First green lacewing (Insecta: Neuroptera: Chrysopidae) from the palaeocene 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 nothochrysin lacewing, are described and illustrated from the Palaeocene Buxin Formation, Sanshui Basin, Foshan City, Guangdong Province, South China. The new taxon is the oldest described representative and first reports this subfamily in China. It is also the first formally described fossil insects from the Buxin Formation of the Sanshui Basin.

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Introduction

The family Chrysopidae, also called green lacewings due to the colour 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://fossil works.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 Palaeogene. 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 into 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 Palaeocene and the Eocene representatives, namely, three species in the genus Protochrysa (Willmann and Brooks 1991) from the Palaeocene-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 Palaeocene, 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).

The position of the family Chrysopidae is not fully elucidated and alternative hypotheses are proposed depending on the methods or the analysed data (e.g. Engel and Grimaldi 2007; Vasilikopoulos et al. 2020). Winterton et al. (2019) proposed a molecular phylogentic 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 be related to the clade (Mantispidae + Berothidae) according to recent molecular analyses (Vasilikopoulos et al. 2020: fig., p. 1) with a divergence estimate to the early Jurassic. However, the calibration used in this most recent work seems 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 constraint 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, 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 correlated to Karatuu biota of Kazakhstan (Huang 2015, 2016) that yielded some very similar insects such as Cicadomorpha (Fu et al. 2019). An ash layer appeared less than one metre up the fossil insect layer at the Guancaishan locality providing a SIMS zircon U-Pb dating as 157.3 ± 1.5 Ma that supports 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 Chrysopidae (a superfamily that also comprises the Mesozoic Ascalthrysidae), 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 authors did not use Protoaristenymphes to calibrate their datings. Vasilikopoulos et al. (2020) also ignored the Mesochrysopidae and the genus Protoaristenymphes in their list of fossils used as calibra-
| Subfamily/Tribe/Genus                  | Species                          | Distribution           | Age           | Locality/Formation                          | Reference                  |
|---------------------------------------|----------------------------------|------------------------|---------------|--------------------------------------------|----------------------------|
| **Subfamily uncertain**               | C. moleniensis Schlüter 1982     | Denmark                | Ypresian      | Gullerup/Fur Formation                      | Schlüter 1982              |
|                                       | C. martynovi Makarkin 1994       | Russian Federation     | Campanian     | Obeschchayushchyi/Ola Formation            | Makarkin 1994              |
