

The oldest Inocelliidae (Raphidioptera) from the Eocene of western North America

Vladimir N. Makarkin, S. Bruce Archibald¹, and James E. Jepson

Abstract—One new genus of Inocelliidae (Raphidioptera) with one new species and one undetermined specimen is described from the Eocene of North America: *Paraksenocellia borealis* **new genus, new species** from the early Eocene (Ypresian) Okanagan Highlands shale at Driftwood Canyon, British Columbia, Canada (a forewing), and *Paraksenocellia* species from the middle Eocene (Lutetian) of the Coal Creek Member of the Kishenehn Formation, northwestern Montana, United States of America (a hind wing). These are the oldest records of the family. The new genus possesses many character states that are rare in Inocelliidae, e.g., a very long pterostigma extending to ScP in both the forewings and hind wings; the forewing subcostal space has three crossveins; the forewing and hind wing AA1 are deeply forked; the crossvein between CuA and CuP is located far distad the crossvein 1r-m. *Paraksenocellia* is confidently a member of the Inocelliidae, as it possesses a proximal shift of the basal crossvein 1r-m (connecting R and M) in the forewing and the loss of the basal crossvein 1r-m in the hind wing, both apomorphies of the family. It shares some character states with the Mesozoic Mesoraphidiidae, which we consider to be mostly stem-group plesiomorphies.

Introduction

The order Raphidioptera includes two extant families, Raphidiidae and Inocelliidae, which are distributed almost exclusively outside of the tropics in the northern hemisphere. The majority of their fossils in the Cenozoic belong to these families, with the exception of one species of the otherwise Mesozoic Baissopteridae from the late Eocene locality of Florissant, Colorado (Makarkin and Archibald 2014).

The extant Inocelliidae is a small family of seven genera and about 40 species (Oswald 2018). Their fossil record comprises two extinct genera with a single species each, *Electrinocellia* Engel and *Succinofibla* Aspöck and Aspöck from

late Eocene Baltic amber (Carpenter 1957; Engel 1998; Aspöck and Aspöck 2004), and four species of the extant *Fibla* Navás from Baltic amber, Florissant, and the late Miocene of Spain (Carpenter 1957; Nel 1993; Engel 1998, 2002; Makarkin and Archibald 2014). One species was described from the late Miocene of Murat, France (Nel 1993), which was not named or assigned to a genus.

Here, we describe a new genus of Inocelliidae with one new species and one undetermined specimen, based on a hind wing from the Kishenehn Formation in Nevada, United States of America (Lutetian, i.e., middle Eocene) and a forewing from Driftwood Canyon in British Columbia, Canada (Ypresian, i.e., early Eocene). These are the oldest known records of the family.

Received 4 December 2018. Accepted 28 January 2019. First published online 18 June 2019.

V.N. Makarkin, Laboratory of Entomology, Federal Scientific Centre of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, 100 let Vladivostoku 159, 690022, Vladivostok, Russia
S.B. Archibald¹, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada; Museum of Comparative Zoology, 26 Oxford Street, Cambridge, Massachusetts, 02138, United States of America; Royal British Columbia Museum, 675 Belleville Street, Victoria, British Columbia, V8W 9W2, Canada

J.E. Jepson, School of Biological, Earth and Environmental Science, University College Cork, Distillery Fields, North Mall, Cork, T23 N73K, Ireland

¹Corresponding author (e-mail: sba48@sfu.ca)

Subject editor: Bradley Sinclair

doi:10.4039/tce.2019.26

<http://zoobank.org/urn:lsid:zoobank.org:pub:3BF85EFE-9564-4176-96F1-5D7E15A0F7F8>

Fig. 1. Localities of fossil Inocelliidae in western North America.

Materials and methods

We examined two specimens: a single forewing preserved in lacustrine shale from the Okanagan Highlands locality at Driftwood Canyon Provincial Park, near the town of Smithers in northwestern British Columbia, Canada; and a single hind wing preserved in lacustrine sediment-derived oil shale of the Coal Creek Member of the Kishenehn Formation exposed along the Middle Fork of the Flathead River between Paola and Stanton Creeks, approximately 27 km south of West Glacier, northwestern Montana, United States of America (Fig. 1).

The Driftwood Canyon locality

Driftwood Canyon is the northernmost known occurrence of the Okanagan Highlands series, which were deposited in early Eocene lake basins

scattered over roughly 1000 km southeast to Republic in northcentral Washington, United States of America. An Ypresian age for Driftwood Canyon sediments of 51.77 ± 0.34 million years ago (mya) is indicated by U–Pb analysis of zircons recovered from a tephra layer intercalated within the fossil-bearing shale (Moss *et al.* 2005). Okanagan Highlands sites preserve fossils of life from temperate (mostly upper microthermal) montane forests during the warmest sustained interval of the Cenozoic (Archibald *et al.* 2011). Various floristic proxy analyses indicate that Driftwood Canyon was the coolest of the series (Greenwood *et al.* 2005). The climate and flora have been characterised by Greenwood *et al.* (2005) and Moss *et al.* (2005).

