

EARLY GREEN LACEWINGS (INSECTA: NEUROPTERA: CHRYSOPIDAE) FROM THE JURASSIC OF CHINA AND KAZAKHSTAN

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Abstract: Two new species of Jurassic Chrysopidae are described: *Mesypochrysa sinica* sp. nov. (Limaiinae) from the Middle–Upper Jurassic boundary interval of Daohugou (China) and *Baisochrysa pumila* sp. nov. (Limaiinae) from the Upper Jurassic of Karatau (Kazakhstan). *Mesypochrysa intermedia* Panfilov, 1980, previously known from Karatau, is recorded from Daohugou. *Mesypochrysa sinica* sp. nov. and *M.* cf. *intermedia* from Daohugou are considered to be the earliest known, unquestionable green lacewings. *Lembochrysa* Ren and Guo, 1996 is synonymized with *Mesypo-*

chrysa Martynov, 1927. *Mesypochrysa makarkini* Nel *et al.*, 2005 is synonymized with *M. intermedia*, and the size range of their forewings is discussed. Male and female terminalia of the Mesozoic green lacewings are described for the first time. The diversification of ants is considered a possible cause of the extinction of Limaiinae during the early Eocene.

Key words: Daohugou, Karatau, Middle Jurassic, Chrysopidae, Neuroptera, green lacewings.

TODAY, the Chrysopidae is the second largest family of lacewings after Myrmeleontidae and has a worldwide distribution. They comprise *c.* 1200 Recent species in approximately 80 genera belonging to three subfamilies: Chrysopinae, Apochrysininae and Nothochrysininae (Brooks and Barnard 1990). Larvae of green lacewings are one of the most important biological control agents of aphids, psyllids, scale insects and other soft-bodied pest insects (New 2001).

The earliest known occurrence of Chrysopidae, *Liasochrysa stigmatica* Ansoerge and Schlüter, 1990, was reported from the Upper Lias of Dobbartin (Ansoerge and Schlüter 1990). The status of this taxon, however, is controversial. Nel *et al.* (2005) placed *L. stigmatica* in the separate family Liassochrysidae, within Chrysopoidea, whereas Wedmann and Makarkin (2007) assigned it to Mantispididae based on the structure of the pterostigmal region and the other venational characters. Liu *et al.* (2015) also accepted a mantispid affinity for *Liassochrysa*.

The earliest unequivocal green lacewings were five species of *Mesypochrysa* Martynov, 1927 described from the Upper Jurassic of Karatau, Kazakhstan (Martynov 1927; Panfilov 1980; Nel *et al.* 2005). All other known fossil

green lacewings are Cretaceous or younger in age (see the list in Archibald *et al.* 2014), such that the Jurassic record of Chrysopidae is quite sparse. Here, we describe two new Jurassic species of Chrysopidae – one from the Upper Jurassic of Karatau and another from the Middle–Upper Jurassic boundary interval of Daohugou, China. The precise ages of two these localities are not established, but judging by the estimated age ranges (see Material and methods below), Daohugou is somewhat older than Karatau, such that *M. sinica* sp. nov. and *M.* cf. *intermedia* Panfilov, 1980 from Daohugou should be considered as the earliest known representatives of Chrysopidae.

MATERIAL AND METHODS

The specimens NIGP161886 and NIGP161887 described in this paper were collected from the Middle–Upper Jurassic boundary interval Daohugou beds at Daohugou Village, Wuhua Township, Ningcheng County, near Chifeng City in Inner Mongolia, China. The Daohugou beds, consisting of grey tuff, tuffaceous siltstone and mudstone, are now considered to be one of the most important of

Mesozoic terrestrial Lagerstätten (Rasnitsyn and Zhang 2004; Ponomarenko and Ren 2010), from which approximately 2000 specimens of Neuroptera have been collected (Yang *et al.* 2012). The fossil-bearing beds at Daohugou were previously considered to be Bathonian to Callovian in age and thought to belong to the Jiulongshan Formation (Yang *et al.* 2012). However, recent radiometric dating suggests that the age of Daohugou beds falls near the Callovian–Oxfordian boundary (Liu *et al.* 2006, 2012; Cohen *et al.* 2013; Wang *et al.* 2013), so the deposits should be correlated with the Lanqi Formation (or Tiaojishan Formation; Liu *et al.* 2006, 2012; Chang *et al.* 2009; Wang *et al.* 2013; Zhang *et al.* 2014). Based on comparisons with similar palyno-assemblages in the Jurassic of China, the age of the Daohugou locality recently was interpreted to be the late Middle Jurassic (Na *et al.* 2015).

All other specimens were collected from the Upper Jurassic Karabastau Formation, consisting of lacustrine deposits. Several adjacent outcrops of the Karabastau Formation, known as the Karatau locality, are situated near Big Karatau Range in South Kazakhstan (formerly Chimkent) Province. The characteristic lithology of the Karabastau Formation consists of lithographic shales: highly laminated, fissile claystone which provides exceptional preservation of fossil inclusions. Spore and pollen analysis indicates a late Callovian to Kimmeridgian (Doludenko and Orlovskaya 1976) or possibly Oxfordian–Kimmeridgian (Doludenko *et al.* 1990) age for these deposits. More than 18 000 insects have been found in Karatau, with lacewings comprising 543 of the specimens collected and accounting for about 3% of the total.

The photographs of specimens NIGP161886 and NIGP161887 were taken using a Canon EOS 5D digital camera; photographs of all other specimens were taken with a Nikon D200 digital camera. An ethanol–water solution was dropped on specimens in some cases to make structural details more discernible. The overlay line drawings were prepared on photographs using the image-editing software Photoshop CS6.

Abbreviations. The traditional nomenclature of wing venation was used following Adams (1967): C, costa; Sc, subcosta; R, radius; R1, first branch of R; Rs, radial sector; Rs1, most basal branch of Rs; M, media; MA, media anterior; MP, media posterior; MP1, anterior branch of MP; MP2, posterior branch of MP; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; A1–A3, first to third anal veins; im, basal intramedian cell; 2m-cu is the second crossvein connecting MP and CuA, and 2m-cu cell is wing area posterior to crossvein 2m-cu and bounded by CuA and MP1.

Institutional abbreviations. Specimens NIGP161886 and NIGP161887 are housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. All other specimens mentioned in the paper are at the Borissiak Paleontologi-

cal Institute of the Russian Academy of Sciences in Moscow, Russia (PIN).

