

# A new species of *Archaeochrysa* Adams (Neuroptera: Chrysopidae) from the early Eocene of Driftwood Canyon, British Columbia, Canada

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**Abstract**—*Archaeochrysa sanikwa* new species (Neuroptera: Chrysopidae: Nothochrysinæ) is described from early Eocene (Ypresian) Okanagan Highlands shale at Driftwood Canyon, British Columbia, Canada. The evolutionary trends of three chrysopid wing venation characters (the shape of the intramedian cell, the position of the crossvein 2m-cu, and the development of the pseudocubitus) are analysed. The forewing venation of this species is very plesiomorphic compared with the vast majority species of Nothochrysinæ, both fossil and extant.

## Introduction

Green lacewings (Neuroptera: Chrysopidae) constitute one of largest families of Neuroptera (Brooks and Barnard 1990). They are popularly known for their use in biological control of aphids (Hemiptera: Aphidoidea) and other small arthropod plant pests (*e.g.*, Bigler 1984; Ridgway and Murphy 1984; Tulisalo 1984).

The fossil record of Chrysopidae is relatively rich, with 22 named genera and 58 named species (including that described here) assigned to three subfamilies: the extinct Limaiinae, and the extant and fossil Nothochrysinæ and Chrysopinae. Limaiinae has eight described Mesozoic genera with 25 species (from the Late Jurassic to Late Cretaceous), and one Eocene genus with two named species (Table 1). Other Mesozoic Chrysopidae have not been assigned to subfamily. Fossil Nothochrysinæ include 12 named genera and 23 species (including the new species) from the early Eocene to the Pliocene of Europe, Asia and North America (Table 1). Fossil Chrysopinae are assigned to eight species of one extinct genus and two extant genera, from the late Eocene and Miocene of Europe and the Caribbean region.

Chrysopinae is the dominant subfamily today with over 1200 species, which are distributed globally; and Nothochrysinæ is a small, relict, sporadically distributed subfamily, with 21–22 species (Yang 1986; Brooks and Barnard 1990; Adams and Penny 1992a; Kovanci and Canbulat 2007). A third, small extant mainly tropical subfamily, Apochrysinæ, has no known fossil record (Winterton and Brooks 2002).

Here, we describe a new species of Nothochrysinæ from Driftwood Canyon, British Columbia, Canada, which we assign to the genus *Archaeochrysa* Adams. This genus is the most species rich among fossil nothochrysinæ, with its five species known from the early Eocene of British Columbia, Canada, the late Eocene of Florissant, Colorado, United States of America, and the early Oligocene of Creede, Colorado.

## Materials and methods

### Locality and material

We base this species on a single fossil forewing preserved in lacustrine shale from the Okanagan Highlands locality at Driftwood Canyon Provincial

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**Table 1.** A checklist of named fossil species of Chrysopidae