|                                       | D. madseni Willmann 1993         | Denmark                | Ypresian      | Sundby Klint, Mors/Fur Formation           | Willmann 1993              |
|                                       | P. splendida Nel et al. 2005     | China                  | Aptian        | Huangbanjigou, Chaomidian Village/Yixian Formation | Nel et al. 2005 |
|                                       | S. multifurcata Willmann 1993    | Denmark                | Ypresian      | Ejerslev Industrial Pit/Fur Formation      | Willmann 1993              |
|                                       | P. monteisensis Séméria and Nel 1990 | France             | Priabonian    | Alès-Monteils/Monteils Formation          | Séméria and Nel 1990       |
|                                       | P. baltica Makarkin et al. 2018  | Russian Federation    | Priabonian    | Baltic amber                               | Makarkin et al. 2018       |
| **Chrysopinae Schneider, 1851**       | C. glaesaria Engel and Grimaldi 2007 | Dominican Republic | Burdigalian/ | Dominican amber                           | Engel and Grimaldi 2007    |
|                                       | C. martynovae Makarkin 1991      | Russian Federation    | Miocene       | Vishnevaya Balka creek, outcrop 4, Stavropol | Makarkin 1991              |
|                                       | C. miocenea Makarkin 1991        | Russian Federation    | Miocene       | Vishnevaya Balka creek, outcrop 4, Stavropol | Makarkin 1991              |
|                                       | C. sarmatica Handschin 1937      | Romania                | Middle        | Magyar Sáros                              | Handschin 1937             |
|                                       | C. stavropolitana Makarkin 1991  | Russian Federation    | Miocene       | Vishnevaya Balka creek, outcrop 3 bed IX, Stavropol | Makarkin 1991 |
|                                       | C. vetula Engel and Grimaldi 2007 | Dominican Republic    | Burdigalian/ | Dominican amber                           | Engel and Grimaldi 2007    |
|                                       | L. (Nodita) prisca Engel and Grimaldi 2007 | Dominican Republic | Burdigalian/ | Dominican amber                           | Engel and Grimaldi 2007    |
| **Limaiinae Martins-Neto and Vulcano 1988** | A. buryatica Khramov 2018       | Russian Federation    | Aptian        | Khasurity                                 | Khramov 2018               |
|                                       | A. pulchella Khramov 2018        | Russian Federation    | Aptian        | Khasurity                                 | Khramov 2018               |
|                                       | A. magnifica Martins-Neto and Vulcano 1988 | Brazil              | Aptian        | Crato/Crato Formation                      | Martins-Neto and Vulcano 1988 |
| **Baisochrysa Makarkin 1997**         | B. multineris Makarkin 1997      | Russian Federation    | Aptian        | Baissa/Zaza Formation                      | Makarkin 1997              |
|                                       | B. pumila Khramov et al. 2015    | Kazakhstan            | Callovian/Oxfordian | Karatau-Mihailovka/Karabastau Formation | Khramov et al. 2015       |
| **Drokochrysa Yang and Hong 1990**    | D. sina Yang and Hong 1990       | China                  | Aptian        | 84GT1, west Tuanwang Village/Laiyang Formation | Yang and Hong 1990       |

