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First brown lacewings (Neuroptera: Hemerobiidae) from the early Eocene Green River Formation

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Abstract

Pseudonotherobius kohlsi **gen. et sp. nov.** and *Megalomus? coloradensis* **sp. nov.** (Neuroptera: Hemerobiidae) are described from the early Eocene of the Parachute Creek Member of the Green River Formation, Colorado, U.S.A. The main diagnostic character states of *Pseudonotherobius* **gen. nov.** are the presence of a crossvein between the proximal branch of RP and RA in the forewing, and the costal space being dilated medially in the hind wing. The latter condition is unique in the family. The genus is preliminarily assigned to the subfamily Carobiinae due to the similarity of its venation to that of the extant Australian genus *Notherobius* New, 1988.

Key words: Neuroptera, Hemerobiidae, Carobiinae, Eocene, Green River Formation

Introduction

Today the family Hemerobiidae comprises about 600 species distributed world-wide (Oswald & Machado 2018). To date, 33 fossil species of the family have been described in 19 genera (Pictet-Baraban & Hagen 1856; Scudder 1878, 1890; Henriksen 1922; Krüger 1923; Jarzembowski 1980; Panfilov 1980; Klimaszewski & Kevan 1986; Makarkin 1991, 1994, 2023; Ponomarenko 1992; Oswald 2000; Makarkin *et al.* 2003, 2016; Makarkin & Wedmann 2009; Jepson *et al*. 2010, 2012; Yang *et al*. 2018; Nel & Jarzembowski, 2019; Makarkin & Gröhn, 2020; Perkovsky & Makarkin, 2020; Makarkin & Perkovsky, 2020; Liu *et al*. 2022; Nakamine *et al*. 2022; Li *et al*. 2023). Of these, 13 genera are extinct, eight from the Mesozoic, five from the Cenozoic. Of the Cenozoic genera, *Prolachlanius* Krüger, 1923, *Proneuronema* Makarkin *et al*., 2016 and *Archibaldia* Makarkin, 2023 are represented by well-preserved specimens and can be easily diagnosed (Makarkin *et al*. 2016, 2019; Makarkin 2023), while the status and systematic position of the monotypic *Bothromicromus* Scudder, 1878 and *Prospadobius* Krüger, 1923 are unclear, one type species holotype missing, the other poorly described. Four extant genera are also known from the Paleogene: *Drepanepteryx* Leach, 1815, *Megalomus* Rambur, 1842, *Sympherobius* Banks, 1904 and *Wesmaelius* Krüger, 1922.

A few species have been described from the Paleogene of North America: *Archibaldia wehri* (Makarkin *et al*., 2003) from the early Eocene of Republic (Washington, U.S.A.); *Wesmaelius mathewesi* Makarkin *et al.*, 2003 from the early Eocene of Quilchena (British Columbia, Canada); and *Bothromicromus lachlani* Scudder, 1878 from the Oligocene of Quesnel (British Columbia, Canada) (Makarkin *et al*. 2016; Makarkin 2023). There are several more undescribed specimens from the early Eocene of British Columbia and Washington.

The Hemerobiidae are represented in the New World Neogene by four species of three to four extant genera from Miocene Dominican amber (Hispaniola Island of the Greater Antilles). At least ten specimens of *Notiobiella thaumasta* Oswald, 2000 are known, the most abundant of these (see Oswald 2000; Engel & Grimaldi 2007). Two specimens of Hemerobiinae are illustrated, but not described and the generic affinity of one of these is difficult to determine from its photograph (see Poinar 1992: Fig. 71; Poinar & Poinar 1999: Fig. 130). Oswald (2000) referred to it as “a hemerobiinae apparently near *Hemerobius* or *Wesmaelius*” (p. 297). The second specimen is probably a

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member of *Wesmaelius* Krüger, 1922 judging from its photograph (Scheven 2004: Fig. on p. 144). A specimen of *Sympherobius* sp. was described, but not illustrated (Engel & Grimaldi 2007).

Previously, four species in four neuropteran families have been described from the early Eocene of the Green River Formation (Colorado, U.S.A): *Xenoberotha angustialata* Makarkin, 2017a (Berothidae), *Epignopholeon sophiae* Makarkin, 2017b (Myrmeleontidae), *Protonolima mantispinoformis* Makarkin, 2019 (Mantispidae), and *Osmylidia taliae* Makarkin *et al*., 2021 (Osmylidae) (Makarkin 2017a, b, 2019; Makarkin *et al*. 2021). Here, two new species of Hemerobiidae from the Green River Formation are described based on three specimens.

Materials and methods

The three specimens of Hemerobiidae examined were collected from the upper part of the Parachute Creek Member of the Green River Formation in Garfield County **(**Colorado, U.S.A.). Two were found at the Anvil Points Labandeira and Kohls sites within the so-called 'B-Groove' laying *ca*. 30 m below the Mahogany Bed (see Young 1995: Fig. 4). The third specimen is from the Radar Dome site (also known as the Douglass Pass locality), which is *ca*. 30 m above the Mahogany Bed (Dayvault *et al*. 1995). This formation is considered to span from 53.5 to 48.5 Ma ago based on $^{40}Ar/^{39}Ar$ dating (Smith *et al*. 2003, 2008). The Parachute Creek Member was accumulated during *ca*. 2.8 million years within the Ypresian, from 51.3 to 48.5 Ma. These specimens are approximately 48.5–49.0 Ma old judging from the age of the Mahogany Bed (Smith *et al*. 2008: Fig.2B).

