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3 Historical Biology
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8 First green lacewing (Insecta: Neuroptera: Chrysopidae) from the Paleocene Sanshui Basin of
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10 Guangdong, South China
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38 **ABSTRACT**
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40 *Sinonothochrysa zhangii* Huang and Nel gen. et sp. nov., a new genus and species of
41 nothochrysinine lacewing, is described and illustrated from the Paleocene Buxin Formation,
42 Sanshui Basina, Foshan City, Guangdong Province, South China. The new taxon is the oldest
43 described representative and first report this subfamily in China. It is also the first formally
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53 **KEYWORDS**
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55 Neuroptera; Nothochrysininae; fossil insects; Buxin Formation; middle Paleocene
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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. Apochrysinæ + Chrysopinæ + Nothochrysinæ + Limaiinæ), with the Limaiinæ is a strictly fossil subfamily. Each subfamilies present huge disparities in their fossil species diversity (Table. 1) since the subfamily Apochrysinæ 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 Limaiinæ 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 Nothochrysinæ and Chrysopinæ (Table 1).

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2
3 The position of the family Chrysopidae is not fully elucidated and alternative hypotheses
4 are proposed depending on the methods or the analyzed data (e.g. Engel et al. 2018;
5 Vasilikopoulos et al. 2020). Winterton et al. (2019) proposed a molecular phylogenetic analysis
6 of the Chrysopidae, dating the separation of their stem group from their putative sister group
7 Myrmeleontoidea from the late Triassic and their crown group from the early Cretaceous.
8 However, it seems that the Chrysopidae would closely related to the clade (Mantispidae +
9 Berothidae) according to recent molecular analyses (Vasilikopoulos et al. 2020: fig. 1) with a
10 divergence estimate to the early Jurassic. However, the calibration used in this most recent work
11 seem to provide questionable age for the group. In fact, Vasilikopoulos et al. (2020) used the
12 chrysopid fossil species *Mesypochrysa cf. intermedia* to calibrate the crown-group
13 (Chrysopidae + (Mantispidae + Berothidae)) using a soft minimum constrain set to 158.1 Ma
14 (Vasilikopoulos et al., 2020: additional file 1: table S10), which fits with the datation of the
15 Karabastau Formation of Kazakhstan, dated back to the Callovian/Kimmeridgian (Doludenko
16 and Orlovskaya 1976a, Doludenko and Orlovskaya 1976b) or possibly Oxfordian–
17 Kimmeridgian (Doludenko et al. 1990). Recent study on Yanliao Biota late assemblage i.e.
18 Linglongta biota at the Guancaishan locality was considered correlate to Karatau biota of
19 Kazakhstan (Huang 2015, 2016) that yielded some very similar insects such as *Cicadomorpha*
20 (Fu et al. 2020). An ash layer appeared less one meter up the fossil insect layer at the
21 Guancaishan locality providing a SIMS zircon U-Pb dating as 157.3 ± 1.5 Ma that support
22 Karabastau Formation is more likely an Oxfordian–Kimmeridgian age (Huang 2016). However,
23 the Toarcian genus *Protoaristenymphes* Nel and Henrotay, 1994 is currently placed in the
24 Mesozoic family Mesochrysopidae and the Chrysopoidea (a superfamily that also comprises
25 the Mesozoic Ascalochrysidae), and would be the oldest known representative of this clade
26 (Nel and Henrotay 1994; Yang et al. 2012; Makarkin et al. 2013), supporting a possible older
27 age for the superfamily, more in accordance with Winterton et al. (2019), even if these last
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3 authors did not used *Protoaristenymphes* to calibrate theirs datations. Vasilikopoulos et al.
4
5 (2020) also ignored the Mesochrysopidae and the genus *Protoaristenymphes* in their list of
6
7 fossils used as calibration points. We are aware that the choice of fossil taxa in calibrations is
8
9 difficult and that applying too much constraints on trees may results in dubious results, but, at
10
11 least the putative oldest records of the concerned clades should be discussed. Therefore, we
12
13 wonder if the clade or at least the Chrysopidae could be older than previously thought, and
14
15 suggest that it would be interesting to explore the Neuroptera phylogeny testing different
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17 calibrations of the stem- and crown-groups for each family.
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21 Herein we described a new genus and species of Nothochrysinæ from the Paleocene,
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23 confirming the important diversity of this subfamily at that time.
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26 27 28 **Geological setting**

