Zootaxa 5306 (4): 427–444
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5306.4.2
http://zoobank.org/urn:lsid:zoobank.org:pub:24CBC353-2E5E-47E9-A4B9-92913B0D56BC

Fossil Neuropterida (Insecta: Neuroptera and Raphidioptera) from the middle Eocene Kishenehn Formation, Montana, USA

JAMES E. JEPSON[1*] & VLADIMIR N. MAKARKIN[2]
[1]*Department of Earth and Environmental Sciences, University of Manchester, Williamson Building, Manchester, M13 9PL, UK.*
james.jepson@manchester.ac.uk; https://orcid.org/0000-0003-3184-8277
[2]*Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok 690022, Russia. vnmakarkin@mail.ru; https://orcid.org/0000-0002-1304-0461*
**Corresponding author: james.jepson@manchester.ac.uk*

Abstract

The neuropterid (Neuroptera and Raphidioptera) fauna of the middle Eocene Coal Creek Member (Kishenehn Formation), U.S.A. is documented. Three families of Neuroptera (Ascalaphidae, Chrysopidae, Hemerobiidae) and two families of Raphidioptera (Raphidiidae, Inocelliidae) are recorded. Five new species and three new genera are described: *Pseudoameropterus ambiguus* **gen. et sp. nov.** (Ascalaphidae), *Minimochrysa latialata* **gen. et sp. nov.**, *Palaeochrysa greenwalti* **sp. nov.**, *P. minor* **sp. nov.** (Chrysopidae: Nothochrysinae), *Macrostigmoraphia diluta* **gen. et sp. nov.** (Raphidiidae). Two indeterminate species are also recorded: *Megalomus*-group gen. et sp. indet. (Hemerobiidae) and Neuroptera fam. gen. et sp. indet. The only previously described neuropterid from the deposit is the raphidiopteran *Paraksenocellia australis* Makarkin *et al*. 2019 (Inocelliidae). The neuropterid assemblage suggests a subtropical semi-arid climate of the Coal Creek Member.

Key words: Ascalaphidae, Chrysopidae, Hemerobiidae, Inocelliidae, Raphidiidae, middle Eocene, North America

Introduction

Neuropterida is a superorder of holometabolous insects that comprise the orders Neuroptera (lacewings and allies), Raphidioptera (snakeflies), and Megaloptera (alderflies and allies). Today Neuropterida are found on all continents, except Antarctica, and are represented by approximately 6,500 species (Oswald 2021). Neuropterida, in particular Neuroptera, has a diverse fossil record extending back to the Permian, with a major period of diversification in the mid-Mesozoic. In North America today all three orders are present. With regard to the neuropterid fossil record, there are numerous localities in North America that have yielded specimens, these ranging from the Permian (Elmo, Kansas), Cretaceous ambers (New Jersey and Canadian), the Eocene Green River (Colorado), Okanagan Highlands (British Columbia) and Florissant (Colorado), to the Miocene ambers of Mexico and the Dominican Republic.

The Eocene Kishenehn Formation has yielded numerous insect fossils, with at least 15 orders present. The majority are Diptera, and most of those are aquatic; with dipteran pupae common (Greenwalt *et al*. 2015). The fossil Neuropterida described herein are represented by the orders Neuroptera (Ascalaphidae, Chrysopidae, and Hemerobiidae) and Raphidioptera (Raphidiidae, Inocelliidae). The neuropteran fossils represent the first descriptions of the order from the Kishenehn Formation, Montana, U.S.A., whereas one species of raphidiopteran has been previously described (Makarkin *et al*. 2019). The order Megaloptera, which has a relatively poor fossil record, has not been found in this deposit.

The fossil neuropterids described herein are from the Coal Creek Member of the Kishenehn Formation, of the Kishenehn Basin, northwestwern Montana, U.S.A. The Coal Creek Member consists of sandstone, siltstone, lignite and oil shale, which form a heterogenous 1150 m thick basin fill (Greenwalt *et al*. 2015). The fossil insects are found within the lacustrine oil shale from the middle sequence of the Coal Creek Member (Greenwalt *et al*. 2015). The insect fauna includes the orders, in order of abundance, Diptera, Hemiptera, Hymenoptera, Coleoptera, Trichoptera, Thysanoptera, Orthoptera, Lepidoptera, Odonata, Dermaptera, Isoptera, Neuroptera, Blattodea, Psocoptera, and Raphidioptera (Greenwalt *et al*. 2015).

Accepted by X.-Y. Liu: 3 Apr. 2023; published: 22 Jun. 2023

The climate is usually interpreted as humid subtropical to tropical (Harbach & Greenwalt 2012; Dawson & Constenius 2018; Downen & Selden 2020). For example, the early arboreal primate *Tarkadectes montanensis*, originally described from the Coal Creek member and recently assigned to the extinct family Omomyidae, is closely related to the extant insectivorous Tarsiidae that are now restricted to islands of Southeast Asia (McKenna 1990; Groves & Shekelle 2010). A more detailed paleoclimate analysis for the Coal Creek Member is needed (see Makarkin *et al*. 2019).

The preservation of insects in the Coal Creek Member shale is strongly biased towards the fossilization of small (lengths less than 1 cm) specimens with the exception of those that are composed of a wing only. Evidence suggests that insects were captured on or within cyanobacterial mats prior to falling to the bottom of a relatively shallow, near-shore lake. Unlike fossils from other major North American Lagerstätten such as the Green River and Florissant, the Coal Creek Member specimens are preserved only on one side of the split shale; counterparts do not exist (Greenwalt *et al*. 2015).

The age of the insect bearing middle sequence of the Coal Creek Member (Kishenehn Formation) has been estimated to be 46.2 ±0.4 million years old (middle Eocene: Lutetian) by $^{40}Ar/^{39}Ar$ analysis and 43.5 ±4.9 million years old by fission-track analysis (Constenius 1996). These dates are supported by biostratigraphic correlations with mammalian, molluscan and pollen fossils (Constenius *et al*. 1989; Pierce & Constenius 2014).

Material and Methods

The specimens are preserved in lacustrine sediment-derived oil shale, which is exposed along the Middle Fork of the Flathead River, between Paola and Stanton Creeks, approximately 17 miles south of West Glacier, Montana. Specimens were collected under United States Forest Service permit HUN 281. Photographs were taken by Dale Greenwalt (USNM), using an Olympus SZX12 microscope equipped with a Q-Color5 Olympus camera. Image-Pro Plus 7.0 software (Media Cybernetics, Inc., Bethesda, MD) was used to capture and record the images. Drawings were made using Inkscape. The wing venation terminology adopted here follows Breitkreuz *et al*. (2017) for Neuroptera, and Makarkin & Archibald (2014) for Raphidioptera.

Abbreviations. A1–A3, anal veins; C, costa; Cu, cubitus, CuA, cubitus anterior, CuP, cubitus posterior; *doi,* discoidal cell; *gc*, gradate cells; *im*, intramedian cell; M, media; MA, media anterior; MP, media posterior; pt, pterostigma; R, radius; RA, radius anterior; RP, radius posterior; RP1, proximal-most branch of RP; Sc, subcosta. Crossveins are named after the longitudinal veins with which they are connected, and they are numbered in sequence from the wing base, *e.g*., 1ra-rp, first (proximal-most) crossvein connecting RA and RP; 2sc-r, second crossvein between Sc and RA; 1im, first crossvein between MA and MP.

Institutional abbreviations. All specimens are housed at the Department of Paleobiology, National Museum of Natural History (USNM PAL), Smithsonian Institution, Washington, DC, U.S.A.

Systematic Palaeontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Ascalaphidae Rambur, 1842

Subfamily incertae sedis

Genus *Pseudoameropterus* gen. nov.
urn:lsid:zoobank.org:act:E5FAC79E-0647-404E-92F5-4577429C98AD

Type and only species. *Pseudoameropterus ambiguus* gen. et sp. nov.

Etymology. From the Greek *pseudos*, false, and *Ameropterus*, a genus-group name of Ascalaphidae. Gender masculine.

Diagnosis. May be distinguished from other genera by a set of the following hind wing characters: RP1 profusely branched; hypostigmal cell relatively long; MP and CuA spaces relatively narrow; CuA long and incurved; branches of CuA and MP interlinked by only one row of crossveins.

Remarks. The status of Ascalaphidae as a family is an area of debate. Many studies based on morphology only have recovered a monophyletic Ascalaphidae closely related to Myrmeleontidae (e.g., Aspöck *et al*. 2001; Aspöck & Aspöck 2008). However, studies that have included molecular data in addition to morphology have recovered conflicting trees supporting monophyly of both Ascalaphidae and Myrmeleontidae, or showing a paraphyletic relationship of Ascalaphidae with respect to Myrmeleontidae (see Machado *et al.* 2018; Winterton *et al.* 2018; Jones 2019 for review). Recently, phylogenomic studies by Machado *et al.* (2018) and Winterton *et al.* (2018) recovered Ascalaphidae and Myrmeleontidae as being paraphyletic with respect to each other, this prompted Machado et *al.* (2018) to synonymize Ascalaphidae with Myrmeleontidae, dividing the family into four subfamilies and 17 tribes. But the family status of Ascalaphidae is still debated (Jones 2019; Cai *et al.* 2023). Here we follow Cai *et al.* (2023) and consider Ascalaphidae to be retained as a family with the inclusion of Stilbopteryginae as a subfamily.

The long and more or less strongly incurved CuA in the hind wing as found in *Pseudoameropterus* **gen. nov.** is present in several genera of Ascalaphidae: all genera of Stilbopteryginae (*Stilbopteryx* Newman, 1838 and *Aeropteryx* Riek, 1968) and Albardiinae (*Albardia* van der Weele, 1903), and most genera of Ululodinae (i.e., *Ameropterus* Esben-Petersen, 1922, *Cordulecerus* Rambur, 1842 and *Ululodes* Currie in Smith, 1900). Interestingly, all these taxa are now distributed in the Americas (Albardiinae, Ululodinae) or Australia (Stilbopteryginae).

The hind wing venation of the new genus is most similar to that of *Ameropterus*, especially e.g. *A. trivialis* (Gerstaecker, 1888) and *A. mexicanus* (van der Weele, 1908) (see Penny 2002: Figs 14, 16). The genus is distributed from southern Mexico in the north to Argentina in the south. However, *Pseudoameropterus* **gen. nov.** differs from that genus in that RP1 is more proximally and profusely branched, which is branched more distally in *Ameropterus* (see van der Weele 1909: Figs 83–85; Penny 2002: Figs 12–15). All species of *Cordulecerus* (except *Cordulecerus praecellens* (Gerstaecker, 1885)) differ from *Pseudoameropterus ambiguus* **sp. nov.** by the hind wings being strongly broadened proximally (see van der Weele 1909: Figs 98–112, 115, 116; Penny 1982: Fig. 11; Ardila-Camacho *et al*. 2019: Fig. 9). The species of *Ululodes* differ from the new species by the presence of a longitudinal crossvein connecting crossveins between RA/Sc+RA and RP below the pterostigma (see van der Weele 1909: Figs 59–68, 73–76; Penny 2002: Figs 22–26).