Venational terminology follows Breitkreuz *et al*. (2017), except details (*e.g.*, spaces, veinlets, traces, oblique radial branches' ("ORB") concept) that follow Oswald (1993). Crossveins are designated by the longitudinal veins to which they connect and are numbered in sequence from the wing base, *e.g.*, 2r-m, crossvein in second gradate series between RP and MA.

Character states of compared taxa are provided in brackets.

Abbreviations: A1–A3, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; MA, anterior media; MP, posterior media; ORB1–ORB3, first to third oblique radial branches; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; rv, recurrent veinlet; Sc, subcosta.

Order Neuroptera Linnaeus, 1758

Family Hemerobiidae Leach, 1815

Subfamily Megalominae Krüger, 1922

Genus *Megalomus* Rambur, 1842

Megalomus? coloradensis sp. nov.

Fig. 1

Type material. Holotype: UCM 86387, collected by David Kohls and deposited in the collections of UCM. An incomplete specimen.

Type locality and horizon. UCM locality 2005025 (Anvil Points Kohls site), Garfield County**,** Colorado, U.S.A. Parachute Creek Member of the Green River Formation; early Eocene (late Ypresian).

Etymology. From Colorado, type area of the species.

Diagnosis. May be distinguished from other species of the genus by possession of all of the following forewing character states: four ORBs; ORB1 deeply forked; distal ORB with three branches originating proximad fourth gradate series.

Description. Head, thorax poorly preserved, details not discernible. Antennae fragmentarily preserved. Prothorax probably very short. Legs partially preserved, with dense short setae, other details not discernible.

Forewing broad-oval, 8.4 mm long, 3.8 mm wide. Costal space very broad. Vast majority of subcostal veinlets forked once including distal ones; two veinlets in proximal portion of each wing forked twice; single veinlets simple; humeral veinlets strongly recurrent, with five branches (three simple, two forked once in left wing; four

simple, one forked once in right wing). One costal crossvein detected in proximal portion of left wing. Subcostal space moderately broad, with one intermediate crossvein detected (right wing). Posterior trace of RA distally forked once, with four veinlets mostly forked once, but one simple in left wing, and one forked twice in both wings. RA space (in this species between RA and distal ORB) rather narrow with two crossveins belonging to third and fourth gradate series (left wing). RP probably with four ORBs. ORB1 at least once deeply forked distad second gradate series. Distal ORB (RP proper) with three branches originating proximad fourth gradate series, forked distally once to three times. M forked slightly distad basal fork of ORB1; distal parts of MA, MP, and one branch partially preserved (it is impossible to determinate if this branch belongs to MA or MP). CuA with four pectinate branches, forked distally once to three times. CuP deeply forked, both branches shallowly once forked. A1 deeply forked, but fragmentarily preserved, its fork not discernible. Branching of A2, A2 unclear. Three gradate series of crossveins preserved (no crossveins in first (basal) series preserved): in second series, two crossveins preserved, 2m-cu located slightly distad 2icu; third ("inner") series incomplete, with seven preserved crossveins from RA to MA; fourth ("outer") series nearly complete, consists of 17 (left wing) from RA to CuA. Veins in costal space mostly dark, other veins mostly with alternate dark and pale sections. Membrane slightly spotted: crossveins in third and fourth gradate series with narrow brown margin; rather large, narrow spot near postero-apical margin.