SYSTEMATIC PALAEOLOGY

This published work and the nomenclatural acts it contains have been registered in ZooBank: <http://zoobank.org/References/11137CD0-D24F-40AC-B628-70CFD01439EB>

Order Neuroptera Linnaeus, 1758
Family Chrysopidae Schneider, 1851
Subfamily Limaiinae Martins-Neto and Vulcano, 1989

Genus MESYPOCHRYSA Martynov, 1927
= LEMBOCHRYSA Ren and Guo, 1996 syn. nov.

Type species. *MesyPOCHrysa latipennis* Martynov, 1927 from the Upper Jurassic of Karatau, South Kazakhstan Province.

Other species. See Table 1 and Appendix.

Diagnosis

Forewing. Two gradate series of crossveins present in Rs, cell im proximally connected by crossvein with stem of Rs, MP connected with CuA distally to point of bifurcation by one crossvein, CuP bifurcated terminally forming quadrangle (sometimes a trapezoid) with wing margin, its vertex connected by crossvein with CuA, Cu + MP with 3–8 unforked branches, Rs with 5–20 branches once or few times forked terminally, A1 and A2 long and simple and sometimes forked terminally, A1 close to CuP connected with it by short crossvein or even fused, A3 short.

Hindwing. Two gradate series of crossveins present in Rs, Rs with 5–18 branches, MP simple or bifurcated, as in forewing, CuA with 3–5 branches, connected with MP by one or two crossveins, CuP same as in forewing, forming quadrangle terminally and connected by crossvein with CuA, A1 close to CuP.

Male. (Figs 1D, 2B) Sternites 8 and 9 not fused, tergite 9 narrow and not fused with ectoproct.

Female. (Fig. 1C) Tergite 9 fused with ectoproct.

Remarks

To date, seven genera have been placed in the subfamily Limaiinae (Archibald *et al.* 2014): *MesyPOCHrysa* Mar-

TABLE 1. Occurrence with comments of the fossil genus *Mesypochrysa* Martynov, 1927 (Chrysopidae: Limaiiinae).

<i>Mesypochrysa</i> species	Wing known (as preserved/drawn in original description)	Locality and age
<i>M. sinica</i> sp. nov.	Forewing and partly preserved hindwing	China, Daohugou, Middle to Upper Jurassic
<i>M. cf. intermedia</i> Panfilov, 1980 (<i>sensu</i> this paper)	Forewing and hindwing	China, Daohugou, Middle to Upper Jurassic
<i>M. latipennis</i> Martynov, 1927	Overlapping wings	Kazakhstan, Karatau, Upper Jurassic
<i>M. intermedia</i> Panfilov, 1980	Forewing	Kazakhstan, Karatau, Upper Jurassic
<i>M. polyclada</i> Panfilov, 1980	Partly preserved forewing	Kazakhstan, Karatau, Upper Jurassic
<i>M. reducta</i> Panfilov, 1980	Hindwing	Kazakhstan, Karatau, Upper Jurassic
<i>M. minuta</i> Jepson <i>et al.</i> , 2012	Hindwing	England, Durlston Formation, upper Berriasian
<i>M. magna</i> Makarkin, 1997	Forewing and hindwing	Russia, Transbaikalia, Baissa, Valanginian–Hauterivian
<i>M. falcata</i> Makarkin, 1997	Hindwing and partly preserved forewing	Russia, Transbaikalia, Baissa, Valanginian–Hauterivian
<i>M. chrysopa</i> Makarkin, 1997	Forewing and hindwing	Russia, Transbaikalia, Baissa, Valanginian–Hauterivian
<i>M. curvimedia</i> Makarkin, 1997	Forewing and hindwing	Russia, Transbaikalia, Baissa, Valanginian–Hauterivian
<i>M. angustialata</i> Makarkin, 1997	Forewing	Russia, Transbaikalia, Baissa, Valanginian–Hauterivian
<i>M. minima</i> Makarkin, 1997	Hindwing	Russia, Transbaikalia, Baissa, Valanginian–Hauterivian
<i>M. chrysopoides</i> Ponomarenko, 1992	Forewing and hindwing	Mongolia, Bon-Tsagan, Aptian

(continued)

TABLE 1. (Continued)

<i>Mesypochrysa</i> species	Wing known (as preserved/drawn in original description)	Locality and age
<i>M. cf. chrysopoides</i> Ponomarenko, 1992 (<i>sensu</i> Nel <i>et al.</i> 2005)	Forewing and hindwing	China, Yixian Formation, early Aptian
<i>M. polyneura</i> (Ren and Guo, 1996) comb. nov.	Forewing and hindwing	China, Yixian Formation, early Aptian
<i>M. miniscula</i> (Ren and Guo, 1996) comb. nov.	Forewing	China, Yixian Formation, early Aptian
<i>M. criptovenata</i> (Martins-Neto and Vulcano, 1989)	Forewing and hindwing	Brazil, Crato Formation, late Aptian – early Albian
<i>M. confusa</i> (Martins-Neto and Vulcano, 1989)	Overlapping wings	Brazil, Crato Formation, late Aptian – early Albian

tynov, 1927; *Lembochrysa* Ren and Guo, 1996; *Baisochrysa* Makarkin, 1997; *Drakochrysa* Yang and Hong 1990; *Protochrysa* Willmann and Brooks, 1991; *Limaia* Martins-Neto and Vulcano, 1989; and *Cretachrysa* Makarkin, 1994. This subfamily is characterized by the following characters: a long im, the crossvein 2m-cu merges into the distal part of im, a short Sc which terminates within the pigmented pterostigma and a long R1 which terminates near wing apex (Makarkin and Archibald 2013). Monotypic *Cretachrysa* from the Upper Cretaceous (Cenomanian) of the Obeshchayushchiy locality (Russia) is known only from a fragmentary forewing, so attribution of it to Limaiiinae is not well established. All venational characters of *Lembochrysa* Ren and Guo, 1996, comprising two species, *L. polyneura* Ren and Guo, 1996 and *L. miniscula* Ren and Guo, 1996 from the Lower Cretaceous (early Aptian) Yixian Formation (China), are in agreement with the diagnosis of *Mesypochrysa*. Consequently, we treat these genera as synonyms.