However, it is possible that the new genus belongs to Stilbopteryginae or Albardiinae. The hind wing venation of *Aeropteryx* Riek, 1968 (Stilbopteryginae) and *Pseudoameropterus* **gen. nov.** are very similar, including the profusely branched RP1 (see Riek 1968: Pl. 1). Moreover, a new undescribed ascalaphid species from the Green River Formation, the venation of which is most similar to that of *Pseudoameropterus ambiguus* **sp. nov.**, possesses entire eyes characteristic of Stilbopteryginae and Albardiinae, while eyes are divided in Ululodinae. But the true subfamilial affinity of *Pseudoameropterus* **gen. nov.** may only be determined when more complete material is found.

***Pseudoameropterus ambiguus* sp. nov.**

urn:lsid:zoobank.org:act:4A61DA82-99EF-410B-BADE-94C6D728246F
Fig. 1

Etymology. From the Latin *ambiguus* [*-a*, *-um*], ambiguous, obscure, mysterious.

Type material. Holotype USNM PAL 626076, deposited in USNM. A nearly complete hind wing.

Type locality and horizon. Middle Fork of the Flathead River, between Paola and Stanton Creeks approximately 17 miles south of West Glacier; the Coal Creek Member of the Kishenehn Formation, north-western Montana, U.S.A. The Middle Eocene (Lutetian).

Diagnosis. As for genus.

Description. Hind wing 30.3 mm long as preserved (estimated complete length 35–37 mm), 8.1 mm wide. Costal space moderately broad, with all veinlets simple, closely spaced. Pterostigma indistinct, short, bound by two simple veinlets, two incorporated veins, one multibranched, one simple. Sc fused with RA in distal part of wing level with centre of the pterostigma. Seven preserved veinlets of Sc+RA connected by 10 preserved crossveins; four proximal veinlets simple or forked once, three distal veinlets strongly forked. Thirteen ra-rp crossveins preserved. RP with seven branches. RP1 originating before mid-point of wing, profusely branched at mid-point of vein. Other branches of RP probably shallowly branched (their terminal parts not preserved). Numerous crossveins (66 preserved) throughout RP spaces. One presectoral crossvein preserved. Between R and M (radiomedial space) 17 crossveins preserved. MA slightly incurved medially, simple. MP terminally simple, stronger incurve medially than MA, pectinately branched with four branches, one of these (MP1) rather shallowly forked, other simple. Stem of MP and its branches connected by four crossveins (one between each pair). In intramedial space (between MA and MP) 15 crossveins preserved. Between MP and CuA (mediocubital space) nine preserved widely spaced crossveins. CuA long, strongly incurved; stem of CuA shallowly forked terminally, with eight pectinate branches; one of these rather shallowly forked, other simple. Stem of CuA and three distal branches connected by three crossveins (one between each pair). One cua-cup crossvein preserved in intracubital space. CuP probably rather long, fragmentarily preserved. Anal veins not preserved.

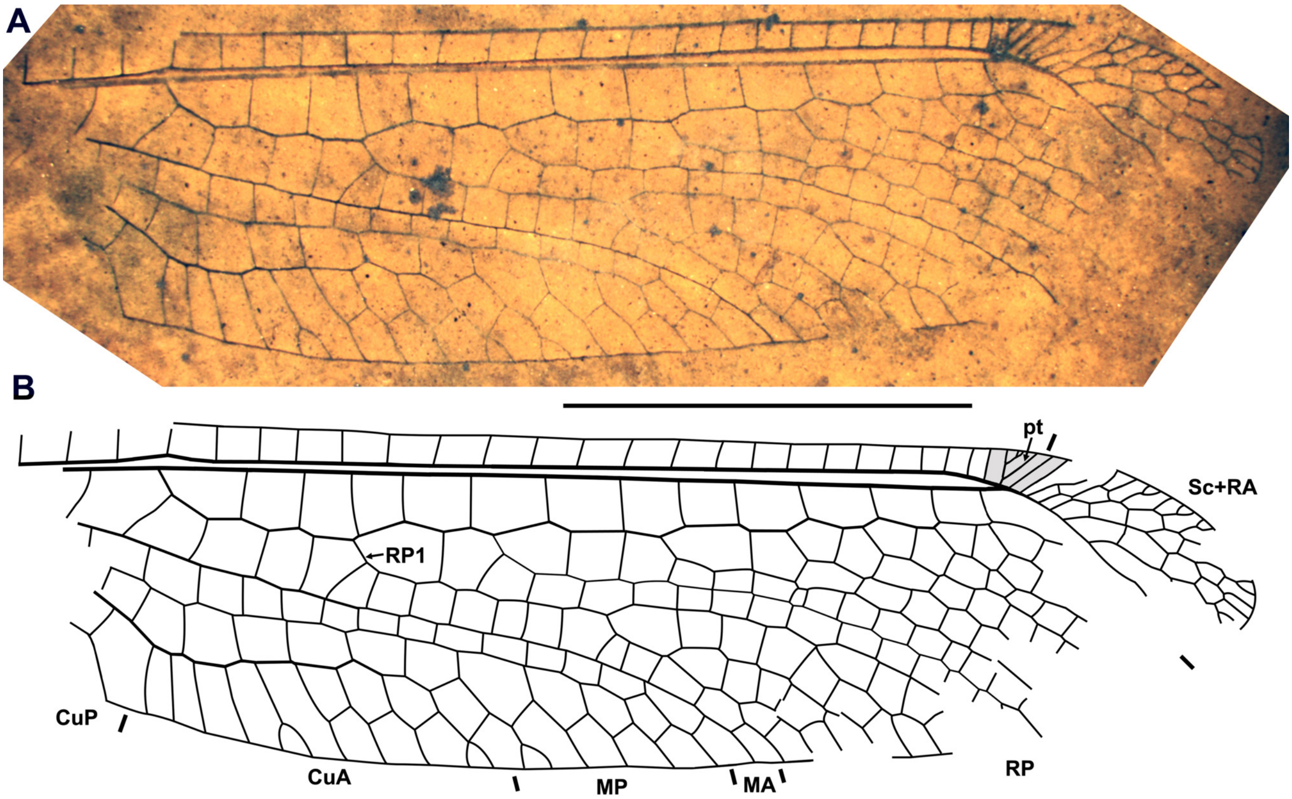

FIGURE 1. *Pseudoameropterus ambiguus* **gen. et sp. nov.**, holotype USNM PAL 626076. A, specimen as preserved; B, hind wing venation. Scale bar 10 mm.

Family Chrysopidae Schneider, 1851

Subfamily Nothochrysinae Navás, 1910

Genus *Minimochrysa* gen. nov.

urn:lsid:zoobank.org:act:1A315754-A548-4BB7-9739-6A3C2E948EA7

Type and only species. *Minimochrysa latialata* **sp. nov.**

Etymology. From the Latin *minimus*, *-a*, *-um*, tiny, smallest, and *Chrysopa*, a genus-group name, in reference to smallest chrysopid genus. Gender feminine.

Diagnosis. Differs from other nothochrysine genera by combination of following forewing character states: extremely short (≤5 mm); broadly-rounded apically; distal branches of RP originating at almost right angles; RA almost reaching wing apex.

Remarks. The Nothochrysinae affinity is based on a very long RA and long Sc. In Chrysopinae, RA is much shorter, terminating at C well proximad of wing apex. In Limaiinae, Sc is much shorter than RA. The venation of Apochrysinae is very different from that of this specimen.

In most other genera of Nothochrysinae, the forewing is apically subacute or at least has a more oval apex, and the distal branches of RP originate more obliquely. In those genera that have a similar broadly-rounded forewing apex and distal branches of RP originating at almost right angles (e.g., *Kimachrysa* Tjeder, 1966), their RA is very short.

Minimochrysa latialata **sp. nov.**
urn:lsid:zoobank.org:act:36FE8A47-EF3A-4718-8374-1DE02063E5FE
Fig. 2

Type material. Holotype USNM PAL 622725, deposited in USNM. A distal part of a forewing.

