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Historical Biology

# First green lacewing (Insecta: Neuroptera: Chrysopidae) from the Paleocene Sanshui Basin of Guangdong, South China

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## ABSTRACT

*Sinonothochrysa zhangi* Huang and Nel gen. et sp. nov., a new genus and species of nothochrysine lacewing, is described and illustrated from the Paleocene Buxin Formation, Sanshui Basina, Foshan City, Guangdong Province, South China. The new taxon is the oldest described representative and first report this subfamily in China. It is also the first formally described fossil insects from the Buxin Formation of the Sanshui Basin.

## KEYWORDS

Neuroptera; Nothochrysinae; fossil insects; Buxin Formation; middle Paleocene

## Introduction

The family Chrysopidae, also called green lacewings due to the color of their extant representatives, is a widespread group of Neuroptera, which has a quite rich fossil record, comprising more than 20 fossil genera and more than 60 fossil species (compared to other Neuroptera as the Myrmeleontidae) (Table. 1; http://fossilworks.org). Their oldest representatives are dated back from the Jurassic of China and Kazakhstan (e.g. Martynov 1927; Panfilov, 1980; Khramov et al. 2015), but their highest species diversity, in the fossil record, is known during the Paleogene. Representatives of the stem-group appear early in the evolutionary history of the family as the subfamily Limaiinae is known since the Jurassic period (Table. 1), suggesting that the family may be older.

Currently, the family is divided in four subfamilies (viz. Apochrysinae + Chrysopinae + Nothochrysinae + Limaiinae), with the Limaiinae is a strictly fossil subfamily. Each subfamilies present huge disparities in their fossil species diversity (Table. 1) since the subfamily Apochrysinae is completely absent from the fossil record while the two other extant subfamilies possess fossil representatives. Interestingly, while the majority of the fossil record of the Limaiinae is Mesozoic, this group survived the Cretaceous-Cenozoic crisis with some Paleocene and the Eocene representatives, viz. three species in the genus *Protochrysa* Willmann and Brooks, 1991 from the Paleocene-Eocene of Denmark and the Early Eocene of British Columbia (Nel et al. 2005; Makarkin and Archibald 2013). This scenario is very similar to the fate of the Mammalia Multituberculata that were very diverse during the Mesozoic and became extinct during the Paleocene, well after the K-T crisis. The fossil record of the crown group Chrysopidae is currently only represented by Cenozoic Nothochrysinae and Chrysopinae (Table 1).

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The position of the family Chrysopidae is not fully elucidated and alternative hypotheses are proposed depending on the methods or the analyzed data (e.g. Engel et al. 2018; Vasilikopoulos et al. 2020). Winterton et al. (2019) proposed a molecular phylogenetic analysis of the Chrysopidae, dating the separation of their stem group from their putative sister group Myrmeleontoidea from the late Triassic and their crown group from the early Cretaceous. However, it seems that the Chrysopidae would closely related to the clade (Mantispidae + Berothidae) according to recent molecular analyses (Vasilikopoulos et al. 2020: fig. 1) with a divergence estimate to the early Jurassic. However, the calibration used in this most recent work seem to provide questionable age for the group. In fact, Vasilikopoulos et al. (2020) used the chrysopid fossil species *Mesypochrysa cf. intermedia* to calibrate the crown-group (Chrysopidae + (Mantispidae + Berothidae)) using a soft minimum constrain set to 158.1 Ma (Vasilikopoulos et al., 2020: additional file 1: table S10), which fits with the datation of the Karabastau Formation of Kazakhstan, dated back to the Callovian/Kimmeridgian (Doludenko and Orlovskaya 1976a, Doludenko and Orlovskaya 1976b) or possibly Oxfordian–Kimmeridgian (Doludenko et al. 1990). Recent study on Yanliao Biota late assemblage i.e. Linglongta biota at the Guancaishan locality was considered correlate to Karatau biota of Kazakhstan (Huang 2015, 2016) that yielded some very similar insects such as *Cicadomorpha* (Fu et al. 2020). An ash layer appeared less one meter up the fossil insect layer at the Guancaishan locality providing a SIMS zircon U-Pb dating as 157.3±1.5 Ma that support Karabastau Formation is more likely an Oxfordian–Kimmeridgian age (Huang 2016). However, the Toarcian genus *Protoaristenymphes* Nel and Henrotay, 1994 is currently placed in the Mesozoic family Mesochrysopidae and the Chrysopoidea (a superfamily that also comprises the Mesozoic Ascalochrysidae), and would be the oldest known representative of this clade (Nel and Henrotay 1994; Yang et al. 2012; Makarkin et al. 2013), supporting a possible older age for the superfamily, more in accordance with Winterton et al. (2019), even if these last

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authors did not used *Protoaristenymphes* to calibrate theirs datations. Vasilikopoulos et al. (2020) also ignored the Mesochrysopidae and the genus *Protoaristenymphes* in their list of fossils used as calibration points. We are aware that the choice of fossil taxa in calibrations is difficult and that applying too much constraints on trees may results in dubious results, but, at least the putative oldest records of the concerned clades should be discussed. Therefore, we wonder if the clade or at least the Chrysopidae could be older than previously thought, and suggest that it would be interesting to explore the Neuroptera phylogeny testing different calibrations of the stem- and crown-groups for each family.

