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The second genus and species of the extinct neuropteroid family Corydasialidae, from early Eocene McAbee, British Columbia, Canada: do they belong to Megaloptera?

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Abstract

Ypresioneura obscura **gen. et sp. nov.** from the early Eocene (Ypresian) McAbee locality (Canada, British Columbia) is described. It is assigned to the extinct neuropteroid family Corydasialidae, as the second known genus and species. The Corydasialidae was previously known only from late Eocene (Priabonian) Baltic amber. It was originally assigned to the Megaloptera, but the character states that support this conclusion are not strongly diagnostic. There is still doubt as to whether this family belongs to Megaloptera or to the Neuroptera. If this is a megalopteran (which we favor), it is the first specimen of the order from the insect-rich Okanagan Highlands series of Ypresian localities, which occur sporadically across the southern interior of British Columbia, Canada into north-central Washington, USA.

Key words: Megaloptera, Neuroptera, Corydasialidae, Ypresian, Eocene, Okanagan Highlands

Introduction

The Megaloptera is a small holometabolous order of about 380 extant species, distributed across much of the globe (Yang & Liu 2010, Oswald 2013). The larvae are primarily aquatic predators, feeding on a variety of invertebrates. They emerge as winged adults who live only a few days and apparently do not usually eat, although known to feed on small quantities of liquid food such as nectar (e.g. females of Corydalinae: Anderson 2003). Adults range from moderate sized, with wingspans less than 2 cm, to very large, with wingspans reaching 18 cm, and male dobsonflies (*Corydalus* spp.) bear impressively-sized sickle-shaped mandibles of unknown function (Grimaldi & Engel 2005).

The order is currently divided into five families, the extant Sialidae (alderflies) (Early Jurassic to Recent) and the Corydalidae (dobsonflies, Corydalinae; and fishflies, Chauliodinae) (Middle Jurassic to Recent) and three extinct families, the Parasialidae (Permian), Euchauliodidae (Late Triassic), and Corydasialidae (late Eocene) (Riek 1974; Ponomarenko 1976, 1977; Ansorge 2001; Wang & Zhang 2010; Liu *et al*. 2012). The venation of the minute Permian Nanosialidae is similar to that of Parasialidae, and it probably also belongs to the Megaloptera as we treat it here. Originally, it was assigned to the monotypic suborder Siarapha of the order Panmegaloptera, which included three other suborders: Archimegaloptera (including only Parasialidae), Megaloptera s. str., and Raphidioptera (Shcherbakov 2013). The position of the Euchauliodidae, however, is unclear. It consists of one species, *Euchauliodes distinctus* Riek, 1974, known from a single incomplete forewing from the Late Triassic of the South African Republic (Molteno Formation). Its wing venation is similar to that of some insects in the order Grylloblattodea, e.g., Megakhosaridae, particularly in that M is basally fused for a short distance with CuA (cf. Riek 1974: Fig. 4 and Storozhenko & Aristov 2014: Fig. 16). Ansorge (2001) suggested that it might in fact belong to the Grylloblattodea. As there is too little evidence to consider *E. distinctus* to belong to Megaloptera, we treat it here as Grylloblattodea *incertae sedis*.

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The fossil record of Megaloptera is very poor. Most Mesozoic specimens are larvae; only the Early Jurassic *Dobbertinia reticulata* Handlirsch, 1920 from Dobbertin (Germany), the Middle Jurassic *Eochauloides striolatus* Liu *et al*. 2012 and *Jurochauliodes ponomarenkoi* Wang et Zhang, 2010 from Daohugou (China), and the Early Cretaceous *Cretochaulus lacustris* Ponomarenko, 1976 from Baissa (Transbaikalian Russia) are known confidently as adults (although other recently reported adult specimens remain to be described, in particular from the Early Cretaceous Crato Formation in Brazil (Martins-Neto *et al*. 2007)).