Species	Subfamily	Age	Locality
<i>Mesypochrysa intermedia</i> Panfilov <sup>1</sup>	LIMN	Oxfordian/Kimmeridgian <sup>2</sup>	Karatau, Kazakhstan
<i>Mesypochrysa latipennis</i> Martynov <sup>3</sup>	LIMN	Oxfordian/Kimmeridgian <sup>2</sup>	Karatau, Kazakhstan
<i>Mesypochrysa makarkini</i> Nel, Delclòs, and Hutin <sup>4</sup>	LIMN	Oxfordian/Kimmeridgian <sup>2</sup>	Karatau, Kazakhstan
<i>Mesypochrysa polyclada</i> Panfilov <sup>3</sup>	LIMN	Oxfordian/ Kimmeridgian <sup>2</sup>	Karatau, Kazakhstan
<i>Mesypochrysa reducta</i> Panfilov <sup>3</sup>	LIMN	Oxfordian/Kimmeridgian <sup>2</sup>	Karatau, Kazakhstan
<i>Mesypochrysa minuta</i> Jepson, Makarkin, and Coram <sup>5</sup>	LIMN	late Berriasian <sup>5</sup>	Durlston Formation, England
<i>Baisochrysa multinervis</i> Makarkin <sup>6</sup>	LIMN	Pre-Barremian/early Barremian <sup>7</sup>	Baissa, Russia
<i>Mesypochrysa angustialata</i> Makarkin <sup>6</sup>	LIMN	Pre-Barremian/early Barremian <sup>7</sup>	Baissa, Russia
<i>Mesypochrysa chrysopa</i> Makarkin <sup>6</sup>	LIMN	Pre-Barremian/early Barremian <sup>7</sup>	Baissa, Russia
<i>Mesypochrysa curvimedia</i> Makarkin <sup>6</sup>	LIMN	Pre-Barremian/early Barremian <sup>7</sup>	Baissa, Russia
<i>Mesypochrysa falcata</i> Makarkin <sup>6</sup>	LIMN	Pre-Barremian/early Barremian <sup>7</sup>	Baissa, Russia
<i>Mesypochrysa magna</i> Makarkin <sup>6</sup>	LIMN	Pre-Barremian/early Barremian <sup>7</sup>	Baissa, Russia
<i>Mesypochrysa minima</i> Makarkin <sup>6</sup>	LIMN	Pre-Barremian/early Barremian <sup>7</sup>	Baissa, Russia
<i>Lembochrysa miniscula</i> Ren and Guo <sup>8</sup>	LIMN	Barremian <sup>7</sup>	Yixian Formation, China
<i>Lembochrysa polyneura</i> Ren and Guo <sup>8</sup>	LIMN	Barremian <sup>7</sup>	Yixian Formation, China
<i>Paralembochrysa splendida</i> Nel, Delclòs and Hutin <sup>4</sup>	Incertae sedis	Barremian <sup>7</sup>	Yixian Formation, China
<i>Drakochrysa sinica</i> Yang and Hong <sup>9</sup>	LIMN	Barremian <sup>7</sup>	Laiyang Formation, China
<i>Mesypochrysa chrysopoides</i> Ponomarenko <sup>10</sup>	LIMN	Barremian/Aptian <sup>2</sup>	Bon-Tsagaan, Mongolia
<i>Araipechrysa magnifica</i> Martins-Neto and Vulcano <sup>11</sup>	Incertae sedis	Late Aptian <sup>12</sup>	Crato Formation, Brazil
<i>Limaia conspicua</i> Martins-Neto and Vulcano <sup>11</sup>	LIMN	Late Aptian <sup>12</sup>	Crato Formation, Brazil
<i>Limaia adicotomica</i> Martins-Neto <sup>14</sup>	LIMN	Late Aptian <sup>12</sup>	Crato Formation, Brazil
<i>Mesypochrysa confusa</i> (Martins-Neto and Vulcano) <sup>11</sup>	LIMN	Late Aptian <sup>12</sup>	Crato Formation, Brazil
<i>Mesypochrysa criptovenata</i> (Martins-Neto and Vulcano) <sup>11</sup>	LIMN	Late Aptian <sup>12</sup>	Crato Formation, Brazil
<i>Mesypochrysa skulda</i> (Martins-Neto) <sup>13</sup>	LIMN	Late Aptian <sup>12</sup>	Crato Formation, Brazil
<i>Cretachrysa martynovi</i> Makarkin <sup>15</sup>	Incertae sedis	Cenomanian <sup>2</sup>	Ola Formation, NE Siberia
<i>Cimbrochrysa moleriensis</i> Schlüter <sup>18</sup>	NOTN	Eocene (~54–56 mya: Ypresian) <sup>17</sup>	Fur Formation, Denmark
<i>Danochrysa madseni</i> Willmann <sup>19</sup>	NOTN	Eocene (~54–56.0 mya: Ypresian) <sup>17</sup>	Fur Formation, Denmark
<i>Stephenbrooksia multifurcata</i> Willmann <sup>19</sup>	NOTN	Eocene (~54–56.0 mya: Ypresian) <sup>17</sup>	Fur Formation, Denmark
<i>Protochrysa aphrodite</i> Wilmann and Brooks <sup>16</sup>	LIMN	Eocene (~54–56.0 mya: Ypresian) <sup>17</sup>	Fur Formation, Denmark
<i>Adamschrysa aspera</i> Makarkin and Archibald <sup>20</sup>	NOTN	Eocene (52.90 ± 0.83 mya: Ypresian) <sup>21</sup>	McAbee, Canada
<i>Archaeochrysa profracta</i> Makarkin and Archibald <sup>20</sup>	NOTN	Eocene (52.90 ± 0.83 mya: Ypresian) <sup>21</sup>	McAbee, Canada
<i>Okanaganochrysa coltsunae</i> Makarkin and Archibald <sup>20</sup>	NOTN	Eocene (52.90 ± 0.83 mya: Ypresian) <sup>21</sup>	McAbee, Canada