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30 The Paleogene deposit of the Sanshui Basin of South Guangdong Province, South China is
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32 developed and detailed hereafter (Fig. 1). This strata is divided into the Xinzhuangcun, the
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34 Buxin, the Baoyue, and the Huachong formations from bottom to top. Buxin Formation was
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36 established at 1964 for a set of lacustrine deposit comprised dark gray oil shale, mud stone,
37
38 chalky clay, and sand stone. It was firstly considered as an Eocene or Early Oligocene strata.
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40 The age of the Buxin Formation was argued by authors based on different biochronometer with
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42 various opinions, summarized by Zhang et al. (1993): 1) Early Eocene by ostracodes,
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44 conchostracans, gastropods, and fishes; 2) Late Paleocene-Early Eocene by bivalves; 3) Early-
45
46 Middle Eocene by plant fossils and spore-pollen studies; 4) Middle Eocene by stoneworts. Later,
47
48 a systematical biostratigraphic study on ostracods suggested that the Xinzhuangcun, Buxin, and
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50 Baoyue formations would be assigned to the Paleocene and the Huachong Formation would be
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52 assigned to the Early Eocene. Therefore, the above authors indicated that the age of Buxin
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54 Formation could be assigned to the Middle Paleocene (Zhang et al. 2008). A recent integrative
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3 study on China's Paleogene stratigraphy and timescale indicated that the age of Buxin
4 Formation would range from 62.2 Ma to 59.2 Ma, i.e. late Danian to Selandian-Thanetian
5 boundary, mainly based on a paleomagnetism study (Wang et al. 2019). According to this
6 opinion, the age of the present fossil material could be even as old as 62 Ma.
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12 Most isotopic dating of volcanic rocks in the Sanshui Basin used K-Ar method
13 (Guangdong Provincial Bureau of Geology and Mineral Resources 1997) could not provide
14 convincing geochronological ages. A Paleocene age of the Buxin Formation was also supported
15 by a geochronological study that indicated that the volcanic eruption started at approximately
16 60 Ma in the Sanshui Basin. These authors got two set of ages by zircon U-Pb dating as 59.3 ± 0.2
17 Ma and 56.2 ± 0.3 Ma. The Buxin Formation is subdivided into four members as Honggang
18 Member, Dagang Member, Fenggang Member, and Gaogang Member from bottom to top. The
19 herein described fossil insect was collected from the lower part of the Honggang Formation.
20 The volcanic rocks in the Paleogene of Sanshui Basin initially appeared in the Honggang
21 Member and particularly occurred at the bottom of the Gaogang Member, and then were widely
22 distributed in the lower parts of the Huachong Formation (Zhang et al. 1993). Therefore, the
23 above isotopic age 59.3 ± 0.2 Ma and 56.2 ± 0.3 Ma more likely corresponds to the volcanic
24 events of the bottom Gaogang Member of Buxin Formation and the Lower part of the Huachong
25 Formation respectively. This opinion would indicate that the age of the present insect layer is
26 about 61–62 Ma approximately. A correspondence of these two volcanic rock layers with the
27 lower and upper parts of the Buxin Formation cannot be excluded. Then, the age of this fossil
28 insect layer would be 60–59 Ma approximately. To briefly summarize, the age of the lower part
29 of the Buxin Formation that yielded numerous fossil insects would belong to the Middle
30 Paleocene, very close to the famous French volcano-sedimentary maar deposit of Menat in age
31 ($60\text{--}61$ Ma; e.g. Nel and Auvray 2006; Wappler et al. 2009). Nevertheless, both localities with
32 rich fossil entomofaunas need future better accurate isotopic dating.
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3 The fossil insects from the Sanshui Basin have been found from the Buxin and the Baoyue
4 formations but without a systematically collecting and study. These fossil insects were
5 identified by Qibin Lin (NIGPAS) including *Laodiscis melanis*, *Nisocercopis* sp., *Platokoleos*
6 sp. etc., all taxa that firstly described from the Paleogene of Mengla County, Yunnan Province,
7 Southwestern China (Zhang et al. 1993). The so-called Mengyejing Formation at Shangyong
8 of Mengla County yielded a very rich fossil entomofauna (e.g. Lin 1977; Lin et al. 2010a, b),
9 and its age was also discussed by authors. Analyses of spore-pollen assemblages suggested a
10 Paleogene age for the 'Mengyejing' Formation at Shangyong, but a Late Cretaceous age was
11 not excluded (Nanjing Institute of Geology and Palaeontology et al. 1975). Study of
12 conchostracans suggested an early Eocene age i.e. Ypresian (Chen and Shen 1980; Shen and
13 Chen 1984; Shen et al. 2006). This entomofauna was considered as Eocene (Lin 1977) or
14 Paleocene (Hong 1984) respectively. For the general analysis, the insect-rich layer of the Buxin
15 Formation at the Sanshui Basin and 'Mengyejing' Formation at Shangyong are correlated and
16 both would be Paleocene.

