZ without original labels, which were presumably lost during this loan to F. M. Carpenter decades before (A. Ross, pers. comm.). There is now only one small red label that says "HOLOTYPE Raphidia funerata Michael S. Engel". The specimen has a small label glued to the rock that says "Brit. Mus. Geol. Dep."; black ink writing on the side of the specimen block that says "I –32-" [the original number of G. F. Sternberg, from whom the specimen was purchased in October 1926]; writing on the back of the specimen on an oval yellow disc says "In 26922". The old register/catalogue in NHM says "Tenebrionites alatus, Miocene, Florissant, Colorado; No. 32 Purchd. G. F. Sternberg Oct 1926." (C. Mellish, pers. comm.).

Type locality. Florissant (precise collecting locality unknown).

Remarks. The left forewing is slightly deformed basally (CuA appears zigzagged; CuP and AA1 appear to be fused; AA1 is not normally running).

Family Inocelliidae Navás, 1913

Diagnostic character states of venation. Pterostigma not enclosed by crossvein proximally; incorporated pterostigmal branches of RA absent. Forewing: 2scp-r located near termination of Sc; 3ra-rp always distad pterostigma; three crossveins between RA, RP (few exceptions, below); stem of M+CuA always long (except *Sininocellia* Yang, 1985, where relatively short); four crossveins between R/RP, M/MA; basal crossvein between R, M (1r-m) connect M, R; 4r-m present; in medial space, three crossveins forming three *doi*; *4doi* present, formed by MP, CuA, and two crossveins between MP, CuA (except few species, below); MP, CuA connect by two crossveins (MP, CuA apparently fused as in Raphidiidae in few species with two *doi*, below); AA1 usually simple (few exceptions, below); rather long free basal portions of AA2, AA3 (before their fusion).

Hind wing: 2scp-r connects ScP and RA; 3ra-rp always distad pterostigma; CuP not fused with AA1.

Composition. Seven extant genera (40 valid species): *Inocellia* Schneider, 1843 [22 species;Palaearctic region]; *Fibla* [4 species; Mediterranean]; *Parainocellia* Aspöck *et* Aspöck, 1968c [4 species; Europe; Burma, Vietnam]; *Sininocellia* [2 species; China]; *Amurinocellia* Aspock *et* Aspock, 1973 [3 species; East Asia]; *Indianoinocellia* [2 species; Mexico]; *Negha* [3 species; North America] (Liu *et al*. 2009a,b, 2010b,c, 2012a,b, 2013, 2014; Aspöck *et al*. 2011, 2012b).

Seven fossil species (six named), all recorded from the Cenozoic: *Electrinocellia peculiaris*, *Succinofibla aperta* Aspöck *et* Aspöck, 2004, '*Fibla*' *erigena* (Menge in Pictet-Baraban *et* Hagen, 1856), '*Fibla' carpenteri* Engel, 1998, and an undesribed specimen (Janzen 2002: Figs 54, 547) from late Eocene Baltic amber; '*Fibla' exusta* (Cockerell *et* Custer, 1925) from the late Eocene of Florissant (Colorado); *Miofibla cerdanica* Nel, 1993 from the late Miocene of Bellver-en-Cerdaña (Spain) and the unnamed 'Species G' from the late Miocene of Murat (France). Inocelliid larvae are known from Baltic amber (Weidner 1958; Janzen 2002: Figs 55, 548).

Comments on characters. ***Radial crossveins.*** All species of extant Inocelliidae have three radial crossveins between RA and RP in the forewing, with the exception of two species of *Sininocellia* (four crossveins) and individual specimens of the highly variable *Inocellia folvostigmata* Aspöck *et* Aspöck, 1968 (Aspöck & Aspöck 1968: Fig. 1h) (two crossveins); other specimens of this species have three of these crossveins (e.g., Aspöck *et al.* 1982: Figs 26–29). *Electrinocellia peculiaris* from Baltic amber has only two radial crossveins (Carpenter 1957: Fig. 3A).