Adults are better known from the Cenozoic, but are always rare. Two specimens of Sialidae are known from the late Paleocene/early Eocene of Dinmore (Australia) and the early Eocene of Oise amber (France) (Lambkin 1992, Nel *et al.* 2002). Most species of Megaloptera (Sialidae and Corydalidae) have been described from Priabonian (late Eocene) Baltic amber (Wichard 1997, 2002, 2003; Ansorge 2006; Wichard & Engel 2006). Several species of Sialidae have been described from the Neogene of Europe, Asia Minor and the Caribbean (e.g. Illies 1967, Nel 1988, Engel & Grimaldi 2007).

In North America, the few fossils reported as belonging to the order are either of questionable status as megalopterans or are currently little known. In the Mesozoic, there are larvae of the Triassic *Mormolucoides articulatus* Hitchcock, 1858 from Turner's Falls, Massachusetts (New Arc Group), which, however, are often considered not to be megalopterans (e.g., Ponomarenko 2002), and an egg clutch of the Maastrichtian *Corydalites fecundum* Scudder, 1878 from Crow Creek, Colorado (Laramie Formation), whose megalopteran affinity needs to be confirmed. Reported adult Sialidae from the early Eocene Green River Formation, Colorado (Dayvault *et al*. 1995) and the Miocene of Stewart Valley, Nevada (Ansorge 2001) remain undescribed.

The extinct family Corydasialidae is problematic in possessing the most generalized wing venation of the order. It was placed in the Megaloptera by its tarsomere and maxillary palp morphologies (see below). However, these are not diagnostic of the order (see below), and so here, we treat it as having a currently unknown neuropteroid order-level affinity, although we favor a megalopteran affinity. The family is currently known by a single specimen of its sole species, *Corydasialis inexspectata* Wichard *et al*., 2005 (Wichard *et al*. 2005), from Baltic amber. Here, we describe *Ypresioneura obscura* **gen. et sp. nov.**, a second species and genus of the family, from the Ypresian (early Eocene) Okanagan Highlands locality at McAbee, British Columbia, Canada. If corydasialids do belong to the Megaloptera, *Y. obscura* **gen. et sp. nov.** would be the first known occurrence of the order in the Okanagan Highlands.

Material and methods

We examined one fossil forewing preserved in lacustrine shale of an unnamed formation from the McAbee locality, about eight kilometers east of the town of Cache Creek in southcentral British Columbia, Canada. The McAbee is part of the Okanagan Highlands series of Ypresian upland localities scattered across roughly a thousand kilometers of south-central British Columbia into north-central Washington, United States of America. It is radiometrically dated 52.90 ± 0.83 Ma (Archibald *et al*. 2010). The McAbee forest had a temperate but equable climate in an upland setting (summarized by Archibald *et al*. 2013).

Terminology follows Kukalova-Peck & Lawrence (2004) as interpreted by Yang *et al*. (2012, 2014), except for wing spaces and details of venation (e.g., spaces, veinlets), which follows Oswald (1993).

Venational abbreviations are: AA, analis anterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M, media; MA, media anterior; MP, media posterior; R, radius; RA, radius anterior; RP, radius posterior; RP1, proximal-most branch of RP; ScP, subcosta posterior.

Institution abbreviations: TRU, Thompson Rivers University, Kamloops, British Columbia, Canada.

Order Megaloptera Latreille, 1802

Family Corydasialidae Wichard *et al*., 2005

Genus *Ypresioneura* gen. nov.

Type and only species. *Ypresioneura obscura* sp. nov.

Diagnosis. May be easily distinguished from only other genus of Corydasialidae by longer, wider forewing, ca. 25 mm long, length/width ratio ca. 2.9 [19 mm, 3.5 in *Corydasialis* Wichard *et al*., 2005]; CuP, probably MP pectinately branched, with two branches each [both once rather deeply forked in *Corydasialis*]; AA1 terminating on hind margin distad level of M fork [proximad level of M fork in *Corydasialis*].

Etymology. From the Ypresian age, and *neura*, plural form of the Ancient Greek noun *neuron*, nerve, vein, and a traditional ending of Neuroptera-like genera. Gender feminine.