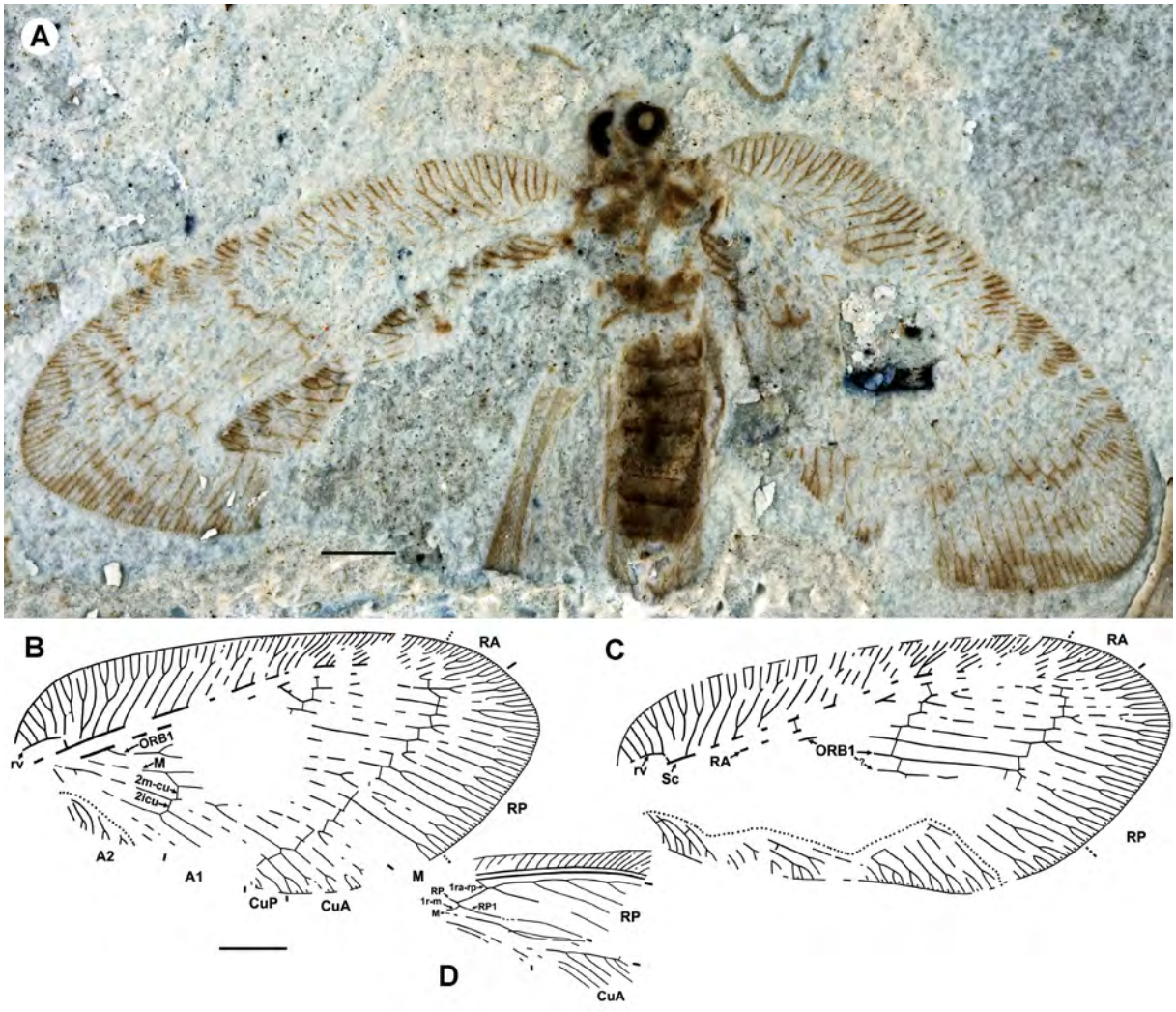

FIGURE 1. *Megalomus? coloradensis* **sp. nov**., holotype UCM 86387. A, specimen as preserved (ventral aspect); B, left forewing venation; C, right forewing venation; D, right hind wing venation. Scale = 1 mm (B–D to same scale).

Hind wings fragmentarily preserved. Costal space slightly dilated towards wing apex. All preserved subcostal veinlets simple. RP with at least five branches. Basal crossvein 1r-m terminating on RP1 near its origin. CuA with at least five pectinate branches.

Abdomen rather well preserved, but no diagnostic details visible.

Subfamily Carobiinae Oswald, 1993 *sensu* Garzón-Orduña *et al*. 2016

Genus *Pseudonotherobius* gen. nov.

Type and only species. *Pseudonotherobius kohlsi* sp. nov.

Diagnosis. In forewing: three ORB's [two in *Notherobius* New, 1988, *Carobius* Banks, 1909]; ORB1 deeply forked one or (rarer) two times [shallowly forked in *Carobius*]; anterior branch of ORB1 connected with RA by crossvein [shared with *Notherobius*, *Carobius*]; distal-most ORB with two branches proximad fourth ("outer") gradate series of crossveins [one branch in *Notherobius*]; CuP deeply forked [shallowly forked in *Carobius*]. In hind wing: costal space dilated medially [unique in the family]; costal space almost entirely dark [dark only in pterostigmal area of *Notherobius, Carobius*].

Etymology. From the Greek *pseudes*, false, and *Notherobius*, a genus-group name, referring to similarity of its venation to that of the genus *Notherobius*. Gender masculine.

***Pseudonotherobius kohlsi* sp. nov.**
Figs 2–5

Description. *Holotype UCM 61905*. Body 3.9 mm long; details poorly discernible. Antennae short, *ca*. 2.5 mm (approximately half forewing length). Prothorax probably very short. Legs fragmentarily preserved.