Discoidal cells. Until recently, the vast majority of extant Inocelliidae species were known to have four (3+1) *doi* in the forewing (Fig. 2A). Probably, the single documented exception was three (2+1) *doi* in the two species *Negha meridionalis* Aspöck, 1988 (Aspöck 1988: Fig. 1) from California and *Inocellia f. fulvostigmata* from India (Aspöck *et al*. 1982: Figs 26, 27), and two (2+0) *doi* in *Inocellia fulvostigmata nigrostigmata* Aspöck *et al*. 1982 from India (Aspöck & Aspöck 1968: Fig. 1h; Aspöck *et al*. 1982: Figs 28, 29). However, the rich inocelliid fauna from eastern and southeastern Asia reported in the last few years shows remarkable venational diversity including three (2+1) *doi* present in *Inocellia biprocessus* Liu *et al*., 2010 from Shandong Province in China, and two *doi* (2+0) in *Inocellia bilobata* Aspöck *et al*., 2011; *I. cornuta* Aspöck *et al*., 2011; *Inocellia longispina* Aspöck *et al*., 2011; *Inocellia striata* (all from Thailand, southernmost findings of Raphidioptera in the Old World); and *Inocellia yunnanica* Liu *et al*., 2012 from Yunnan Province in China (Liu *et al*. 2010c: Fig. 1; Aspöck *et al*. 2011: Figs 1, 10, 19–28, 40–43; Liu *et al*., 2012a: Figs 3, 4). *Electrinocellia peculiaris* from late Eocene Baltic amber also has two *doi.*

Most probably, in these few species of Inocelliidae that have two *doi*, MP and CuA are fused for some distance similarly to Raphidiidae. At least, the venation of this area in these inocelliid species is not different from that of Raphiididae.

Forewing AA1. The inocelliid AA1 is usually simple. Occasionally, AA1 is forked (often in only one of the forewings) in some extant species, e.g., *Sininocellia gigantos* Yang, 1985, *S. chikum* Liu *et al*., 2012 (Liu *et al.* 2012b: Figs 1–3), *Fibla hesperica* Navás, 1915 (Aspöck *et al.* 1991: Fig. 45) and *Negha inflata* (Hagen, 1861) (Carpenter 1936: Fig. 7); in the fossil *Fibla carpenteri*, and the unnamed species 'Espèce G (probablement *Fibla*)' (Nel 1993: Fig. 12). It is noteworthy that all of these species (except *Negha inflata*) possess a long basal 1r-m crossvein (brace) in the hind wing, a plesiomorphic character state. We suspect that the forked AA1 is a plesiomorphic state in this family as well.

Remarks. All but one fossil species have wings similar to those of the extant genera *Fibla* and *Sininocellia* in the presence of the long basal r-m brace (1r-m), a plesiomorphic state in Neuropterida. The exception is *Electrinocellia peculiaris*. This species has two discoidal cells, two radial and medial crossveins in the forewing (as in raphidiids) and 1r-m in the hind wing is lost (as in most extant inocelliids; this condition is only known in this species among fossil taxa of the family). Grimaldi (2000) believed that "it shares inocelliid and raphidiid features" (p. 262). Engel (1998) separated it into the monotypic inocelliid subfamily Electrinocelliinae. However, some recently described species of *Inocellia* from southeastern Asia have very similar venation (see Aspöck *et al.* 2011: Figs 23–28), discrediting the validity of this subfamily.

Two Mesozoic species have been assigned to the Inocelliidae. The Early Cretaceous *Sinoinocellia liaoxiensis* Wang, 1987 was attributed to this family (Wang 1987: Fig. 17); however, the drawing of this incompletely-preserved species clearly shows that it belongs to Mesoraphidiidae (s.l.) by its forewing character states, e.g., only two crossveins between RA and RP (three in Inocelliidae); three crossveins between R/RP and M/MA (four in Inocelliidae); 1r-m connects R with MA, not M as in all Inocelliidae. Also, an undescribed species from the Late Cretaceous (Turonian) locality of Kzyl-Dzhar (now Kyzylzhar) was thought as belonging to Inocelliidae (Zherikhin 1978, p. 78). This specimen also belongs with certainty to Mesoraphidiidae (s.l.); it is most similar to *Alloraphidia dorfi* Carpenter, 1968 (VM, pers. obs.).