Remarks. The differences in the forewings of the two species of Corydasialidae appear great enough to justify treating them as separate genera. As far as we know, the pectinate CuP of the new species is a unique condition in the order. It is simple in the vast majority of Megaloptera species with a maximum of a single fork in the few others. Generally, the venation within the Megaloptera is much more uniform than that within the Neuroptera, and its differences between genera of Megaloptera are minimal.

The gender of *Corydasialis* is feminine, not masculine, as the name is ending in *Sialis* whose gender is feminine (ICZN 1999: Article 3.1.1); therefore, the specific epithet should be *inexspectata*.

Ypresioneura obscura sp. nov.

(Fig. 1)

Description. Forewing narrowed basally, slightly broader in distal half, length 21.5 mm as preserved (estimated complete length ca. 25 mm), maximum width 8.5 mm. Trichosors not detected. Costal space narrowed basad, most dilated near proximal 1/4, then gradually narrowed towards apex. Subcostal veinlets simple, rather dense; nearly straight with tips directed apicad in proximal portion of costal space. Subcostal space narrow, slightly dilated distad; crossveins not detected. RP originated near wing base at very acute angle, somewhat zigzagged distal to mid-point. RA space (between RA, RP) strongly narrow basally, dilated towards apex; ten preserved crossveins in proximal part, more closely spaced basally than distally; eight crossveins proximad origin of RP1. RP with two preserved branches; RP1 origin at nearly half wing length; origins of RP1, RP2, probably RP3 widely spaced. Crossveins between branches of RP not detected, except one proximal. M appears fused basally with R for rather short distance; running concave proximad fork; forked far from wing base, but much proximad origin of RP1. MA somewhat arched in proximal portion; distal-most portion poorly preserved, but probably rather deeply forked. MP with probably three pectinate branches (proximal-most branch very poorly preserved, partly destroyed). Fork of Cu not detected, apparently near wing base. CuA nearly straight (only little-zigzagged); probably once rather deeply forked (distal-most portion poorly preserved). CuP, CuA slightly diverged distad. CuP distally zigzagged, with two branches. AA1 long, with two pectinate oblique branches. AA2 much shorter than AA1, pectinate, with two oblique branches. Origins of AA1, AA2 join basally. AA3 short, probably simple. Crossvenation irregular, comparatively dense. Gradate series of crossveins not developed.

Etymology. The specific epithet is formed from the Latin *obscurus* [*-a*, *-um*], obscure, unclear, in reference to the hazy preservation of this wing.

Holotype. Specimen TRU F-1547 (part only), deposited in the collection of TRU. A poorly preserved incomplete forewing lacking apical portion, and with a fissure across it at approximately mid-length.

Type locality and horizon. McAbee, British Columbia, Canada; Ypresian (early Eocene).

Discussion

Although the forewing venation of *Ypresioneura* **gen. nov.** firmly associates it with *Corydasialis* (Corydasialidae) from the Eocene Baltic amber, some shared character states appear to be significantly similar in ways to those of *Raphia* Rust, 1999 (Raphidioptera: family unknown) from the early Eocene Fur Formation of Denmark, and *Cratochrysa* Martins-Neto, 1994 (Neuroptera: Cratochrysidae) from the Early Cretaceous Crato Formation in Brazil. The names *Raphia* and Cratochrysidae are *nomen nudum*, as the former was described in an unpublished dissertation (ICZN 1999: Article 9, see "Example"), and the family-group name Cratochrysidae appeared only in lists of taxa or mentioned without description (Martins-Neto 1994, 1997, 2003) (ICZN 1999: Article 13). Of these, only the family name Corydasialidae is valid. We preliminary believe that all these genera may belong to Corydasialidae; however, this supposition awaits examination of the specimens of *Cratochrysa* and *Raphia*.