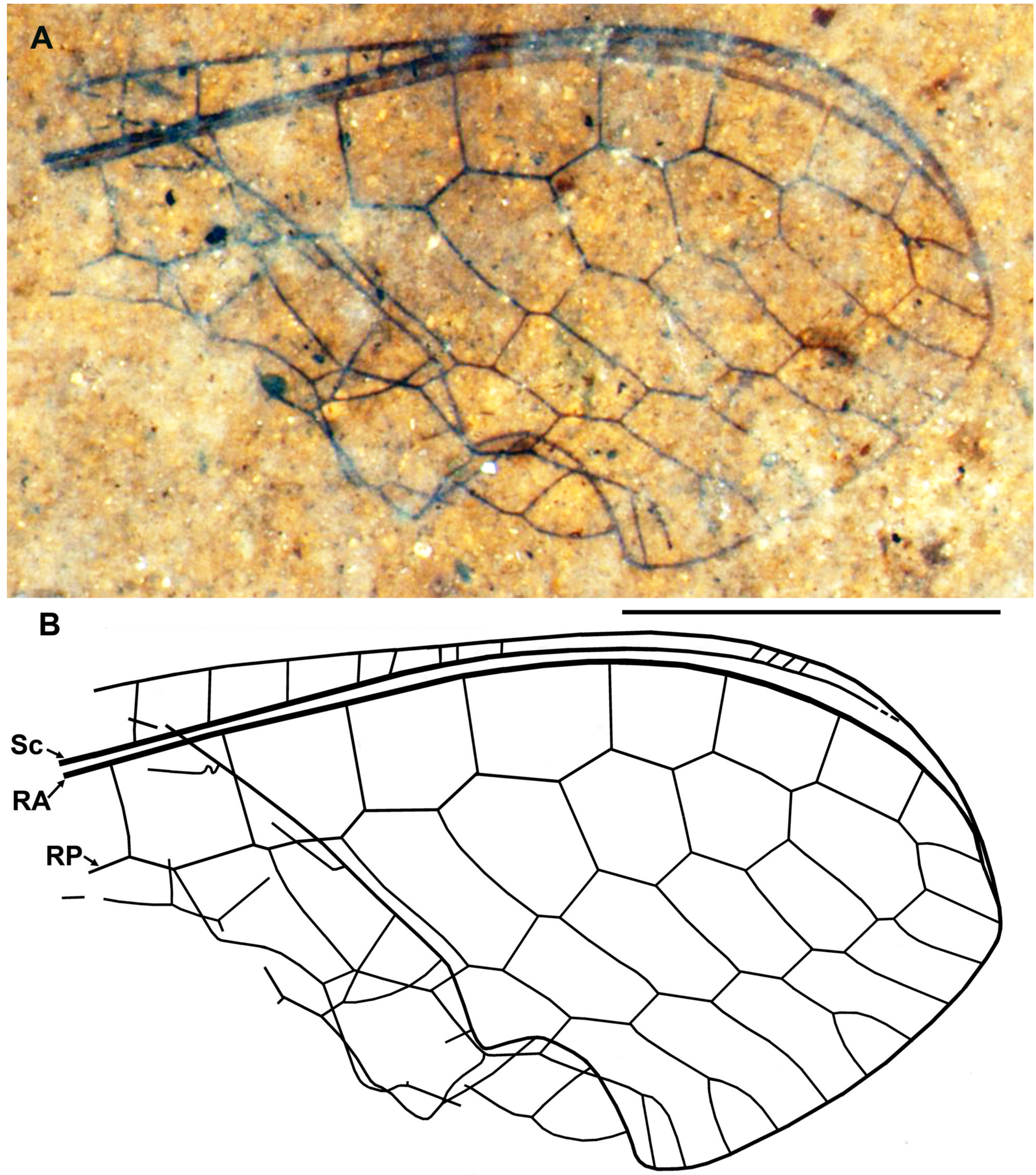

FIGURE 2. *Minimochrysa latialata* **sp. nov.**, holotype USNM PAL 622725. A, specimen as preserved; B, forewing venation. Scale bar 1 mm.

Type locality and horizon. Middle Fork of the Flathead River, between Paola and Stanton Creeks approximately 17 miles south of West Glacier; the Coal Creek Member of the Kishenehn Formation, north-western Montana, U.S.A. The Middle Eocene (Lutetian).

Etymology. From the Latin *latus*, broad, and *ala*, wing, in reference to broad distal part of the forewing (broadly-rounded apically).

Description. Forewing 2.5 mm long as preserved (estimated complete length *ca*. 4.5–5.0 mm), 1.4 mm wide as preserved. Forewing broadly rounded apically. Costal space with 12 preserved simple crossveins, narrowing distally. No crossveins present in subcostal space. Sc long terminating well before apex of wing. RA long almost reaching apex of the wing. Radial space wide with eight regularly spaced ra-rp crossveins preserved. RP with eight preserved branches, majority simple, four forked distally near wing margin. RP crossveins forming two gradate series. Basal portion of wing not preserved.

Remarks. *Minimochrysa latialata* **sp. nov.** is the smallest known chrysopid species. The species of the smallest extant genera have a minimum forewing length of 6 mm, *e.g*., the chrysopine *Suarius* Navás, 1914 and the nothochrysine *Kimochrysa* Tjeder, 1966 (Brooks & Barnard 1990). The smallest known fossil chrysopid species *Pseudochrysopa harveyi* Makarkin & Archibald, 2013 from the early Eocene Driftwood Canyon (Canada) with a minimum forewing length of *ca*. 8.2 mm is nearly twice as long as the new species (Makarkin & Archibald 2013).

Genus *Palaeochrysa* Scudder, 1883

Remarks. The genus *Palaeochrysa* was recently revised to include only one species *P. stricta* Scudder, 1890 from the late Eocene of Florissant (Makarkin *et al*. 2022). Two more species in this genus are described below from the Kishenehn Formation. Makarkin *et al*. (2022) diagnosed the genus with the following characters: in the fore- and hind wings (1) two gradate series are present in the radial space; (2) inner gradate series is arranged in a strongly broken line; (3) Psm is nearly straight, slightly zigzagged; (4) Psm is formed by five branches of RP; in the forewing (5) *im* is elongate; and in the hind wing (6) three branches of CuA proximad fusion with MP. Two of the species (*P. stricta* and *P. greenwalti* **sp. nov.**) share the whole set of these character states. The character states (2) and (4) are slightly different in *P. minor* **sp. nov**.: in this species the inner gradate series is arranged in a curved line, but not broken, and Psm is formed by three branches of RP (most likely related to its small size).

We found a new feature distinguishing *Palaeochrysa* from most other genera of Nothochrysinae. This genus possesses a proximal cell between two gradate series of crossveins in the hind wing (located at the termination of Psm; labelled *gc1* in Figs. 3C and 4E). The cell is acute anteriorly as the very oblique crossvein of the inner series and a part of a RP branch (which are limited the cell anteriorly) coincide in the same direction, which continues the Psm. All gradate cells are principally similar in shape at least in other fossil genera from North America.

Therefore, the assignment of *Palaeochrysa greenwalti* sp. nov. to *Palaeochrysa* is undoubted, while *P. minor* **sp. nov.** is very probable.

***Palaeochrysa greenwalti* sp. nov.**

urn:lsid:zoobank.org:act:A0BCCD17-AA0C-4961-89AD-BBC32456AC1C
Fig. 3

Type material. Holotype USNM PAL 622159, deposited in USNM. One nearly complete forewing, one incomplete forewing, and one incomplete hind wing.

Type locality and horizon. Middle Fork of the Flathead River, between Paola and Stanton Creeks approximately 17 miles south of West Glacier; the Coal Creek Member of the Kishenehn Formation, north-western Montana, U.S.A. Middle Eocene (Lutetian).

Etymology. From the surname of Dale E. Greenwalt, in recognition of his work on the Kishenehn Formation.

Diagnosis. Similar to *Palaeochrysa stricta* differing from it by smaller size [forewing length *ca*. 11.2 mm in *P. greenwalti* **sp. nov.**; 15.5 mm in *P. stricta*] and proximal-most crossvein of inner gradate series in hind wing (after RP5) shifted posteriorly, so that it terminates on Psm [terminates on RP5 far anterior to Psm in *P. stricta*]; it differs from *P. minor* **sp. nov.** by larger size and wider forewing [length/width ratio *ca*. 2.95 in *P. greenwalti* **sp. nov.**; *ca*. 3.17 in *P. minor* **sp. nov.**].

Description. Forewing *ca*. 11.2 mm long, 3.8 mm wide. Costal space moderately broad. Subcostal veinlets simple, relatively closely spaced. Sc long (its termination not discernible). Subcostal space narrow, crossveins not detected. RA terminated at margin slightly proximad wing apex. RA space broad, narrowed distad, with 14 regularly spaced crossveins. RP with 13 pectinate branches. RP1 to RP5 terminated at Psm; two distal branches simple; forking of most other branches unclear, at least two in distal portion forked once in one of forewings. Psm straight, only slightly zigzagged. M poorly preserved proximally, forked slightly distad origin of RP. *im* incompletely preserved (its shape probably similar to that of other species of the genus: narrow, elongate). Presumable MA forked once distad Psc; presumable MP forked at Psc. Crossvein 2m-cu long, located in proximal part of *im*. Psc straight, slightly zigzagged only distally. CuA presumably with three branches. CuP forked, with both branches widely spaced. 1A partially preserved. Two gradate series of crossveins nearly parallel; inner series forming distinct angle with Psm at RP5, with six preserved crossveins after RP5 (probably eight in life); outer series continuing Psc, with nine crossveins after RP5.

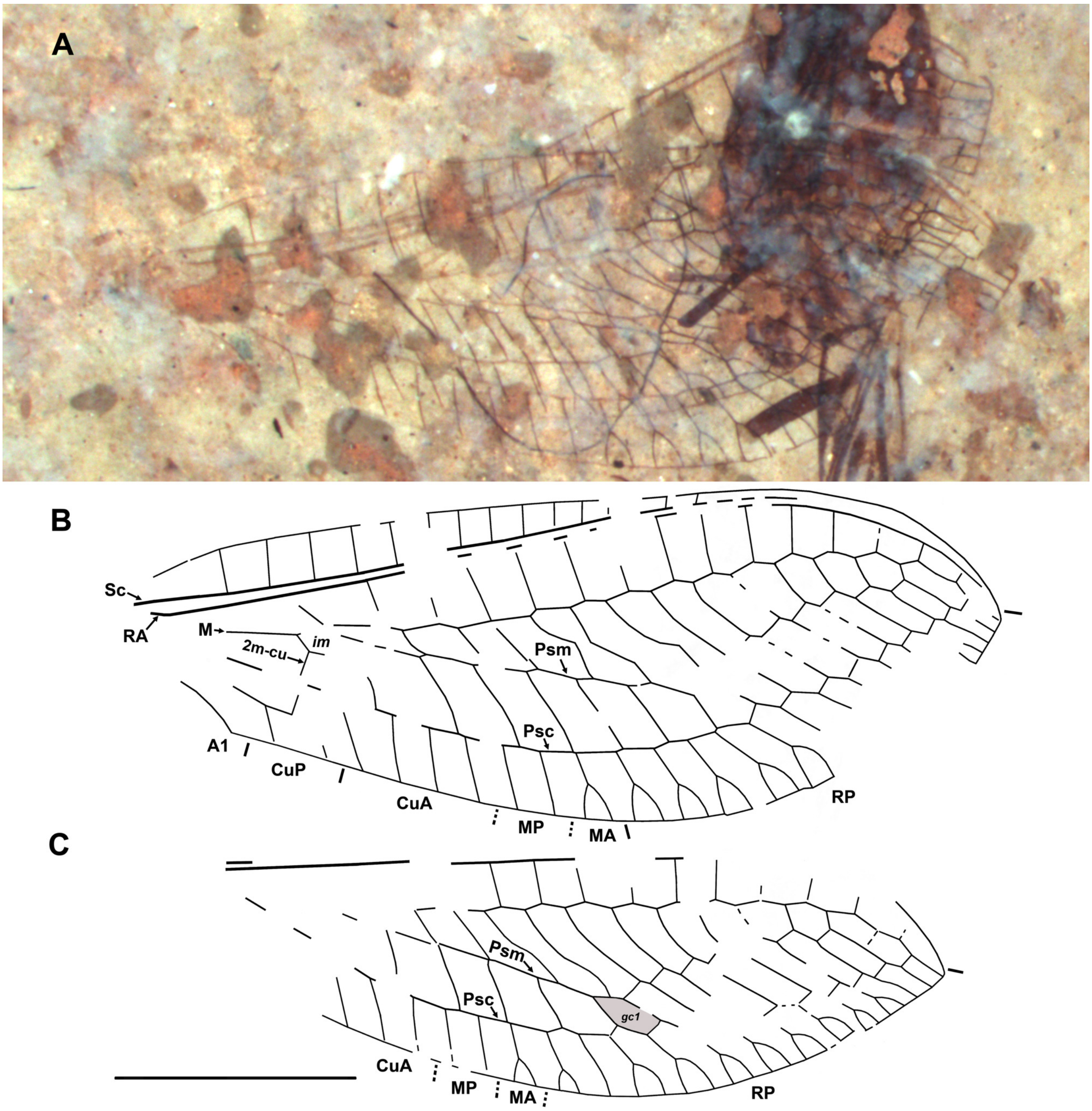

FIGURE 3. *Palaeochrysa greenwalti* **sp. nov.**, holotype USNM PAL 622159. A, specimen as preserved; B, forewing venation; C, hind wing venation. Scale bar 3 mm (all to same scale).