Herein we described a new genus and species of Nothochrysinae from the Paleocene, confirming the important diversity of this subfamily at that time.

**Geological setting**

The Paleogene deposit of the Sanshui Basin of South Guangdong Province, South China is developed and detailed hereafter (Fig. 1). This strata is divided into the Xinzhuangcun, the Buxin, the Baoyue, and the Huachong formations from bottom to top. Buxin Formation was established at 1964 for a set of lacustrine deposit comprised dark gray oil shale, mud stone, chalky clay, and sand stone. It was firstly considered as an Eocene or Early Oligocene strata. The age of the Buxin Formation was argued by authors based on different biochronometer with various opinions, summarized by Zhang et al. (1993): 1) Early Eocene by ostracodes, conchostracans, gastropods, and fishes; 2) Late Paleocene-Early Eocene by bivalves; 3) Early-Middle Eocene by plant fossils and sporo-pollen studies; 4) Middle Eocene by stoneworts. Later, a systematical biostratigraphic study on ostracods suggested that the Xinzhuangcun, Buxin, and Baoyue formations would be assigned to the Paleocene and the Huachong Formation would be assigned to the Early Eocene. Therefore, the above authors indicated that the age of Buxin Formation could be assigned to the Middle Paleocene (Zhang et al. 2008). A recent integrative

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study on China's Paleogene stratigraphy and timescale indicated that the age of Buxin Formation would range from 62.2 Ma to 59.2 Ma, i.e. late Danian to Selandian-Thanetian boundary, mainly based on a paleomagnetism study (Wang et al. 2019). According to this opinion, the age of the present fossil material could be even as old as 62 Ma.

Most isotopic dating of volcanic rocks in the Sanshui Basin used K-Ar method (Guangdong Probincial Bureau of Geology and Mineral Resources 1997) could not provide convincing geochronological ages. A Paleocene age of the Buxin Formation was also supported by a geochronological study that indicated that the volcanic eruption started at approximately 60 Ma in the Sanshui Basin. These authors got two set of ages by zircon U-Pb dating as 59.3±0.2 Ma and 56.2±0.3 Ma. The Buxin Formation is subdivided into four members as Honggang Member, Dagang Member, Fenggang Member, and Gaogang Member from bottom to top. The herein described fossil insect was collected from the lower part of the Honggang Formation. The volcanic rocks in the Paleogene of Sanshui Basin initially appeared in the Honggang Member and particularly occurred at the bottom of the Gaogang Member, and then were widely distributed in the lower parts of the Huachong Formation (Zhang et al. 1993). Therefore, the above isotopic age 59.3±0.2 Ma and 56.2±0.3 Ma more likely corresponds to the volcanic events of the bottom Gaogang Member of Buxin Formation and the Lower part of the Huachong Formation respectively. This opinion would indicate that the age of the present insect layer is about 61–62 Ma approximately. A correspondence of these two volcanic rock layers with the lower and upper parts of the Buxin Formation cannot be excluded. Then, the age of this fossil insect layer would be 60–59 Ma approximately. To briefly summarize, the age of the lower part of the Buxin Formation that yielded numerous fossil insects would belong to the Middle Paleocene, very close to the famous French volcano-sedimentary maar deposit of Menat in age (60–61 Ma; e.g. Nel and Auvray 2006; Wappler et al. 2009). Nevertheless, both localities with rich fossil entomofaunas need future better accurate isotopic dating.

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The fossil insects from the Sanshui Basin have been found from the Buxin and the Baoyue formations but without a systematically collecting and study. These fossil insects were identified by Qibin Lin (NIGPAS) including *Laodiscis melanis*, *Nisocercopis* sp., *Platokoleos* sp. etc., all taxa that firstly described from the Paleogene of Mengla County, Yunnan Province, Southwestern China (Zhang et al. 1993). The so-called Mengyejing Formation at Shangyong of Mengla County yielded a very rich fossil entomofauna (e.g. Lin 1977; Lin et al. 2010a, b), and its age was also discussed by authors. Analyses of spore-pollen assemblages suggested a Paleogene age for the 'Mengyejing' Formation at Shangyong, but a Late Cretaceous age was not excluded (Nanjing Institute of Geology and Palaeontology et al. 1975). Study of conchostracans suggested an early Eocene age i.e. Ypresian (Chen and Shen 1980; Shen and Chen 1984; Shen et al. 2006). This entomofauna was considered as Eocene (Lin 1977) or Paleocene (Hong 1984) respectively. For the general analysis, the insect-rich layer of the Buxin Formation at the Sanshui Basin and 'Mengyejing' Formation at Shangyong are correlated and both would be Paleocene.

**Material and method**

The specimen describe herein derives from the chalky clay of lower part of Honggang Member, Buxin Formation at western of Sanshui District, Foshan City, Guangdong Province, about 40 km west of Guangzhou, the capital of the province (Fig. 1).

The holotype of *Sinonothochrysa zhangi* Huang and Nel gen. et sp. nov. is an imprint/compression fossil with three-dimensional preservation. It is a nearly complete insect with well-preserved wing venation but the body structures are damaged by crystallization. The specimen was examined and photographed with a LeicaMZ APO and a Canon EOS 5DMark II camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using a Zeiss Discovery V20 stereo microscope. The figures

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and drawings were composed with Adobe Illustrator CC2019 and Photoshop CC2019 softwares. The holotype specimen presented herein is housed in NIGPAS, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, China under the accession number NIGP175154. Wing venation nomenclature follows Breitkreuz et al. (2017) and in part Brooks and Barnard (1990).