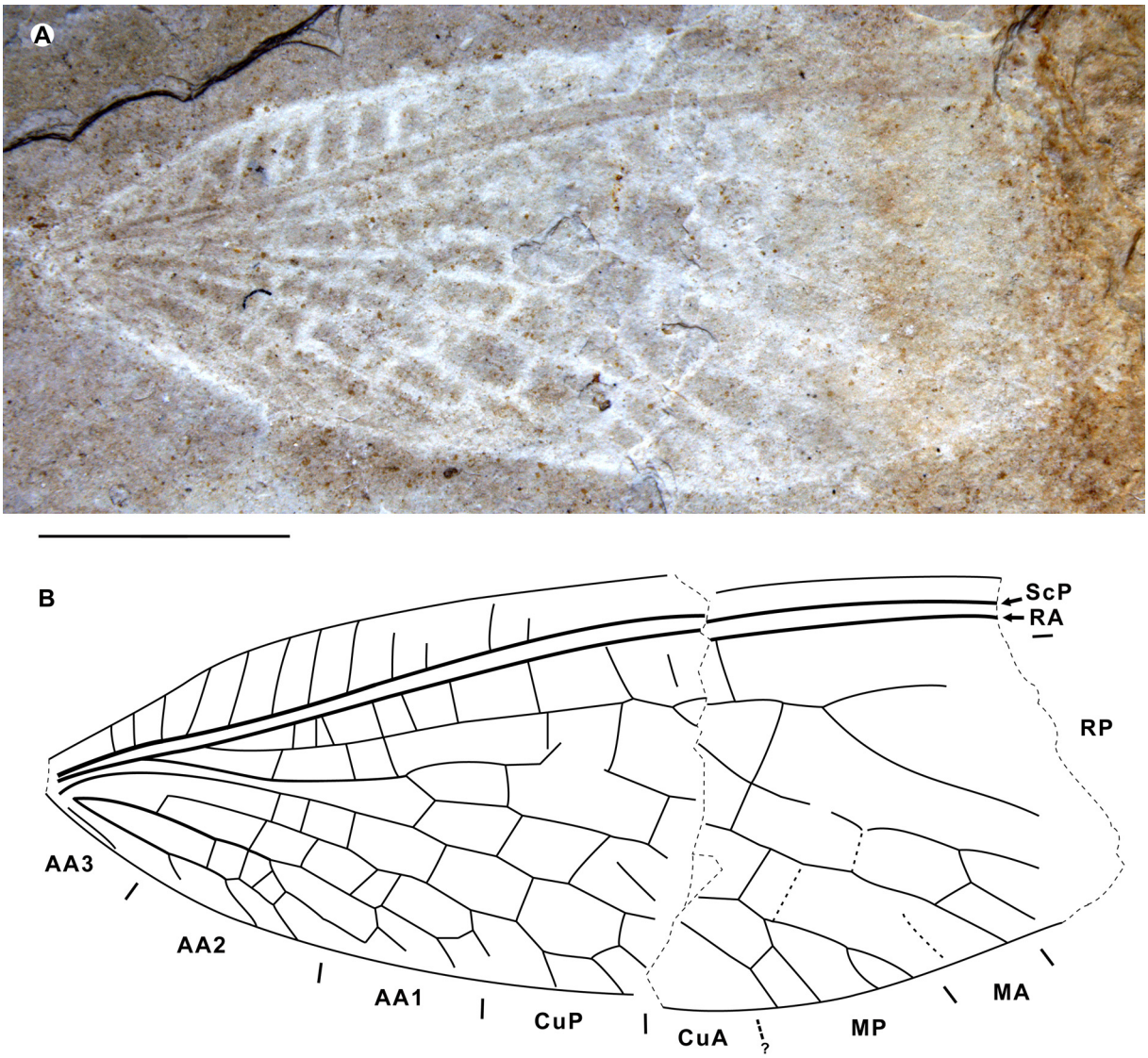

FIGURE 1. Forewing of *Ypresioneura obscura* **gen. et sp. nov.**, holotype TRU F-1547. A, photograph; B, drawing. Scale bar = 5 mm (both to scale).