The other two Early Cretaceous genera of Limaiiinae, *Limaia* Martins-Neto and Vulcano, 1989 from the Crato Formation and monotypic *Drakochrysa* Yang and Hong, 1990 from the Laiyang Formation (late Barremian, according to Makarkin *et al.* 2012), are also likely synonyms of *Mesypochrysa*. The only significant character of *Drakochrysa* distinguishing it from *Mesypochrysa*,

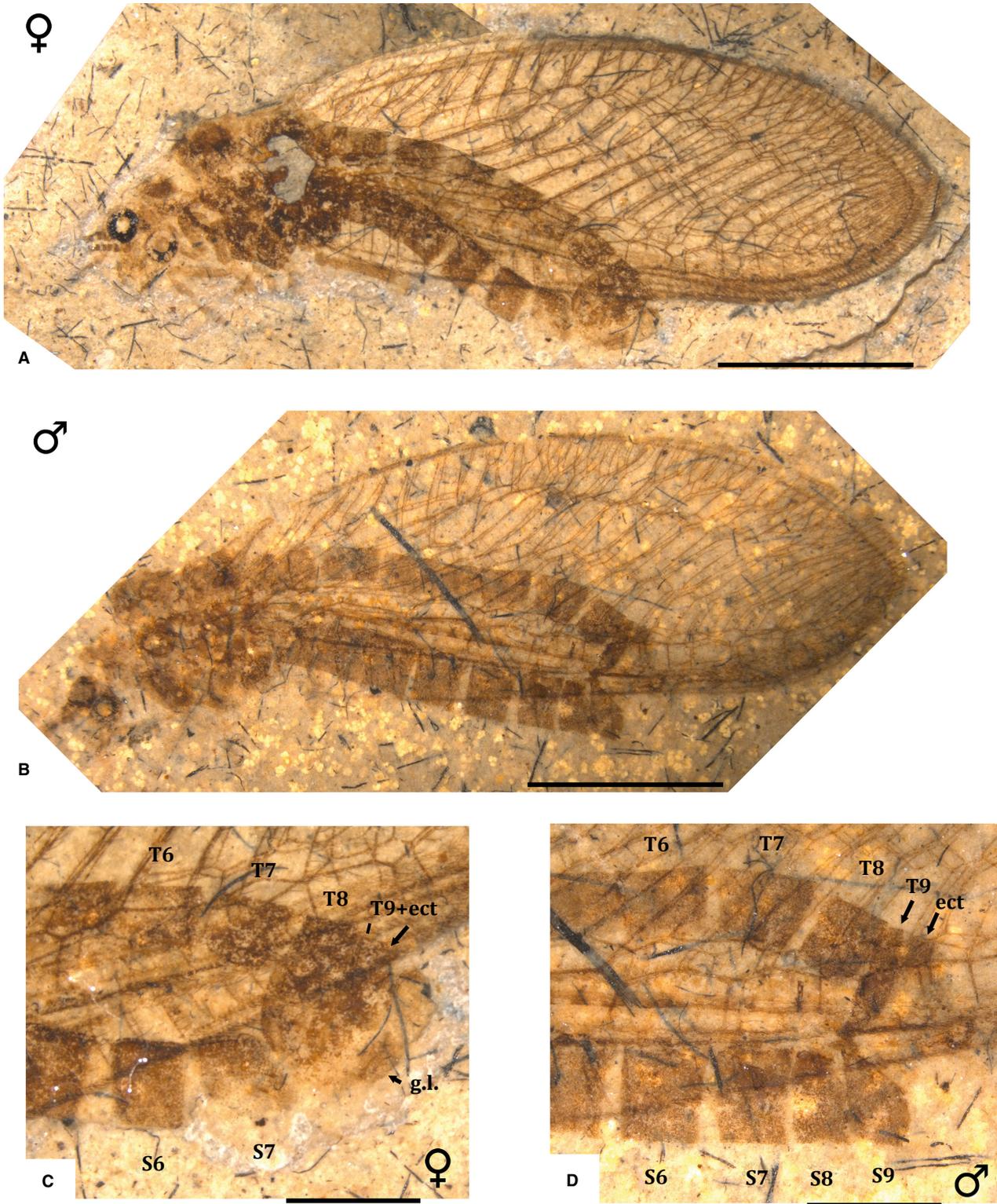


FIG. 1. *Mesypochrysa* sp. from the Upper Jurassic of Karatau, Kazakhstan. A, C, female, PIN 2239/1709. B, D, male, PIN 2904/676. Abbreviations: T, tergite; S, sternite; ect, ectoproct; g.l., gonapophysis lateralis (see text for venation nomenclature). Scale bars represent 5 mm (A–B); 2 mm (C–D). Colour online.