37 **Material and method**

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

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

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3 and drawings were composed with Adobe Illustrator CC2019 and Photoshop CC2019 softwares.
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5 The holotype specimen presented herein is housed in NIGPAS, Nanjing Institute of Geology
6
7 and Palaeontology, Chinese Academy of Science, China under the accession number
8
9 NIGP175154. Wing venation nomenclature follows Breitkreuz et al. (2017) and in part Brooks
10
11 and Barnard (1990).
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14 Abbreviations are as follows: A anal vein; bsx basal subcostal crossvein; C costa; C1 and C2
15
16 first and second cubital cells; CuA cubitus anterior; CuP cubitus posterior; dcc discal cubital
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18 cell; ig inner gradate crossveins; im intramedian cell; MA media anterior; MP media posterior;
19
20 M1 and M2 first and second median cells; og outer gradate crossveins; Psc Pseudo-cubital vein;
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22 Psm pseudo-median vein RA radius anterior; RP radius posterior; ScP subcostal posterior.
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26 Published work and nomenclatural acts are registered in ZooBank
27
28 urn:lsid:zoobank.org:pub:16ED73C0-9126-4313-837E-D2A76B8738C8.
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32 33 **Systematic palaeontology**

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37 Order Neuroptera Linnaeus, 1758

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39 Family Chrysopidae Schneider, 1851

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41 Subfamily ?Nothochrysinæ Navás, 1910
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47 ***Sinonothochrysa*** Huang and Nel, gen. nov.

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49 urn:lsid:zoobank.org:act:176B7F87-BA8C-4CCF-80A5-2121B79C9FEF
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54 *Type species*

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56 *Sinonothochrysa zhangii* n. sp.
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3 *Diagnosis*
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5 Forewing characters. Two series of gradate crossveins; cell im nearly quadrangular and very
6 broad, twice as long as broad, with its anterior side curved; vein Psm with three branches of RP
7 entering it, Psm continued by inner gradates; crossvein 2m-cu at basal third of cell im; series of
8 cells between Psm and Psc distinctly broader than long; inner gradate series anteriorly curved.
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17 *Etymology*
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19 Named after the Latin name 'Sina' for China, and the extant genus name *Nothochrysa*
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21 McLachlan, 1868.
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26 ***Sinonhothochrysa zhangi*** Huang and Nel sp. nov.
27

28 Figs 2–3
29

30 urn:lsid:zoobank.org:act:0238777A-68AE-453D-A83B-2A793B4F06DC
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35 *Etymology*
36

37 Named after Prof. Xianqiu Zhang, Chinese senior palaeontologist who made a systematically
38 biostratigraphic study of the Sanshui Basin. The specific epithet is to be treated as a noun in the
39 genitive case.
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47 *Type material*
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49 Holotype NIGP175154 (crystallized body with complete but superposed right fore- and hind
50 wings and fragments of the left fore- and hind wings).
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56 *Type locality*
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58 Sanshui District, Foshan City, Guangdong Province, China.
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5 *Stratigraphic occurrence*
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7 Middle Paleocene, Buxin Formation at Western of Sanshui District.
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12 *Diagnosis*
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14 As for the genus.
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19 *Description*
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21 Body ca. 5.0 mm long; thorax ca. 1.0 mm wide.
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23 Forewing (Figs 2–3), 9.0 mm long, ca. 2.2 mm wide; apex rounded; costal space poorly
24 preserved, with simple subcostal veinlets relatively widely spaced; ScP very long, with apex
25 not preserved but probably entering margin near wing apex; subcostal space moderately broad;
26 proximal subcostal crossvein (bsx or 1scp-r) present; no other crossvein between ScP and RA
27 detected; tympanum not detectable; RA long, entering margin at wing apex; origin of RP
28 relatively close to wing base, at 3.0 mm of it; length of RP proximad 1r-m 10 times as long as
29 1r-m; RA space (between RA and RP) broad, with 10 crossveins, the most basal one being well
30 distal to 1r-m; RP weakly zigzagged, with 10 branches, two of them entering Psm; basal
31 crossvein 1r-m very short, perpendicular to M, connecting RP with MA; M forked at an open
32 angle opposite origin of RP; intramedian cell very broad, only two times as long as broad,
33 broadly rectangular with anterior side strongly curved; MA not proximally fused with RP1;
34 Psm well-developed, slightly zigzagged and distally prolonged by inner row of gradates; MP
35 distally fused with CuA; Psc with three-four simple branches between it and posterior wing
36 margin; cells between Psm and Psc rather short but very broad; Psc distally prolonged by outer
37 row of gradates; basal crossvein 1m-cu short, apparently located basal to origin of CuP; 2m-
38 cu present between MP and CuA at basal third of cell im; anal and CuP veins incompletely;
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3 two complete gradate series of crossveins, outer series not parallel to posterior wing margin;
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5 inner series not parallel to outer series; wing membrane apparently hyaline, only darkened in
6
7 distal part of ScP (pterostigma).
8
9