Abbreviations are as follows: A anal vein; bsx basal subcostal crossvein; C costa; C1 and C2 first and second cubital cells; CuA cubitus anterior; CuP cubitus posterior; dcc discal cubital cell; ig inner gradate crossveins; im intramedian cell; MA media anterior; MP media posterior; M1 and M2 first and second median cells; og outer gradate crossveins; Psc Pseudo-cubital vein; Psm pseudo-median vein RA radius anterior; RP radius posterior; ScP subcostal posterior.

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## Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Family Chrysopidae Schneider, 1851

Subfamily ?Nothochrysinae Navás, 1910

***Sinonothochrysa*** Huang and Nel, gen. nov.

urn:lsid:zoobank.org:act:176B7F87-BA8C-4CCF-80A5-2121B79C9FEF

*Type species*

*Sinonothochrysa zhangi* n. sp.

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*Diagnosis*

Forewing characters. Two series of gradate crossveins; cell im nearly quadrangular and very broad, twice as long as broad, with its anterior side curved; vein Psm with three branches of RP entering it, Psm continued by inner gradates; crossvein 2m-cu at basal third of cell im; series of cells between Psm and Psc distinctly broader than long; inner gradate series anteriorly curved.

*Etymology*

Named after the Latin name 'Sina' for China, and the extant genus name *Nothochrysa* McLachlan, 1868.

***Sinonhothochrysa zhangi*** Huang and Nel sp. nov.

Figs 2–3

urn:lsid:zoobank.org:act:0238777A-68AE-453D-A83B-2A793B4F06DC

*Etymology*

Named after Prof. Xianqiu Zhang, Chinese senior palaeontologist who made a systematically biostratigraphic study of the Sanshui Basin. The specific epithet is to be treated as a noun in the genitive case.

*Type material*

Holotype NIGP175154 (crystallized body with complete but superposed right fore- and hind wings and fragments of the left fore- and hind wings).

*Type locality*

Sanshui District, Foshan City, Guangdong Province, China.

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*Stratigraphic occurrence*

Middle Paleocene, Buxin Formation at Western of Sanshui District.

*Diagnosis*

As for the genus.

*Description*

Body ca. 5.0 mm long; thorax ca. 1.0 mm wide.

Forewing (Figs 2–3), 9.0 mm long, ca. 2.2 mm wide; apex rounded; costal space poorly preserved, with simple subcostal veinlets relatively widely spaced; ScP very long, with apex not preserved but probably entering margin near wing apex; subcostal space moderately broad; proximal subcostal crossvein (bsx or 1scp–r) present; no other crossvein between ScP and RA detected; tympanum not detectable; RA long, entering margin at wing apex; origin of RP relatively close to wing base, at 3.0 mm of it; length of RP proximad 1r–m 10 times as long as 1r–m; RA space (between RA and RP) broad, with 10 crossveins, the most basal one being well distal to 1r–m; RP weakly zigzagged, with 10 branches, two of them entering Psm; basal crossvein 1r–m very short, perpendicular to M, connecting RP with MA; M forked at an open angle opposite origin of RP; intramedian cell very broad, only two times as long as broad, broadly rectangular with anterior side strongly curved; MA not proximally fused with RP1; Psm well-developed, slightly zigzagged and distally prolonged by inner row of gradates; MP distally fused with CuA; Psc with three-four simple branches between it and posterior wing margin; cells between Psm and Psc rather short but very broad; Psc distally prolonged by outer row of gradates; basal crossvein 1m–cu short, apparently located basal to origin of CuP; 2m–cu present between MP and CuA at basal third of cell im; anal and CuP veins incompletely;

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two complete gradate series of crossveins, outer series not parallel to posterior wing margin; inner series not parallel to outer series; wing membrane apparently hyaline, only darkened in distal part of ScP (pterostigma).

Hind wing (Figs 2–3) ca. 8.8 mm long, ca. 2.1 mm wide; apex acute; costal space not preserved; only basal part of ScP visible, subcostal space as broad as that of forewing; proximal subcostal crossvein (bsx or 1scp–r) present; no other crossvein between ScP and RA detected; RA long, entering margin at wing apex; origin of RP relatively close to wing base, at ca. 1.1 mm of it; length of basal part of RP as long as part fused with MA; RA space (between RA and RP) broad, with 11 crossveins; RP weakly zigzagged, with eigth branches, three of them entering Psm; M forked at an open angle slightly basal to origin of RP; MA distally fused with RP1 and separating again; Psm well-developed, slightly zigzagged and distally prolonged by inner row of gradates; MP distally fused with CuA; Psc with four simple branches between it and posterior wing margin; cells between Psm and Psc large, rather short but very broad; Psc distally prolonged by outer row of gradates; intracubital crossveins C1 and C2 and anal veins not preserved except for forked first anal vein; two complete gradate series of crossveins, wing membrane apparently hyaline.