Table 1. Continued

Species	Subfamily	Age	Locality
<i>Protochrysa fuscobasalis</i> Makarkin and Archibald <sup>20</sup>	LIMN	Eocene (52.90 ± 0.83 mya: Ypresian) <sup>21</sup>	McAbee, Canada
<i>Adamsochrysa wilsoni</i> Makarkin and Archibald <sup>20</sup>	NOTN	Eocene (49.4 ± 0.5 mya: Ypresian) <sup>22</sup>	Republic, United States of America
<i>Archaeochrysa sanikwa</i> new species	NOTN	Eocene (51.77 ± 0.34 mya: Ypresian) <sup>23</sup>	Driftwood Canyon, Canada
<i>Pseudochrysopa harveyi</i> Makarkin and Archibald <sup>20</sup>	NOTN	Eocene (51.77 ± 0.34 mya: Ypresian) <sup>23</sup>	Driftwood Canyon, Canada
<i>Asiachrysa tadushiella</i> Makarkin <sup>24</sup>	NOTN	Eocene (Ypresian/Lutetian) <sup>24</sup>	Tadushi Formation, Russia
<i>Archaeochrysa fracta</i> (Cockerell) <sup>25</sup>	NOTN	Eocene (34.07 ± 0.10 mya: Priabonian) <sup>26</sup>	Florissant, United States of America
<i>Archaeochrysa paranervis</i> Adams <sup>27</sup>	NOTN	Eocene (34.07 ± 0.10 mya: Priabonian) <sup>26</sup>	Florissant, United States of America
<i>Dyspetochrysa vetuscula</i> (Scudder) <sup>28</sup>	NOTN	Eocene (34.07 ± 0.10 mya: Priabonian) <sup>26</sup>	Florissant, United States of America
<i>Palaeochrysa concinnula</i> Cockerell <sup>29</sup>	NOTN	Eocene (34.07 ± 0.10 mya: Priabonian) <sup>26</sup>	Florissant, United States of America
<i>Palaeochrysa stricta</i> Scudder <sup>28</sup>	NOTN	Eocene (34.07 ± 0.10 mya: Priabonian) <sup>26</sup>	Florissant, United States of America
<i>Palaeochrysa wickhami</i> Cockerell <sup>25</sup>	NOTN	Eocene (34.07 ± 0.10 mya: Priabonian) <sup>26</sup>	Florissant, United States of America
<i>Tribochrysa inaequalis</i> Scudder <sup>30</sup>	NOTN	Eocene (34.07 ± 0.10 mya: Priabonian) <sup>26</sup>	Florissant, United States of America
<i>Tribochrysa firmata</i> Scudder <sup>28</sup>	NOTN	Eocene (34.07 ± 0.10 mya: Priabonian) <sup>26</sup>	Florissant, United States of America
<i>Paleochrysopa monteilsensis</i> Séméria and Nel <sup>31</sup>	CHRN	Eocene (Priabonian) <sup>31</sup>	Monteils Formation, France
<i>Nothochrysa stampieni</i> Nel and Séméria <sup>32</sup>	NOTN	late Oligocene <sup>2</sup>	Aix-en-Provence, France
<i>Archaeochrysa creedei</i> (Carpenter) <sup>33</sup>	NOTN	late Oligocene <sup>34</sup>	Creede, United States of America
<i>Nothochrysa praeclara</i> Statz <sup>35</sup>	NOTN	Miocene (Aquitanian) <sup>2</sup>	Rott, Germany
<i>Pronothochrysa vivesi</i> Peñalver, Nel, and Martínex-Delclòs <sup>36</sup>	NOTN	Miocene (Burdigalian?) <sup>37</sup>	Ribesalbes, Spain
<i>Chrysopa glaesaria</i> Engel and Grimaldi <sup>38</sup>	CHRN	Miocene (15–20 mya: Burdigalian-Langhian) <sup>39</sup>	Dominican Amber
<i>Chrysopa vetula</i> Engel and Grimaldi <sup>38</sup>	CHRN	Miocene (15–20 mya: Burdigalian-Langhian) <sup>39</sup>	Dominican Amber
<i>Leucochrysa prisca</i> Engel and Grimaldi <sup>38</sup>	CHRN	Miocene (15–20 mya: Burdigalian-Langhian) <sup>39</sup>	Dominican Amber
<i>Chrysopa miocenea</i> Makarkin <sup>40</sup>	CHRN	Middle/late Miocene <sup>41</sup>	Stavropol, Russia
<i>Chrysopa martynovae</i> Makarkin <sup>40</sup>	CHRN	Middle/late Miocene <sup>41</sup>	Stavropol, Russia
<i>Chrysopa stavropolitana</i> Makarkin <sup>40</sup>	CHRN	Middle/late Miocene <sup>41</sup>	Stavropol, Russia
<i>Chrysopa sarmatica</i> Handschin <sup>42</sup>	CHRN	Late Miocene <sup>43</sup>	Delenii, Romania
<i>Hypochrysa hercyniensis</i> Schlüter <sup>18</sup>	NOTN	Pliocene (Piacenzian) <sup>44</sup>	Willerhausen, Germany

