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

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### Abstract

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

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

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

## Introduction

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

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

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

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

Here, we examined all of the type material (specimens or high-resolution photographs) and revise their taxonomy, finding nine valid species. We propose that none of these belong to *Raphidia*, but that they belong to extinct genera, in general agreement with the original assignments of Handlirsch (1910). Besides the previously established presence of the extant families Raphidiidae and Inocelliidae, we find, surprisingly, that *Dictyoraphidia* Handlirsch, 1910 belongs to the Baissopteridae, previously only known from the Cretaceous. Although the status

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

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

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

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

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