10 Hind wing (Figs 2–3) ca. 8.8 mm long, ca. 2.1 mm wide; apex acute; costal space not preserved;
11
12 only basal part of ScP visible, subcostal space as broad as that of forewing; proximal subcostal
13
14 crossvein (bsx or 1scP–r) present; no other crossvein between ScP and RA detected; RA long,
15
16 entering margin at wing apex; origin of RP relatively close to wing base, at ca. 1.1 mm of it;
17
18 length of basal part of RP as long as part fused with MA; RA space (between RA and RP)
19
20 broad, with 11 crossveins; RP weakly zigzagged, with eighth branches, three of them entering
21
22 Psm; M forked at an open angle slightly basal to origin of RP; MA distally fused with RP1 and
23
24 separating again; Psm well-developed, slightly zigzagged and distally prolonged by inner row
25
26 of gradates; MP distally fused with CuA; Psc with four simple branches between it and posterior
27
28 wing margin; cells between Psm and Psc large, rather short but very broad; Psc distally
29
30 prolonged by outer row of gradates; intracubital crossveins C1 and C2 and anal veins not
31
32 preserved except for forked first anal vein; two complete gradate series of crossveins, wing
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34 membrane apparently hyaline.
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42 **Discussion**

43
44 After the key to the extant chrysopid subfamilies of Brooks and Barnard (1990: 132),
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46 *Sinonothochrysa* gen. nov. falls in the Nothochrysinae because of the character ‘forewing Psm
47
48 continuous with inner row of gradates’. Tauber (2014) proposed a list of putative apomorphies
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50 of the Nothochrysinae and two groups of genera, but none of these are preserved in our
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52 specimen. Makarkin and Archibald (2013) considered the character ‘Psm not extending to the
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54 outer row of gradates’ as possibly characteristic of the Nothochrysinae. They also have the
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3 crossvein 2m-cu located in the proximal half of im. This character is also present in some
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5 Chrysopinae, but not in the Cretaceous-Paleogene Limaiinae.
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8 Garzón-Orduña et al. (2019) listed nine extant genera in the Nothochrysinæ, viz.
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10 *Nothochrysa* McLachlan, 1868, *Pimachrysa* Adams, 1957, and *Hypochrysa* Hagen, 1866,
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12 *Asthenochrysa* Adams and Penny, 1992, *Leptochrysa* Adams and Penny, 1992, *Pamochrysa*
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14 Tjeder, 1966, *Kimochrysa* Tjeder, 1966 (considered as a subjective synonym of *Hypochrysa* by
15
16 Tauber, 2014), *Triplochrysa* Kimmins, and *Dictyochrysa* Esben-Petersen (Tjeder 1966; Adams
17
18 1967; Adams and Penny 1992). Several fossil genera are currently put in this subfamily (Table
19
20 1), viz. *Adamsochrysa* Makarkin and Archibald, 2013 (Eocene), *Archaeochrysa* Adams, 1967
21
22 (Eocene to Oligocene), *Asiachrysa* Makarkin, 2014 (Eocene), *Dyspetochrysa* Adams, 1967
23
24 (Oligocene), *Lithochrysa* Carpenter, 1935 (Oligocene), *Okanaganochrysa* Makarkin and
25
26 Archibald, 2013 (Eocene), *Palaeochrysa* Scudder, 1890 (Oligocene), *Pronothochrysa* Peñalver
27
28 et al., 1995 (Miocene), *Pseudochrysopa* Makarkin and Archibald, 2013 (Eocene), and
29
30 *Tribochrysa* Scudder, 1890 (Oligocene). As Winterton et al. (2019) found the Nothochrysinæ
31
32 as paraphyletic in their phylogenetic analysis, the exact positions of all these fossils remain
33
34 questionable.
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41 *Dictyochrysa* and *Triplochrysa* are excluded from consideration because the gradate
42
43 crossveins in *Sinonothochrysa* gen. nov. are arranged in two series only (vs. more than two in
44
45 these genera, see respectively Brooks and Barnard 1990: fig. 527; New 1980: fig. 13).
46
47 *Pamochrysa* has the forewing cell im rhomboidal, while it is nearly quadrangular in
48
49 *Sinonothochrysa* gen. nov. (Brooks and Barnard 1990: fig. 554).
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51
52 *Sinonothochrysa* gen. nov. shares with *Kimochrysa* a forewing cell im ca. twice as long
