

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

S. Bruce Archibald, Vladimir N. Makarkin<sup>1</sup>

**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

Received 6 March 2014. Accepted 15 May 2014. First published online 23 September 2014.

**S.B. Archibald**, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada; and Museum of Comparative Zoology, Cambridge, Massachusetts, United States of America; and Royal BC Museum, Victoria, British Columbia, Canada

**V.N. Makarkin**,<sup>1</sup> Institute of Biology and Soil Sciences, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia

<sup>1</sup>Corresponding author (e-mail: vnmakarkin@mail.ru).

Subject editor: Bradley Sinclair

doi:10.4039/tce.2014.53

<http://zoobank.org/urn:lsid:zoobank.org:pub:5C9ADAEF-844A-47B7-A822-D0648F48DFA4>

**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 preservation (*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 Osmyliidae. Chrysopids were recently the first named species from this site (Makarkin and Archibald 2013). Osmyliidae 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.

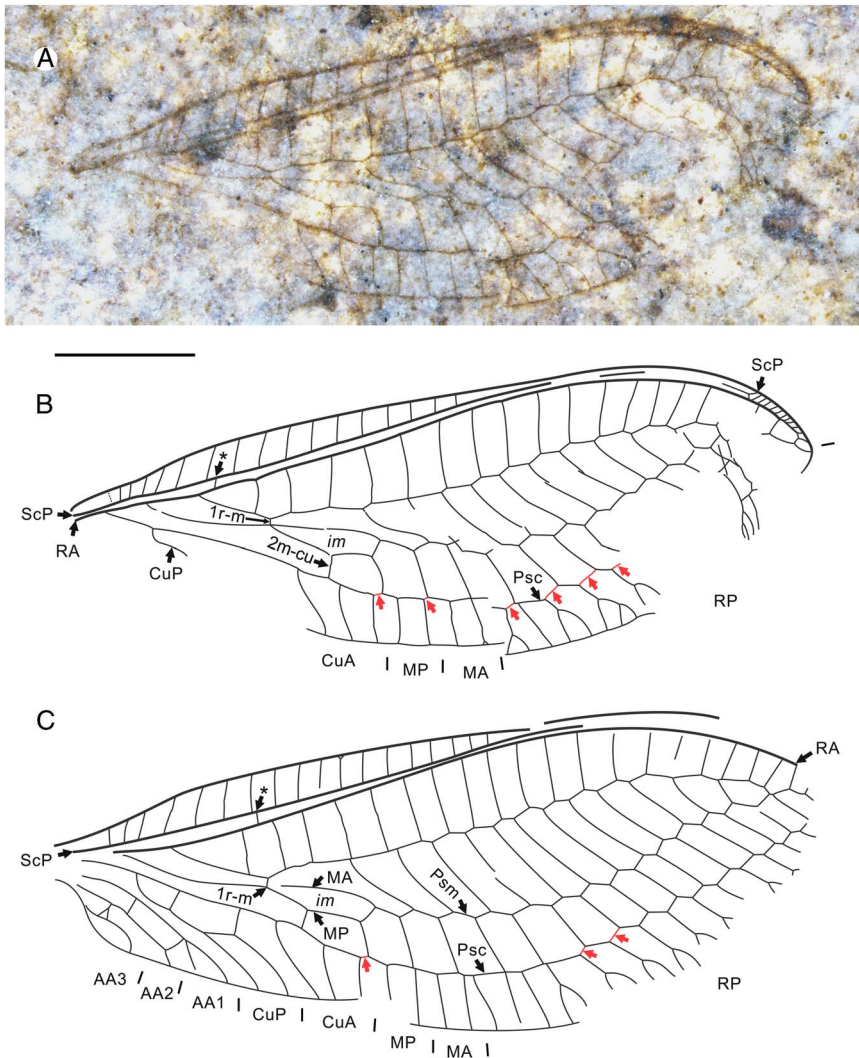
### Genus *Archaeochrysa* Adams (Chrysopidae: Nothochrysinae)

#### *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 (proximad 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*).