## Discussion

After the key to the extant chrysopid subfamilies of Brooks and Barnard (1990: 132), *Sinonothochrysa* gen. nov. falls in the Nothochrysinae because of the character ‘forewing Psm continuous with inner row of gradates’. Tauber (2014) proposed a list of putative apomorphies of the Nothochrysinae and two groups of genera, but none of these are preserved in our specimen. Makarkin and Archibald (2013) considered the character ‘Psm not extending to the outer row of gradates’ as possibly characteristic of the Nothochrysinae. They also have the

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crossvein 2m-cu located in the proximal half of im. This character is also present in some Chrysopinae, but not in the Cretaceous-Paleogene Limaiinae.

Garzón-Orduña et al. (2019) listed nine extant genera in the Nothochrysinae, viz. *Nothochrysa* McLachlan, 1868, *Pimachrysa* Adams, 1957, and *Hypochrysa* Hagen, 1866, *Asthenochrysa* Adams and Penny, 1992, *Leptochrysa* Adams and Penny, 1992, *Pamochrysa* Tjeder, 1966, *Kimochrysa* Tjeder, 1966 (considered as a subjective synonym of *Hypochrysa* by Tauber, 2014), *Triplochrysa* Kimmins, and *Dictyochrysa* Esben-Petersen (Tjeder 1966; Adams 1967; Adams and Penny 1992). Several fossil genera are currently put in this subfamily (Table 1), viz. *Adamsochrysa* Makarkin and Archibald, 2013 (Eocene), *Archaeochrysa* Adams, 1967 (Eocene to Oligocene), *Asiachrysa* Makarkin, 2014 (Eocene), *Dyspetochrysa* Adams, 1967 (Oligocene), *Lithochrysa* Carpenter, 1935 (Oligocene), *Okanaganochrysa* Makarkin and Archibald, 2013 (Eocene), *Palaeochrysa* Scudder, 1890 (Oligocene), *Pronothochrysa* Peñalver et al., 1995 (Miocene), *Pseudochrysopa* Makarkin and Archibald, 2013 (Eocene), and *Tribochrysa* Scudder, 1890 (Oligocene). As Winterton et al. (2019) found the Nothochrysinae as paraphyletic in their phylogenetic analysis, the exact positions of all these fossils remain questionable.

*Dictyochrysa* and *Triplochrysa* are excluded from consideration because the gradate crossveins in *Sinonothochrysa* gen. nov. are arranged in two series only (vs. more than two in these genera, see respectively Brooks and Barnard 1990: fig. 527; New 1980: fig. 13). *Pamochrysa* has the forewing cell im rhomboidal, while it is nearly quadrangular in *Sinonothochrysa* gen. nov. (Brooks and Barnard 1990: fig. 554).

*Sinonothochrysa* gen. nov. shares with *Kimochrysa* a forewing cell im ca. twice as long as broad, unlike the genus *Nothochrysa* in which im is much narrower (Adams 1967: fig. 3; Kovanci and Canbulat 2007; Tauber 2019). But the forewing cells im of the *Kimochrysa* spp. are triangular or pentagonal (Tjeder 1966; Adams 1978; Brooks and Barnard 1990: fig. 539).

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*Hypochrysa elegans* (Burmeister, 1839) and *Asthenochrysa* (type species *A. viridula* (Adams, 1978)) have also a triangular cell im (Adams 1967: fig. 5, 1978: fig. 1; Brooks and Barnard 1990: fig. 533). In *Sinonothochrysa* gen. nov., the anterior side of the cell im is curved, while in *Kimochrysa impar* Tjeder, 1966, it is slightly angular, rendering im pentagonal (Tjeder 1966: fig. 785), the difference being rather weak. Nevertheless, the vein 'distal part of MA – Psm' is much shorter in *K. impar* and *K. africana* (Kimmins, 1937) than in *Sinonhothochrysa* gen. nov., with only two short cells above it basal to the first i.g. vein instead of three large ones.

While *Pimachrysa grata* Adams, 1957, *P. fusca* Adams, 1967 and *P. intermedia* Adams, 1967 have rather narrow cells im, *P. nigra* Adams, 1967 has one nearly ca. twice as long as broad as in *Sinonothochrysa* gen. nov. (Adams 1957: fig. 1, 1967: figs 1-2, 4). They all differ from *Sinonothochrysa* gen. nov. in the crossvein 2m-cu basal or very close to basal angle of cell im and the series of cells between Psm and Psc nearly as long as broad.

*Leptochrysa* has a very particular cell im, quadrangular but with the cell below it strongly reduced (Adams and Penny 1992: fig. 10; Tauber 2019), strongly differing from the configuration of im in *Sinonothochrysa* gen. nov. (pentagonal without reduction of the cell below it).

*Okanaganochrysa* has two series of cells between Psm and Psc (Makarkin and Archibald 2013: fig. 4). The *Adamsochrysa* spp. have a hexagonal cell im, but broadly similar to that of *Sinonothochrysa* gen. nov. (Makarkin and Archibald 2013: fig. 6), but they also have four rows of gradate crossveins. The *Archaeochrysa* spp. have a quadrangular cell im, but much narrower than in *Sinonothochrysa* gen. nov. (Adams 1967; Makarkin and Archibald 2013). Makarkin and Archibald (2013) provisionally put *Pseudochrysopa* in the Nothochrysinae because of the two following characters: 'Psm does not extend to the outer gradate series'; and '2m-cu is located in the proximal half of im'. The exact position of this genus needs to be re-

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evaluated. Nevertheless, it strongly differs from *Sinonothochrysa* gen. nov. in the narrower cell im and vein Psm not continued by the inner gradates.