The fossils from Driftwood Canyon were recovered from very fine-grained shale and, unlike fossils from other Okanagan Highlands localities,

are often preserved only on one side of the split rock, without a counterpart, and only become visible upon wetting.

The Coal Creek Member

The geology of the Coal Creek Member of the Kishenehn Formation was described by Greenwalt *et al.* (2015). It has been estimated to be Lutetian, 46.2 ± 0.4 mya by $^{40}\text{Ar}/^{39}\text{Ar}$ analysis and 43.5 ± 4.9 mya by fission-track analysis (Constenius 1996), supported by biostratigraphic correlation of mammal fossils (Pierce and Constenius 2014; Dawson and Constenius 2018). Fossil insects are found at the base of the middle sequence of this member.

High mean annual temperature has been assumed for the Kishenehn Formation based on the presence of vertebrates and invertebrates that today range in tropical low latitudes (Greenwalt *et al.* 2015). However, plants and animals today restricted to the tropics also occur in the Okanagan Highlands, which has estimates of cooler, mostly upper microthermal mean annual temperature values (Archibald *et al.* 2010, 2013, 2014). This may be explained by their restriction to low latitudes today by coldest month mean temperatures, *i.e.*, their inability to persist in regions of harsh winters (Archibald and Farrell 2003), and so mild winters with few if any frost days in the Okanagan Highlands may have allowed their presence there despite cooler mean annual temperature. Therefore, the presence of such organisms in the Kishenehn Formation does not exclude the possibility of mean annual temperature values similar to those of the Okanagan Highlands. Detailed paleoclimate analysis for the Kishenehn Formation, as has been done in the Okanagan Highlands, is needed to resolve this question.

Greenwalt *et al.* (2015) published a study of the lithology of Coal Creek Member shale and the taphonomy of its fossils. Preservation of its insects is strongly biased towards small (lengths < 1 cm) specimens, except for larger disarticulated wings. Evidence suggests that insects were captured on or within cyanobacterial mats prior to sinking to the bottom of a relatively shallow, near-shore lake. Like those of Driftwood Canyon, Coal Creek Member specimens are often preserved only on one side of the split shale and usually only become visible when wetted;

counterparts usually do not exist (Greenwalt *et al.* 2015). In this way, the Kishenehn Coal Creek and Driftwood Canyon shales appear more similar to each other than they do to shales of any other Okanagan Highlands site or of the Green River or Florissant Formations.

Terminology

We use the venational terminology of Makarkin and Archibald (2014) with the following alterations. First, the forewing CuA of Inocelliidae is here restricted to two proximal branches, conforming to the configuration of CuA in the hind wing of Inocelliidae and the forewings and hind wings of Raphidiidae. Accordingly, the distal part of CuA of Makarkin and Archibald (2014, Fig. 2A) is here the posterior branch of MP, and the designations of respective crossveins are changed (see Fig. 2).

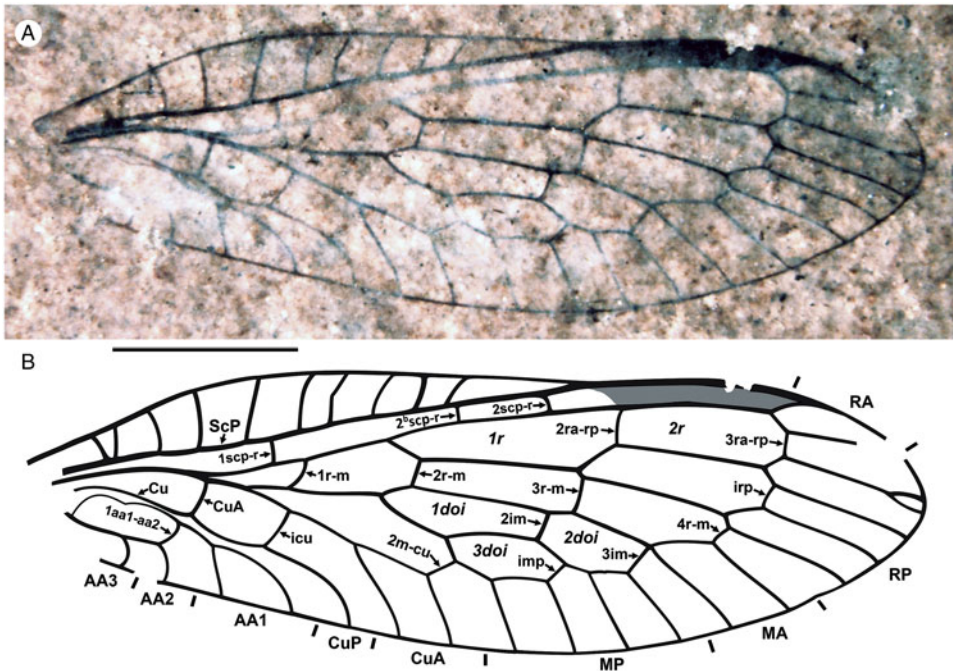
Secondly, we use a different interpretation of the anal veins of the hind wing. It is now generally accepted that Raphidiomorpha plesiomorphically possess three anal veins in both forewings and hind wings, although only two are apparent in the hind wing of extant members of both extant families. This is supported in Raphidiidae by pupal tracheation (Withycombe 1923; Fig. 2A).