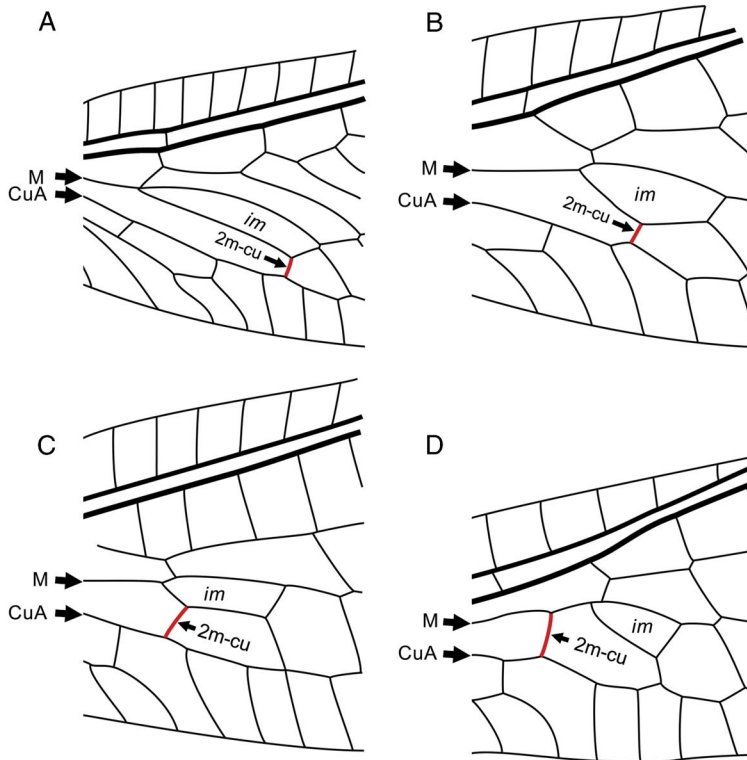
Condition 1: *im* is narrow, quite long, tapering, that is, its sides (MA and MP) converging basally at a low angle (Figs. 1B, 1C; and see Makarkin and Archibald 2013, fig. 15). This includes the early Eocene *A. profracta* and *A. sanikwa* from the Okanagan Highlands, and *A. fracta* from the late Eocene 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 proximal 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 Nothochrysininae. *Archaeochrysa sanikwa* occupies an important place in this chain, as the only representative of the Nothochrysininae 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 Nothochrysininae 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 Nothochrysininae (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 Nothochrysininae (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 Apochrysininae (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 Nothochrysininae, 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).

## Acknowledgements

The authors thank the Elders of the Wet'suwet'en Nation for providing us with the word *sanikwa* with which to form the specific epithet, and Mike Ridsdale of the Office of the Wet'suwet'en for connecting us with the Elders and communicating their wishes to us (missiyh: thank you); BC Parks, and in particular John Howard (Babine Area Supervisor, BC Parks) for permitting and facilitating work at Driftwood Canyon; the above and other people of the Smithers, British Columbia region for their warm welcome at Driftwood Canyon Provincial Park. We thank Richard Hebda (curator) and Marji Johns (collections manager) at the Royal British Columbia Museum for facilitating this specimen's study, and Marlow Pellatt of Parks Canada of access to microphotography equipment. Funding for S.B.A. has been generously provided by Rolf Mathewes (Simon Fraser University) for laboratory space and general funding, and David



Greenwood (Brandon University, Brandon, Manitoba, Canada) who also provided Driftwood Canyon fieldwork support. The study is partly supported by a President's Grant for Government Support of the Leading Scientific Schools of the Russian Federation No.HIII-150.2014.4, and the grant of the Far Eastern Branch of the Russian Academy of Sciences No. 12-I-II30-03 for V.M.