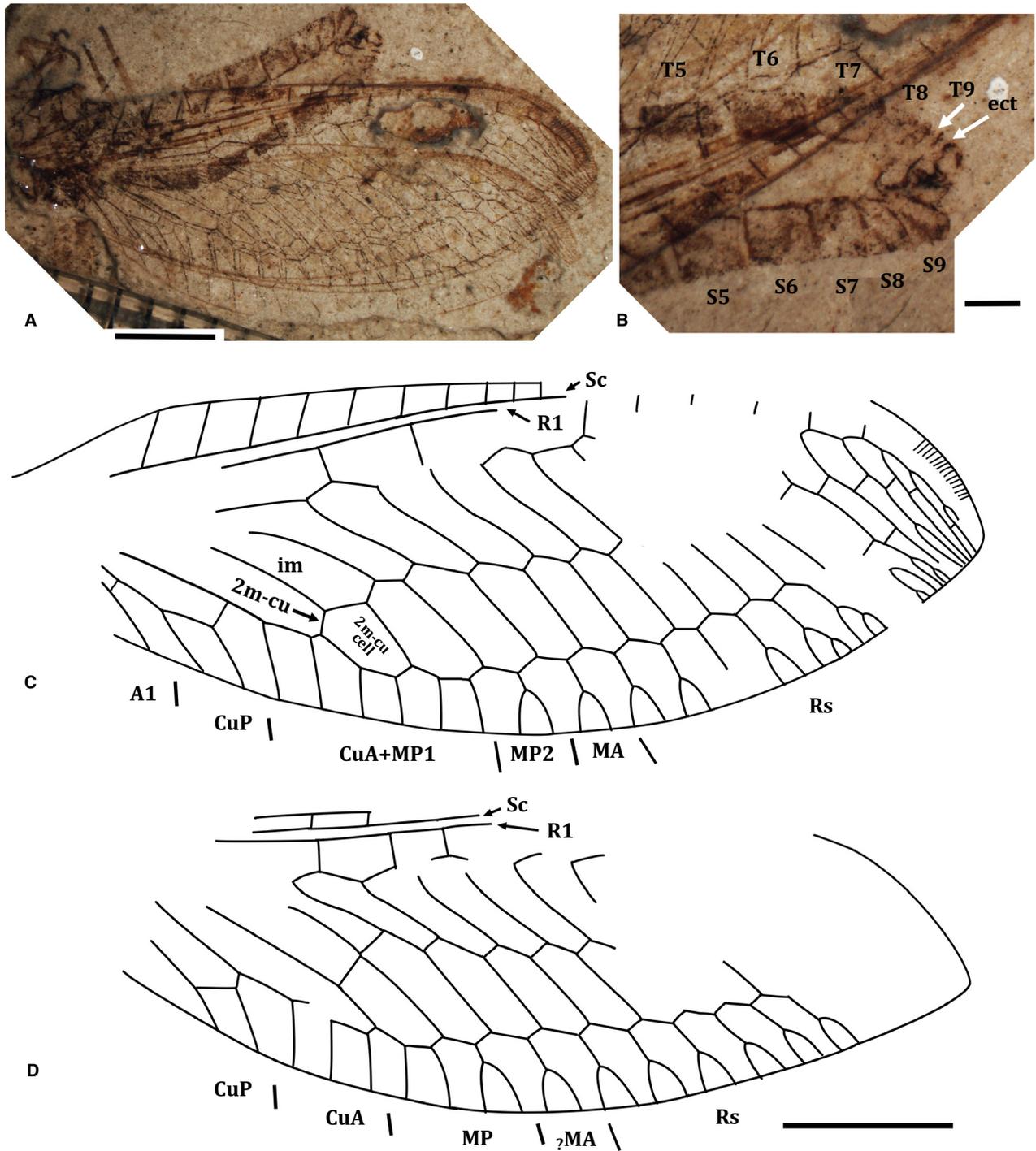


FIG. 2. A, *Mesepochrysa* cf. *intermedia* Panfilov, 1980, male, NIGP161886, from the Middle–Upper Jurassic of Daohugou. B, enlargement of the terminal segments of the abdomen. C, overlay drawing of the forewing. D, overlay drawing of the hindwing. Abbreviations: T, tergite; S, sternite; ect, ectoproct; im, basal intramedian cell; 2m-cu, second crossvein connecting MP and CuA. See text for venation nomenclature. Scale bars represent 3 mm (A, C–D); 1 mm (B). Colour online.

according to the drawing in the original description (Yang and Hong 1990), is the greater number of anal veins. However, this indication is almost certainly the result of misinterpretation due to vein multiplication

from overlapping wings. *Limaia adicotomica* Martins-Neto, 1997, judging by the venation, seems to belong to *Mesepochrysa*. The venation of the type species, *L. conspicua* Martins-Neto and Vulcano, 1989, is quite unclear.

The decision about whether or not to synonymize *Drakochrysa* and *Limaia* with *Mesypochrysa*, however, is postponed until their holotypes can be re-examined.

Currently, only three genera of Limaiainae seem to be well established: *Mesypochrysa*, *Baisochrysa* from the Upper Jurassic of Karatau and the Lower Cretaceous of Baissa (which differs from the others by three gradate series of crossveins in the Rs), and *Protochrysa* from the lower Eocene of Denmark and Canada (which is clearly distinguished due to the presence of the additional crossvein 3m-cu between the CuA and MP; Makarkin and Archibald 2013).

Mesypochrysa cf. *intermedia* Panfilov, 1980
= *M. makarkini* Nel et al., 2005, syn. nov.

Figure 2

Material. NIGP161886, an impression of a nearly complete male (head absent) with overlapping wings.

Locality and horizon. Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China; Daohugou beds, Middle to Upper Jurassic.

Description. Male: sternite 9 seems to consist of two parts with suture between them, proximal part small and narrow, distal part large and extended; ventral end of tergite 9 somewhat expanded and rounded. Forewing: length 16.8 mm, width 6.2 mm, Rs with 14 branches, last 3 unforked, CuA + MP1 with 6 unforked branches, crossvein 2m-cu fused with CuA somewhat distad of second branch of CuA + MP1, short crossvein discernible between CuP and A1, longest diagonal of CuP 'trapezoid' longer than that of 2m-cu cell. Hindwing: length 14.7 mm, width 5.3 mm, MP two-branched (?), crossvein between two branches of MP situated slightly posterior to inner gradate series of crossveins, CuA with two branches and connected with MP by one crossvein, space between stem of CuA where it branches and wing margin two times as wide as space between CuA and MP.

Comparisons. The specimen NIGP161886 is clearly distinguished (see Appendix) from the four minute species: *M. latipennis* Martynov, 1927, *M. miniscula* (Ren and Guo, 1996; whose forewings are 11–12 mm in length, with few branches of Rs (5–6)), *M. minuta* Jepson et al., 2012 and *M. reducta* Panfilov, 1980 (whose hindwings are 7–10 mm with 5 branches of Rs). *M. magna* Makarkin, 1997 and *M. chrysopa* Makarkin, 1997 from Baissa are also apparently dissimilar to NIGP161886 because of their small cell 2m-cu (length ratio of cell 2m-cu to im in forewings of both species is 1:3, while this ratio is 1:2 in all other species of *Mesypochrysa*). *Mesypochrysa falcata* Makarkin, 1997 is distinguished from NIGP161886 by its narrow cells in Rs, *M. polyclada* Panfilov, 1980, *M. sinica* sp. nov. by branches of Rs, which extensively branched

terminally, and *M. minima* Makarkin, 1997 by the smaller size of hindwing. Comparison with *M. confusa* (Martins-Neto and Vulcano, 1989) is impossible because the latter's venation is not drawn with sufficient detail in the original description.