1, Panfilov (1980); 2, Rasnitsyn and Zherikhin (2002); 3, Martynov (1927); 4, Nel *et al.* (2005); 5, Jepson *et al.* (2012); 6, Makarkin (1997); 7, Makarkin *et al.* (2012); 8, Ren and Guo (1996); 9, Yang and Hong (1990); 10, Ponomarenko (1992); 11, Martins-Neto and Vulcano (1989); 12, Martill and Heimhofer (2008); 13, Martins-Neto (2003); 14, Martins-Neto (1997); 15, Makarkin (1994); 16, Willmann and Brooks (1991); 17, Chambers *et al.* (2003), and see discussion by Archibald *et al.* (2006); 18, Schlüter (1982); 19, Willmann (1993); 20, Makarkin and Archibald (2013); 21, Archibald *et al.* (2010); 22, Wolfe *et al.* (2003); 23, Moss *et al.* (2005); 24, Makarkin (2014); 25, Cockerell (1914); 26, Evanoff *et al.* (2001); 27, Adams (1967); 28, Scudder (1890); 29, Cockerell (1909); 30, Scudder (1885); 31, Séméria and Nel (1990); 32, Nel and Séméria (1986); 33, Carpenter (1935); 34, Lanphere (2000); 35, Statz (1936); 36, Peñalver *et al.* (1995); 37, Barron *et al.* (2010); 38, Engel and Grimaldi (2007); 39, Iturralde-Vinent and MacPhee (1996); 40, Makarkin (1991); 41, Goncharova (1989); 42, Handschin (1937); 43, Sziráki and Dulai (2002); 44, Thil *et al.* (2012). CHRN, Chrysopinae; LIMN, Limaiinae; NOTN, Nothochrysiniae; mya, million years ago.

Park, near the town of Smithers in northwestern British Columbia, Canada. It was collected under BC Parks park use permit SK08116495.

Driftwood Canyon is the northernmost known occurrence of the series, which were deposited in early Eocene lake basins scattered over roughly 1000 km southeast to Republic in north-central Washington, United States of America (Archibald *et al.* 2011). This fossil, like many from Driftwood Canyon, was recovered from very fine-grained shale, and, unlike fossils from other Okanagan Highlands localities, was preserved only on one side of the split rock, without a counterpart. Fossil insects there are commonly found in layers that are at times very dense with insect fossils. This piece of shale, roughly 65 × 20 cm also bears wings of Ichneumonidae (Hymenoptera), Tipulidae (Diptera), various Sciaroidea (Diptera) wings and bodies, as well as other insect body parts (RBCM numbers RBCM.EH2014.033.0001.002 to RBCM.EH2014.033.0001.009). Driftwood Canyon insects often show a notably fine degree of perseveration (*e.g.*, see Archibald *et al.* 2011, fig. 6).

A preliminary age for Driftwood Canyon sediments of  $51.77 \pm 0.34$  million years ago (mya) is indicated by U–Pb analysis of zircons recovered from a tephra layer intercalated within the fossil-bearing shale (Mortensen and Archibald work in progress cited by Moss *et al.* 2005).

Okanagan Highlands sites preserved cooler (mostly upper microthermal) montane forests during the warmest sustained interval of the Cenozoic; 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 insect fauna has been extensively collected in recent years by S.B.A. (with Greenwood and associates). Neuroptera are represented at this locality by the families Chrysopidae and Osmylidae. Chrysopids were recently the first named species from this site (Makarkin and Archibald 2013). Osmylidae and Raphidioptera are known by one undescribed species each (S.B.A. and V.N.M., personal observation).

### Terminology

We use the venational terminology of Kukulová-Peck and Lawrence (2004) as modified by Yang *et al.* (2012), except for anal veins, which in general follows that applied to other Neoptera by,

for example, Béthoux (2005) and Béthoux and Jarzembowski (2010) wherein all anal veins are considered as branches of the anterior analis. Crossveins are designated after the longitudinal veins with which are they connected and are numbered in sequence from the wing base, *e.g.*, 1scp-r, first (proximal-most) crossvein connecting ScP and R/RA; icu, crossvein between CuA and CuP. Terminology of wing spaces and details of venation (*e.g.*, veinlets) follows Oswald (1993).