*Dyspetochrysa vetuscula* (Scudder, 1890), *Tribochrysa inaequalis* Scudder, 1885, *Tribochrysa firmata* Scudder, 1890, *Lithochrysa wickhami* (Cockerell, 1914), *Palaeochrysa stricta* Scudder, 1890 and *P. creedei* Carpenter, 1935 differ from *Sinonothochrysa* gen. nov. in the elongate cell im, a course of the inner gradates parallel to posterior wing margin, instead of being anteriorly curved (Carpenter 1935: figs 1, 3-4, 6-7). *Palaeochrysa fracta* Cockerell, 1914 has also a narrow cell im and an irregular series of inner gradates (maybe an aberrant feature) (Carpenter 1935: fig. 2).

*Pronothochrysa vivesi* Peñalver et al., 1995 has also a narrow cell im, plus a much longer vein 'distal part of MA – Psm' than in *Sinonothochrysa* gen. nov. with six cells between it and RP instead of three (Peñalver et al. 1995: fig. 4).

*Asiachrysa tadushiella* Makarkin, 2014 has a cell im similar to that of *Sinonothochrysa* gen. nov., although slightly narrower. Nevertheless, its cells between Psm and Psc are longer and narrower than in *Sinonothochrysa* gen. nov. and overall, the crossvein 2m-cu is situated below mid part of cell im instead of being in the basal third of this cell (Makarkin 2014: fig. 3).

## Conclusion

Except for a Miocene genus, the fossil record of the subfamily Nothochrysinae is restricted to the Eocene – Oligocene, with an impressive diversity during the Eocene to the earliest Oligocene with ten described extinct genera contra only one (*Nothochrysa*) during the Middle – Late Oligocene, confirmed by the newly described genus. Possibly this subfamily collapsed during the Oligocene in relation to the general cooling and/or bat diversification, as already suggested by Archibald et al. (2014) and Ngô-Muller et al. (2019). The Paleocene

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*Sinonothochrysa zhangi* Huang and Nel gen. nov. et sp. nov. is the oldest record of the Nothochrysinae.

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**Table 1.** Fossil record of the family Chrysopidae

**Figure 1.** Fossil locality map.

**Figure 2.** *Sinonhothochrysa zhangi* Huang and Nel gen. et sp. nov., holotype NIGP175154. (**A**) photograph of habitus; (**B**) forewing reconstruction; arrows: course of forewing CuP; (**C**) hind wing reconstruction. Scale bars = 1 mm.

**Figure 3.** *Sinonhothochrysa zhangi* Huang and Nel gen. et sp. nov., holotype NIGP175154. Photographs. (**A**) thorax with bases of wings; (**B**) detail of bases of wings. Scale bars = 1 mm (A), 0.5 mm (B)