## References

- Adams, P.A. 1957. A new genus and new species of Chrysopidae from the western United States, with remarks on the wing venation of the family (Neuroptera). *Psyche*, **63**: 67–74.
- Adams, P.A. 1967. A review of the Mesochrysinæ and Nothochrysinæ (Neuroptera: Chrysopidae). *Bulletin of the Museum of Comparative Zoology*, **135**: 215–238.
- Adams, P.A. and Penny, N.D. 1992a. Review of the South American genera of Nothochrysinæ (Insecta: Neuroptera: Chrysopidae). *In Current research in Neuropterology. Proceedings of the fourth international symposium on Neuropterology. Edited by M. Canard, H. Aspöck, and M.W. Mansell. SACCO, Toulouse, France. Pp. 35–41.*
- Adams, P.A. and Penny, N.D. 1992b. New genera of Nothochrysinæ from South America (Neuroptera: Chrysopidae). *Pan-Pacific Entomologist*, **68**: 216–221.
- 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., Cover, S.D., and Moreau, C.S. 2006. Bulldog ants of the Eocene Okanagan Highlands, and the history of the subfamily (Hymenoptera: Formicidae: Myrmecinae). *Annals of the Entomological Society of America*, **99**: 487–523.
- 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.
- Barron, E., Rivas-Carballo, R., Postigo-Mijarra, J.M., Alcalde-Olivares, C., Vieira, M., Castro, L., *et al.* 2010. The Cenozoic vegetation of the Iberian Peninsula: a synthesis. *Review of Palaeobotany and Palynology*, **162**: 382–402.
- Béthoux, O. 2005. Wing venation pattern of Plecoptera (Insecta: Neoptera). *Illiesia*, **1**: 52–81.
- Béthoux, O. and Jarzembowski, E.A. 2010. New basal neopterans from Writhlington (UK, Pennsylvanian). *Alavesia*, **3**: 87–96.
- Bigler, F. 1984. Biological control by chrysopids: integration with pesticides. *In Biology of Chrysopidae. Edited by M. Canard, Y. Séméria, and T.R. New. Dr. W. Junk Publishers, The Hague, The Netherlands. Pp. 233–245.*
- Brooks, S.J. and Barnard, P.C. 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). *Bulletin of the British Museum of Natural History (Entomology)*, **59**: 117–286.
- Carpenter, F.M. 1935. Tertiary insects of the family Chrysopidae. *Journal of Paleontology*, **9**: 259–271.
- Chambers, L., Pringle, M., Fitton, G., Larsen, L.M., Pedersen, A.K., and Parrish, R. 2003. Recalibration of the Palaeocene-Eocene boundary (P-E) using high precision U-Pb and Ar-Ar isotopic dating. EGS-AGU-EUG Joint Assembly, Nice, 6–11 April 2003. *Geophysical Research Abstracts* 5: 9681. Copernicus Publications, Göttingen, Germany.
- Cockerell, T.D.A. 1909. Two fossil Chrysopidae. *The Canadian Entomologist*, **41**: 218–219.
- Cockerell, T.D.A. 1914. New and little-known insects from the Miocene of Florissant, Colorado. *Journal of Geology*, **22**: 714–724.
- Engel, M.S. and Grimaldi, D. 2007. The neuropterid fauna of Dominican and Mexican amber (Neuroptera: Megaloptera, Neuroptera). *American Museum Novitates*, **3587**: 1–58.
- Evanoff, E., McIntosh, W.C., and Murphey, P.C. 2001. Stratigraphic summary and <sup>40</sup>Ar/<sup>39</sup>Ar geochronology of the Florissant Formation, Colorado. *In Fossil flora and stratigraphy of the Florissant Formation, Colorado. Volume 1. Proceedings of the Denver Museum of Nature and Science. Volume 4. Edited by E. Evanoff, K. Gregory-Wodzicki, and K. Johnson. Denver Museum of Nature and Science, Denver, Colorado. Pp. 1–16.*
- Goncharova, I.A. 1989. Dvustvorchatye molluski Tarkhanskogo i Chokrakskogo basseinov [Bivalve molluscs of Tarkhanian and Tshokrakian Basins]. *Trudy Paleontologicheskogo Instituta*, **234**: 1–200. (In Russian).
- 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.
- Handschin, E. 1937. Fossile Insekten aus Siebenbürgen. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **17**: 25–29.
- Iturralde-Vinent, M.A. and MacPhee, R.D.E. 1996. Age and paleogeographical origin of Dominican amber. *Science*, **273**: 1850–1852.
- Jepson, J.E., Makarkin, V.N., and Coram, R.A. 2012. Lacewings (Insecta: Neuroptera) from the Lower Cretaceous Purbeck Limestone Group of southern England. *Cretaceous Research*, **34**: 31–47.
- Kovanci, B. and Canbulat, S. 2007. A new species of the genus *Nothochrysa* McLachlan 1868 from northwestern Turkey (Neuroptera: Chrysopidae) with a key to western Palearctic species. *Annales de la Société Entomologique de France (N.S.)*, **43**: 165–168.