Forewing 4.9 mm long (left wing), 5.1 mm (right wing); 2.1 mm wide (both wings). Costal space broad, narrowed distally. Preserved subcostal veinlets once forked; humeral veinlet recurrent, with three preserved simple branches (probably four simple branches in life). Sc, RA slightly curved sigmoidally. Posterior trace of RA distally forked, one branch forked once in left wing. Venation in pterostigmal region of Sc and RA unclear. Subcostal space moderately narrow; one basal crossvein detected, located slightly proximad origin of RP1. RP consists of three ORBs. ORB1 deeply forked once (left wing) and twice (right wing) proximad third ('inner') gradate series; in left wing, both branches forked proximad or at fourth ('outer') gradate series, in right wing, posterior trace forked at fourth gradate series, two other branches distad it. ORB2 shallowly dichotomously forked at fourth gradate series. ORB3 (distal) with two branches proximad fourth gradate series; distally forked one to three times. M forked at level of origin of basal branch of ORB1; MA, MP not forked proximad fourth gradate series; distally forked one to three times. CuA pectinate, with three branches originating proximad fourth gradate series; proximal branch deeply forked. CuP deeply forked; each branch forked once distally. A1 deeply forked; each branch probably forked once distally. A2 deeply forked; anterior branch forked two to three times, posterior branch with two pectinate simple branches. A3 simple. Jugal lobe well developed. Coloration: all crossveins with brown margin; large brownish patch between third and fourth gradate series; smaller indistinct patch between second and third gradate series; broad brown area along costal, apical and outer margins; five pale spots along margins: two along costal margin (one at pterostigma and one in proximal portion), two along outer and posterior margins); posterior margin narrowly brown.

Hind wing 3.2 mm long (left wing), 3.8 mm (right wing) (as preserved; presumed complete length of right wing *ca*. 4.2 mm); 1.85 mm wide (left wing), 1.75 mm (right wing). Costal space strongly dilated in medial part so that costal margin is convex; pterostigma very long, dark. Subcostal veinlets indiscernible pterostigmal area, simple proximad it. Sc in pterostigmal area poorly discernible. Posterior trace of RA curved posteriorly in distal part, with one (left wing) veinlet. Sc and RA not fused distally. Subcostal space narrow; no crossveins detected. RA space strongly constricted at 1ra-rp, them dilated towards origin of proximal veinlet of RA, then narrowed; with two crossveins: basal one (1ra-rp) strongly oblique; distal one belonging to fourth gradate series. RP with three branches proximad fourth gradate series. RP1 rather deeply, dichotomously forked. RP2, RP2 shallowly forked two to three times. MA, MP shallowly forked one to two times. CuA pectinate, with three preserved branches; presumable basal branch dichotomously forked; other once forked. Distal part of presumable CuP preserved; A1 fragmentarily preserved, parallel to posterior margin (alternatively, CuP lost and A1 pectinate). Outer gradate series contains eight crossveins from RA to CuA, mainly very poorly discernible. Other crossveins not detected. Coloration: membrane towards margins slightly brownish; costal space almost entirely dark brown.