Abbreviations: AA1–AA3, first to third branches of anterior anal vein; CuA, anterior cubitus; CuP, posterior cubitus; *im*, intramedian cell; MA and MP, anterior and posterior branches of media; Psc, pseudocubitus; Psm, pseudomedia; RA, anterior radius; RP, posterior radius; RP1, proximal-most branches of RP; ScP, subcosta posterior.

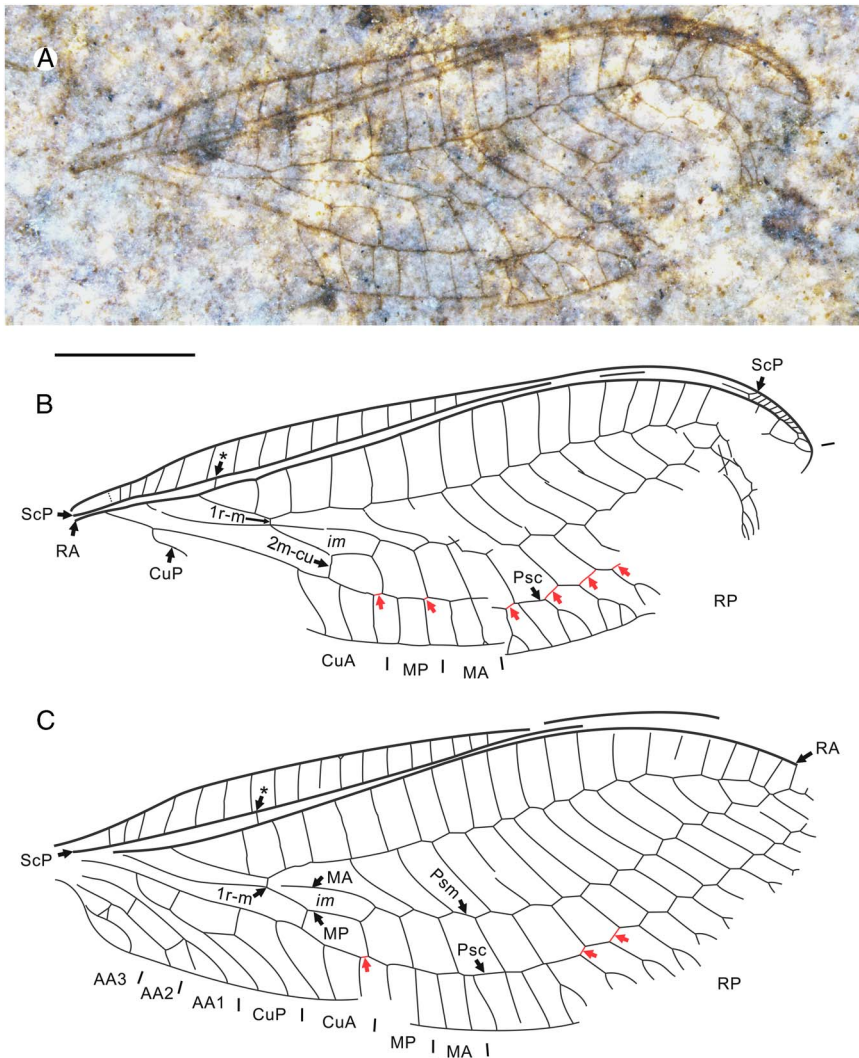
### Genus *Archaeochrysa* Adams (Chrysopidae: Nothochrysinae)

#### *Archaeochrysa sanikwa* Archibald and Makarkin, new species (Figs. 1A, 1B)

**Diagnosis.** Forewing may be distinguished from that of other species of the genus by a combination of the following character states: 2 m-cu located slightly distad middle of intramedian cell (slightly proximad middle of intramedian cell in *A. profracta* Makarkin and Archibald; distinctly proximad in *A. fracta* Adams, *A. paranervis* Adams, *A. creedei* (Carpenter)); sides (MA and MP) of intramedian cell converging basally at low angle (sides of intramedian cell parallel and converging basally at steeper angle in *A. paranervis*, *A. creedei*); distance from origin of RP to crossvein 1r-m markedly shorter than length of intramedian cell (nearly equal in *A. profracta*, *A. paranervis*, *A. creedei*); only one crossvein of Psc lost, others confidently identified (most crossveins lost or indefinable in *A. profracta*); basal crossvein 1scp-r located between origin of RP, proximal-most crossvein between RA, RP (between two proximal crossveins between RA, RP in *A. profracta*).