In the hind wing of Inocelliidae, AA1 is a separate vein for its entire length, but the distal or only middle parts of AA2 and AA3 are fused for most of their distances. This is inferred from the short free basal parts of AA2 and AA3 that are sometimes visible (see, *e.g.*, Aspöck *et al.* 1991, fig. 44; Liu *et al.* 2012; Figs. 1–3). The AA2 of Inocelliidae of Makarkin and Archibald (2014; Fig. 2B) is then AA2+3, *i.e.*, in that species the distal parts of AA2 and AA3 are fused to the wing margin. In the new genus (as in many other extant species), only the middle parts of AA2 and AA3 are fused, and the distal parts of AA2 and AA3 are separate.

It appears that this is quite different in the Raphidiidae. Aspöck *et al.* (1991, fig. 23) interpreted AA1 and AA2 as fused basally for quite a long distance and AA3 as entirely separate. We agree with this, finding it highly likely. Therefore, the anterior (distal) branch of AA1 of Raphidiidae of Makarkin and Archibald (2014; Fig. 2D) is AA1, the posterior (proximal) branch is AA2, and AA2 is AA3.

Genera of the paraphyletic family Mesoraphidiidae show different tendencies in the fusion of

Fig. 2. *Paraksenocellia borealis* from Driftwood Canyon, holotype RBCM.EH2018.129.1. **A**, Specimen wetted with ethanol; **B**, forewing venation (both converted to standard view, with apex to the right). Scale = 2 mm (both to scale).



their anal veins in the hind wing, indicating that this family might be polymorphic in this regard. Unfortunately, basal parts of the hind wings are not clearly preserved in most Mesoraphidiidae, but AA1 and AA2 are clearly medially fused in *Burmorphidia reni* Liu *et al.* and appear to be basally fused in *Nanoraphidia electroburmica* Engel, both from mid-Cretaceous Burmese amber (Engel 2002; Fig. 3; Liu *et al.* 2016, fig. 9).

Crossveins are designated after the longitudinal veins with which they are connected and are numbered in sequence from the wing base, *e.g.*, 2scp-r, distal crossvein connecting ScP and RA; 2^bscp-r, intermediate crossvein connecting ScP and RA; icu, crossvein between CuA and CuP; 1im-3im, first to third crossvein between MA and MP. Terminology of wing spaces and details of venation (*e.g.*, veinlets) follows Oswald (1993).

Abbreviations. AA1–AA3, first to third branches of anterior analis; CuA, anterior cubitus; CuP, posterior cubitus; 1doi–3doi, first to