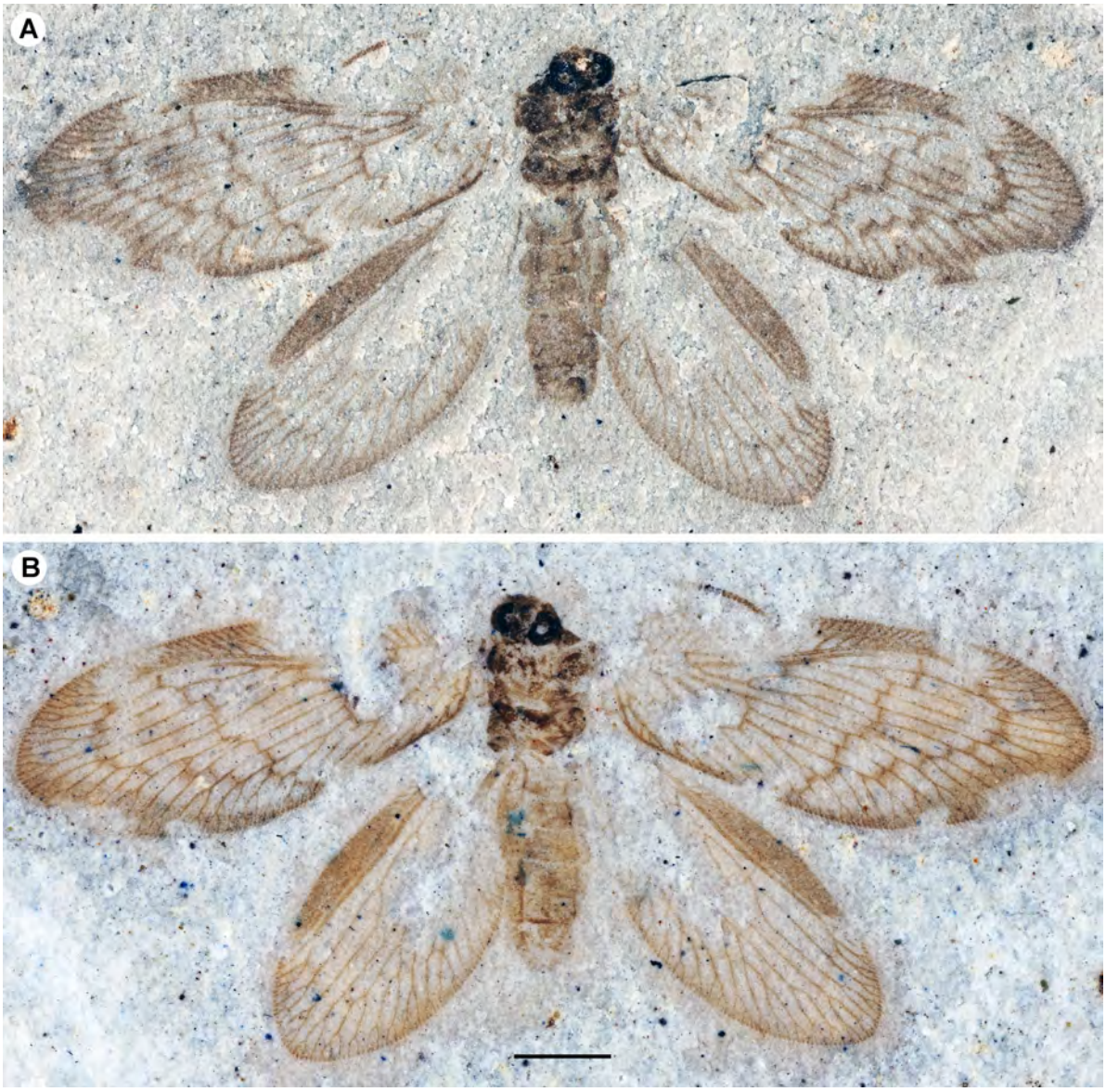

FIGURE 2. *Pseudonotherobius kohlsi* **gen. et sp. nov.**, holotype UCM 61905. A, part (dry); B, counterpart (wetted with ethanol). Scale = 1 mm (both to same scale).

Paratype UCM 86385. Body 2.6 mm long; details poorly discernible. Abdominal apex possibly with a long, slender process of a possible ectoproct (see Remarks).

Forewing *ca*. 5.1 mm long (left wing), *ca*. 4.9 mm (right wing); 2.2 mm wide (left wing), 2.1 mm (right wing). Venation similar to holotype. RP consists of three ORBs. ORB1 deeply forked once in both wings proximad third gradate series. ORB2 shallowly, dichotomously forked at or slightly distad fourth gradate series. ORB3 (distal) with two branches proximad fourth gradate series. CuA pectinate, with three branches originating proximad fourth gradate series. Color pattern similar to holotype.

Preserved venation of hind wings similar holotype. Costal space in left wing folded.

Type material. Holotype: UCM 61905a, b (part, counterpart), collected on 6 July 2004 by David Kohls and deposited in the collections of UCM. A nearly complete specimen with all four wings spread. Paratype: UCM 86385a, b (part, counterpart), collected by W.D. Bateman and deposited in the collections of UCM. A nearly complete specimen with all four wings spread.

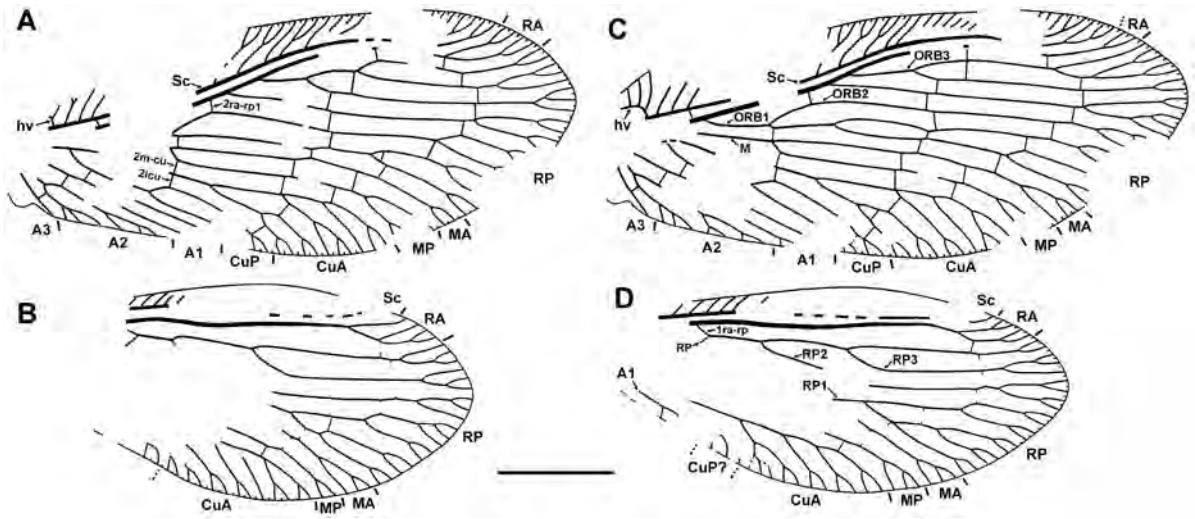

FIGURE 3. Wing venation of *Pseudonotherobius kohlsi* **gen. et sp. nov.**, holotype UCM 61905. A, right forewing; B, right hind wing; C, left forewing; D, left hind wing (C, D converted to standard view, with apex to the right). Scale = 1 mm (all to same scale).