53
54 as broad, unlike the genus *Nothochrysa* in which im is much narrower (Adams 1967: fig. 3;
55
56 Kovanci and Canbulat 2007; Tauber 2019). But the forewing cells im of the *Kimochrysa* spp.
57
58 are triangular or pentagonal (Tjeder 1966; Adams 1978; Brooks and Barnard 1990: fig. 539).
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3 *Hypochrysa elegans* (Burmeister, 1839) and *Asthenochrysa* (type species *A. viridula* (Adams,
4 1978)) have also a triangular cell im (Adams 1967: fig. 5, 1978: fig. 1; Brooks and Barnard
5 1990: fig. 533). In *Sinonothochrysa* gen. nov., the anterior side of the cell im is curved, while
6
7 in *Kimochrysa impar* Tjeder, 1966, it is slightly angular, rendering im pentagonal (Tjeder 1966:
8 fig. 785), the difference being rather weak. Nevertheless, the vein ‘distal part of MA – Psm’ is
9
10 much shorter in *K. impar* and *K. africana* (Kimmins, 1937) than in *Sinonothochrysa* gen. nov.,
11
12 with only two short cells above it basal to the first i.g. vein instead of three large ones.
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19 While *Pimachrysa grata* Adams, 1957, *P. fusca* Adams, 1967 and *P. intermedia* Adams,
20 1967 have rather narrow cells im, *P. nigra* Adams, 1967 has one nearly ca. twice as long as
21 broad as in *Sinonothochrysa* gen. nov. (Adams 1957: fig. 1, 1967: figs 1-2, 4). They all differ
22 from *Sinonothochrysa* gen. nov. in the crossvein 2m-cu basal or very close to basal angle of
23 cell im and the series of cells between Psm and Psc nearly as long as broad.
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30 *Leptochrysa* has a very particular cell im, quadrangular but with the cell below it
31 strongly reduced (Adams and Penny 1992: fig. 10; Tauber 2019), strongly differing from the
32 configuration of im in *Sinonothochrysa* gen. nov. (pentagonal without reduction of the cell
33 below it).
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40 *Okanaganochrysa* has two series of cells between Psm and Psc (Makarkin and
41 Archibald 2013: fig. 4). The *Adamsochrysa* spp. have a hexagonal cell im, but broadly similar
42 to that of *Sinonothochrysa* gen. nov. (Makarkin and Archibald 2013: fig. 6), but they also have
43 four rows of gradate crossveins. The *Archaeochrysa* spp. have a quadrangular cell im, but much
44 narrower than in *Sinonothochrysa* gen. nov. (Adams 1967; Makarkin and Archibald 2013).
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50
51 Makarkin and Archibald (2013) provisionally put *Pseudochrysopa* in the Nothochrysinæ
52 because of the two following characters: ‘Psm does not extend to the outer gradate series’; and
53
54 ‘2m-cu is located in the proximal half of im’. The exact position of this genus needs to be re-
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3 evaluated. Nevertheless, it strongly differs from *Sinonothochrysa* gen. nov. in the narrower cell
4 im and vein Psm not continued by the inner gradates.
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8 *Dyspetochrysa vetuscula* (Scudder, 1890), *Tribochrysa inaequalis* Scudder, 1885,
9
10 *Tribochrysa firmata* Scudder, 1890, *Lithochrysa wickhami* (Cockerell, 1914), *Palaeochrysa*
11
12 *stricta* Scudder, 1890 and *P. creedei* Carpenter, 1935 differ from *Sinonothochrysa* gen. nov. in
13
14 the elongate cell im, a course of the inner gradates parallel to posterior wing margin, instead of
15
16 being anteriorly curved (Carpenter 1935: figs 1, 3-4, 6-7). *Palaeochrysa fracta* Cockerell, 1914
17
18 has also a narrow cell im and an irregular series of inner gradates (maybe an aberrant feature)
19
20 (Carpenter 1935: fig. 2).
21
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24 *Pronothochrysa vivesi* Peñalver et al., 1995 has also a narrow cell im, plus a much
25
26 longer vein ‘distal part of MA – Psm’ than in *Sinonothochrysa* gen. nov. with six cells between
27
28 it and RP instead of three (Peñalver et al. 1995: fig. 4).
29

30
31 *Asiachrysa tadushiella* Makarkin, 2014 has a cell im similar to that of *Sinonothochrysa*
32
33 gen. nov., although slightly narrower. Nevertheless, its cells between Psm and Psc are longer
34
35 and narrower than in *Sinonothochrysa* gen. nov. and overall, the crossvein 2m-cu is situated
36
37 below mid part of cell im instead of being in the basal third of this cell (Makarkin 2014: fig. 3).
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40 41 42 **Conclusion**