(Continued)
| Subfamily/Tribe/Genus | Species                  | Distribution | Age      | Locality/Formation       | Reference                  |
|-----------------------|--------------------------|--------------|----------|--------------------------|----------------------------|
| Mesychrysa Martynov   | *L. conspicua* Martins-Neto and Vulcano 1988 | Brazil       | Aptian   | Crato/Crete Formation    | Martins-Neto and Vulcano 1988 |
|                       | *M. angustialata* Makarkin 1997 | Russian Federation | Aptian   | Baissa/Zaza Formation    | Makarkin 1997              |
|                       | *M. cannabinina* Khramov 2018 | Russian Federation | Aptian   | Khasury                  | Khramov 2018               |
|                       | *M. chrysopea* Makarkin 1997 | Russian Federation | Aptian   | Baissa/Zaza Formation    | Makarkin 1997              |
|                       | *M. chrysopeoides* Ponomarenko 1992 | Mongolia     | Aptian   | Bon Tsagaan/Dzun-Bain Formation | Ponomarenko 1992           |
|                       | *M. curvmeedia* Makarkin 1997 | Russian Federation | Aptian   | Baissa/Zaza Formation    | Makarkin 1997              |
|                       | *M. falcata* Makarkin 1997 | Russian Federation | Aptian   | Baissa/Zaza Formation    | Makarkin 1997              |
|                       | *M. intermedia* Panfilov 1980 | Kazakhstan   | Callovian/Oxfordian | Karatau-Mikhailovka/Karabastau Formation | Panfilov 1980          |
|                       | *M. latipennis* Martynov 1927 | Kazakhstan   | Callovian/Oxfordian | Galkino/Karabastau Formation | Martynov 1927          |
|                       | *M. magna* Makarkin 1997 | Russian Federation | Aptian   | Baissa/Zaza Formation    | Makarkin 1997              |
|                       | *M. minima* Makarkin 1997 | Russian Federation | Aptian   | Baissa/Zaza Formation    | Makarkin 1997              |
|                       | *M. miniscula* Ren and Guo 1996 | China       | Aptian   | Near Chaomidian Village/Yixian Formation | Ren and Guo 1996         |
|                       | *M. minuta* Jepson et al. 2012 | United Kingdom | Berriasian | Durlston Bay, Bed DB175, Swanage (Manchester Mus)/Durlston Formation | Jepson et al. 2012        |
|                       | *M. naranica* Khramov 2018 | Russian Federation | Aptian   | Khasury                  | Khramov 2018               |
|                       | *M. polyclada* Panfilov 1980 | Kazakhstan   | Callovian/Oxfordian | Karatau-Mikhailovka/Karabastau Formation | Panfilov 1980          |
|                       | *M. polyneura* Ren and Guo 1996 | China       | Aptian   | Near Chaomidian Village/Yixian Formation | Ren and Guo 1996         |
|                       | *M. reducera* Panfilov 1980 | Kazakhstan   | Callovian/Oxfordian | Karatau-Mikhailovka/Karabastau Formation | Panfilov 1980          |
|                       | *M. sinica* Khramov et al. 2015 | China       | Aptian   | Daohugou/Daohugou Formation | Khramov et al. 2015       |
| Parabaisochrysa Lu et al. 2018 | *P. xingkei* Lu et al. 2018 | Myanmar     | Cenomanian | Burmese amber              | Lu et al. 2018             |
| Protochrysa Willmann and Brooks 1991 | *P. aphrodite* Willmann and Brooks 1991 | Denmark     | Ypresian | Fur Formation             | Willmann and Brooks 1991  |
|                       | *P. fuscobasalis* Makarkin and Archibald 2013 | Canada      | Ypresian | McAbee                    | Makarkin and Archibald 2013 |
| Nothochrysinae Navas 1910 | *A. aspera* Makarkin and Archibald 2013 | Canada      | Ypresian | McAbee                    | Makarkin and Archibald 2013 |
|                       | *A. wilsoni* Makarkin and Archibald 2013 | Canada      | Ypresian | McAbee                    | Makarkin and Archibald 2013 |
| Archaeochrysa Adams 1967 | *A. creedei* Carpenter 1935 | USA         | Oligocene | Creede/Creede Formation   | Carpenter 1935             |
|                       | *A. fracta* Cockerell 1914 | USA         | Earliest Oligocene | Wilson Ranch, Florissant | Cockerell 1914            |
|                       | *A. paraneris* Adams 1967 | USA         | Oligocene | Florissant, Station 14/Florissant Formation | Adams 1967               |
|                       | *A. profracta* Makarkin and Archibald 2013 | Canada      | Ypresian | McAbee                    | Makarkin and Archibald 2013 |
|                       | *A. sanikwa* Archibald and Makarkin 2015 | Canada      | Ypresian | Driftwood Canyon          | Archibald and Makarkin 2015 |
| Asiachrysa Makarkin 2014 | *A. tadushiella* Makarkin 2014 | Russian Federation | Ypresian | Tadushi locality/Tadushi Formation | Makarkin 2014             |
| Dysptochrysa Adams 1967 | *D. vetuscula* Scudder 1890 | USA         | Earliest Oligocene | Florissant/Florissant Formation | Scudder 1890              |
| Hypochrysa Gould, 1866 | -                         | -            | -        | -                        | -                          |
tion points. We are aware that the choice of fossil taxa in calibrations is difficult and that applying too much constraints on trees may result 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 describe a new genus and species of Nothochrysa from the Palaeocene, confirming the important diversity of this subfamily at that time.