Hind wing 9.5 mm long as preserved, 2.9 mm wide as preserved. Costal space not preserved. Sc preserved only basally. RA not preserved in distal part. RA with 10 preserved crossveins. RP with 11 preserved pectinate branches (probably 12 in life). RP1 (presumably) to RP5 terminating at Psm; two distal branches simple; other branches forked once. Psm straight, almost not zigzagged. Proximal part of M not preserved; presumable MA forked distad Psc; presumable MP forked at Psc. Psc straight, zigzagged only in distal part. Presumable CuA with two preserved branches. Anal veins not preserved. Two gradate series of crossveins: inner series convex, forming distinct angle with Psm at RP5, with seven preserved crossveins before RP5 (eight in life); outer series continuing Psc, with six preserved crossveins before RP5 (eight in life).

Remarks. The apex of the forewing of *P. greenwalti* **sp. nov.** appears more rounded than in the other species. No body parts are preserved and some parts of the forewing venation and the basal part of the hind wing are difficult to interpret.

Palaeochrysa minor **sp. nov.**

urn:lsid:zoobank.org:act:ECE45B39-18B0-45CC-97C1-07942C4A2BC7
Fig. 4

Type material. Holotype USNM PAL 722497, deposited in USNM. An incomplete, crumpled specimen.

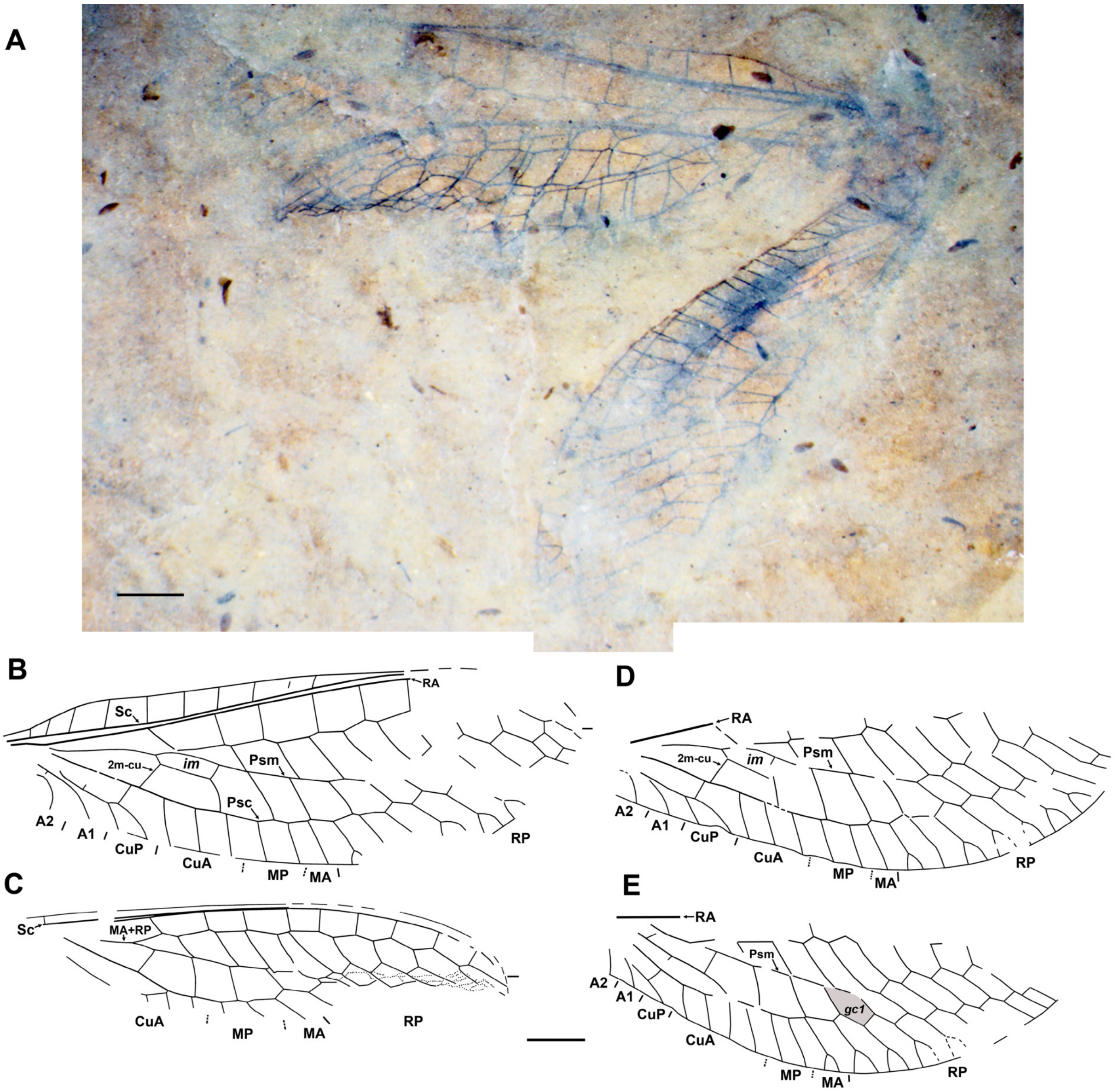

FIGURE 4. *Palaeochrysa minor* **sp. nov.**, holotype USNM PAL 722497. A, specimen as preserved; B, right forewing venation; C, right hind wing venation; D, left forewing venation; E, left hind wing venation. Scale bars 1 mm (B–E to same scale).

Type locality and horizon. Middle Fork of the Flathead River, between Paola and Stanton Creeks approximately 17 miles south of West Glacier; the Coal Creek Member of the Kishenehn Formation, north-western Montana, U.S.A. The Middle Eocene (Lutetian).

Etymology. From the Latin *parvus*, -*a*, -*um* (comparative *minor*), meaning "small (smaller)".

Diagnosis. Differs from two other species by smaller size, subcostal veinlets widely spaced [closely spaced in other species], and three branches of RP terminating on Psm [five in other species].

Description. Body very poorly preserved, details not discernible.

Forewing *ca*. 9.5 mm long, *ca*. 3.0 mm wide. Costal space relative narrow. Subcostal veinlets simple, relatively widely spaced. Distal parts of Sc, RA not preserved. Subcostal space narrow, crossveins not detected. RA space with five detected, widely spaced crossveins. RP with nine pectinate branches. RP1 to RP3 terminated at Psm; two or three distal branches simple; RP1 deeply forked at Psc and its proximal branch shallowly forked in left forewing; other branches rather shallowly once forked. Basal crossvein 1r-m very short, connecting anterior trace of RP and MA within *im* at proximal one-third length. Psm straight, only slightly zigzagged. M forked slightly distad origin of RP. *im* narrow, elongate (3.8 times as long as wide). Crossvein 2m-cu long, connecting *im* and CuA at nearly proximal one-fifth of *im*. Psc straight, slightly zigzagged distally. CuA probably with two simple branches. CuP deeply forked. Two intracubital crossveins; *c1*: *c2* length ratio 0.82:1 in right wing. A1 simple. A2 strongly arched, simple. Two gradate series of crossveins nearly parallel; inner series with six crossveins after RP3; outer series continuing Psc, with six crossveins after RP3.

Hind wing 6.8 mm long as preserved, 2.3 mm wide as preserved. Costal space very narrow. Sc preserved proximally. Subcostal space appears to be very narrow. RA long, terminating at margin probably near wing apex. RA space with eight regularly spaced crossveins. RP with nine pectinate branches. RP1 to RP3 terminated at Psm; three distal branches simple; forking of other branches mostly unknown. Psm straight, slightly zigzagged. M proximally fused with RP. Presumable MA forked distad Psc; presumable MP forked at Psc. Psc slightly zigzagged. CuA with three simple branches; probably all originating before fusion of CuA with MP. CuP, A1, A2 simple. Two nearly parallel gradate series of crossveins: inner series with four preserved crossveins after RP (probably six in life); outer series continuing Psc, with six crossveins after RP3.

Remarks. *Palaeochrysa minor* **sp. nov.** is the smallest member of the genus and has a more elongate forewing than the other species. The small size is reflected in the venation with it having only three branches of RP terminating on Psm [five in the other species of the genus].

Family Hemerobiidae Latreille, 1802

Megalomus-group gen. et sp. indet.

Fig. 5

Material. Specimen USNM PAL 624842, deposited in USNM. An incomplete specimen.

Locality and horizon. Middle Fork of the Flathead River, between Paola and Stanton Creeks approximately 17 miles south of West Glacier; the Coal Creek Member of the Kishenehn Formation, north-western Montana, U.S.A. The Middle Eocene (Luteian).

Description. Body poorly preserved, fine details not discernable. Head poorly preserved, only both eyes well discernible (0.5 mm wide). Prothorax 0.6 mm long, mesothorax 1.5 mm long, metathorax 0.8 mm long. Legs and abdomen not preserved.

Forewing fragmentary, poorly preserved, *ca.* 6.8 mm long (as preserved; estimated complete length *ca*. 8 mm), 2.7 mm wide (as preserved; estimated width *ca.* 3 mm). Recurrent humeral veinlet well developed, with four preserved branches. Costal space narrowing distally, with *ca*. 15 partially preserved costal veinlets, mainly forked; trichosors present on costal margin. Sc and RA partially preserved; subcostal crossveins not detected. RP poorly preserved, with five to six branches separately originating on RA. RP1 at least deeply-forked once near origin. Three gradate series of crossveins partially preserved. Second series consists of two preserved crossveins (right wing), between M and CuP. Third ('inner') series consists of eight preserved crossveins anterior to CuA (probably nine in life) (left wing); fourth ('outer') series with four preserved crossveins (left wing). M forked nearly opposite fork of RP1; posterior branch probably forked again at inner gradate series. Cubital veins fragmentarily preserved; proximal branch of CuA originating at second gradate series. Anal veins not preserved.