In distinguishing between the rest of the species of *Mesypochrysa* one character which seems to be useful is the number of unforked branches of CuA and MP running into the forewing margin between the always distinct 'fork' of CuP and the first terminally forked branch (usually MP2 or MA). This number is three in the case of *M. sinica* sp. nov.; four in *M. chrysopoides* Ponomarenko, 1992, *M. cf. chrysopoides* Ponomarenko, 1992 (Nel et al. 2005) and *M. polyneura* (Ren and Guo, 1996); six in NIGP161886, *M. intermedia* Panfilov, 1980 and *M. makarkini* Nel et al., 2005; seven in *M. angustialata* Makarkin, 1997 and *M. curvimedia* Makarkin, 1997; and eight (?) in *M. criptovenata* (Martins-Neto and Vulcano, 1989). Besides the same number of unforked branches of CuA and MP1 in the forewing, NIGP161886, *M. intermedia* (Fig. 3C) and *M. makarkini* (Fig. 3G) share a 2m-cu cell of the same shape, an unforked A1, and nearly the same number of branches of Rs (14, 12 and 13, respectively), the most distal 4–5 which are unforked. Judging by the forewing length (16.8 mm), NIGP161886 is more similar to *M. makarkini* (16.3 mm), than to *M. intermedia* (20.3 mm). Nevertheless, the wing lengths can vary within species of recent Chrysopidae; for example, the forewing length range of *Kymachrysa intacta* (Navás, 1912) is 11–15 mm (Tauber and Garland 2014), and that of *Leucochrysa boxi* Navás, 1930 is 21.9–27.3 mm (Tauber et al. 2011). Significantly, the forewings of specimens from Karatau belonging to *M. intermedia* vary by the same range (Fig. 3): the forewing length of specimen PIN 2997/2757 (Fig. 3E) is about 16.5 mm, PIN 2997/2660 (Fig. 3F) is about 17 mm (length of preserved part of wing is 11, 2 mm), PIN 2066/1142 (Fig. 3A) and PIN 2784/1063 (Fig. 3D) are 17.5 mm, and PIN 2997/718 (Fig. 3B) is 19 mm.

As the length of the forewing is the only discernible difference between *M. intermedia* and *M. makarkini*, and both are collected from the same locality at Karatau, we propose to synonymize these taxa. As NIGP161886 appears to be indistinguishable from *M. intermedia* in venation, it is reasonable to assign it to this species.

Remarks. It is insufficient to conclude with certainty that southern Kazakhstan and north-eastern China were indeed inhabited by the same biological species of green lacewing during the Middle to Upper Jurassic. One of the most common extant green lacewings, *Chrysoperla carnea* (Stephens, 1836), which was considered to be a single cosmopolitan species with a Holarctic distribution, has turned out to be a group of cryptic species (Henry and Wells 2007). The same could have been true for the Mesozoic green lacewings with

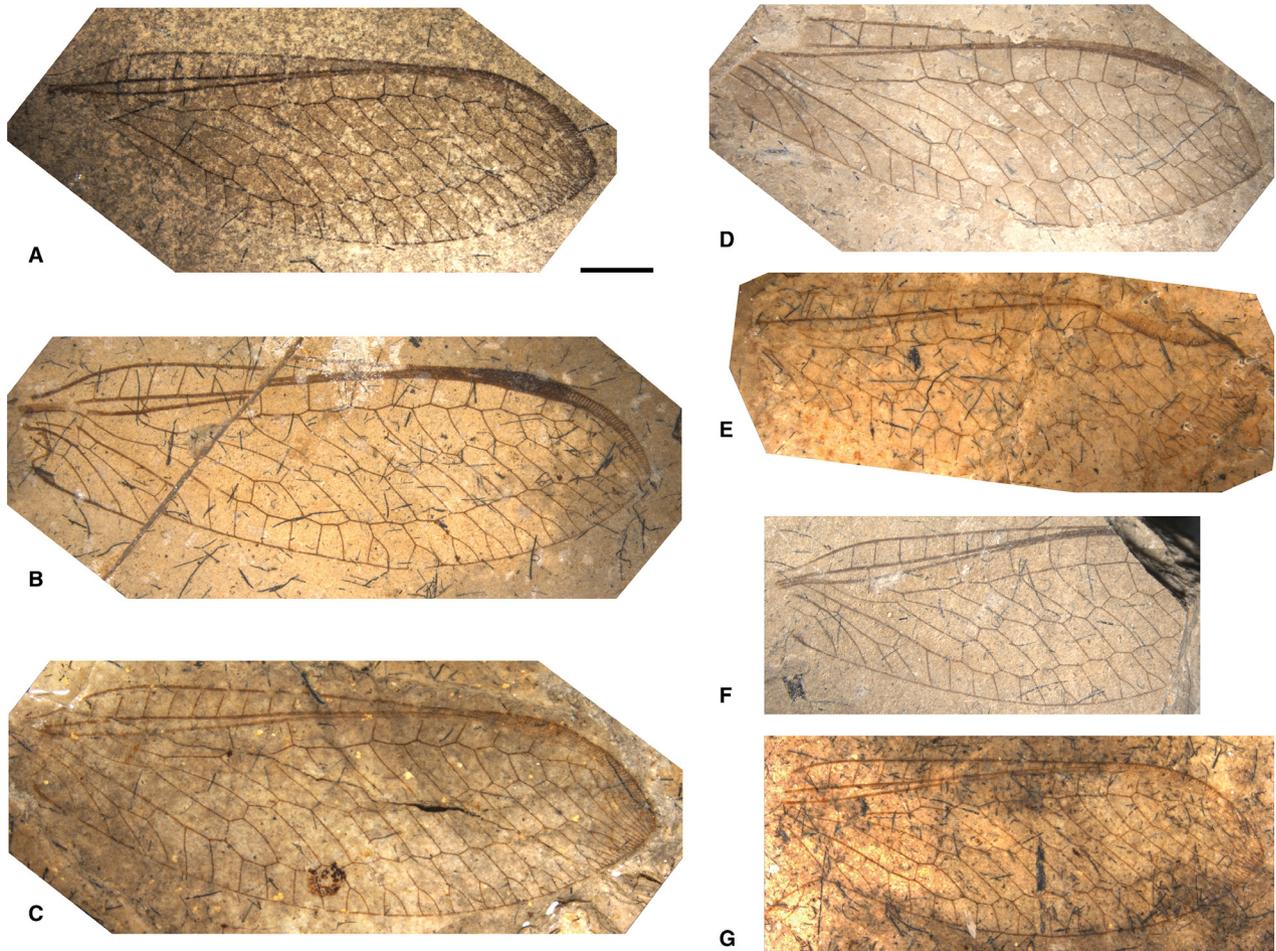


FIG. 3. Forewings of *Mesypochrysa intermedia* Panfilov, 1980 from the Upper Jurassic of Karatau, Kazakhstan. A, PIN 2066/1142. B, PIN 2997/718. C, holotype of *M. intermedia*. D, PIN 2784/1063. E, PIN 2997/2757. F, PIN 2997/2660. G, holotype of *M. makarkini* Nel et al., 2005 (= *M. intermedia*). Scale bar represents 2 mm. Colour online.

identical venation, especially when taking into account that we do not know the characters of their colouration, genitalia and other important features.