**Etymology.** The specific epithet *sanikwa* was suggested to us by Elders of the Wet'suwet'en Nation of northwest British Columbia, whose traditional territory includes Driftwood Canyon

**Fig. 1.** *Archaeochrysa* species. (A) *A. sanikwa* **new species** from Driftwood Canyon, holotype RBCM. EH2014.033.0001.001, photograph; (B) same, drawing (both converted to standard view, with apex to the right); (C) *A. profracta* Makarkin and Archibald (2013) from McAbee, holotype UCCIPR L-18F-1527, re-drawn from Makarkin and Archibald (2013) with new labelling and addition of 1scp-r. Crossveins of the pseudocubitus (Psc) and proximal part of outer gradate series (proximal RP5) are shown in red and further indicated by red arrows. The asterisk (\*) indicates 1scp-r, the crossvein connecting ScP and RA. Scale = 2 mm (all to scale).



Provincial Park. It is formed from the word *sanikwa* (or spelled *Sani kwa*) in the Wet'suwet'en language, which refers to the transformation of insects, specifically metamorphosis as seen in butterflies, but here referring to the appearance of this ancient insect in our time. It also makes reference here to the Wet'suwet'en connection to the environment.

**Material.** Holotype: RBCM.EH2014.033.0001.001 (original collection number: SBA 4922), part only. An almost complete forewing, mostly well preserved but slightly crumpled and torn. Housed in the collection of the Royal British Columbia Museum, Victoria, British Columbia, Canada. Collected by S.B.A. at Driftwood Canyon on 13 July 2008.

**Description.** Forewing 10.5 mm long; 3.8 mm wide as preserved (estimated complete width 3.9 mm). Costal space moderately wide, most dilated at level of proximal-most ra-rp crossvein. Humeral veinlet not distinctly visible. Subcostal veinlets simple, 16 in number (proximal-most pterostigmal region), rather closely spaced. Pterostigma rather distinct, only slightly darker than other membrane as preserved; presence of incorporated veinlets, crossveins unclear. ScP long, entering wing margin rather far from apex. Subcostal space narrow; basal crossvein 1scp-r located between origin of RP, proximal-most crossvein between RA, RP. RA entering margin at wing apex, strongly zigzagged apically, with 10 short distal veinlets. RA space broad, with 19 crossveins (distal ones not completely preserved). Stem of RP slightly zigzagged, with 11 branches (or 12; distal-most branch possibly not preserved); all preserved branches deeply forked except distal-most; three branches with additional shallower fork of one of branch each. Basal crossvein 1r-m very short, connecting stem of RP, stem of M at its fork. M dividing into MA, MP far distad origin of RP. MA strongly arched, deeply forked at Psc; MP zigzagged, deeply forked at Psc; MA, MP weakly divergent towards Psc. Between MA, MP one crossvein before Psc. Intramedian cell rather long, narrow, tapering basally. Psm weakly developed, strongly zigzagged. Crossvein 2m-cu (between intramedian cell, CuA) shifted distally, placed in distal portion of intramedian cell. CuA with three simple branches. CuA continuing into well-developed Psc, which continues into outer gradate series of crossveins. Basal part of CuP; other posterior portions of forewing (rest of CuP, licu, 2icu, anal veins) not preserved. Two gradate series of crossveins parallel; inner series with 11 crossveins distal to MA; outer series incompletely preserved.

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

**Remarks.** The two species *Archaeochrysa sanikwa* and *A. profracta* from Okanagan Highlands are certainly closely related (see Figs. 1B, 1C); both are from the interior of British Columbia, Driftwood Canyon and McAbee and both are

from the mid-Ypresian, with a million years or so separating them (see Table 1). Their venation differs only in small details. However, *Archaeochrysa sanikwa* is hypothesised to be more primitive than the McAbee species (see below).

## Discussion

Some character states found in the new species are of phylogenetic interest.

(1) *The shape of the intramedian cell.* Species of *Archaeochrysa* may be divided into two groups based on the shape of the intramedian cell (*im*).