Hind wing fragmentarily preserved, 5.5 mm long (as preserved; estimated complete length *ca*. 7 mm), 1.8 mm wide (as preserved; estimated complete width *ca*. 2.4 mm). Costal space narrow, narrowest at mid-way point. Costal veinlets partially preserved, proximally simple, distally few forked; trichosors preserved on costal margin. Subcostal space narrow. Sc and RA partially preserved, not fused; reaching wing margin before apex. RA distally with three to four branches. RP partially preserved, at least with five branches. Third ('outer') gradate series with five preserved crossveins. Cubital and anal veins not preserved.

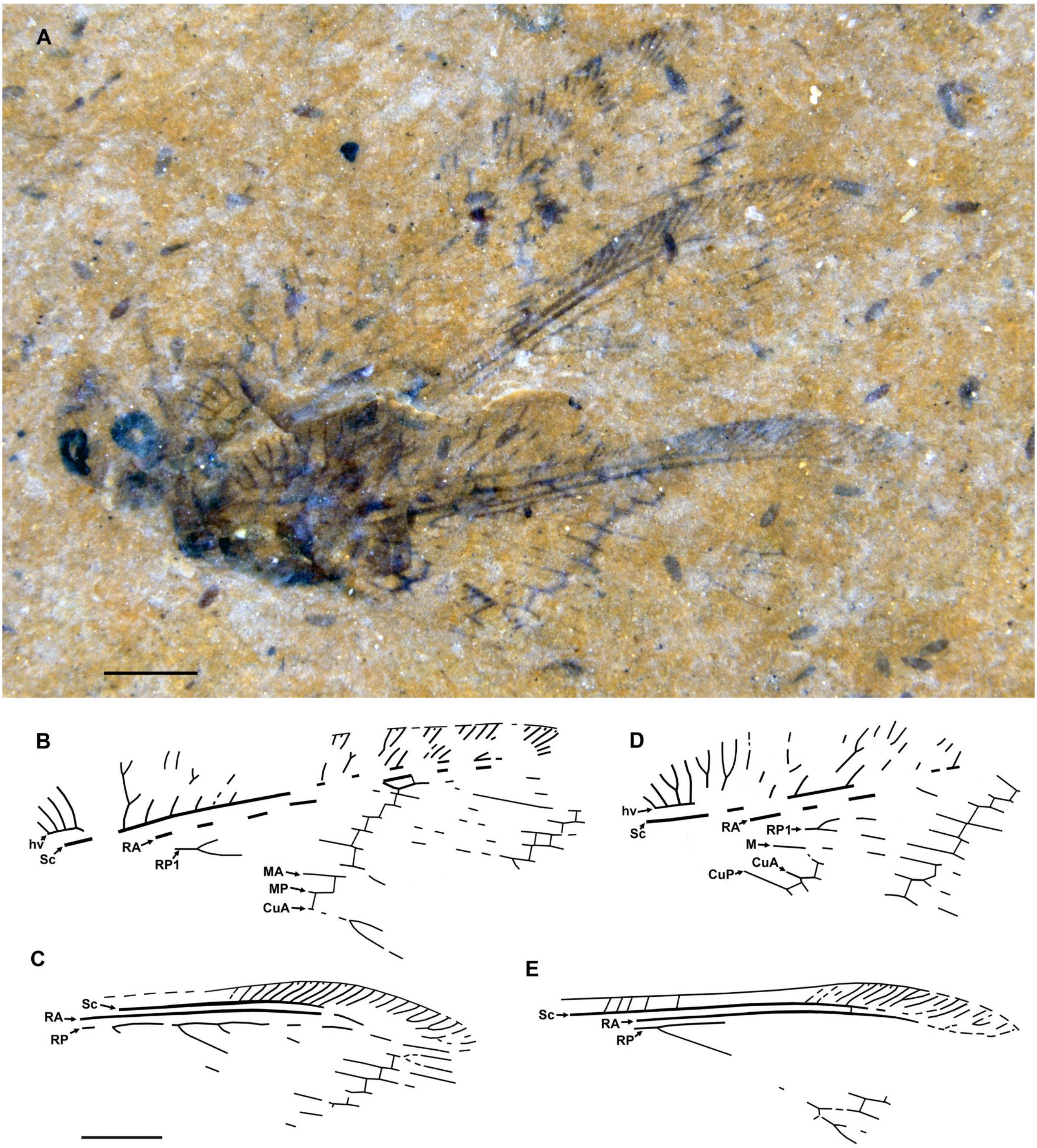

FIGURE 5. *Megalomus*-group gen. et sp. indet., specimen Holotype USNM PAL 624842. A, specimen as preserved; B, left forewing venation; C, left hind wing venation; D, right forewing venation; E, right hind wing venation. Scale bar 1 mm.

Remarks. This specimen obviously belongs to a genus of the *Megalomus*-group (Drepanepteryginae, Drepanacrinae or Megalominae). These hemerobiids share the wing character states such as a dense venation; a deeply forked CuP in the forewing; and a fully developed CuP in the hind wing (see Makarkin *et al.* 2016 for detailed discussion). The venation of the specimen is fragmentarily preserved, and it is therefore difficult to place into a particular genus. However, the preserved venation is most similar to that of *Proneuronema* Makarkin *et al.* 2016, in particular the presence of at least once deeply-forked RP1. This genus was widely distributed in the Eocene in North America, Europe, and East Asia (see Makarkin & Perkovsky 2020).

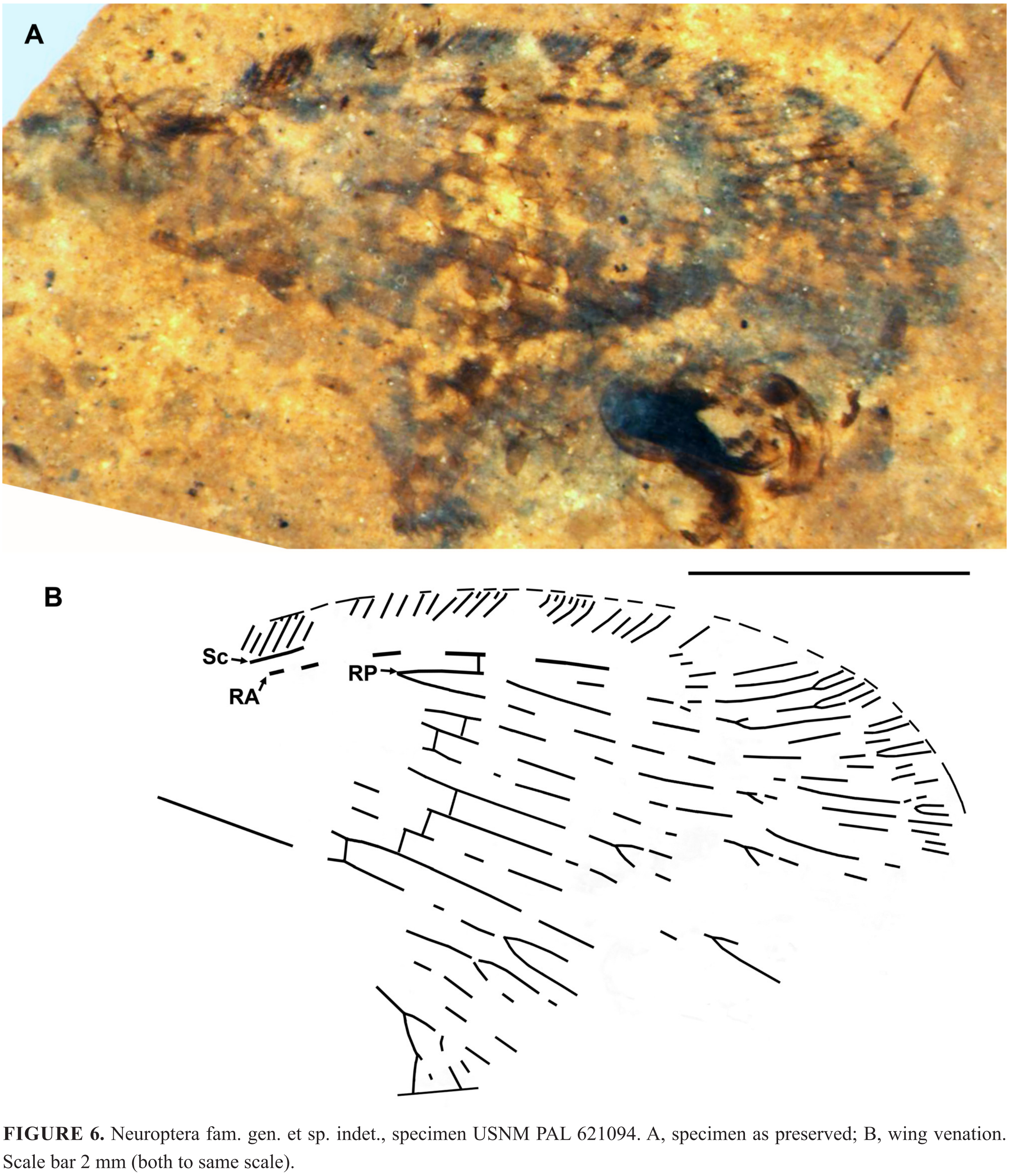

FIGURE 6. Neuroptera fam. gen. et sp. indet., specimen USNM PAL 621094. A, specimen as preserved; B, wing venation. Scale bar 2 mm (both to same scale).

Neuroptera incertae sedis

Neuroptera fam. gen. et sp. indet.
Fig. 6

Material examined. Specimen USNM PAL 621094, deposited in USNM. A fragmentary wing.

Locality and horizon. Middle Fork of the Flathead River, between Paola and Stanton Creeks approximately 17 miles south of West Glacier; the Coal Creek Member of the Kishenehn Formation, north-western Montana, U.S.A. The Middle Eocene (Luteian).

Description. Wing *ca*. 5.8 mm long as preserved (estimated complete length approximately 8–10 mm). Costal space relatively narrow. Subcostal veinlets simple, closely spaced. RA space narrow; one crossvein well discernible. Branches of RP closely spaced, dichotomously forked distally. One or two gradate series of crossveins discernible in proximal part of fragment; other crossveins in distal part are possible.