Mesypochrysa sinica sp. nov.

Figure 4

LSID. urn:lsid:zoobank.org:act:5A4C3AA6-6956-454E-A751-E794623257A7

Derivation of name. The species name is derived from the Latin word ‘*sinica*’ meaning ‘Chinese’ or ‘of China’.

Holotype. NIGP161887, an imprint of a complete insect, right fore and hindwings poorly preserved.

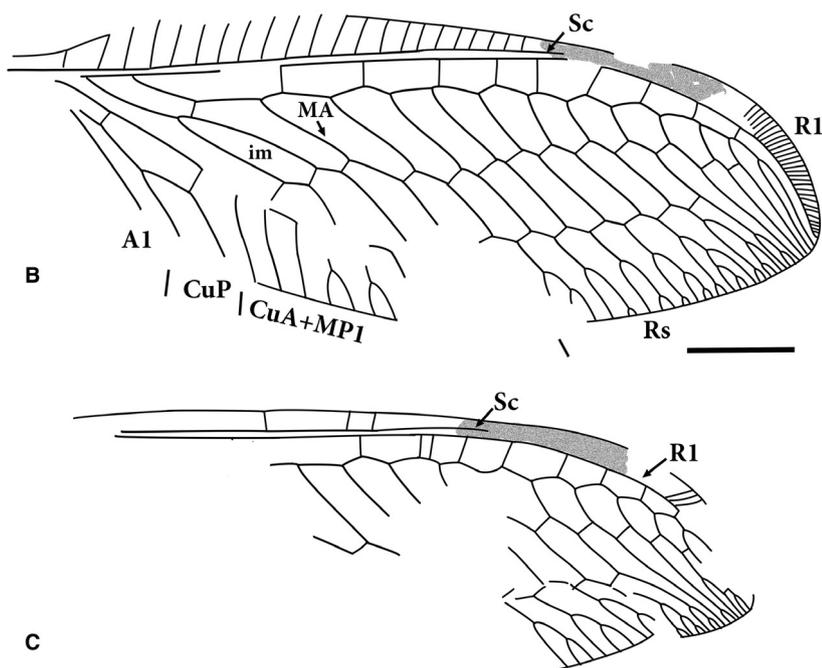
Type locality and horizon. Daohugou Village, Wuhua Township, Ningcheng County, near Chifeng City in Inner Mongolia, China; Daohugou beds, Middle to Upper Jurassic.

Description. Forewing: length 15.1 mm, width 5.6 mm, Rs with 11 branches, last four unforked, some branches of Rs extensively branched at distal ends, all branches of Rs branched anteriorly to the middle one-third (the section of Rs branches between outer series of gradate crossveins and wing margin), cell im narrow, CuA + MP1 with three branches of Rs which are rather long (their length to widest part of forewing is *c.* 1:4), fork of CuP large, elongate. Hindwing: branches of Rs extensively branched distally.

Comparisons. *Mesypochrysa sinica* sp. nov. differs from all species of the genus described from hindwings by branches of Rs which are extensively branched at distal ends of the hindwing. It differs from the other species by the smallest number of unforked branches of CuA + MP1 in the forewings (3 in contrast to 3–8 in other representatives of *Mesypochrysa*) and their greater length. (In *M. sinica* sp. nov., the length of the branches of CuA + MP1 to widest expanse of forewing at its greatest width is about 1:4; in other species, it is 1:4.5–5.) The distinguishing feature of the forewing venation of *M. sinica* sp. nov. is the terminal



FIG. 4. *Mesypochrysa sinica* sp. nov. from the Middle–Upper Jurassic of Daohugou. A, holotype NIGP161887. B, drawing of the forewing. C, overlay drawing of the hindwing. See text for venation nomenclature. Scale bars represent 4 mm (A), 2 mm (B–C). Colour online.



branching pattern of the Rs branches, which are branched anteriorly to the middle of their third section, whereas they branch more posteriorly in other species, including those with an extensively dichotomizing branches of Rs, for example *M. polyclada*.

Genus *Baisochrysa* Makarkin, 1997

Type species. *Baisochrysa multinervis* Makarkin, 1997 from the Lower Cretaceous of Baissa.

Other species. *Baisochrysa pumila* sp. nov. from the Upper Jurassic of Karatau.

Diagnosis. As in Makarkin (1997).

Baisochrysa pumila sp. nov.