No venational autapomorphies of Inocelliidae were identified by Aspöck and Aspöck (2004). However, we find two forewing character states to be autapomorphies of this family: (1) the presence of the crossvein 1ra-rp, and (2) the crossvein 1r-m connects M and R (see above).

'Fibla' exusta (Cockerell & Custer, 1925)

(Fig. 23)

Inocellia exusta Cockerell & Custer, 1925: 296, Fig.; Rodeck 1938: 290.
Fibla exusta: Carpenter 1936: 144, 152, Fig. 13; Oswald 1990: 161; Engel 1998: 190; Engel 2003: 125; Aspöck & Aspöck 2004: 15, 17; Engel 2009: Tabl. 1; Engel 2011: 79 (Tabl. 2).
"Inocellia" exusta: Aspöck *et al*. 1991: 543, 666, Fig. 3060, Map 194.
"Fibla" exusta: Engel 2002: 17.

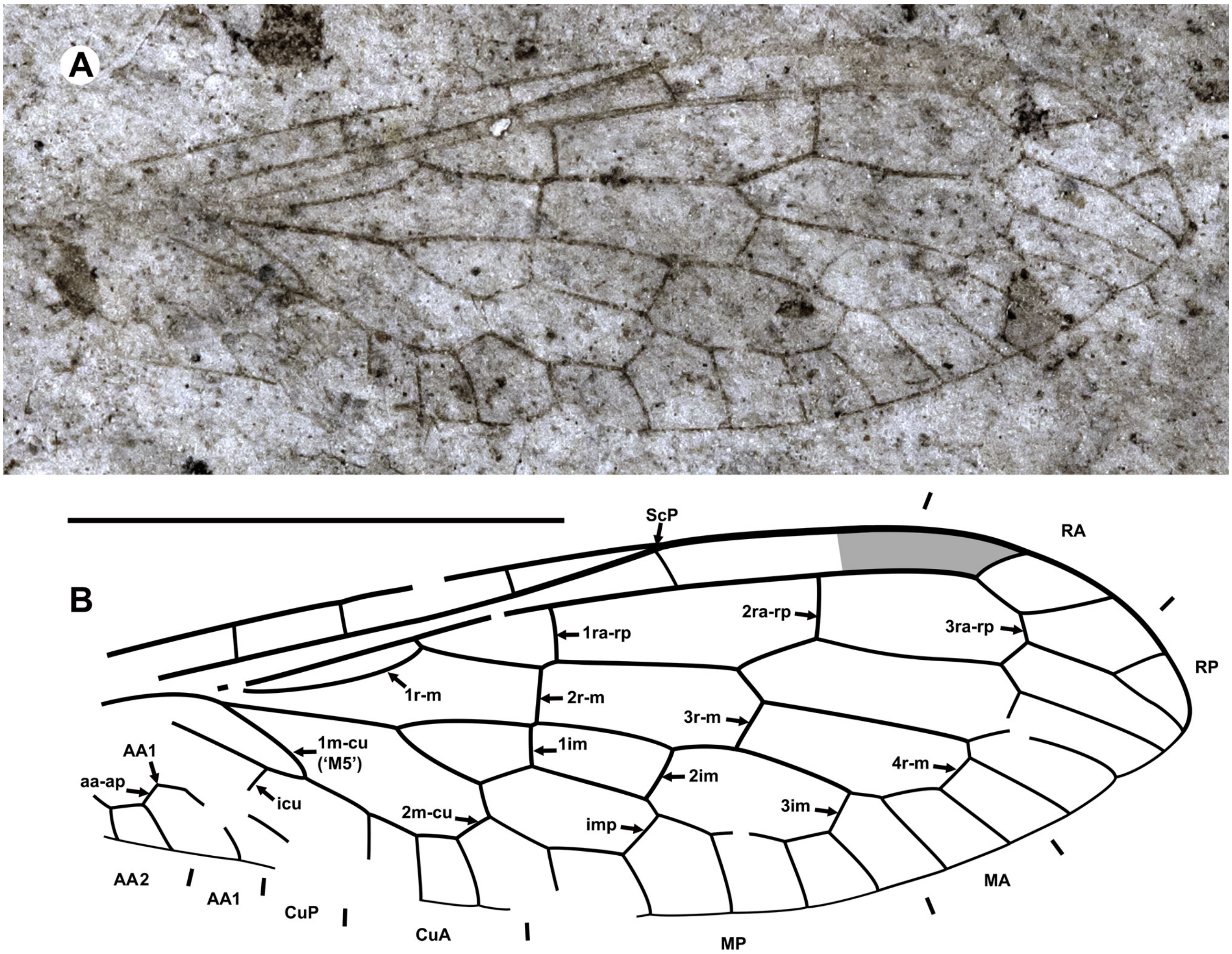

FIGURE 23. *'Fibla' exusta* (Cockerell *et* Custer, 1925). Holotype UCM 4923. A, specimen as preserved. B, hind wing venation. Scale bar = 4 mm.

Redescription. Hind wing 8.6 mm long as preserved (estimated complete length ca. 9.5 mm), 3.1 mm wide. Costal space moderately broad; subcostal veinlets widely spaced. ScP relatively short; length from termination of ScP to pterostigma nearly equal to length of pterostigma. In subcostal space, one crossvein between ScP near its termination, RA. Pterostigma rather short. RA with one branch, closed pterostigma distally; posterior trace RA distad pterostigma angulated at 3ra-rp. Three crossveins between RA, RP; 2ra-rp located clearly proximad pterostigma; 3ra-rp short, distad pterostigma. Anterior trace of RP forked apically, with two branches proximad 3ra-rp. RP1 deeply forked; RP2 simple. One intraradial crossvein, between stem of RP2, anterior branch of RP1. Four crossveins between R, M: 1r-m very long, connecting RP, M at its separation from R; 2r-m connects stem of