- Kukulová-Peck, J. and Lawrence, J.F. 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. *European Journal of Entomology*, **101**: 95–144.
- Lanphere, M.A. 2000. Duration of sedimentation of the Creede Formation from 40Ar/39Ar age. *In* Ancient Lake Creede: its volcano-tectonic setting, history of sedimentation, and relation to mineralization in the Creede Mining District, Special Paper. Volume 346. *Edited by* P.M. Bethke and R.L. Hay. Geological Society of America, Boulder, Colorado. Pp. 71–76.
- Makarkin, V.N. 1991. Miotsenovyie setchatokrylye (Neuroptera) Severnogo Kavkaza i Sikhote-Alinya [Miocene Neuroptera from North Caucasus and Sikhote-Alin']. *Paleontologicheskii Zhurnal*, **1991**: 57–68. (In Russian, English summary).
- Makarkin, V.N. 1994. Upper Cretaceous Neuroptera from Russia and Kazakhstan. *Annales de la Société Entomologique de France*, **30**: 283–292.
- Makarkin, V.N. 1997. Fossil Neuroptera of the lower Cretaceous of Baisa, East Siberia. Part 3. Chrysopidae. *Spixiana*, **20**: 107–118.
- Makarkin, V.N. 2014. A new fossil green lacewing (Neuroptera: Chrysopidae) from the Eocene Tadushi Formation, eastern Sikhote-Alin. *Far Eastern Entomologist*, **272**: 1–7.
- Makarkin, V.N. and Archibald, S.B. 2013. A diverse new assemblage of green lacewings (Insecta: Neuroptera: Chrysopidae) from the Early Eocene Okanagan Highlands, western North America. *Journal of Paleontology*, **87**: 122–145.
- Makarkin, V.N., Yang, Q., Peng, Y.Y., and Ren, D. 2012. A comparative overview of the neuropteran assemblage of the Early Cretaceous Yixian Formation (China), with description of a new genus of Psychopsidae (Insecta: Neuroptera). *Cretaceous Research*, **35**: 57–68.
- Martill, D.M. and Heimhofer, U. 2008. Stratigraphy of the Crato Formation. *In* The Crato fossil beds of Brazil. Window into an ancient world. *Edited by* D.M. Martill, G. Bechly, and R.F. Loveridge. Cambridge University Press, Cambridge, United Kingdom. Pp. 25–43.
- Martins-Neto, R.G. 1997. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. X - Descrição de novos táxons (Chrysopidae, Babinskaiidae, Myrmeleontidae, Ascalaphidae e Psychopsidae). *Revista Universidade de Guarulhos, Série Ciências Exatas e Tecnológicas*, **2**: 68–83.
- Martins-Neto, R.G. 2003. The Santana Formation Paleontofauna reviewed. Part I – Neuropteroida (Neuroptera and Raphidioptera): systematic and phylogeny, with description of new taxa. *Acta Geologica Leopoldensia*, **25**: 35–66.
- Martins-Neto, R.G. and Vulcano, M.A. 1989. Neurópteros (Insecta: Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. I - Família Chrysopidae. *Anais da Academia Brasileira de Ciências*, **60**: 189–201.