### Geological setting

The Palaeogene deposit of the Sanshui Basin of South Guangdong Province, South China is developed and detailed hereafter (Figure 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 grey oil shale, mud stone, chalky clay, and sandstone. It was first considered as an Eocene or Early Oligocene strata. The age of the Buxin Formation was argued by authors based on different biochronometers with various opinions, summarised by Zhang et al. (1993), p. 1) Early Eocene by ostracodes, conchoceratans, gastropods, and fishes; 2) Late Palaeocene-Early Eocene by bivalves; 3) Early-Middle Eocene by plant fossils and sporo-pollen studies; 4) Middle Eocene by stenoworts. Later, a systematical biostratigraphic study on ostracods suggested that the Xinzhuangcun, Buxin, and Baoyue formations would be assigned to the Palaeocene 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 Palaeocene (Zhang et al. 2008). A recent integrative study on China’s Palaeogene 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 Selndian-Thanetian boundary, mainly based on a palaeomagnetism 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 Probinicial Bureau of Geology and Mineral Resources 1997) could not provide convincing geochronological ages. A Palaeocene age of the Buxin Formation was also supported by a geochronological study that indicated that the

### Table 1. (Continued).

| Subfamily/Tribe/Genus | Species | Distribution | Age | Locality/Formation | Reference |
|-----------------------|---------|--------------|-----|--------------------|-----------|
| Liotochrysa Carpenter | *H. hercyniensis* Schlüter 1982 | Germany | Pliocene | Willershausen clay pit | Schlüter 1982 |
|                       | *L. borealis* Archibald and Makarkin 1977 | Canada | Ypresian | Driftwood Canyon | Archibald and Makarkin 2017 |
|                       | *L. wickhami* Cockerell 1914 | USA | Earliest Oligocene | Florissant/Florissant Formation | Cockerell 1914 |
| Nothochrysa MacLachlan, 1868 | *N. praeclara* Statz 1936 | Germany | Chattian | Rott/Rott Formation | Statz 1936 |
|                       | *N. stampiensis Nel and Séméria 1986 | France | Chattian | Plâtières, Aix-en-Provence | Nel and Séméria 1986 |
|                       | *N. praeclara* Statz 1936 | Germany | Chattian | Rott/Rott Formation | Statz 1936 |
| Okanaganochrysa Makarkin and Archibald 2013 | *O. coltsunae* Makarkin and Archibald 2013 | Canada | Ypresian | McBee | Makarkin and Archibald 2013 |
| Palaeochrysa Scudder 1890 | *P. concinnula* Cockerell 1909 | USA | Chadronian | Florissant/Florissant Formation | Cockerell 1909 |
|                       | *P. stricta* Scudder 1890 | USA | Chadronian | Florissant/Florissant Formation | Scudder 1890 |
| Pronothochrysa Peñalver et al. 1995 | *P. rivesi* Peñalver et al. 1995 | Spain | Miocene | La Rinconada, Ribesalbes | Peñalver et al. 1995 |
| Pseudochrysa Makarkin and Archibald 2013 | *P. harveyi* Makarkin and Archibald 2013 | Canada | Ypresian | Driftwood Canyon | Makarkin and Archibald 2013 |
| Sinonothochrysa gen. nov. | *Sinonothochrysa eocenica* sp. nov. | China | Middle Palaeocene | Sanshui District/Buxin Formation | This paper |
| Tribochrysa Scudder 1885 | *T. firmata* Scudder 1890 | USA | Chadronian | Florissant/Florissant Formation | Scudder 1890 |
|                       | *T. inequalis* Scudder 1885 | USA | Chadronian | Florissant/Florissant Formation | Scudder 1885 |

![Figure 1. Fossil locality map.](image-url)
volcanic eruption started at approximately 60 Ma in the Sanshui Basin. These authors got two sets 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 Palaeogene 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; Zhou et al. 2009). 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 summarise, the age of the lower part of the Buxin Formation that yielded numerous fossil insects would belong to the Middle Palaeocene, very close to the famous French volcanosedimentary 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.

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, Nisocercopsis sp., Platykoleos sp. etc., all taxa that first described from the Palaeogene 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 Palaeogene 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 Palaeocene (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 Palaeocene.

Figure 2. Sinonithochrysa 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.
Material and method

The specimen described 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 (Figure 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 crystallisation. The specimen was examined and photographed with a LeicaMZ APO and a Canon EOS 5D Mark 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 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; bxs—basal subcostal crossvein; C—costa; C1 and C2—first and second cubital cells; CuA—cubitus anterior; CuP—cubitus posterior; dcc—disclial cubital cell; gmg—inner gradate crossveins; int—intramedian cell; MA media anterior; MP media posterior; M1 and M2—first and second median cells; gmg—outer gradate crossveins; Psc—pseudo-cubital vein; Psms—pseudo-median vein; RA—radius anterior; RP—radius posterior; ScP subcostal posterior.

Published work and nomenclatural acts are registered in ZooBank (urn:lsid:zoobank.org:act:176B7F87-BA8C-4CCF-80A5-2121B79C9FEF).