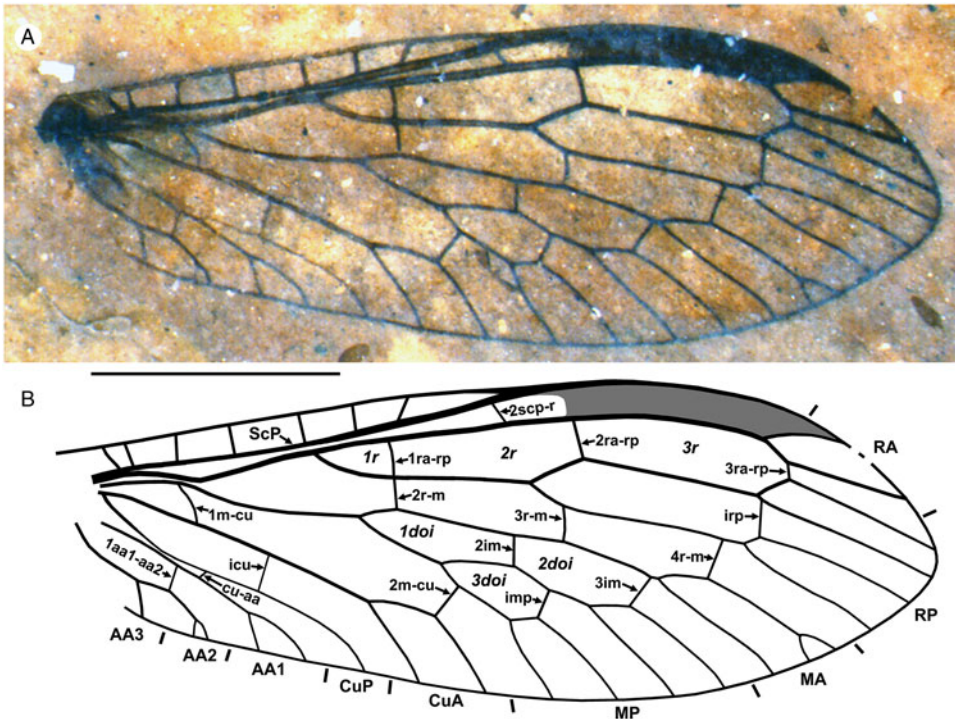
third discoidal cells; MA and MP, anterior and posterior branches of media; 1r–3r, first to third radial cells; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; ScP, posterior subcosta.

***Paraksenocellia* Makarkin, Archibald, and Jepson, new genus**

<http://zoobank.org/urn:lsid:zoobank.org:act:5D0B1CC2-DE20-40F9-BD0F-2B21FFBDA1DE>

Diagnosis (contrary character states of compared taxa are provided in parentheses). Distinguished within Inocelliidae by: both forewings and hind wings: pterostigma very long, extending to ScP in both wings (other genera: not extending to ScP); very long terminal parts of branches of RA and RP (*i.e.*, distad distal crossveins) (other genera: moderately long to short); forewing: three crossveins in subcostal

Fig. 3. *Paraksenocellia* species from the Coal Creek Member of the Kishenehn Formation, holotype USNM 625900. **A**, Specimen wetted with ethanol; **B**, hind wing venation (both converted to standard view, with apex to the right). Scale = 2 mm (both to scale).



space (possibly adventitious in this specimen) (other genera: two); two radial cells (other genera: normally three); three discoidal cells (four discoidal cells in vast majority of species with few exceptions, see below); AA1 deeply forked (other genera: simple, with few exceptions, see below); hind wing: basal crossvein 1r-m absent (shared with most genera of Inocelliidae); icu (crossvein between CuA, CuP) far distad 1m-cu (proximad or opposite 1m-cu in other Inocelliidae with few exceptions, see below); AA1 deeply forked (other genera: simple with few exceptions, see below).

Etymology. From the Greek *paraksenos*, strange, and *Inocellia*, a genus group name, referring to its unusual venation. Gender feminine.

Type species. *Paraksenocellia borealis* new species, here designated.

Species included. *Paraksenocellia borealis* new species.

***Paraksenocellia borealis* Makarkin, Archibald, and Jepson, new species**

<http://zoobank.org/urn:lsid:zoobank.org:act:4061A2A7-A16D-47E8-B768-9AF2C22C0424>
See Fig. 2.

Diagnosis. See forewing character states in the genus diagnosis.

Material. Holotype: RBCM.EH2018.129.1 (also bearing collector number SBA-5915), collected by S.B. Archibald on 12 June 2012, and deposited in Royal British Columbia Museum (Victoria, British Columbia, Canada). A well-preserved complete forewing.

Etymology. From the Latinised Greek *boreus* -a, -um, northern, as the holotype is the more northern occurrence of the genus.

Description. Forewing elongate, 9.6 mm long, 2.9 mm wide. Costal space strongly dilated at one-fifth wing length; subcostal veinlets simple (including humeral veinlet), widely spaced. ScP