- Martynov, A.V. 1927. Jurassic fossil insects from Turkestan. 7. Some Odonata, Neuroptera, Thysanoptera. *Izvestia Akademii Nauk SSSR (Series 6)*, **21**: 757–768.
- 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., Delclòs, X., and Hutin, A. 2005. Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta: Neuroptera). *Annales de la Société Entomologique de France (N.F.)*, **41**: 29–68.
- Nel, A. and Séméria, Y. 1986. Une nouvelle espèce de Chrysopide fossile du Stampien supérieur (Oligocène) d'Aix-en-Provence *Notochrysa stampieni* n. sp. (Neuroptera, Chrysopidae, Notochrysinæ). *Neuroptera International*, **4**: 23–30.
- New, T.R. 1980. A revision of the Australian Chrysopidae (Insecta: Neuroptera). *Australian Journal of Zoology, Supplementary Series*, **77**: 1–143.
- 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.
- Panfilov, D.V. 1980. Novye predstaviteli setcharokrylykh (Neuroptera) iz yury Karatau [New representatives of lacewings (Neuroptera) from the Jurassic of Karatau]. *In* Iskopaemye nasekomye mezozoya [Fossil insects of the Mesozoic]. *Edited by* V.G. Dolin, D.V. Panfilov, A.G. Ponomarenko, and L.N. Pritykina. Naukova Dumka, Kiev, Ukraine. Pp. 82–111. (In Russian).
- Peñalver, E., Nel, A., and Martínez-Delclòs, X. 1995. New Nothochrysinæ from the Spanish Miocene (Neuroptera, Chrysopidae). *Bulletin de la Société entomologique de France*, **100**: 481–487.
- Ponomarenko, A.G. 1992. Novye setchatokrylye (Insecta, Neuroptera) iz mezozoya Mongolii [New lacewings (Insecta, Neuroptera) from the Mesozoic of Mongolia]. *In* Novye taksony iskopaemykh bespozvonochnykh Mongolii [New taxa of fossil invertebrates of Mongolia]. *Transactions of the joint Soviet-Mongolian paleontological expedition. Volume 41. Edited by* T.A. Grunt, Nauka Press, Moscow, Pp. 101–111. (In Russian)
- Rasnitsyn, A.P. and Zherikhin, V.V. 2002. 4. Appendix: alphabetic list of selected insect fossil sites. 4.1. Impression fossils. *In* History of insects. *Edited by* A.P. Rasnitsyn and D.L.J. Quicke. Kluwer Academic Publishers, Dordrecht, The Netherlands. Pp. 437–444.
- Ren, D. and Guo, Z.G. 1996. On the new fossil genera and species of Neuroptera (Insecta) from the Late Jurassic of northeast China. *Acta Zootaxonomica Sinica*, **21**: 461–479.
- Ridgway, R.L. and Murphy, W.L. 1984. Biological control in the field. *In* Biology of Chrysopidae. *Edited by* M. Canard, Y. Séméria, and T.R. New. Dr. W. Junk Publishers, The Hague, The Netherlands. Pp. 220–228.