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.

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 2 m–cu at basal third of cell im; series of cells between Psm and Psc distinctly broader than long; inner gradate series anteriorly curved.

Etyymology

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

Sinonothochrysa zhangi Huang and Nel sp. nov.

Figures 2–3

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

Type material

Holotype NIGP175154 (crystallised 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.

Stratigraphic occurrence

Middle Palaeocene, 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 (Figures 2–3), 9.0 mm long, ca. 2.2 mm wide; apex rounded; costal space poorly preserved, with simple subcostal veinslets relatively widely spaced; ScP very long, with apex not preserved but probably entering margin near wing apex; subcostal space moderately broad; proximal subcostal crossvein (bxs or 1sc–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 proximal 1 r–m 10 times as long as 1 r–m; RA space (between RA and RP) broad, with 10 crossoveins, the most basal one being well distal to 1 r–m; RP weakly zigzagged, with 10 branches, two of them entering Psm; basal crossvein 1 r–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 1 m–cu short, apparently located basal to origin of CuP; 2 m–cu present between MP and CuA at basal third of cell im; anal and CuP veins incompletely; 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 (Figures 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 (bxs or 1sc–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 crossoveins; RP weakly zigzagged, with eight 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 crossoveins C1 and C2 and anal veins not preserved except for forked first anal vein; two complete gradate series of crossveins, wing membrane apparently hyaline.

Etyymology

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

After the key to the extant chrysopid subfamilies of Brooks and Barnard (1990, p. 132), Sinonothochrysa gen. nov. falls in the Nothochrysinae because of the character ‘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 possible characteristic of the Nothochrysinae. They also have the crosseeve 2 m-cu located in the proximal half of im. This character is also present in some Chrysopinae, but not in the Cretaceous-Palaeogene Limaliinae.

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), Pamachrysa (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. Adamssochrysa (Makarkin and Archibald 2013) (Eocene), Archaeochrysa (Adams 1967) (Eocene to Oligocene), Asiachrysa (Makarkin 2014) (Eocene), Dyspetochrysa (Adams 1967) (Oligocene), Lithochrysa (Carpenter 1935) (Oligocene), Okanganachrysa (Makarkin and Archibald 2013) (Eocene), Palaeochrysa (Scudder 1890) (Oligocene), Pronothechrysa (Peñalver et al. 1995) (Miocene), Pseudochnyopa (Makarkin and Archibald 2013) (Eocene), and Tribochrysa (Scudder 1890) (Oligocene). As Winton 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 crosseve 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., p. 13). Pamachrysa has the following cell im rhomboidal, while it is nearly quadrangular in Sinonothochrysa gen. nov. (Brooks and Barnard 1990: fig., p. 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: Figure 3; Kovanci and Canbulat 2007; Tauber 2019a, 2019b). But the forewing cells im of the Kimochrysa spp. are triangular or pentagonal (Tjeder 1966; Adams 1978; Brooks and Barnard 1990: fig., p. 539). Hypochrysa elegans (Burmeister 1839) and Asthenochrysa (type species A. viridula (Adams 1978)) have also a triangular cell im (Adams 1967: fig. 5, 1978: Figure 1; Brooks and Barnard 1990: fig., p. 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., p. 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 Sinonothochrysa 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. fuscua (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: Figure 1, 1967: Figures 1–2, 4). They all differ from Sinonothochrysa gen. nov. in the crosseeve 2 m-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 2019b), 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., p. 4). The Adamssochrysa spp. have a hexagonal cell im, but broadly similar to that of Sinonothochrysa gen. nov. (Makarkin and Archibald 2013: fig., p. 6), but they also have four rows of gradate crosseve. 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 Pseudochnyopa in the Nothochrysinae because of the two following characters: ‘Psm does not extend to the outer gradate series’; and ‘2 m-cu is located in the proximal half of im’. The exact position of this genus needs to be re-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. creedii (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: Figures 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., p. 2).

Pronothechrysa vivae (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., p. 4).

Figure 3. Sinonothochrysa 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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