The forewing venation of Corydasialidae (especially its type, *Corydasialis inexspectata*) is in general Megaloptera-like, as the absence of nygmata, trichosors, and terminal twigging of veins is characteristic of the order. However, no autapomorphy of Megaloptera is present in this venation; each of its character states is present in at least some neuropteran families. If it is a megalopteran, its venation is the most generalized of the order: (1) ScR and RA are distally separated (fused in Sialidae and most Corydalidae, except in a few taxa, e.g. *Protohermes* van der Weele, 1907); (2) CuP is forked (simple in Parasialidae, Sialidae, and Corydalidae), and; (3) M and CuA are separated (fused for some distance in Parasialidae and Sialidae). In general, the venation of Corydasialidae is more similar to that of Corydalidae than to that of the Sialidae or Parasialidae, although Wichard *et al*. (2005) considered it to be the sister of Sialidae, based on its bilobed fourth tarsomere. The venation of *Ypresioneura obscura* **gen. et sp. nov.** differs from that of *Corydasialis inexspectata* only in bearing more numerous forks of CuP and MP, more closely spaced subcostal veinlets, and slightly denser crossvenation. These features make the wing of *Y. obscura* **gen. et sp. nov.** somewhat Neuroptera-like, providing at least weak support for the notion that the Corydasialidae belongs to that order – or, if to the Megaloptera, that the Neuroptera is its sister, the currently most accepted view (e.g. Haring & Aspöck 2004; Aspöck & Aspöck 2008; Aspöck *et al.* 2012; Peters *et al*. 2014).

The Corydasialidae was assigned to the Megaloptera based on its bilobed fourth tarsomere, shared with Sialidae, and its four-segmented maxillary palps, shared with Sialidae and Chauliodinae (Corydalidae) (Contreras-

Ramos 2004; Wichard *et al*. 2005). The specialized mouthparts of the neuropteran family Nemopteridae, however, also have four-segmented maxillary palps in most species (Tjeder 1967). Thus this cannot be considered a strong enough character state to confidently associate the Corydasialidae with the Megaloptera.

The third tarsomere in Raphidioptera is also bilobed, but the wing venation of the order (even in the basal suborder Priscaenigmatomorpha; see for example Liu *et al*. 2013) differs greatly from that of Corydasialidae. They are not snakeflies.

Bilobed tarsomeres are also known in Neuroptera. The fourth tarsomere of most Coniopterygidae is flattened and slightly cordate in a dorsal view (Killington 1936; Meinander 1972). Moreover, in the subfamily Brucheiserinae (Neuroptera, Coniopterygidae: three species in Chile and Argentina), this tarsomere is similar to that found in the Sialidae: clearly expanded, with two lateral lobes connected by a sclerite (Riek 1967: Figs 6, 12, 13; Sziraki 2007). Initially, the Brucheiseridae was established as a family of Megaloptera (Navás 1927); only the discovery and description of their larvae confirmed that this taxon belongs to the Coniopterygidae (Sziráki & Flint 2007).

Finally, these apparently shared tarsus morphologies of Corydasialidae and Sialidae might be convergent, as they differ in possibly significant ways. The lateral lobes of the fourth tarsomere in Sialidae are connected by a sclerite and this tarsomere appears ventrally like an expanded (usually conical) structure (see Vshivkova 1987: Fig. 7.5a; Yang & Liu 2010: Fig. 17). In Corydasialidae, these lobes are not connected by a sclerite and bear a brush of sucker disc-shaped hairs, which is considered an autapomorphy of the family (Wichard *et al*. 2005: Fig. 6).

What we are left with is Corydasialidae belonging to either Megaloptera or Neuroptera and composed of *Corydasialis*, *Ypresioneura* **gen. nov.**, and possibly *Raphia* and *Cratochrysa*. We favor a megalopteran affinity for the family, as all of the character states present in these are characteristic of the order, and none are confidently diagnostic of the Neuroptera. However, this assessment is provisional, based on current knowledge from the fossils discussed here. Two new and undescribed specimens of *Cratochrysa* (VM, current research) may clarify this issue.

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