RP, M; 3r-m connects RP1, MA; 4r-m connects posterior branch of RP1, anterior branch of MA. M forked slightly proximad origin of RP. MA once deeply forked. MP pectinately branched; anterior trace simple; proximal-most branch (MP1) long, forked; two other branches short, simple. Three intramedian crossveins forming three *doi*; crossvein between anterior trace of MP, anterior branch of MP1 forming fourth *doi*. 1m-cu ('M5') long, oblique connecting basal MP, CuP; 2m-cu connects MP1 between origin, forking, and CuA. CuA pectinately forked, with two simple branches. CuP probably simple. Intercubital crossvein (icu) located proximad 1m-cu. AA1 with two simple branches.

Type material. Holotype UCM 4923 (coll. S.A. Rohwer). A well-preserved nearly complete hind wing. Verbatim label data [typed and hand written]: "F / B / UCM Paleontology TYPE Collection / Neuroptera: Raphidiidae / UCM#: 4923 / Locality #: 18130 Description: wing / ID: Inocellia exusta Cockerell / Age: Late Eocene Collector: SA Rohwer / Fm: Florissant Citation: Toohey". The specimen has black ink writing on the rock that says "neurop. / UCM 4923a (AP) / R"; red ink writing "TYPE", and a white hand written label glued to the rock that says "Inocellia / exusta Ckll & Custer / TYPE [in red square] / Florissant / Miocene".

Type locality. Florissant (UCM locality No. 18130).

Remarks. The generic affinity of this species is provisional. The hind wing character states are fully concordant with those of the extant *Fibla* and *Sininocellia*, and the Baltic amber *Succinofibla* Aspöck *et* Aspöck, 2004, in particular by the presence of the long basal r-m brace (1r-m), a plesiomorphic condition in Neuropterida. These genera are mainly distingiushed by genetalic features (Aspöck & Aspöck 2004; Liu *et al*. 2012b).

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