Figure 5

LSID. urn:lsid:zoobank.org:act:3115CFAD-E089-4B29-B6CF-11BDB7653527

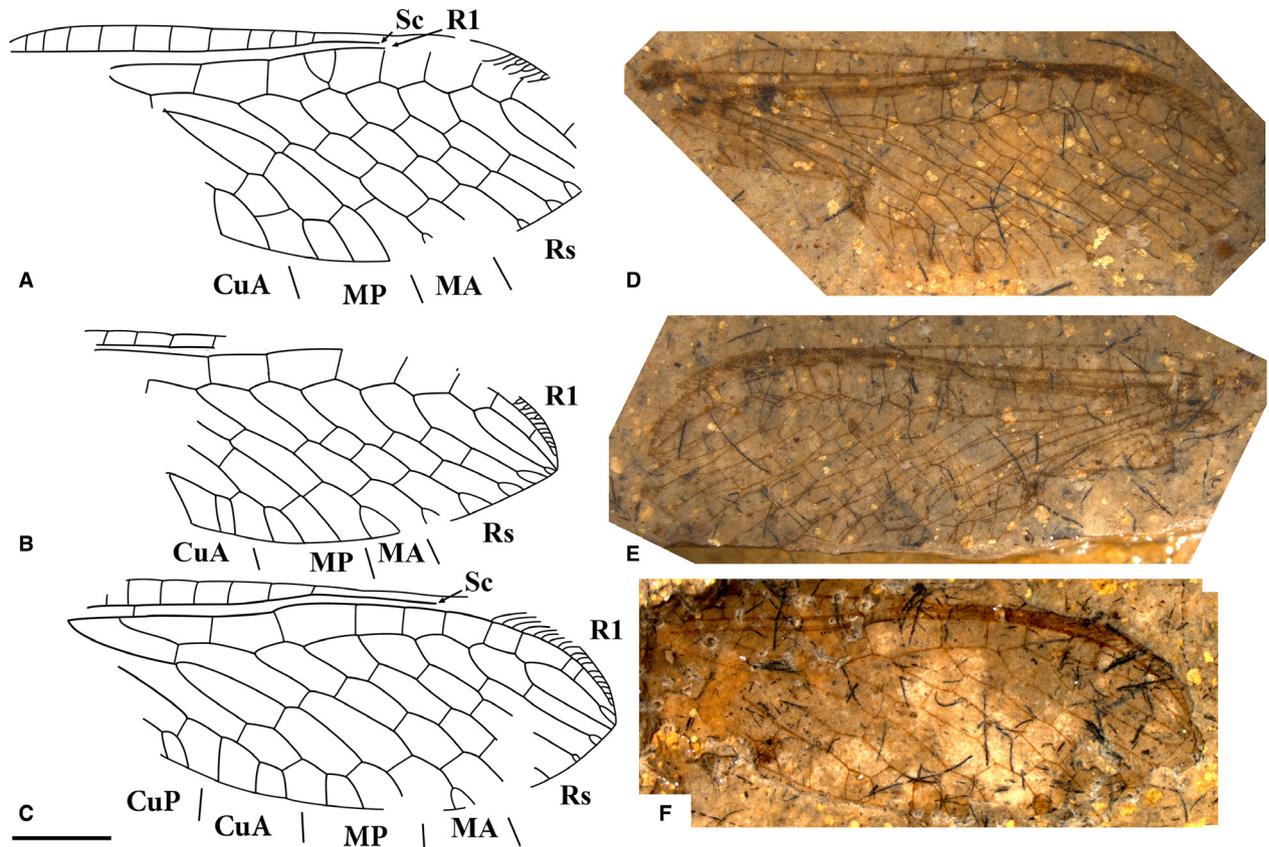


FIG. 5. *Baisochrysa pumila* sp. nov. from the Upper Jurassic of Karatau. A–B, D–E, holotype PIN 2239/1696; A, overlay drawing of the forewing; B, overlay drawing of the hindwing; D–E, photographs of part and counterpart. C, F, paratype PIN 2284/838, forewing; C, overlay drawing; F, photograph. See text for venation nomenclature. Scale bar represents 2 mm. Colour online.

Derivation of name. The species name is derived from the Latin word ‘pumilus’ meaning ‘dwarf’.

Holotype. PIN 2239/1696, an impression of an overlapping forewing and hindwing.

Paratype. PIN 2284/838, an impression of an isolated forewing.

Type locality and horizon. Karatau, South Kazakhstan Province, Karabastau Formation, Upper Jurassic.

Description. Forewing: length 11.5 mm (holotype), 11 mm (paratype); width 4 mm (both holotype and paratype); crossveins arranged into three gradate series, Sc and R1 distally curved towards anterior wing margin, Rs with five branches, each with single terminal fork, CuA with two branches. Hindwing: length about 10 mm, width 3.4 mm, Rs with five branches, crossveins arranged in two gradate series, additional crossvein situated between first and second branches of Rs.

Comparison. The affinity of this species with *Baisochrysa* is clearly indicated by the presence of three gradate series of crossveins in the radial sector. *B. pumila* sp. nov.

differs from *B. multinervis* from Baissa by its smaller size and the lesser number of branches of the Rs (the forewing length of *B. multinervis* is 19 mm, the number of Rs branches is no less than nine). Species of *Mesypochrysa*, which is closely related to *Baisochrysa*, also vary greatly in size: the forewing length of *M. latipennis* Martynov, 1927 from Karatau is 12 mm, while that of *M. magna* Makarkin, 1997 from Baissa is 26 mm.

DISCUSSION

Green lacewings have been relatively abundant since their known appearance during the Middle–Upper Jurassic. They account for 1.2% of all Neuroptera from Daohugou and 11.4% from Karatau (AK pers. obs.). The Early Cretaceous localities are characterized by an especially high percentage of Chrysopidae. According to Makarkin *et al.* (2012), green lacewings accounted for 11.5% of all Neuroptera from Baissa and 30.3% from Yixian. Chrysopidae seem to be completely absent from deposits earlier than the latest Middle Jurassic. For example, no green lacewings have been found in the late Early to early Middle

Jurassic deposits of Sai-Sagul, Kyrgyzstan (AK pers. obs.), where about 260 other lacewings have been collected (Khramov 2012). Except for *L. stigmatica* of uncertain chrysopid affinity, green lacewings have not been mentioned from European Liassic (Early Jurassic) deposits, where at least 240 other lacewings have been found (Anson 2003).

Almost all Mesozoic green lacewings belong to the extinct subfamily Limaiinae, except for *Paralembochrysa* Nel *et al.*, 2005 from the Yixian Formation of China and *Araripechrysa* Martins-Neto and Vulcano, 1989 from the Crato Formation of Brazil. These genera, whose subfamily affiliation is not established, are rather rare; for example, only three specimens of *Paralembochrysa* are known from the Yixian Formation (Archibald *et al.* 2014). By contrast, Limaiinae are known from dozens of specimens. The venation of Limaiinae could be regarded as plesiomorphic because of the presence of a distinct MP, which is, however, fused with the zigzagged proximal branches of the Rs to form the pseudomedia (Psm) in both Chrysopinae and Apochrysininae. The absence of a well-developed Psm is also typical of some Nothochrysininae (Adams 1967); the venational differences between Nothochrysininae and Limaiinae were discussed by Makarkin and Archibald (2013). The male terminalia of Limaiinae (Figs 2D, 3B) also are quite plesiomorphic in having separate eighth and ninth sternites, which are fused in modern green lacewings, except in some Nothochrysininae (Aspöck and Aspöck 2008).