Remarks. The family assignment of this wing fragment is unclear. It may theoretically belong to Hemerobiidae, Berothidae or Dilaridae. The narrow costal space and simple closely-spaced costal veinlets in the distal part of the wing show that this is likely a hind wing. In this case, a dilarid affinity is most probable as the hind wings are heavily maculated only in Dilaridae, especially in the American genus *Nallachius* Navás, 1909, and some East Asian species of *Dilar* Rambur, 1838 (see Adams 1970: Figs 1, 11, 12; Martins *et al*. 2018: Fig. 3A). The arrangement of the preserved crossveins also shows that a dilarid affinity is most probable. However, the mode of terminal branching of the longitudinal veins in *Nallachius* strongly differs from that of this specimen. The venation of the extant *Dilar* is more similar to that of the fragment, but still different. Hind wings of Hemerobiidae and Berothidae are hyaline (not maculated), and their crossveins are arranged otherwise.

If this is a forewing, a hemerobiid affinity is most probable, but a berothid affinity is also possible (although very unlikely).

Order Raphidioptera Navás, 1916

Family Raphidiidae Latreille, 1810

Genus *Macrostigmoraphia* gen. nov.
urn:lsid:zoobank.org:act:67388462-CDFA-46FA-8803-B2978E50605C

Type and only species. *Macrostigmoraphia diluta* **sp. nov.**

Etymology. From the Greek *macros*, long, *stigma*, spot, and *Raphidia*, a genus-group name of Raphidiidae. Gender feminine.

Diagnosis. May be distinguished from other genera by configuration of pterostigma: it is very long (10 times as long as wide), very pale, and lacks any incorporated veinlets or crossveins.

Remarks. The specimen has been placed within Raphidiidae based on the combination of 2sc-r being far distad the termination of Sc [Inocelliidae: located near termination of Sc], closing the proximal end of pterostigma [Inocelliidae: sc-r not closing pterostigma proximally].

The long pterostigma closed proximally by crossvein 2sc-r and often without incorporated veinlets is also present in the genera of the Cretaceous tribe Nanoraphidiini (Mesoraphidiidae). In general, their venation is very similar to that of some Raphidiidae, particularly the late Eocene subfamily Succinoraphidiinae Aspöck & Aspöck, 2004 (Perkovsky & Makarkin 2019). Apart from the long pterostigma, the rest of the forewing venation of *Macrostigmoraphia* **gen. nov.** is typical of the Eocene Raphidiidae. The venation of all species of Nanoraphidiini (except one wing of *Rhynchoraphidia burmana* Liu *et al*., 2016: Fig. 6B) differs from it, in particular by the simple (not forked) anterior trace of RP distad of 3ra-rp [two branches are present in *Macrostigmoraphia* **gen. nov.**]. It cannot be ruled out, however, that the new genus may theoretically belong to Nanoraphidiini or another group of Mesoraphidiidae, but currently there is insufficient data for this conclusion.

The few crossveins and a lack of an enriched venation separate the specimen from Baissopteridae.

The slight bend of RA proximad 3ra-rp might be indicative of the last distal veinlet, closing the pterostigma distally (indiscernible by preservation). In this case, 3ra-rp would be located distad the pterostigma, but it is very unlikely as this crossvein is located within the pterostigma in all known Eocene Raphidiidae (see Archibald & Makarkin 2021). In Nanoraphidiini, both conditions are present: 3ra-rp may be located proximad or distad the pterostigma (see Makarkin 2023). If the indiscernible veinlet exists, then RA has two distal veinlets, but all known Nanoraphidiini only have one. Therefore, if this is either Raphidiidae or Nanoraphidiini, the very long pterostigma is characteristic of the genus, not an artefact.

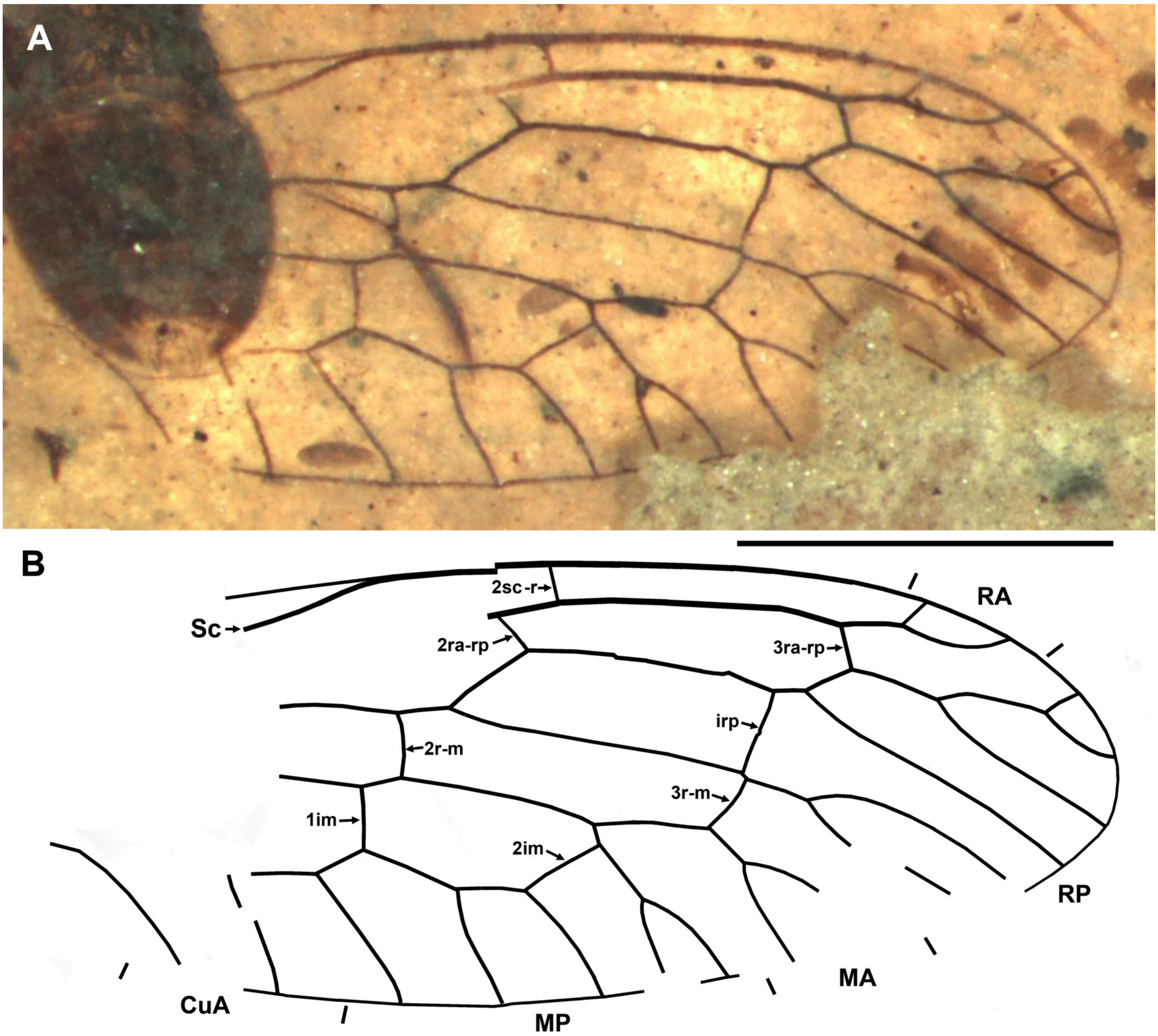

FIGURE 7. *Macrostigmoraphia diluta* **sp. nov.**, holotype USNM PAL 620478. A, specimen as preserved; B, forewing venation. Scale bar 2 mm.

Macrostigmoraphia diluta sp. nov.

urn:lsid:zoobank.org:act:23A6E686-5B20-4BD9-B4CC-F211B33B870A
Fig. 7

Type material. Holotype USNM PAL 620478, deposited in USNM, a distal part of a forewing.

Type locality and horizon. Middle Fork of the Flathead River, between Paola and Stanton Creeks approximately 17 miles south of West Glacier; the Coal Creek Member of the Kishenehn Formation, north-western Montana, U.S.A. The Middle Eocene (Lutetian).

Etymology. From the Latin *dilutus*, pale.

Description. Forewing 5.7 mm as preserved (estimated complete length 8.5 mm), 2.4 mm wide. Costal space poorly preserved, no veinlets preserved. Sc terminates on C proximad 2sc-r. Pterostigma very long (10 times as long as wide), pale, no incorporated veinlets detected within. One crossvein preserved between Sc and RA, 2sc-r, closing pterostigma proximally. RA long terminating before wing apex, with one distal veinlet closing pterostigma distally. Two crossveins between RA and RP, 2ra-rp, 3ra-rp. RP origin not preserved, RP with three branches. RP1 long forking distad irp, RP2, RP3 simple. One crossvein preserved between RP1 and RP2, irp. Between stem of RP, RP1 and MA two crossveins preserved, 2r-m, 3r-m. M origin not preserved, MA long, forking distally distad 3r-m. Two crossveins between MA and MP, 1im, 2im, forming two *doi*. MP partially preserved, pectinately branched, first branch proximad 1im, second between 1im, 2im. MP probably fused with CuA proximally. Cu origin not preserved. CuA partially preserved, distal part of its anterior trace and one branch. CuP, anal veins, basal part of wing not preserved.

Family Inocelliidae Navás, 1913

Genus *Paraksenocellia* Makarkin *et al.*, 2019

Paraksenocellia australis Makarkin *et al.*, 2019

Fig. 8

Type material. Holotype USNM PAL 625900, deposited in USNM. A complete hind wing.

Type locality and horizon. Middle Fork of the Flathead River, between Paola and Stanton Creeks approximately 17 miles south of West Glacier; the Coal Creek Member of the Kishenehn Formation, north-western Montana, U.S.A. The Middle Eocene (Luteian).

Remarks. *Paraksenocellia* includes two Eocene species, *P. borealis* Makarkin *et al.*, 2019 from the mid-Ypresian Driftwood Canyon Provincial Park, near Smithers, British Columbia, Canada (type species) and *P. australis*. This is the oldest genus in Inocelliidae, and possesses some rare character states for the family (see Makarkin *et al*. 2019 for discussion).