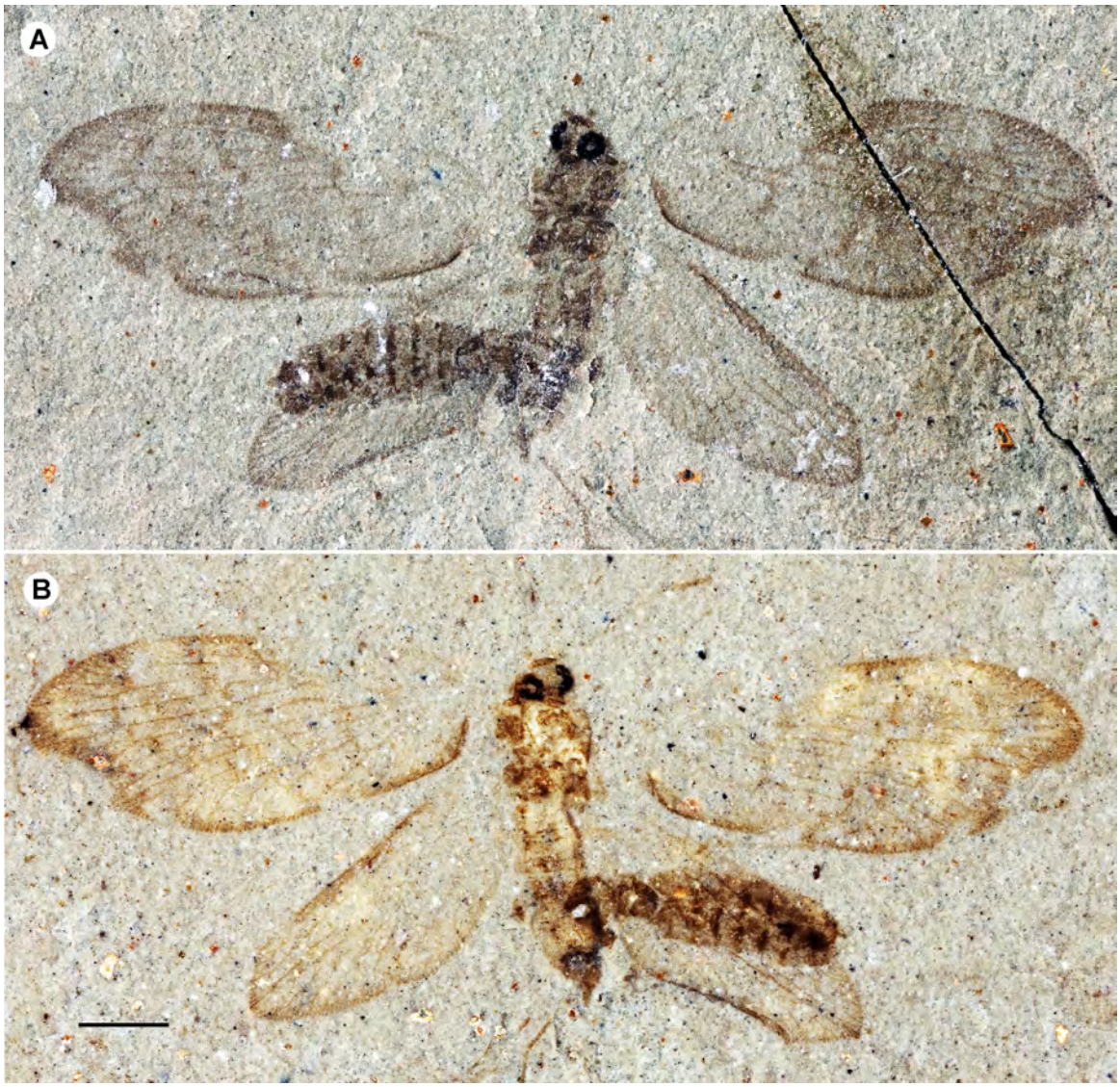

FIGURE 4. *Pseudonotherobius kohlsi* **gen. et sp. nov.**, paratype UCM 86385. A, part (dry); B, counterpart (wetted with ethanol). Scale = 1 mm (both to same scale).

Type locality and horizon. Holotype: UCM locality 2005026 (Labandeira site), Garfield County**,** Colorado, U.S.A. Paratype: UCM locality 2012762 (Radar Dome [=Douglas Pass] site), Garfield County**,** Colorado, U.S.A. Parachute Creek Member of the Green River Formation; early Eocene (late Ypresian).

Etymology. From the surname of the collector of the holotype, David Kohls, in recognition of his great contribution to paleontology by the donation of a huge number of fossil insects to the Museum of Natural History at the University of Colorado in Boulder, and the United States National Museum (Smithsonian Institution) in Washington, D.C.

Remarks. The paratype is possibly a male with a slender long process of presumed ectoproct resembling that of *Carobius* (Fig. 5). Unfortunately, this cannot be identified with certainty because there is a small wingless insect preserved there, and it could be part of its legs.