terminating on costal margin at about three-fifth wing length. Subcostal space broad, with three crossveins: basal crossvein 1scp-r located proximad 1r-m; intermediate crossvein 2^bscp-r located slightly distad distal-most subcostal veinlet; distal crossvein 2scp-r located well proximad termination of ScP. Pterostigma long, extended to termination of ScP, heavily pigmented. Branch (veinlet) of RA at distal end of pterostigma strongly oblique, distinctly curved (convex). RA stem probably simple (as preserved, but incomplete), strongly bent posteriorly after origin of distal branch, terminating at margin before wing apex. RA space with two crossveins: 2ra-rp located opposite proximal end of pterostigma; 3ra-rp located well distad end of pterostigma. RP originates far from wing base (at about 40% complete wing length), with two branches: RP1 deeply forked at outer gradate series of crossveins; RP2 simple. Stem of RP shallowly forked near wing margin. One crossvein in radial space, between anterior branch of RP1, RP2. Four crossveins between R/RP, M: 1r-m curved, connecting R, M; 2r-m connects stem of RP, MA; 3r-m connects RP1 near its origin and MA; 4r-m connects posterior branch of RP1 and anterior branch of MA. M appears fused basally with R for considerable distance, then with CuA for short distance; forked nearly opposite origin of RP. MA deeply forked. MP dichotomously branched, with four terminal branches. Three intramedian crossveins form three *doi*: two crossveins between MA, MP, one between branches of MP. One crossvein between M, Cu (2m-cu) connecting posterior branch of MP, stem of CuA. Cu basally not fused with R+M; divided into CuA, CuP far from wing base. CuA crossvein-like before fusion with M, perpendicular to Cu, then fused with M for short distance, deeply forked distally. CuP simple, rather aligned with Cu. One crossvein between CuA, CuP (icu). AA1 deeply forked. AA2, AA3 fused proximally; separate, simple distally. One crossvein between AA1, AA2 connecting AA1 well proximad its fork, AA2.

Locality and age. Driftwood Canyon Provincial Park (public face exposure), near Smithers, British Columbia; mid-Ypresian, 51.77 ± 0.34 mya.

Remarks. An oblique incorporated pterostigmal veinlet of RA appears possibly visible in the middle of the pterostigma with some lighting;

however, this is clearly not present when clarified by wetting with ethanol.

***Paraksenocellia* species**

See Fig. 3.

Material. Specimen: USNM 625900, deposited in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (Washington, District of Columbia, United States of America). A well-preserved complete hind wing.

Description. Hind wing 7.2 mm long, 2.6 mm wide. Costal space moderately broad; all seven subcostal veinlets simple. ScP stout, short. RA stout, distally with one strongly oblique, smoothly curved (convex) branch (veinlet); RA distad 3ra-rp long, straight. Subcostal space with one distal crossvein 2scp-r, connecting ScP, RA near termination of ScP. Pterostigma very long, heavily pigmented, extended to ScP. RA space (between RA, RP) with three crossveins: 1ra-rp located opposite to 2r-m; 2ra-rp located opposite proximal end of pterostigma; short 3ra-rp located distad termination of pterostigma. RP originates relatively close to wing base (at 33% complete wing length), with two branches. RP1 deeply forked, with branches very long; RP2 very long, straight, simple. One crossvein between branches of RP as part of a gradate series. Three crossveins between RP, MA; 1r-m lost; 2r-m connects stems of RP, MA; 3r-m connects RP1, stem of MA; 4r-m connects RP1 before fork and anterior branch of MA. M not fused basally with R, forked into MA, MP distad origin of RP. MA deeply forked, with branches very long; its anterior branch shallowly forked. Two crossveins between MA, anterior part of MP form two long cells (*1doi*, *2doi*), nearly equal in length. MP dichotomously branched, with four very long terminal branches. One crossvein between branches of MP forming slightly elongate *3doi*. Two crossveins between M, Cu: basal 1m-cu rather long, oblique, slightly sinuate, located near wing base; 2m-cu connecting posterior branch of MP, anterior branch of CuA. CuA deeply forked. CuP thin, simple. One long crossvein between CuA, CuP (icu), located far distad 1m-cu. One short crossvein between CuP, AA1 located distad level of 1m-cu. AA1 deeply forked. AA2, AA3 fused proximally; distal (free) part of AA2 long, shallowly forked terminally; distal (free) part of AA3 rather long,

simple. One long crossvein between AA1, AA2, joining AA2 in middle distal (free) part.

Locality and age. Middle Fork of the Flathead River, between Paola and Stanton Creeks, approximately 27 km south of West Glacier; the Coal Creek Member of the Kishenehn Formation, northwestern Montana, United States of America; Lutetian (see age discussion above).

Remarks. We assign the Coal Creek specimen to the same genus as *P. borealis*, as they share the distinctive pterostigma and very long terminal parts of the branches of RA and RP. These character states are unusual and do not occur or are very rare in other members of the family.

The specimens present difficulties in separating them at the species level, however, as *P. borealis* is based on a forewing with no known hind wing, and the Coal Creek specimen is a hind wing with no associated forewing. Their age difference suggests that they might represent distinct species – Driftwood Canyon is a maximum of about nine million years older than Coal Creek – but this is not conclusive. Grimaldi and Engel (2005) speculated that insect species persist on average perhaps 3–10 million years, and Hörnschemeyer *et al.* (2010) discussed cases of much greater time spans; indeed, Möller Andersen *et al.* (1993) reported a specimen of the water strider genus *Limnopus* Stål (Hemiptera: Gerridae) in Driftwood Canyon shale that is extremely close to a modern species.