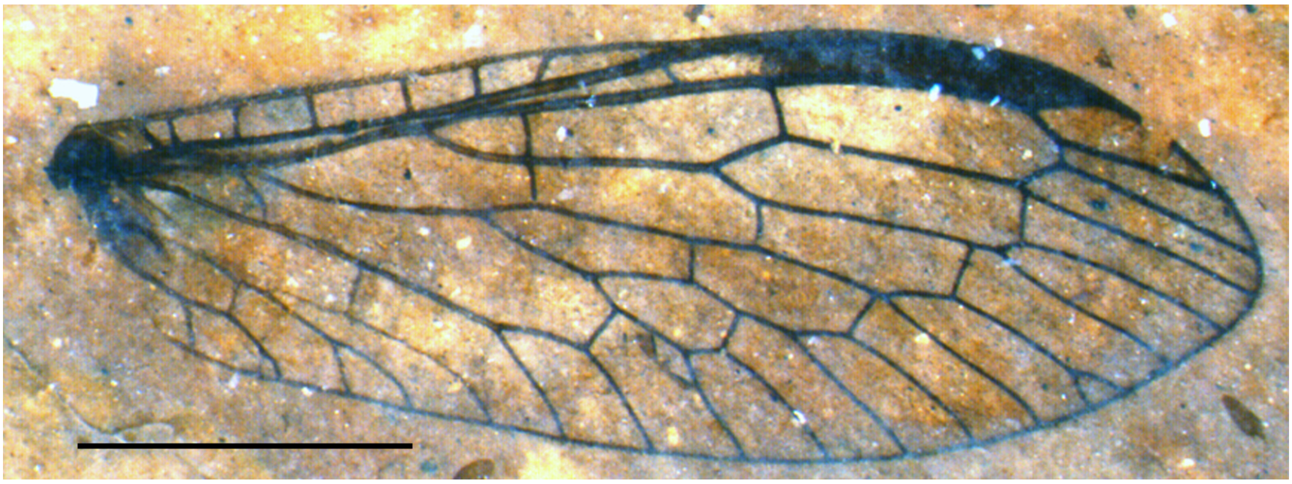

FIGURE 8. *Paraksenocellia australis* Makarkin *et al*., 2019, holotype USNM PAL 625900 (hind wing). Scale bar 2 mm.

Discussion

The Neuropterida assemblage of the Coal Creek Member (Kishenehn Formation) are represented mainly by isolated wings, as is the case with the majority of the large (greater than 1 cm) insects from the deposit. This is likely due to the insects being too large to be buried by a single layer of sediment, therefore leaving the insect vulnerable to predation and other destructive processes (Greenwalt & Labandeira 2013).

In North America, fossil Chrysopidae were previously known from some localities of the early Eocene Okanagan Highlands (McAbee and Driftwood Canyon in British Columbia, Canada; Republic in Washington, U.S.A.) and the late Eocene Florissant (Colorado, U.S.A.), all of which are from the subfamily Nothochrysinae (Makarkin &

Archibald 2013; Archibald. & Makarkin 2015, 2017; Makarkin *et al.* 2022). Currently the family has not been found in the hot climate of the Green River Formation. The possible reason for the absence of Nothochrysinae in this formation is the presence of a relatively numerous population of bats. Nothochrysinae do not possess a tympanum that detects echolocation sounds of bats (see Archibald *et al*. 2014), therefore making them more vulnerable to predation. The presence of three nothochrysine species in the Kishenehn Formation shows that bats could be rarer there.

The occurrence of Ascalaphidae and Raphidioptera may indicate a semi-arid climate. The raphidiopterans of North America are today distributed only in the western (more arid) regions, although they are associated with trees and bushes (see Aspöck & Aspöck 2014). Raphidiidae are diverse in the extremely arid Central Asia, but the order is only represented by a few species of Raphidiidae and Inocelliidae in the humid forested regions of Asia (e.g., Japan, Ussuri region, north-western Caucasus). Southern-most Inocelliidae inhabit humid montane forests in Thailand and southern Mexico (Aspöck *et al*. 1992, 2011). In general, extant inocelliids extend to the south further than raphidiids. Therefore, the occurrence of both Raphidiidae and Inocelliidae in the Coal Creek Member might indicate that they could live in a subtropical semi-arid (at least regionally) climate, but humid conditions are also possible.

Ascalaphidae are also most diverse in semi-arid hot regions, such as sub-Saharan Africa. At least five specimens, of three species, of Ascalaphidae and one species of the non-forest-dwelling Myrmeleontidae are recorded from the Parachute Creek Member of the Green River Formation (Makarkin 2017; pers. data), which has climatic conditions interpreted as being relatively dry and warm (Wilf *et al*. 1998). It is important to note that the venation of *Pseudoameropterus ambiguus* **sp. nov.** from the Coal Creek Member is similar to one of the Green River ascalaphids.

In summary, the neuropteroid assemble suggests a subtropical semi-arid climate of the Coal Creek Member.

Acknowledgements

We thank Dale Greenwalt (Smithsonian Institution, U.S.A.) for bringing the Kishenehn Neuropterida to the attention of JEJ, taking the images, and supplying information on the geology of the Kishenehn Formation. Thanks to Conrad Labandeira (Smithsonian Institution, U.S.A.) for arranging the loan of the Kishenehn material. Many thanks to Xingyue Liu and two anonymous reviewers for their comments. The research of VNM was carried out within the state assignment of Ministry of Science and Higher Education of the Russian Federation (project no. 121031000151-3).

References

Adams, P.A. (1970) A review of the New World Dilaridae. *Postilla*, 148, 1–30.

Ardila-Camacho, A., Noriega, J.A. & Acevedo-Ramos, F. (2019) New genera records of split-eyed owlflies (Neuroptera: Myrmeleontidae: Ascalaphinae) from Colombia. *Papéis Avulsos de Zoologia*, 59, e20195951. http://doi.org/10.11606/1807-0205/2019.59.51

Archibald, S.B. & Makarkin, V.N. (2015) A new species of *Archaeochrysa* Adams (Neuroptera: Chrysopidae) from the Early Eocene of Driftwood Canyon, British Columbia, Canada. *Canadian Entomologist*, 147 (4), 359–369. https://doi.org/10.4039/tce.2014.53

Archibald, S.B. & Makarkin, V.N. (2017) A new fossil green lacewing (Neuroptera: Chrysopidae) from the early Eocene Driftwood Canyon, Canada. *Zootaxa*, 4324 (2), 397–400. https://doi.org/10.11646/zootaxa.4324.2.13

Archibald, S.B. & Makarkin, V.N. (2021) Early Eocene snakeflies (Raphidioptera) of western North America from the Okanagan Highlands and Green River Formation. *Zootaxa*, 4951(1), 41–79. [erratum: 4964 (3), 600] https://doi.org/10.11646/zootaxa.4951.1.2

Archibald, S.B., Makarkin, V.N., Greenwood, D.R. & Gunnell, G.F. (2014) The Red Queen and Court Jester in green lacewing evolution: bat predation and global climate change. *Palaios*, 29 (5), 185–191. https://doi.org/10.2110/palo.2013.089

Aspöck, U. & Aspöck, H. (2004) Two significant new snakeflies from Baltic amber, with discussion on autapomorphies of the order and its included taxa (Raphidioptera). *Systematic Entomology*, 29, 11–19. https://doi.org/10.1111/j.1365-3113.2004.00245.x

Aspöck, U. & Aspöck, H. (2008) Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). *Systematic Entomology*, 33, 97–127. https://doi.org/10.1111/j.1365-3113.2007.00396.x

Aspöck, H. & Aspöck, U. (2014) Die nördlichen und südlichen Verbreitungsgrenzen der Ordnung Raphidioptera (Insecta: Endopterygota: Neuropterida). *DGaaE-Nachrichten*, 28, 16–20.

Aspöck, U., Aspöck, H. & Rausch, H. (1992) Rezente Südgrenzen der Ordnung Raphidioptera in Amerika (Insecta: Neuropteroidea). *Entomologia Generalis*, 17, 169–184. https://doi.org/10.1127/entom.gen/17/1992/169

Aspöck, U., Liu, X.Y., Rausch, H. & Aspöck, H. (2011) The Inocelliidae of southeast Asia: a review of present knowledge (Raphidioptera). *Deutsche Entomologische Zeitschrift*, Neue Folge, 58, 259–274. https://doi.org/10.1002/mmnd.201100029

Aspöck, U., Plant, J.D. & Nemeschkal, H.L. (2001) Cladistic analysis of Neuroptera and their systematic position within the Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera). *Systematic Entomology*, 26, 73–86. https://doi.org/10.1046/j.1365-3113.2001.00136.x

Breitkreuz, L.C.V., Winterton, S.L. & Engel, M.S. (2017) Wing tracheation in Chrysopidae and other Neuropterida (Insecta): A resolution of the confusion about vein fusion. *American Museum Novitates*, 3890, 1–44. https://doi.org/10.1206/3890.1

Brooks, S.J. & Barnard, P.C. (1990) The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). *Bulletin of the British Museum of Natural History*, Entomology, 59, 117–286.

Cai, C.Y., Tihelka, E., Liu, X.Y. & Engel, M.S. (2023) Improved modelling of compositional heterogeneity reconciles phylogenomic conflicts among lacewings. *Palaeoentomology*, 6 (1), 49–57. https://doi.org/10.11646/palaeoentomology.6.1.8

Constenius, K.N. (1996) Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. *Geological Society of America Bulletin*, 108, 20–39.

Constenius, K.N., Dawson, M.R., Pierce, H.G., Walter, R.C. & Wilson, M.V.H. (1989) Reconnaissance paleontologic study of the Kishenehn Formation, northwestern Montana and southeastern British Columbia. *In:* French, D.E. & Grabb, R.F. (Eds.), *1989 Field Conference Guidebook: Montana Centennial Edition. Geological Resources of Montana. Vol. 1*. Montana Geological Society, Billings, Motana, pp. 189–203.

Downen, M.R. & Selden, P.A. (2020) Fossil spiders (Araneae) from the Eocene Kishenehn Formation of Montana, USA. *Palaeontologia Electronica*, 23 (3), a56. https://doi.org/10.26879/1135

Dawson, M.R. & Constenius, K.N. (2018) Mammalian fauna of the Middle Eocene Kishenehn Formation, Middle Fork of the Flathead River, Montana. *Annals of Carnegie Museum*, 85 (1), 25–60. https://doi.org/10.2992/007.085.0103.

Esben-Petersen, P. (1922) New species of Neuroptera in the British Museum. *Annals and Magazine of Natural History*, Series 9, 10, 617–621.