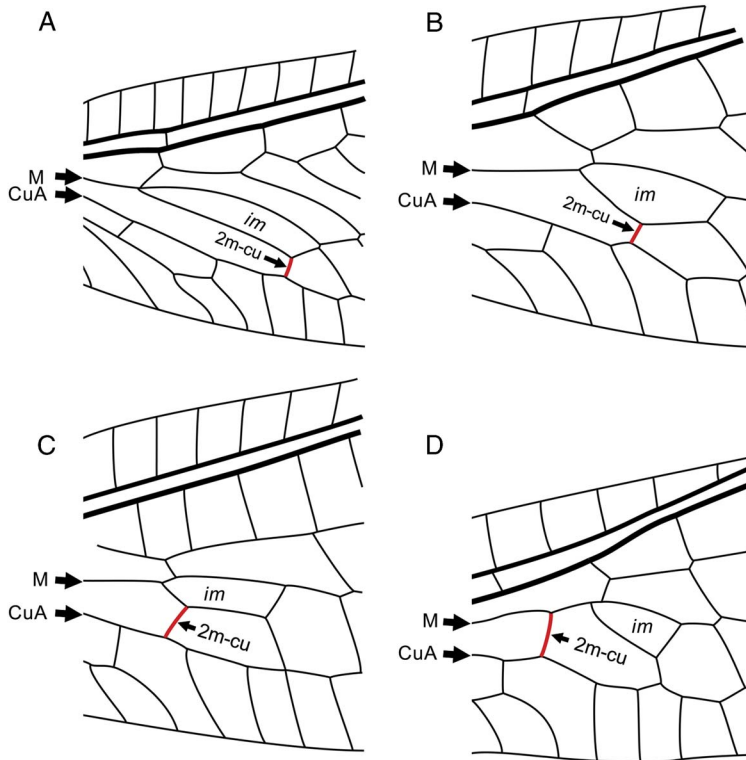
Condition 1: *im* is narrow, quite long, tapering, that is, its sides (MA and MP) converging basally at a low angle (Figs. 1B, 1C; and see Makarkin and Archibald 2013, fig. 15). This includes the early Eocene *A. profracta* and *A. sanikwa* from the Okanagan Highlands, and *A. fracta* from the late Eocene of Florissant. This condition is very likely plesiomorphic for the subfamily, as a similar configuration is found in the vast majority of Mesozoic chrysopid species (including all Limaiinae; Fig. 2A), and MA and MP also diverge at acute angle in other families of Neuroptera with generalised venation. The shape of *im* varies in other nothochrysinines, but never appears in such a plesiomorphic condition as this.

Condition 2: *im* differs by its sides (MA and MP) being more parallel (Fig. 2C), and MP basad 2m-cu converge at a steeper angle (*i.e.*, *im* remains wider basally: see Adams 1967, figs. 40, 41). This includes *A. paranervis* from Florissant and *A. creedei* from Oligocene of Creede. A similarly shaped *im* is found in all other fossil Nothochrysininae from the late Eocene Florissant and early Oligocene Creede deposits (*i.e.*, *Palaeochrysa* Scudder, *Tribochrysa* Scudder, *Dispetochrysa* Adams), and is also seen in many extant species (of *Nothochrysa* McLachlan, most *Pimachrysa* Adams, some *Kimochrysa* Tjeder) (Adams 1967, figs. 1–3; Tjeder 1966, fig. 839; Brooks and Barnard 1990, figs. 545, 561).

(2) *The position of the crossvein 2m-cu.* The position of this crossvein is especially illustrative of evolutionary trends in chrysopid wing venation (see Makarkin and Archibald 2013). Several conditions may be identified for the location of crossvein 2m-cu in the family.

Condition 1: located in the distal part of an elongated *im* (Fig. 2A); this condition is most

**Fig. 2.** Evolution of the position of the crossvein 2m-cu in Chrysopidae. (A) *Mesypochrysa magna* Makarkin from the Early Cretaceous, re-drawn from Makarkin (1997); (B) *Asiachrysa tadushiella* Makarkin from the early/middle Eocene, re-drawn from Makarkin (2014); (C) *Palaeochrysa stricta* Scudder from the late Eocene, re-drawn from Adams (1967); (D) the extant *Kimochrysa africana* (Kimmins), re-drawn from Tjeder (1966). Drawings are slightly schematic. To various scales.



likely plesiomorphic in the family. This occurs in the vast majority of Mesozoic Chrysopidae, and in the limaiine genus *Protochrysa* that is found in the early Eocene of Denmark and the Okanagan Highlands (Willmann and Brooks 1991; Makarkin and Archibald 2013). The only other occurrence of this condition is in the enigmatic extant monotypic genus *Leptochrysa* Adams and Penny from South America, which has 2m-cu positioned distally (Adams and Penny 1992b, fig. 10); however, this genus might belong to the Limaiinae (Makarkin and Archibald 2013).

Condition 2: located slightly distad mid-point of *im*; this condition is found in the new species and is most likely plesiomorphic in Nothochrysinæ (Fig. 1B).

Condition 3: located nearly at middle of *im* (Fig. 2B); this occurs in the early Eocene

*Cimbrochrysa* Schlüter and *Stephenbrooksia* Willmann, and the early/middle Eocene *Asiachrysa* Makarkin.