The distance between Driftwood Canyon and Coal Creek appears consistent with their separation, as most modern raphidiopteran species have small ranges (Aspöck 2002) – but some do range more widely. They differ in size, but this might be accounted for by sexual dimorphism. While we suspect that they may represent two species, lacking sufficient differences between the Driftwood Canyon forewing and the Coal Creek hind wing, we treat the Coal Creek wing as *P. sp.* pending discovery of a complete specimen of either that clarifies their relationship.

Discussion

Paraksenocellia is assigned to the Inocelliidae with confidence based on several character states. In both forewings and hind wings: 1) the crossvein 2scp-r is shifted proximally, clearly proximad the pterostigma (located at proximal end of the

pterostigma in all Raphidiidae and many Mesoraphidiidae); in the forewing: 2) the basal crossvein 1r-m connects R and M (shifted distally in other Raphidiomorpha connecting the stem of RP and M/MA, except in the Middle Jurassic *Styporaphidia magia* Engel and Ren); 3) the crossvein 2ra-rp is located within (rarely just proximad) the pterostigma (it is markedly proximad the pterostigma in the vast majority of Raphidiidae); in the hind wing: 4) the basal crossvein 1r-m is lost (it is normally present in all other Raphidiomorpha); and 5) CuP and AA1 are separate (they are partially fused in all Raphidiidae, except the Baltic amber *Succinoraphidia* Aspöck and Aspöck). A combination of character states 2 and 4 occurs exclusively in Inocelliidae. We consider character state 2 in *Styporaphidia magia* to be homoplasious relative to its presence in Inocelliidae.

In Inocelliidae, only *Paraksenocellia* has a very long pterostigma, extending to ScP in both wings. This is most similar to the pterostigmata of some Mesoraphidiidae, especially the Jurassic *Mesoraphidia* Martynov, which is long and lacks veinlets of RA within it, and has a far proximal location of the distal crossvein 2scp-r, which sometimes connects ScP and RA, not closing the pterostigma proximally (see, *e.g.*, Lü *et al.* 2015, figs. 1–10; Lyu *et al.* 2017; Figs. 1–2). However, the venation of these Mesoraphidiidae differs from that of Inocelliidae by many other features, in particular by character states 2 and 4.

The following character states of the venation of *Paraksenocellia* are also absent or rare in other Inocelliidae. The three subcostal crossveins of the forewing are unique within Inocelliidae; in other genera of the family there are two. In Raphidiidae, a third (intermediate) subcostal crossvein (2^bscp-r) is also rare but can occur more often (see Makarkin and Archibald 2014: 413), at times as an individual aberration (see, *e.g.*, Aspöck and Aspöck 1974; Fig. 1b).

The two radial cells in the forewing, as found in *Paraksenocellia*, were hitherto only known in the Baltic amber *Electrinocellia* (*i.e.*, 1ra-rp is absent in these). All other genera of Inocelliidae normally have three (*i.e.*, 1ra-rp is present). Conversely, all genera of Raphidiidae have two radial cells (except for *Mongoloraphidia abnormis* Liu *et al.* with three radial cells: Liu *et al.* 2010; Fig. 1), as do the great majority of Mesoraphidiidae. Therefore, we assume that the presence of two radial

cells (*i.e.*, the absence of 1r-rp) is a plesiomorphic state in Raphidiomorpha (see also Makarkin and Archibald 2014: 407).

The presence of three discoidal cells and the forked AA1 in the forewing were discussed in detail by Makarkin and Archibald (2014: 437), who considered these conditions to be very rare in Inocelliidae. They also considered the forked AA1 to be a probable plesiomorphic character state at the family level.

The loss of the basal crossvein 1r-m in the hind wing is clearly an apomorphic character state for the Inocelliidae, which occurs in the family only in five extant genera and the Baltic amber *Electrinocellia*. A plesiomorphic condition at the level of the order – the long and longitudinally oriented 1r-m – occurs in three inocelliid genera: the extant *Fibla* and *Sininocellia* Yang, and the extinct the Baltic amber *Succinofibla*. It occurs in most other Raphidiomorpha. It is interesting that the oldest known genus of Inocelliidae possesses this apomorphic condition.

The far distal location of icu (the crossvein between CuA and CuP) in the hind wing is extremely rare in Inocelliidae. This condition is known to occur only in the Baltic amber *Electrinocellia* (Carpenter 1957; Fig. 1). In other species of Inocelliidae, this crossvein is shifted far proximally, located proximad or opposite 1r-m (extremely rarely slightly distad). Conversely, in all other Raphidiomorpha (including Raphidiidae, fossil, and extant), the crossvein icu is shifted far distally as found in *Paraksenocellia*.