Greenwalt, D.E. & Labandeira, C. (2013) The Amazing fossil insects of the Eocene Kishenehn Formation in Northwestern Montana. *Rocks & Minerals*, 88, 434–441. https://doi.org/10.1080/00357529.2013.809972

Greenwalt, D.E., Rose, T.R., Siljestrom, S.M., Goreva, Y.S., Constenius, K.N. & Wingerath, J.G. (2015) Taphonomy of the fossil insects of the middle Eocene Kishenehn Formation. *Acta Palaeontologica Polonica*, 60, 931–947. http://doi.org/10.4202/app.00071.2014

Gerstaecker, [C.E.] A. (1885) Vier Decaden von Neuropteren aus der Familie Megaloptera Burm. *Mittheilungen aus dem Naturwissenschaftlichen Verein für Neu-Vorpommern und Rugen*, 16 , 1–49. [for 1884]

Gerstaecker, [C.E.] A. (1888) Weitere Beiträge zur artenkenntniss der Neuroptera Megaloptera. *Mittheilungen aus dem Naturwissenschaftlichen Verein für Neu-Vorpommern und Rugen*, 19, 89–130. [for 1887]

Groves, C. & Shekelle, M. (2010) The genera and species of Tarsiidae. *International Journal of Primatology*, 31, 1071–1082. https://doi.org/10.1007/s10764-010-9443-1

Harbach, R.E. & Greenwalt, D. (2012) Two Eocene species of *Culiseta* (Diptera: Culicidae) from the Kishenehn Formation in Montana. *Zootaxa*, 3530, 25–34.

Jones, J.R. (2019) Total-evidence phylogeny of the owlflies (Neuroptera, Ascalaphidae) supports a new higher-level classification. *Zoologica Scripta*, 48 (6), 761–782. https://doi.org/10.1111/zsc.12382

Latreille, P.A. (1802) *Histoire naturelle, générale et particulière de Crustacés et des Insectes. Vol. 3*. Dufart, Paris, 467 pp.

Latreille, P.A. (1810) *Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides et des Insectes; avec un tableau méthodique de leurs genre disposés en famille*. Schoell, Paris, 444 pp.

Linnaeus, C. (1758) *Systema natura per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tenth edition. Laurentius Salvius, Holmiae, 824 pp.

Liu, X.Y., Lu, X.M. & Zhang, W.W. (2016) New genera and species of the minute snakeflies (Raphidioptera: Mesoraphidiidae: Nanoraphidiini) from the mid Cretaceous of Myanmar. *Zootaxa*, 4103 (4), 301–324. http://doi.org/10.11646/zootaxa.4103.4.1

Machado, R.J.P., Gillung, J.P., Winterton, S.L., Garzón-Orduña, I.J., Lemmon, A.R., Lemmon, E.M. & Oswald, J.D. (2018) Owlflies are derived antlions: anchored phylogenomics supports a new phylogeny and classification of Myrmeleontidae (Neuroptera). *Systematic Entomology*, 44 (2), 418–450. https://doi.org/10.1111/syen.12334

Makarkin, V.N. (2017) Oldest new genus of Myrmeleontidae (Neuroptera) from the Eocene Green River Formation, Colorado. *Zootaxa*, 4337 (4), 540–552.
https://doi.org/10.11646/zootaxa.4337.4.5
Makarkin, V.N. (2023) A new species of Mesoraphidiidae (Raphidioptera) from mid-Cretaceous Kachin amber, with discussion on anal veins in Raphidiomorpha. *Cretaceous Research*, 146, 105484.
https://doi.org/10.1016/j.cretres.2023.105484
Makarkin, V.N. & Archibald, S.B. (2013) A diverse new assemblage of green lacewings (Insecta: Neuroptera: Chrysopidae) from the Early Eocene Okanagan Highlands, western North America. *Journal of Paleontology*, 87, 123–146.
https://doi.org/10.1666/12-052R.1
Makarkin, V.N. & Archibald, S.B. (2014) A revision of the late Eocene snakeflies (Raphidioptera) of the Florissant Formation, Colorado, with special reference to the wing venation of the Raphidiomorpha. *Zootaxa*, 3784 (4), 401–444.
https://doi.org/10.11646/zootaxa.3784.4.4
Makarkin, V.N. & Perkovsky, E.E. (2020) A new species of *Proneuronema* (Neuroptera, Hemerobiidae) from the late Eocene Rovno amber. *Zootaxa*, 4718 (2), 292–300.
https://doi.org/10.11646/zootaxa.4718.2.11
Makarkin, V.N., Wedmann, S. & Weiterschan, T. (2016) A new genus of Hemerobiidae (Neuroptera) from Baltic amber, with a critical review of the Cenozoic *Megalomus*-like taxa and remarks on the wing venation variability of the family. *Zootaxa*, 4179 (3), 345–370.
http://doi.org/10.11646/zootaxa.4179.3.2
Makarkin V.N., Archibald, S.B. & Jepson, J.E. (2019) The oldest Inocelliidae (Raphidioptera) from the Eocene of western North America. *Canadian Entomologist*, 151 (4), 521–530.
https://doi.org/10.4039/tce.2019.26
Makarkin, V.N., Antell, G. & Archibald, S.B. (2022) A revision of Chrysopidae (Neuroptera) of the late Eocene Florissant Formation, Colorado, with description of new species. *Zootaxa*, 5133 (3), 301–345.
https://doi.org/10.11646/zootaxa.5133.3.1
Martins, C.C., Flint, O.S. Jr. & Liu, X.Y. (2018) Notes on the pleasing lacewing genus *Dilar* Rambur, 1838 (Neuroptera, Dilaridae), with description of a new species from Vietnam. *Zootaxa*, 4425 (1), 193–200.
http://doi.org/10.11646/zootaxa.4425.1.13
McKenna, M. C. (1990) Plagiomenids (Mammalia: ?Dermoptera) from the Oligocene of Oregon, Montana and South Dakota, and Middle Eocene of northwestern Wyoming. *In*: Brown, T.M. & Rose, K.D. (Eds.), *Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America*. *Geological Society of America, Special Paper 243*. Geological Society of America, Boulder, Colorado, pp. 211–234.
Navás, L. (1909) Monografía de la familia de los Diláridos (Ins. Neur.). *Memorias de la Real Academia de Ciencias y Artes de Barcelona*, Series 3, 7, 619–671.
Navás, L. (1910) Crisópidos (Ins. Neur.) nuevos. *Brotéria*, Zoológica, 9, 38–59.
Navás, L. (1913) Neurópteros del R. Museo Zoológico de Nápoles. *Annuario del [R.] Museo Zoologico della R. Università di Napoli*, New Series, 4 (3), 1–11.
Navás, L. (1914) Neurópteros de la Tripolitania. II serie. *Annali del Museo Civico di Storia Naturale Giacomo Doria*, 46, 202–209.
Navás, L. (1916) Notas sobre el orden de los Rafidiópteros (Ins.). *Memorias de la Real Academia de Ciencias y Artes de Barcelona*, Series 3, 12, 507–513.
Newman, E. (1838) Entomological Notes. *Entomological Magazine*, 5, 168–181 + 372–402, 483–500.
Oswald, J.D. (2021) Neuropterida Species of the World*. Lacewing Digital Library, Research Publication No. 1.* Available from: http://lacewing.tamu.edu/SpeciesCatalog/Main (accessed 18 January 2023)
Penny, N.D. (1982) Review of the generic level classification of the New World Ascalaphidae (Neuroptera). *Acta Amazonica*, 11, 391–406. [for 1981]
Penny, N.D. (2002) Family Ascalaphidae. *In*: Penny, N.D. (Ed.), *A Guide to the Lacewings (Neuroptera) of Costa Rica. Proceedings of the California Academy of Sciences*, Series 4, 53, 176–186 (text), 293–299 (figures).
Perkovsky, E.E. & Makarkin, V.N. (2019) A new species of *Succinoraphidia* Aspöck & Aspöck, 2004 (Raphidioptera: Raphidiidae) from the late Eocene Rovno amber, with venation characteristics of the genus. *Zootaxa*, 4576 (3), 570–580.
https://doi.org/10.11646/zootaxa.4576.3.9
Pierce, H.G. & Constenius, K.N. (2014) Terrestrial and aquatic mollusks of the Eocene Kishenehn Formation, Middle Fork Flathead River, Montana. *Annals of the Carnegie Museum*, 82, 305–329.
https://doi.org/10.2992/007.082.0401
Rambur, J.P. (1838) s.n. *In*: *Faune entomologique de l'Andalousie. Vol. 2*. A. Bertrand, Paris, pl. 9.
Rambur, J.P. (1842) *Histoire Naturelle des Insectes, Névroptères*. Librairie encyclopédique de Roret. Fain et Thunot, Paris, [xviii] + 534 pp.
Riek, E.F. (1968) A new genus and key to the species of Australian Stilbopterygidae (Neuroptera). *Journal of the Australian Entomological Society*, 7, 105–108.
Schneider, W.G. (1851) *Symbolae ad monographiam generis Chrysopae, Leach*. Hirt, Vratislaviae, 178 pp.
Scudder, S.H. (1883) The tertiary Lake Basin at Florissant, Colo., between South and Hayden Parks. *Annual Report of the*

United States Geological and Geographical Survey of the Territories, 12, 271–293.
https://doi.org/10.3133/70159191

Scudder, S.H. (1890) The Tertiary insects of North America. *Report of the United States Geological Survey of the Territories*, 13, 1–734, 28 pls.
https://doi.org/10.5962/bhl.title.44698

Smith, J.B. (1900) Insects of New Jersey: a list of species occurring in New Jersey, with notes on those of economic importance. *Annual Report of the New Jersey State Board of Agriculture*, 27 (Supplement), 1–755. [for 1899]

Tjeder, B. (1966) Neuroptera-Planipennia. The Lace-wings of Southern Africa. 5. Family Chrysopidae. *In*: Hanström, B., Brinck, P. & Rudebec, G. (Eds.), *South African Animal Life. Vol. 12*. Swedish Natural Science Research Council, Stockholm, pp. 228–534.

van der Weele, H.W. (1903) Description of a new genus and species of holophthalmous Ascalaphidae. *Notes from the Leyden Museum*, 23, 234–236.

van der Weele, H.W. (1909) Ascalaphiden. Collections Zoologiques du Baron Edm. de Selys Longchamps. *Catalogue Systématique et Descriptif*, 8 (for 1908), 1–326.

Wilf, P., Wing, S.L., Greenwood, D.R. & Greenwood, C.L. (1998) Using fossil leaves as paleoprecipitation indicators: An Eocene example, *Geology*, 26, 203–206.
https://doi.org/10.1130/0091-7613(1998)026%3C0203:UFLAPI%3E2.3.CO;2

Winterton, S.L., Lemmon, A.R., Gillung, J.P., Garzon, I.J., Badano, D., Bakkes, D.K., Breitkreuz, L.C.V., Engel, M.S., Lemmon, E.M., Liu, X., Machado, R.J.P., Skevington, J.H. & Oswald, J.D. (2018). Evolution of lacewings and allied orders using anchored phylogenomics (Neuroptera, Megaloptera, Raphidioptera). *Systematic Entomology*, 43, 330–354.
https://doi.org/10.1111/syen.12278