43
44 Except for a Miocene genus, the fossil record of the subfamily Nothochrysinæ is restricted to
45
46 the Eocene – Oligocene, with an impressive diversity during the Eocene to the earliest
47
48 Oligocene with ten described extinct genera contra only one (*Nothochrysa*) during the Middle
49
50 – Late Oligocene, confirmed by the newly described genus. Possibly this subfamily collapsed
51
52 during the Oligocene in relation to the general cooling and/or bat diversification, as already
53
54 suggested by Archibald et al. (2014) and Ngô-Muller et al. (2019). The Paleocene
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3 *Sinonothochrysa zhang* Huang and Nel gen. nov. et sp. nov. is the oldest record of the
4
5 Nothochrysinæ.
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11
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14 **Table 1.** Fossil record of the family Chrysopidae
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19 **Figure 1.** Fossil locality map.
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24 **Figure 2.** *Sinonhothochrysa zhangii* Huang and Nel gen. et sp. nov., holotype NIGP175154. (A)
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26 photograph of habitus; (B) forewing reconstruction; arrows: course of forewing CuP; (C) hind
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28 wing reconstruction. Scale bars = 1 mm.
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33 **Figure 3.** *Sinonhothochrysa zhangii* Huang and Nel gen. et sp. nov., holotype NIGP175154.
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35 Photographs. (A) thorax with bases of wings; (B) detail of bases of wings. Scale bars = 1 mm
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37 (A), 0.5 mm (B)
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figure 1

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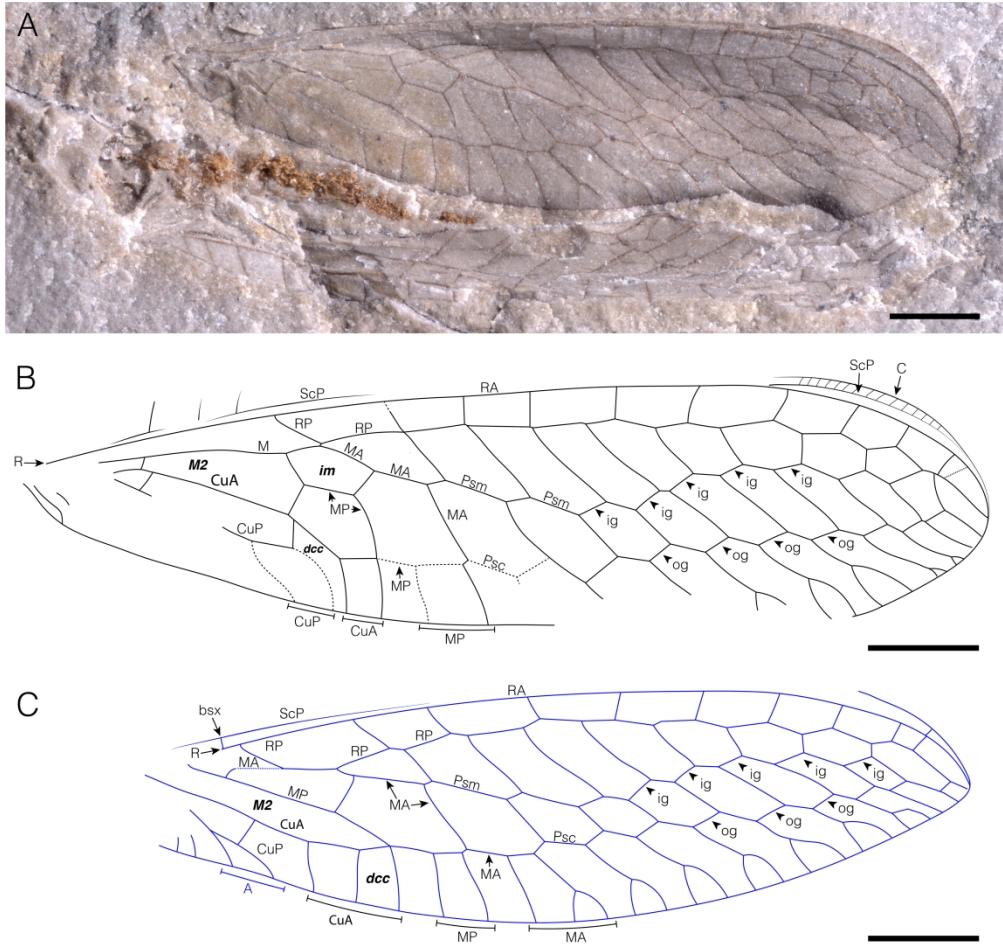