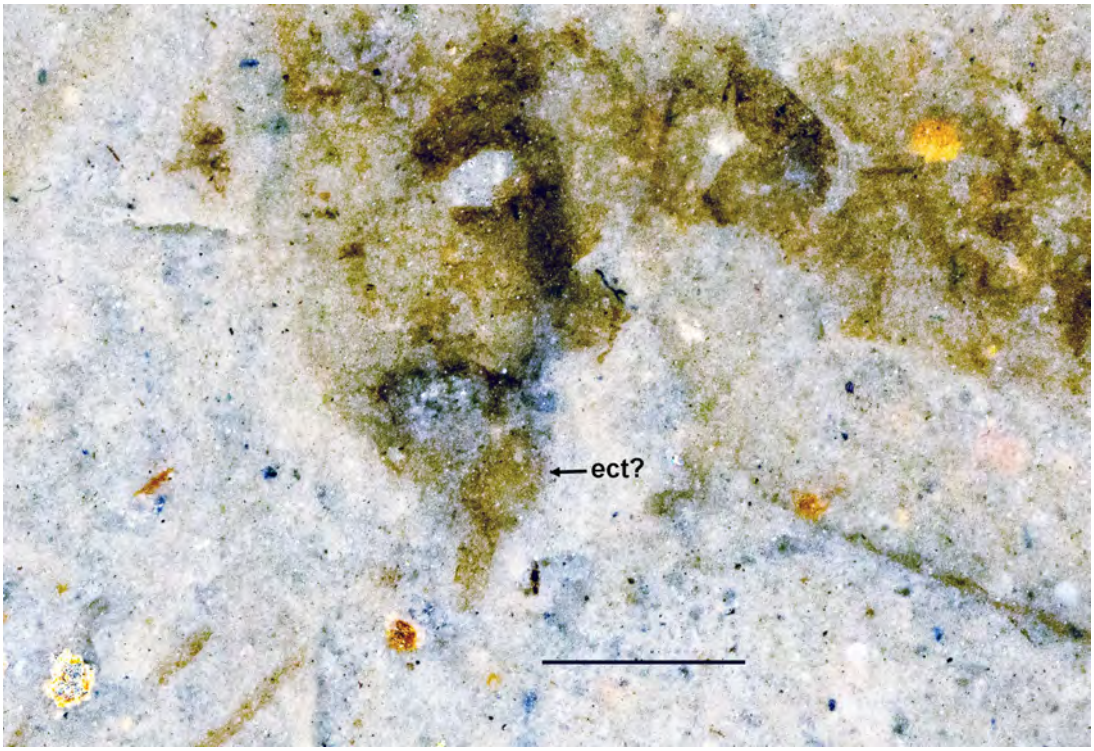

FIGURE 5. *Pseudonotherobius kohlsi* **gen. et sp. nov.**, paratype UCM 86385. Apical portion of abdomen (wetted with ethanol). ect, ectoproct. Scale = 0.5 mm.

Discussion

The generic affinity of *Megalomus? coloradensis* sp. nov. The generic affinity of this species is difficult to determine due to its incomplete preservation. It certainly belongs to the informal *Megalomus*-group, which comprises genera of three subfamilies, *i.e*., Drepanacrinae, Drepanepteryginae and Megalominae (see Makarkin *et al*. 2016 for characteristics of the group). Five genera are known from the Eocene, *i.e*., *Drepanepteryx* Leach, 1815, *Proneuronema*, *Archibaldia* (Drepanepteryginae), *Megalomus* (Megalominae) and *Bothromicromus* Scudder, 1878 (Megalominae?). The preserved venation of the new species is most similar to that of *Megalomus* and *Proneuronema*. In the typical *Megalomus* (*i.e*., those species which are more or less similar to the type species), there are four ORBs or more, RP1 is not forked proximad third gradate series, and the distal ORB has one to two branches. Therefore, the new species does not belong to a typical *Megalomus*, as its RP1 is forked and the distal ORB has three branches. RP1 is forked once to twice in eight New World species currently considered to belong to *Megalomus*, but most of these have six ORBs, and only two species have four and five. In any case, the new species may theoretically be associated with these untypical *Megalomus* as its preserved venation does not contradict this.

Bothromicromus lachlani from the early Oligocene of British Columbia probably belongs to Megalominae and this genus is a possible synonym of *Megalomus* (see Makarkin *et al*. 2016 for further discussion), but it possesses eight ORBs and an unforked ORB1; these character states are strongly dissimilar to these of the new species.

On the other hand, the preserved venation of the new species generally agrees with that of *Proneuronema*. But in all known species of the genus (*i.e*., *Proneuronema minor* Makarkin *et al*., 2016 from Baltic amber, *P. sidorchukae* Makarkin & Perkovsky, 2020 from Rovno amber, and undescribed species from the earliest Eocene of Denmark and northern Germany), there are two to three ORBs [most probably four in the new species] and the distal ORB has at least four branches [three in the new species]. Attribution of the new species to *Proneuronema* is, therefore, less probable than to *Megalomus*.