The forked AA1 of the hind wing occurs very rarely in Inocelliidae, only known in the extant North American *Negha infata* (Hagen) (Carpenter 1936, fig. 7) and the Baltic amber *Succinofibla* (Aspöck and Aspöck 2004, fig. 8).

Therefore, the venation of *Paraksenocellia* is distinctive and markedly differs from that of other genera of the family. It appears to be most closely related to the Baltic amber genus *Electrinocellia*, as they share at least three important character states: 1) the presence of two radial cells in the forewing; 2) the loss of the basal crossvein 1r-m; and 3) the far distal location of the crossvein icu in the hind wing. It is interesting that some character states of *Paraksenocellia* are characteristic of Raphidiidae and occur very rarely in the Inocelliidae, *e.g.*, the presence of two radial cells in the

forewing, and the far distal position of the crossvein icu in the hind wing.

The venation of *Paraksenocellia* resembles many Mesozoic Mesoraphidiidae based on some character states (*e.g.*, the long pterostigma, the presence of three discoidal cells and two radial cells in the forewing, and the distal location of the crossvein icu in the hind wing). These character states do not occur or are very rare in the extant Inocelliidae, but some of them are present in *Electrinocellia*. We interpret this similarity as consistent with the opinion previously expressed by two of us (Makarkin and Archibald 2014) that Mesoraphidiidae is a paraphyletic group in which both extant families (Raphidiidae and Inocelliidae) are separately nested.

Acknowledgements

We thank Dale Greenwalt (Smithsonian Institution, Washington, District of Columbia, United States of America) for bringing the Kishenehn raphidiopteran to the attention of J.E.J., and supplying information on the geology of the Kishenehn Formation; Conrad Labandeira (Smithsonian Institution) for arranging the loan of the Kishenehn raphidiopteran; BC Parks for granting a fieldwork permit for Driftwood Canyon Provincial Park, particularly John Howard of the Smithers office; Marlow Pellatt of Parks Canada for use of microscopes and digital photography equipment; Victoria Arbour of the Royal British Columbia Museum for accessioning the Driftwood Canyon specimen into their collections. S.B.A. received support from Natural Sciences and Engineering Research Council of Canada Discovery grants to Rolf Mathewes (Simon Fraser University) that facilitated research, and to David Greenwood (Brandon University, Brandon, Manitoba, Canada) that funded fieldwork at Driftwood Canyon. The study is supported by grant 16-04-00053 of the Russian Foundation for Basic Research to V.N.M.

References

- Archibald, S.B., Bossert, W.H., Greenwood, D.R., and Farrell, B.D. 2010. Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology*, **36**: 374–398.