figure 2

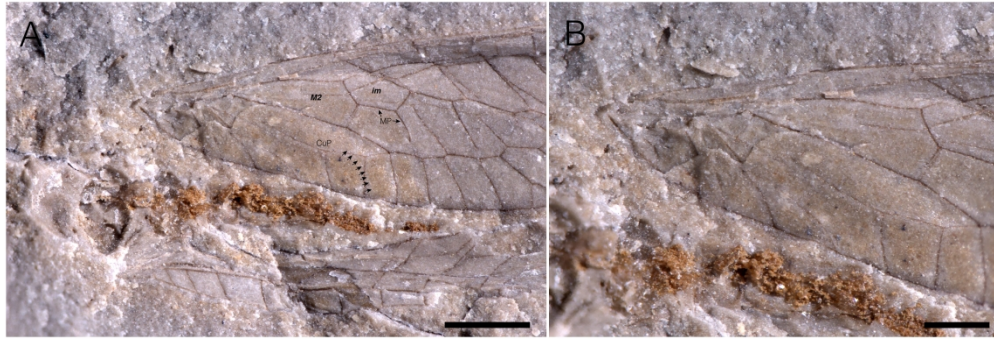


figure 3

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

	<i>L. conspicua</i> Martins-Neto & Vulcano, 1999	Brazil	Aptian
	<i>Mesypochrysa</i> Martynov, 1927		
	<i>M. angustialata</i> Makarkin, 1997	Russian Federation	Aptian
	<i>M. cannabina</i> Khramov, 2018	Russian Federation	Aptian
	<i>M. chrysopa</i> Makarkin, 1997	Russian Federation	Aptian
	<i>M. chrysopoides</i> Ponomarenko, 1992	Mongolia	Aptian
	<i>M. curvimedia</i> Makarkin, 1997	Russian Federation	Aptian
	<i>M. falcata</i> Makarkin, 1997	Russian Federation	Aptian
	<i>M. intermedia</i> Panfilov, 1980	Kazakhstan	Callovian/Oxfordian
	<i>M. latipennis</i> Martynov, 1927	Kazakhstan	Callovian/Oxfordian
	<i>M. magna</i> Makarkin, 1997	Russian Federation	Aptian
	<i>M. minima</i> Makarkin, 1997	Russian Federation	Aptian
	<i>M. miniscula</i> Ren & Guo, 1996	China	Aptian
	<i>M. minuta</i> Jepson et al., 2012	United Kingdom	Berriasian
	<i>M. naranica</i> Khramov, 2018	Russian Federation	Aptian
	<i>M. polyclada</i> Panfilov, 1980	Kazakhstan	Callovian/Oxfordian
	<i>M. polyneura</i> Ren & Guo, 1996	China	Aptian
	<i>M. reducta</i> Panfilov, 1980	Kazakhstan	Callovian/Oxfordian
	<i>M. sinica</i> Khramov et al., 2015	China	Callovian/Oxfordian
	<i>Parabaisochrysa</i> Lu et al., 2018		
	<i>P. xingkei</i> Lu et al., 2018	Myanmar	Cenomanian
	<i>Protochrysa</i> Willmann & Brooks, 1991		
	<i>P. aphrodite</i> Willmann & Brooks, 1991	Denmark	Ypresian
	<i>P. fuscobasalis</i> Makarkin & Archibald, 2013	Canada	Ypresian
	Nothochrysinæ Navas 1910		
	<i>Adamsochrysa</i> Makarkin & Archibald, 2013		
	<i>A. aspera</i> Makarkin & Archibald, 2013	Canada	Ypresian
	<i>A. wilsoni</i> Makarkin & Archibald, 2013	Canada	Ypresian
	<i>Archaeochrysa</i> Adams, 1967		
	<i>A. creedei</i> Carpenter, 1935	USA	Oligocene
	<i>A. fracta</i> Cockerell, 1914	USA	earliest Oligocene
	<i>A. paranervis</i> Adams, 1967	USA	earliest Oligocene
	<i>A. profracta</i> Makarkin & Archibald, 2013	Canada	Ypresian
	<i>A. sanikwa</i> Archibald & Makarkin, 2015	Canada	Ypresian
	<i>Asiachrysa</i> Makarkin, 2014		
	<i>A. tadushiella</i> Makarkin, 2014	Russian Federation	Ypresian
	<i>Dyspetochrysa</i> Adams, 1967		
	<i>D. vetuscula</i> Scudder, 1890	USA	earliest Oligocene
	<i>Hypochrysa</i> Gould, 1861		
	<i>H. hercyniensis</i> Schlüter, 1982	Germany	Pliocene
	<i>Lithochrysa</i> Carpenter, 1935		
	<i>L. borealis</i> Archibald & Makarkin, 2017	Canada	Ypresian
	<i>L. wickhami</i> Cockerell, 1914	USA	earliest Oligocene
	<i>Nothochrysa</i> MacLachlan, 1868		