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figure 1

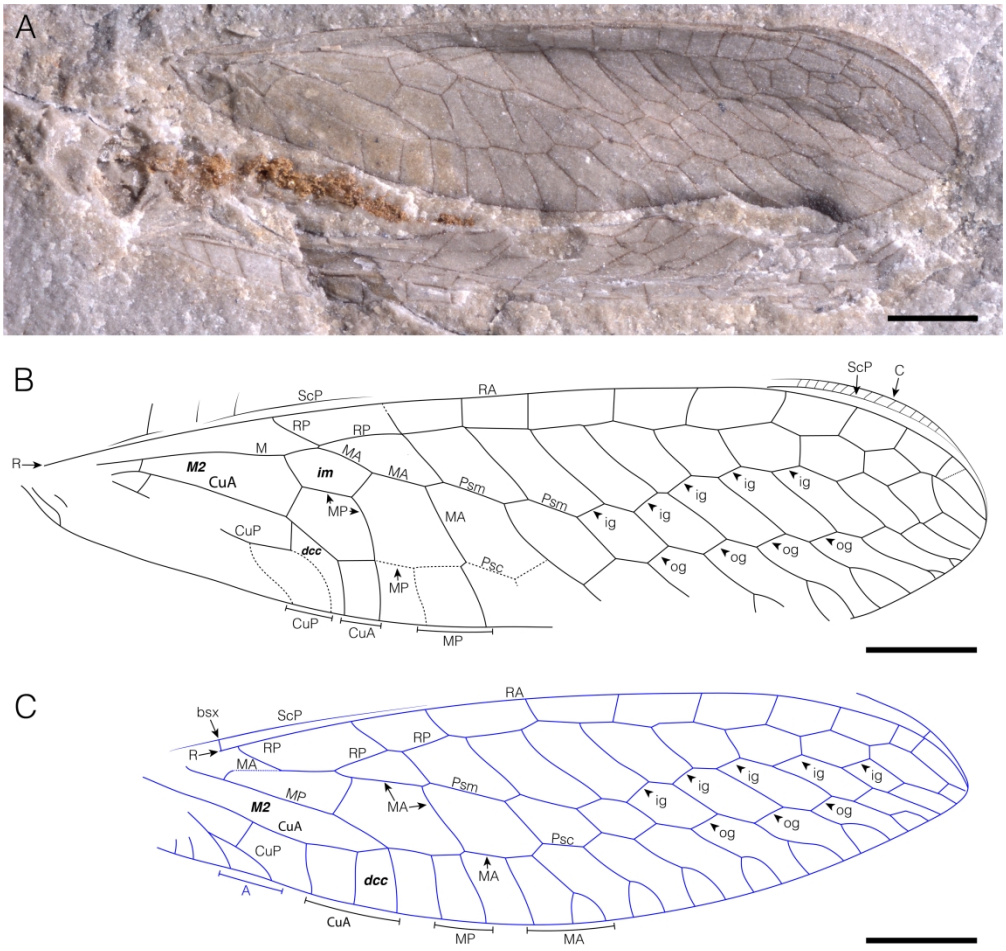

A
B
ScP
RA
RP
RP
M
MA
R
M2
CuA
im
MA
Psm
Psm
MP
MA
ig
ig
ig
ig
CuP
dcc
Psc
og
og
og
og
MP
CuP
CuA
MP
ScP
C
C
bsx
ScP
RA
R
RP
RP
MA
MP
Psm
M2
CuA
MA
ig
ig
ig
ig
ig
CuP
Psc
og
og
og
A
dcc
MA
CuA
MP
MA

figure 2

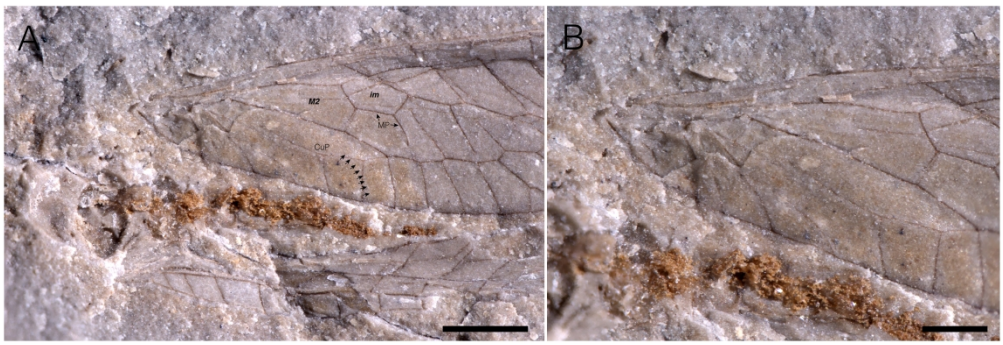



figure 3

| Subfamily / Tribe / Genus | Species | Distribution | Age |
|---|---|---|---|
| **Subfamily uncertain** | | | |
| *Cimbrochrysa* Schlüter, 1982 | | | |
| | *C. moleriensis* Schlüter, 1982 | Denmark | Ypresian |
| | | | |
| *Cretachrysa* Makarkin, 1994 | | | |
| | *C. martynovi* Makarkin, 1994 | Russian Federation | Campanian |
| | | | |
| *Danochrysa* Willmann, 1993 | | | |
| | *D. madseni* Willmann, 1993 | Denmark | Ypresian |
| | | | |
| *Paralembochrysa* Nel et al., 2005 | | | |
| | P. splendida Nel et al., 2005 | China | Aptian |
| | | | |
| *Stephenbrooksia* Willmann, 1993 | | | |
| | *S. multifurcata* Willmann, 1993 | Denmark | Ypresian |
| | | | |
| **Chrysopinae Schneider, 1851** | | | |
| *Paleochrysopa* Séméria & Nel, 1990 | | | |
| | *P. monteilsensis* Séméria & Nel, 1990 | France | Priabonian |
| | | | |
| *Pseudosencera* Makarkin et al., 2018 | | | |
| | *P. baltica* Makarkin et al., 2018 | Russian Federation | Priabonian |
| | | | |
| **Chrysopini Schneider 1851** | | | |
| *Chrysopa* Leach, 1815 | | | |
| | *C. glaesaria* Engel & Grimaldi, 2007 | Dominican Republic | Burdigalian/Langhian |
| | *C. martynovae* Makarkin, 1991 | Russian Federation | Miocene |
| | *C. miocenea* Makarkin, 1991 | Russian Federation | Miocene |
| | *C. sarmatica* Handschin, 1937 | Romania | middle Serravallian |
| | *C. stavropolitana* Makarkin, 1991 | Russian Federation | Miocene |
| | *C. vetula* Engel & Grimaldi 2007 | Dominican Republic | Burdigalian/Langhian |
| | | | |
| **Leucochrysini Adams 1978** | | | |
| *Leucochrysa* McLachlan, 1868 | | | |
| | *L. (Nodita) prisca* Engel & Grimaldi, 2007 | Dominican Republic | Burdigalian/Langhian |
| | | | |
| **Limaiinae Martins-Neto and Vulcano, 1988** | | | |
| *Aberrantochrysa* Khramov, 2018 | | | |
| | *A. buryatica* Khramov, 2018 | Russian Federation | Aptian |
| | *A. pulchella* Khramov, 2018 | Russian Federation | Aptian |
| | | | |
| *Araripechrysa* Martins-Neto & Vulcano, 1988 | | | |
| | *A. magnifica* Martins-Neto & Vulcano, 1988 | Brazil | Aptian |
| | | | |
| *Baisochrysa* Makarkin, 1997 | | | |
| | *B. multinervis* Makarkin, 1997 | Russian Federation | Aptian |
| | *B. pumila* Khramov et al., 2015 | Kazakhstan | Callovian/Oxfordian |
| | | | |
| *Drakochrysa* Yang & Hong, 1990 | | | |
| | *D. sinica* Yang & Hong, 1990 | China | Aptian |
| | | | |
| *Limaia* Martins-Neto & Vulcano, 1988 | | | |
| | *L. adicotomica* Martins-Neto, 1997 | Brazil | Aptian |