Two Eocene species were previously assigned to *Megalomus*: *M. tinctus* (Jarzembowski, 1980) and *M. densistriatus* Henriksen, 1922. The former species was described by Jarzembowski (1980: Fig. 31) as *Hemerobius tinctus* from the latest Eocene Bembridge Marls (England) based on a nearly complete forewing. Makarkin (1991) transferred it to *Megalomus*, and Oswald (1993) mentioned that the forewing venation of this species resembles that of the Australian genus *Psychobiella* Banks, 1909, but differs from this genus by its deeply forked CuP. The genus *Psychobiella* constituted the monotypic subfamily Psychobiellinae (Oswald 1993) which was later synonymized with Drepanacrinae (Garzón-Orduña *et al*. 2016). It is obvious that this species belongs to the *Megalomus*-group, but its generic affinity is unclear (see further Makarkin *et al*. 2016).

The generic affinity of *Megalomus densistriatus* from the earliest Eocene Fur Formation was discussed earlier (Makarkin *et al*. 2016; Makarkin 2023); it probably belongs to the genus *Archibaldia*.

Therefore, all Eocene species currently assigned to *Megalomus*, including the new species, only tentatively belong to it.

Subfamily affinity of *Pseudonotherobius* gen. nov. The family Hemerobiidae is currently divided into 10 subfamilies (Oswald 1993; Garzón-Orduña *et al*. 2016): Sympherobiinae, Zachobiellinae, Notiobiellinae, Hemerobiinae, Adelphohemerobiinae, Microminae, Carobiinae, Megalominae, Drepanepteryginae, and Drepanacrinae. Several of these may be surely excluded from further consideration. The fourth ("outer") gradate series of crossveins is lost in the hind wing of Zachobiellinae, Notiobiellinae and Sympherobiinae, but it is present in the new genus. In Adelphohemerobiinae, Microminae and Hemerobiinae, ORB1 and CuA are simple (except *Noius* Navás, 1929 from Oceania, in which CuA is deeply forked), whereas these veins are deeply forked in the new genus. The venation of these subfamilies is in general dissimilar to that of *Pseudonotherobius* **gen. nov.** The deeply forked ORB1 and CuA are present in the *Megalomus*-group (many Megalominae, Drepanepteryginae and Drepanacrinae) and *Notherobius* New, 1988 (Carobiinae). Most genera of the *Megalomus*-group have much denser venation and more crossveins than in *Pseudonotherobius* **gen. nov.** More importantly, all genera (except *Archibaldia*) in this group lack a crossvein connecting RA and RP1 (2ra-rp1), although they have relatively dense crossvenation. The crossvein 2ra-rp1 is present only in four genera, *i.e*., the extant *Carobius*, *Notherobius* (Carobiinae) and *Zachobiella* (Zachobiellinae), and the Eocene *Archibaldia* (Drepanepteryginae). While the venation of *Notherobius* is similar to that of the new genus, that of *Zachobiella* and *Archibaldia* are not. *Pseudonotherobius* **gen. nov.** and *Notherobius* share the following forewing character states: ORB1 is deeply forked one or two times; the anterior branch of ORB1 is connected with RA by a crossvein; branches of CuA are connected by two crossveins; CuP is deeply forked; and a third gradate series of crossvein is present. Such a combination does not occur in other genera.

The subfamily Carobiinae was established by Oswald (1993) for the Australian genus *Carobius*. He stated that "the most convincing synapomorphy of the genus is the configuration of the forewing radius" (p. 197), *i.e*., the presence of two ORB's, ORB1 shallowly forked. Later, the Australian genus *Notherobius* was added to the subfamily by molecular and morphological phylogenetic analyses (Garzón-Orduña *et al*. 2016). Unfortunately, the authors provided neither a new diagnosis of Carobiinae *sensu lato* nor its synapomorphies. Although *Carobius* and *Notherobius* are considered as belonging to the same subfamily their close relationships may be questioned. Their forewing venation are dissimilar in many aspects: in *Carobius*, ORB1 is shallowly forked [deeply forked one or two times in *Notherobius*]; CuP is shallowly forked [deeply forked in *Notherobius*]; the third gradate series of crossveins is lost [present in *Notherobius*]; and crossveins between branches of CuA are absent [present in *Notherobius*]. The male genitalia are also dissimilar in these two genera. In any case, the venation of *Notherobius* is most like that of *Pseudonotherobius* **gen. nov.**, and the new genus may be preliminary assigned to Carobiinae.

Conclusion

The discovery of the two species of Hemerobiidae described above (*Megalomus? coloradensis* **sp. nov.** and *Pseudonotherobius kohlsi* **sp. nov.**) increases our understanding of the paleodiversity and morphology of Green

River Formation Neuroptera. The medially-dilated costal space in the hind wing as found in *P. kohlsi* **sp. nov.** is unique in the family. Six families of Neuroptera are now recorded from the formation: Osmylidae, Hemerobiidae, Mantispidae, Berothidae, Myrmeleontidae, and Ascalaphidae (not described yet).

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