1		<i>N. praeclara</i> Statz, 1936	Germany	Chattian
2		<i>N. stampieni</i> Nel & Séméria, 1986	France	Chattian
3		<i>N. praeclara</i> Statz, 1936	Germany	Chattian
4				
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6	<i>Okanaganochrysa</i> Makarkin & Archibald, 2013			
7		<i>O. coltsunae</i> Makarkin & Archibald, 2013	Canada	Ypresian
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10	<i>Palaeochrysa</i> Scudder, 1890			
11		<i>P. concinnula</i> Cockerell, 1909	USA	Chadronian
12		<i>P. stricta</i> Scudder, 1890	USA	Chadronian
13				
14	<i>Pronothochrysa</i> Peñalver et al., 1995			
15		<i>P. vivesi</i> Peñalver et al., 1995	Spain	Miocene
16				
17	<i>Pseudochrysopa</i> Makarkin & Archibald, 2013			
18		<i>P. harveyi</i> Makarkin & Archibald, 2013	Canada	Ypresian
19				
20	<i>Sinonothochrysa</i> gen. nov.			
21		<i>Sinonothochrysa eocenica</i> sp. nov.	China	middle Paleocene
22				
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24	<i>Tribochrysa</i> Scudder, 1885			
25		<i>T. firmata</i> Scudder, 1890	USA	Chadronian
26		<i>T. inequalis</i> Scudder, 1885	USA	Chadronian

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
Dominican amber	Engel and Grimaldi, 2007
Khasurty	Khramov, 2018
Khasurty	Khramov, 2018
Crato / Crato Formation	Martins-Neto and Vulcano, 1999
Baissa / Zaza Formation	Makarkin, 1997
Karatau-Mikhailovka / Karabastau Formation	Khramov et al., 2015
84GT1, west Tuanwang Village / Laiyang Formation	Yang and Hong, 1990
Crato / Crato Formation	Martins-Neto, 1997

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2	Crato / Crato Formation	Martins-Neto, 1988
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5	Baissa / Zaza Formation	Makarkin, 1997
6	Khasurty	Khramov, 2018
7	Baissa / Zaza Formation	Makarkin, 1997
8	Bon Tsagaan / Dzun-Bain Formation	Ponomarenko, 1992
9	Baissa / Zaza Formation	Makarkin, 1997
10	Baissa / Zaza Formation	Makarkin, 1997
11	Karatau-Mikhailovka / Karabastau Formation	Panfilov, 1980
12	Galkino / Karabastau Formation	Martynov, 1927
13	Baissa / Zaza Formation	Makarkin, 1997
14	Baissa / Zaza Formation	Makarkin, 1997
15	Near Chaomidian Village / Yixian Formation	Ren and Guo, 1996
16	Durlston Bay, Bed DB175, Swanage (Manchester Mus) / Durlston Formation	Jepson et al., 2012
17	Khasurty	Khramov, 2018
18	Karatau-Mikhailovka / Karabastau Formation	Panfilov, 1980
19	Near Chaomidian Village / Yixian Formation	Ren and Guo, 1996
20	Karatau-Mikhailovka / Karabastau Formation	Panfilov, 1980
21	Daohugou / Daohugou Formation	Khramov et al., 2015
22		
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26	Burmese amber	Lu et al., 2018
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30	Fur Formation	Willmann and Brooks, 1991
31	McAbee	Makarkin and Archibald, 2013
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36	McAbee	Makarkin and Archibald, 2013
37	McAbee	Makarkin and Archibald, 2013
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40	Creede / Creede Formation	Carpenter, 1935
41	Wilson Ranch, Florissant	Cockerell, 1914
42	Florissant, Station 14 / Florissant Formation	Adams, 1967
43		
44	McAbee	Makarkin and Archibald, 2013
45	Driftwood Canyon	Archibald and Makarkin, 2015
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48	Tadushi locality / Tadushi Formation	Makarkin, 2014
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50		
51	Florissant / Florissant Formation	Scudder, 1890
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55	Willershausen clay pit	Schlüter, 1982
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58	Driftwood Canyon	Archibald and Makarkin, 2017
59	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
McAbee	Makarkin and Archibald, 2013
Florissant / Florissant Formation	Cockerell, 1909
Florissant / Florissant Formation	Scudder, 1890
La Rinconada, Ribesalbes	Peñalver et al., 1995
Driftwood Canyon	Makarkin and Archibald, 2013
Sanshui District / Buxin Formation	This paper
Florissant / Florissant Formation	Scudder, 1890
Florissant / Florissant Formation	Scudder, 1885

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