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| | | | |
|---|---|---|---|
| | *L. conspicua* Martins-Neto & Vulcano, 1988 | Brazil | Aptian |
| | | | |
| *Mesypochrysa* Martynov, 1927 | | | |
| | *M. angustialata* Makarkin, 1997 | Russian Federation | Aptian |
| | *M. cannabina* Khramov, 2018 | Russian Federation | Aptian |
| | *M. chrysopa* Makarkin, 1997 | Russian Federation | Aptian |
| | *M. chrysopoides* Ponomarenko, 1992 | Mongolia | Aptian |
| | *M. curvimedia* Makarkin, 1997 | Russian Federation | Aptian |
| | *M. falcata* Makarkin, 1997 | Russian Federation | Aptian |
| | *M. intermedia* Panfilov, 1980 | Kazakhstan | Callovian/Oxfordian |
| | *M. latipennis* Martynov, 1927 | Kazakhstan | Callovian/Oxfordian |
| | *M. magna* Makarkin, 1997 | Russian Federation | Aptian |
| | *M. minima* Makarkin, 1997 | Russian Federation | Aptian |
| | *M. miniscula* Ren & Guo, 1996 | China | Aptian |
| | *M. minuta* Jepson et al., 2012 | United Kingdom | Berriasian |
| | *M. naranica* Khramov, 2018 | Russian Federation | Aptian |
| | *M. polyclada* Panfilov, 1980 | Kazakhstan | Callovian/Oxfordian |
| | *M. polyneura* Ren & Guo, 1996 | China | Aptian |
| | *M. reducta* Panfilov, 1980 | Kazakhstan | Callovian/Oxfordian |
| | *M. sinica* Khramov et al., 2015 | China | Callovian/Oxfordian |
| | | | |
| *Parabaisochrysa* Lu et al., 2018 | | | |
| | *P. xingkei* Lu et al., 2018 | Myanmar | Cenomanian |
| | | | |
| *Protochrysa* Willmann & Brooks, 1991 | | | |
| | *P. aphrodite* Willmann & Brooks, 1991 | Denmark | Ypresian |
| | *P. fuscobasalis* Makarkin & Archibald, 2013 | Canada | Ypresian |
| | | | |
| **Nothochrysinae Navas 1910** | | | |
| *Adamsochrysa* Makarkin & Archibald, 2013 | | | |
| | *A. aspera* Makarkin & Archibald, 2013 | Canada | Ypresian |
| | *A. wilsoni* Makarkin & Archibald, 2013 | Canada | Ypresian |
| | | | |
| *Archaeochrysa* Adams, 1967 | | | |
| | *A. creedei* Carpenter, 1935 | USA | Oligocene |
| | *A. fracta* Cockerell, 1914 | USA | earliest Oligocene |
| | *A. paranervis* Adams, 1967 | USA | earliest Oligocene |
| | *A. profracta* Makarkin & Archibald, 2013 | Canada | Ypresian |
| | *A. sanikwa* Archibald & Makarkin, 2015 | Canada | Ypresian |
| | | | |
| *Asiachrysa* Makarkin, 2014 | | | |
| | *A. tadushiella* Makarkin, 2014 | Russian Federation | Ypresian |
| | | | |
| *Dyspetochrysa* Adams, 1967 | | | |
| | *D. vetuscula* Scudder, 1890 | USA | earliest Oligocene |
| | | | |
| *Hypochrysa* Gould, 1861 | | | |
| | *H. hercyniensis* Schlüter, 1982 | Germany | Pliocene |
| | | | |
| *Lithochrysa* Carpenter, 1935 | | | |
| | *L. borealis* Archibald & Makarkin, 2017 | Canada | Ypresian |
| | *L. wickhami* Cockerell, 1914 | USA | earliest Oligocene |
| | | | |
| *Nothochrysa* MacLachlan, 1868 | | | |

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| | | | |
|---|---|---|---|
| | *N. praeclara* Statz, 1936 | Germany | Chattian |
| | *N. stampieni* Nel & Séméria, 1986 | France | Chattian |
| | *N. praeclara* Statz, 1936 | Germany | Chattian |
| | | | |
| *Okanaganochrysa* Makarkin & Archibald, 2013 | | | |
| | *O. coltsunae* Makarkin & Archibald, 2013 | Canada | Ypresian |
| | | | |
| *Palaeochrysa* Scudder, 1890 | | | |
| | *P. concinnula* Cockerell, 1909 | USA | Chadronian |
| | *P. stricta* Scudder, 1890 | USA | Chadronian |
| | | | |
| *Pronothochrysa* Peñalver et al., 1995 | | | |
| | *P. vivesi* Peñalver et al., 1995 | Spain | Miocene |
| | | | |
| *Pseudochrysopa* Makarkin & Archibald, 2013 | | | |
| | *P. harveyi* Makarkin & Archibald, 2013 | Canada | Ypresian |
| | | | |
| *Sinonothochrysa* gen. nov. | | | |
| | *Sinonothochrysa eocenica* sp. nov. | China | middle Paleocene |
| | | | |
| *Tribochrysa* Scudder, 1885 | | | |
| | *T. firmata* Scudder, 1890 | USA | Chadronian |
| | *T. inequalis* Scudder, 1885 | USA | Chadronian |