- Archibald, S.B. and Farrell, B.D. 2003. Wheeler's dilemma. *Proceedings of the Second Paleontological Congress. Acta Zoologica Crakoviensia*, **46**: 17–23.
- Archibald, S.B., Greenwood, D.R., and Mathewes, R.W. 2013. Seasonality, montane beta diversity, and Eocene insects: testing Janzen's dispersal hypothesis in an equable world. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **371**: 1–8.
- Archibald, S.B., Greenwood, D.R., Smith, R.Y., Mathewes, R.W., and Basinger, J.F. 2011. Great Canadian Lagerstätten 1. Early Eocene Lagerstätten of the Okanagan Highlands (British Columbia and Washington State). *Geoscience Canada*, **38**: 155–164.
- Archibald, S.B., Morse, G.E., Greenwood, D.R., and Mathewes, R.W. 2014. Fossil palm beetles refine upland winter temperatures in the Early Eocene Climatic Optimum. *Proceedings of the National Academy of Sciences of the United States of America*, **111**: 8095–8100.
- Aspöck, H. 2002. The biology of Raphidioptera: a review of present knowledge. *Acta Zoologica Academiae Scientiarum Hungaricae*, **48**: 35–50.
- Aspöck, H. and Aspöck, U. 1974. *Raphidia (Magnoraphidia) flammii* Asp. et Asp. und *Raphidia (Magnoraphidia) horticola* Asp. et Asp. – Taxonomie und Verbreitung (Neuropt., Raphidioptera, Raphidiidae). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen*, **24**: 140–146.
- Aspöck, H., Aspöck, U., and Rausch, H. 1991. Die Raphidiopteren der Erde. Eine monographische Darstellung der Systematik, Taxonomie, Biologie, Ökologie und Chorologie der rezenten Raphidiopteren der Erde, mit einer zusammenfassenden Übersicht der fossilen Raphidiopteren (Insecta: Neuropteroidea). Two volumes. Goecke & Evers, Krefeld, Germany. Pp. 550–730.
- Aspöck, U. and 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.
- Carpenter, F.M. 1936. Revision of the Nearctic Raphidioptera (recent and fossil). *Proceedings of the American Academy of Arts and Science*, **71**: 89–157.
- Carpenter, F.M. 1957. The Baltic amber snake-flies Neuroptera. *Psyche*, **63**: 77–81.
- Constenius, K.N. 1996. Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. *The Geological Society of America Bulletin*, **108**: 20–39.
- Dawson, M.R. and Constenius, K.N. 2018. Mammalian fauna of the middle Eocene Kishenehn Formation, middle fork of the Flathead River, Montana. *Annals of Carnegie Museum*, **85**: 25–60.
- Engel, M.S. 1998. A new fossil snake-fly species from Baltic amber (Raphidioptera: Inocelliidae). *Psyche*, **102**: 187–193.
- Engel, M.S. 2002. The smallest snakefly (Raphidioptera: Mesoraphidiidae): a new species in Cretaceous amber from Myanmar, with a catalog of fossil snakeflies. *American Museum Novitates*, **3363**: 1–22.
- Greenwalt, D.E., Rose, T.R., Siljeström, S.M., Goreva, Y.S., Constenius, K.N., and Wingerath, J.G. 2015. Taphonomy of the fossil insects of the middle Eocene Kishenehn Formation. *Acta Palaeontologica Polonica*, **60**: 931–947.
- Greenwood, D.R., Archibald, S.B., Mathewes, R.W., and Moss, P.T. 2005. Fossil biotas from the Okanagan Highlands, southern British Columbia and northern Washington State: climates and ecosystems across an Eocene landscape. *Canadian Journal of Earth Sciences*, **42**: 167–185.
- Grimaldi, D. and Engel, M.S. 2005. *Evolution of the insects*. Cambridge University Press, New York, New York, United States of America.
- Hörschemeyer, T., Wedmann, S., and Poinar, G. 2010. How long can insect species exist? Evidence from extant and fossil *Micromalthus* beetles (Insecta: Coleoptera). *Zoological Journal of the Linnean Society*, **158**: 300–311.
- Liu, X.Y., Aspöck, H., Yang, D., and Aspöck, U. 2010. Revision of the snakefly genus *Mongoloraphidia* (Raphidioptera, Raphidiidae) from mainland China. *Deutsche Entomologische Zeitschrift*, **57**: 89–98.
- Liu, X.Y., Aspöck, H., Zhang, W.W., and Aspöck, U. 2012. A review of the snakefly genus *Sininocellia* (Raphidioptera, Inocelliidae): discovery of the first male and description of a new species from China. *Deutsche Entomologische Zeitschrift*, **59**: 233–240.
- Liu, X.Y., Lu, X.M., and Zhang, W.W. 2016. New genera and species of the minute snakeflies (Raphidioptera: Mesoraphidiidae: Nanoraphidiini) from the mid Cretaceous of Myanmar. *Zootaxa*, **4103**: 301–324.
- Lü, Y.N., Liu, X.Y., and Ren, D. 2015. First record of the fossil snakefly genus *Mesoraphidia* (Insecta: Raphidioptera: *Mesoraphidiidae*) from the Middle Jurassic of China, with description of a new species. *Zootaxa*, **3999**: 560–570.
- Lyu, Y.N., Ren, D., and Liu, X.Y. 2017. Review of the fossil snakefly family *Mesoraphidiidae* (Insecta: Raphidioptera) in the Middle Jurassic of China, with description of a new species. *Alcheringa*, **41**: 403–412.
- Makarkin, V.N. and 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**: 401–444.
- Möller Andersen, N., Spence, J.R., and Wilson, M.V. H. 1993. 50 Million years of structural stasis in water striders (Hemiptera: Gerridae). *American Entomologist*, **39**: 174–176.
- Moss, P.T., Greenwood, D.R., and Archibald, S.B. 2005. Regional and local vegetation community dynamics of the Eocene Okanagan Highlands (British Columbia-Washington State) from palynology. *Canadian Journal of Earth Sciences*, **42**: 187–204.
- Nel, A. 1993. Nouveaux Raphidioptères fossiles du Cénozoïque de France et d'Espagne (Raphidioptera, Raphidiidae, Inocelliidae). *Ecole Pratique des Hautes Etudes, Biologie et Evolution des Insectes*, **6**: 99–108.

- Oswald, J.D. 1993. Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). *Journal of the New York Entomological Society*, **101**: 143–299.
- Oswald, J.D. 2018. Neuroptera species of the world. Version 6.0 [online]. Available from <http://lacewing.tamu.edu/SpeciesCatalog/Main> [accessed 13 August 2018].
- Pierce, H.G. and 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.
- Withycombe, C.L. 1923. The wing venation of *Raphidia maculicollis* Stephens. *The Entomologist*, **56**: 33–35.