- Schlüter, T. 1982. *Cimbrochrysa moleriensis* n. g. n. sp. und *Hypochrysa hercyniensis* n. sp., zwei fossile Chrysopidae-Arten (Insecta: Planipennia) aus dem europäischen Tertiär. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte, **1982**: 257–264.
- Scudder, S.H. 1885. Systematische Übersicht der fossilen Myriopoden, Arachnoideen und Insekten. In Handbuch der Palaeontologie. Abteilung 1. Palaeozoologie. Band 2. Mollusca und Arthropoda. Edited by K.A. Zittel. Verlag von R. Oldenbourg, Munich, Germany. Pp. 721–831.
- Scudder, S.H. 1890. The tertiary insects of North America. Report of the United States Geological Survey of the Territories, **13**: 1–734.
- Séméria, Y. and Nel, A. 1990. *Paleochrysopa monteilsensis* gen. et sp. nov., a new fossil of Chrysopidae from the Upper Eocene Formation of Monteils (France), with a review of the known chrysopid fossils (Insecta: Neuroptera). In Advances in Neuropterology. Proceedings of the third international symposium on Neuropterology. Edited by M.W. Mansell and H. Aspöck. South African Department of Agricultural Development Pretoria, South Africa. Pp. 27–32.
- Statz, G. 1936. Ueber neue Funde von Neuropteren, Panorpaten und Trichopteren aus den tertiären Schiefen von Rott am Siebengebirge. Decheniana, **93**: 208–255.
- Sziráki, G. and Dulai, A. 2002. Sarmatian (Late Miocene) arthropods from Tallya and neighbouring localities (Tokaj Mts, Hungary): preliminary report. Annales Historico-Naturales Musei Nationalis Hungarici, **94**: 31–44.
- Thil, C., Klotz, S., and Uhl, D. 2012. Palaeoclimate estimates for selected leaf floras from the late Pliocene (Reuverian) of Central Europe based on different palaeobotanical techniques. Turkish Journal of Earth Sciences, **21**: 1–25.
- Tjeder, B. 1966. Neuroptera-Planipennia. The lacewings of southern Africa. 5. Family Chrysopidae. In South African animal life. Volume 12. Edited by B. Hanström, P. Brinck, and G. Rudebec. Swedish Natural Science Research Council, Stockholm, Sweden. Pp. 228–534.
- Tulisalo, U. 1984. Biological control in the greenhouse. In Biology of Chrysopidae. Edited by M. Canard, Y. Séméria, and T.R. New. Dr. W. Junk Publishers, The Hague, The Netherlands. Pp. 228–233.
- Willmann, R. 1993. Insekten aus der Fur-Formation von Dänemark (Moler, ob. Paleozän / unt. Eozän?). 8. Zwei neue Vertreter der Chrysopidae (Neuroptera). Neues Jahrbuch für Geologie und Paläontologie. Monatshefte, **1993**: 239–245.
- Willmann, R. and Brooks, S.J. 1991. Insekten aus der Fur-Formation von Dänemark (Moler, ob. Paleozän/ unt. Eozän?). 6. Chrysopidae (Neuroptera). Meyniana, **43**: 125–135.
- Winterton, S.L. and Brooks, S.J. 2002. Phylogeny of the apochrysin green lacewings (Neuroptera: Chrysopidae: Apochrysininae). Annals of the Entomological Society of America, **95**: 16–28.
- Wolfe, J.A., Gregory-Wodzicki, K.M., Molnar, P., and Mustoe, G. 2003. Rapid uplift and then collapse in the Eocene of the Okanagan? Evidence from paleobotany [CD-ROM]. In Geological Association of Canada–Mineralogical Association of Canada–Society of Economic Geologists, Joint Annual Meeting, Vancouver, Abstracts. Geological Association of Canada – Mineralogical Association of Canada – Society of Economic Geologists, Vancouver, British Columbia, Canada.
- Yang, C.K. 1986. The subfamily Nothochrysininae new to China and a new species of the genus *Nothochrysa* (Neuroptera: Chrysopidae). Entomotaxonomia, **8**: 277–280.
- Yang, C.K. and Hong, Y.C. 1990. *Drakochrysa*, an Early Cretaceous new genus of Chrysopidae (Insecta: Neuroptera) from Laiyang Basin, Shandong Province. Geoscience, **4**: 15–26. (In Chinese, English summary).
- Yang, Q., Makarkin, V.N., Winterton, S.L., Khramov, A.V., and Ren, D. 2012. A remarkable new family of Jurassic insects (Neuroptera) with primitive wing venation and its phylogenetic position in Neuropterida. Public Library of Science One, **7**: e44762.