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| Locality / Formation | Reference |
|---|---|
| | |
| | |
| Gullerup / Fur Formation | Schlüter, 1982 |
| | |
| | |
| Obeshchayushchiy / Ola Formation | Makarkin, 1994 |
| | |
| | |
| Sundby Klint, Mors / Fur Formation | Willmann, 1993 |
| | |
| | |
| Huangbanjigou, Chaomidian Village / Yixian Formation | Nel et al., 2005 |
| | |
| | |
| Ejerslev Industrial Pit / Fur Formation | Willmann, 1993 |
| | |
| | |
| | |
| Alès-Monteils / Monteils Formation | Séméria and Nel, 1990 |
| | |
| | |
| Baltic amber | Makarkin et al., 2018 |
| | |
| | |
| | |
| Dominican amber | Engel and Grimaldi, 2007 |
| Vishnevaya Balka creek, outcrop 4, Stavropol | Makarkin, 1991 |
| Vishnevaya Balka creek, outcrop 4, Stavropol | Makarkin, 1991 |
| Magyar Sáros | Handschin, 1937 |
| Vishnevaya Balka creek, outcrop 3 bed IX, Stavropol | Makarkin, 1991 |
| Dominican amber | Engel and Grimaldi, 2007 |
| | |
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| Dominican amber | Engel and Grimaldi, 2007 |
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| Khasurty | Khramov, 2018 |
| Khasurty | Khramov, 2018 |
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| | |
| Crato / Crato Formation | Martins-Neto and Vulcano, 1988 |
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| | |
| Baissa / Zaza Formation | Makarkin, 1997 |
| Karatau-Mikhailovka / Karabastau Formation | Khramov et al., 2015 |
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| 84GT1, west Tuanwang Village / Laiyang Formation | Yang and Hong, 1990 |
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| Crato / Crato Formation | Martins-Neto, 1997 |

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| Crato / Crato Formation | Martins-Neto, 1988 |
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| Baissa / Zaza Formation | Makarkin, 1997 |
| Khasurty | Khramov, 2018 |
| Baissa / Zaza Formation | Makarkin, 1997 |
| Bon Tsagaan / Dzun-Bain Formation | Ponomarenko, 1992 |
| Baissa / Zaza Formation | Makarkin, 1997 |
| Baissa / Zaza Formation | Makarkin, 1997 |
| Karatau-Mikhailovka / Karabastau Formation | Panfilov, 1980 |
| Galkino / Karabastau Formation | Martynov, 1927 |
| Baissa / Zaza Formation | Makarkin, 1997 |
| Baissa / Zaza Formation | Makarkin, 1997 |
| Near Chaomidian Village / Yixian Formation | Ren and Guo, 1996 |
| Durlston Bay, Bed DB175, Swanage (Manchester Mus) / Durlston Formation | Jepson et al., 2012 |
| Khasurty | Khramov, 2018 |
| Karatau-Mikhailovka / Karabastau Formation | Panfilov, 1980 |
| Near Chaomidian Village / Yixian Formation | Ren and Guo, 1996 |
| Karatau-Mikhailovka / Karabastau Formation | Panfilov, 1980 |
| Daohugou / Daohugou Formation | Khramov et al., 2015 |
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| Burmese amber | Lu et al., 2018 |
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| Fur Formation | Willmann and Brooks, 1991 |
| McAbee | Makarkin and Archibald, 2013 |
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| McAbee | Makarkin and Archibald, 2013 |
| McAbee | Makarkin and Archibald, 2013 |
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| Creede / Creede Formation | Carpenter, 1935 |
| Wilson Ranch, Florissant | Cockerell, 1914 |
| Florissant, Station 14 / Florissant Formation | Adams, 1967 |
| McAbee | Makarkin and Archibald, 2013 |
| Driftwood Canyon | Archibald and Makarkin, 2015 |
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| Tadushi locality / Tadushi Formation | Makarkin, 2014 |
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| Florissant / Florissant Formation | Scudder, 1890 |
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| Willershausen clay pit | Schlüter, 1982 |
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| Driftwood Canyon | Archibald and Makarkin, 2017 |
| Florissant / Florissant Formation | Cockerell, 1914 |
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| Rott / Rott Formation | Statz, 1936 |
| Plâtrières, Aix-en-Provence | Nel and Séméria, 1986 |
| Rott / Rott Formation | Statz, 1936 |
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| McAbee | Makarkin and Archibald, 2013 |
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| Florissant / Florissant Formation | Cockerell, 1909 |
| Florissant / Florissant Formation | Scudder, 1890 |
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| La Rinconada, Ribesalbes | Peñalver et al., 1995 |
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| Driftwood Canyon | Makarkin and Archibald, 2013 |
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| Sanshui District / Buxin Formation | This paper |
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| Florissant / Florissant Formation | Scudder, 1890 |
| Florissant / Florissant Formation | Scudder, 1885 |

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