Condition 4: located slightly proximad mid-point of *im*; this occurs in the early Eocene *Danochrysa* Willmann, *Okanaganochrysa* Makarkin and Archibald, some *Adamsochrysa* Makarkin and Archibald, and *Archaeochrysa profracta* (Fig. 1C).

Condition 5: located distinctly in the proximal part of *im* (Fig. 2C); this occurs in the majority of Nothochrysinæ genera: some early Eocene species (of *Pseudochrysa* Makarkin and Archibald; and *Adamsochrysa wilsoni* Makarkin and Archibald), and all fossil species from the late Eocene onward (except the Pliocene *Hypochrysa* Hagen) and some extant (those of *Nothochrysa*, most *Pimachrysa*, and some *Kimochrysa*: Adams 1967, figs. 1–4; Tjeder 1966, figs. 785, 839; New 1980,

figs. 42, 44; Brooks and Barnard 1990, figs. 527, 545, 561).

Condition 6: located proximad *im* (Fig. 2D); this occurs in the Pliocene to Recent genus *Hypochrysa* and in the majority of extant genera: *Triplochrysa* Kimmins, *Pamochrysa* Tjeder, *Asthenochrysa* Adams, most *Dictyochrysa* Esben-Petersen, some *Pimachrysa* and *Kimochrysa* (Adams 1957, fig. 1; 1967, fig. 5; Tjeder 1966, figs. 822, 835; Brooks and Barnard 1990, figs. 533, 539, 554, 567).

The evolutionary trend of the location of 2m-cu in Chrysopidae is clear, shifting from a distinctly distal position in the Mesozoic Limaiinae to a very proximal one in most extant Nothochrysinae. *Archaeochrysa sanikwa* occupies an important place in this chain, as the only representative of the Nothochrysinae bearing the plesiomorphic condition for the subfamily (condition 2).

(3) *The crossveins of Psc*. The pseudocubitus is formed by the alignment of sections of branches of MA, MP, and Rs, and the crossveins connecting them. The formation of the Psc is a clearly apomorphic condition of Chrysopidae. The Psc continues CuA; its crossveins are part of an outer gradate series, running from CuP to the anterior trace of RP (at most). The configuration of the Psc in Nothochrysinae may also be categorised in distinct conditions.

Condition 1: all crossveins of Psc are present and may be confidently identified. This is most likely primitive in the subfamily (and family) and is found in the Eocene *Asiachrysa*, *Pseudochrysa*, and *Tribochrysa*.

Condition 2: only one crossvein is lost, usually between MA and RP1 (these are touching at Psc), other crossveins are present and identified; it is seen in *Archaeochrysa sanikwa* (Fig. 1B), *A. creedei*, and *A. fracta*.

Condition 3: most crossveins of the proximal Psc are lost or not identifiable; this is found in most fossil Nothochrysinae (e.g., *Cimbrochrysa*, *Stephenbrooksia*, *Danochrysa*, *Okanaganochrysa*, *Adamsochrysa*, *Archaeochrysa profracta* (Fig. 1C)), and in some extant (e.g., *Dictyochrysa*).

Condition 4: Psc is long and straight (or so) with no crossveins identifiable as such with certainty, a most derived condition seen in few Nothochrysinae (late Oligocene to Recent): some *Nothochrysa* and *Pronothochrysa* Peñalver, Nel, and Martínez-Delclòs.

This phylogenetic trend in the development of Psc is also distinct when compared among chrysopid subfamilies. Psc is poorly developed in the predominantly Mesozoic Limaiinae: most of its species show condition 1, only some have condition 2 (e.g., some species of *Mesypochrysa* Martynov from the Early Cretaceous locality of Baissa in Transbaikalia; Makarkin 1997, figs. 1, 4, 13), and conditions 3 and 4 are never known. In all Chrysopinae (which dominate the family today) Psc is very well developed; their species exhibit only conditions 3 and 4, and never have the more plesiomorphic conditions. In the subfamily Apochrysinae (unknown in the fossil record), only condition 4 occurs (see Brooks and Barnard 1990).

Therefore, the forewing venation of this species is very plesiomorphic compared with the vast majority species of Nothochrysinae, both fossil and extant.

*Archaeochrysa sanikwa* is the smallest species of the genus. In general, most chrysopids from the Driftwood Canyon locality are small; in fact, *Pseudochrysopa harveyi* Makarkin and Archibald is the smallest known fossil member of the family, with forewings only 7.2 mm long as preserved, probably about 8.5 mm long in life (Makarkin and Archibald 2013).

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