The majority of Mesozoic Limaiinae belong to the cosmopolitan genus *Mesypochrysa* (Table 1) or very closely allied genera which are probable synonyms of *Mesypochrysa* (see above). For example, 87% of all green lacewings from Karatau are representatives of *Mesypochrysa* (AK pers. obs.); this genus also dominates green lacewings from the Yixian Formation (Makarkin *et al.* 2012). The Jurassic–Cretaceous genus *Baisochrysa* Makarkin, 1997 is much rarer and known only from two localities, Karatau (Late Jurassic) and Baissa (Early Cretaceous). The Late Cretaceous Chrysopidae, as well as other Neuroptera, are scarce, excluding lacewings from Upper Cretaceous ambers, where only small specimens are preserved. *Cretachrysa* Makarkin, 1994, from the Cenomanian of Obeshchayushchiy, Russia, is the only Late Cretaceous taxon probably belonging to Limaiinae (Makarkin 1994). The only other known Late Cretaceous green lacewing is a larva from Canadian amber (Engel and Grimaldi 2008).

During the early Eocene, the Limaiinae were still present but the Nothochrysininae became the most abundant group of green lacewings (Fig. 6). The post-Mesozoic Limaiinae, represented by the genus *Protochrysa* Willmann and Brooks, 1991, are known from the lower Eocene Fur Formation of Denmark (Willmann and Brooks 1991) and the early Eocene deposits of the Okanagan Highlands,

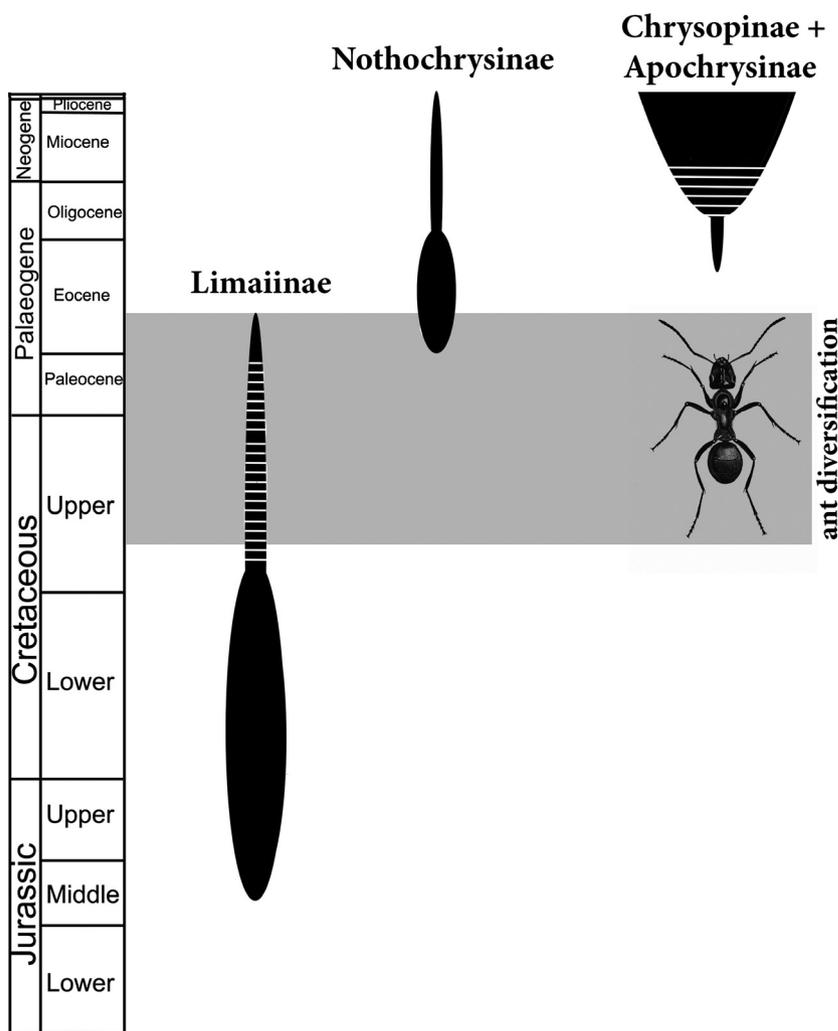
but almost all green lacewings from the latter locality are nothochrysininae (Makarkin and Archibald 2013). Nothochrysininae dominated the Eocene, whereas Oligocene record of green lacewings is sparse and represented by only two species of Nothochrysininae (Archibald *et al.* 2014). The earliest record of Chrysopinae is *Paleochrysopa monteilsensis* Séméria and Nel, 1990 from the upper Eocene of France, the only Palaeogene species of this subfamily described so far. For the Miocene, Chrysopinae became dominant and now they comprise (with Apochrysininae) more than 97% of living chrysopid species (Winterton *et al.* 2012).

Archibald *et al.* (2014) explained that the post-Eocene decline of Nothochrysininae is attributable to global climate change from a warmer greenhouse to a colder icehouse world that was associated with greater seasonality (Katz *et al.* 2008). The decline of Nothochrysininae occurred after the Eocene–Oligocene boundary with the diversification of echolocating bats (Gunnell and Simmons 2005) earlier during the Eocene. Unlike Apochrysininae and Chrysopinae, Nothochrysininae lack the tympanal organ in the base of R in the fore wing and cannot detect bat echolocating sounds. By the end of the Eocene, they could have become extensively predated by bats (Archibald *et al.* 2014).

What was the cause of extinction of Limaiinae, which were so abundant in the Mesozoic? The decline and final disappearance of this lineage also could be explained by biotic factors. A change in food resources was unlikely to be the driving factor of this process. Many recent green lacewings are generalist predators. For example, *Chrysoperla carnea* (Stephens, 1836) is capable of preying on a variety of soft-bodied arthropods including various species of aphids, scale insects, psyllids, lepidopterans and thrips (Shrestha and Enkegaard 2013). Consequently, it is reasonable to suggest that Mesozoic green lacewings could easily have adapted to changes in the diversity of Sternorrhyncha, their principal food resource. The genera *Mesypochrysa* and *Baisochrysa* were not affected by the great shift in sternorrhynchan communities at the Jurassic–Cretaceous boundary, when aphids became a dominant group overtaking psyllids (Shcherbakov and Popov 2002). Hence, the change in the diversity of aphids and other sternorrhynchans following the diversification of angiosperms during the mid-Cretaceous (Peccoud *et al.* 2010; Huang *et al.* 2012) cannot be regarded as the cause of decline of the Limaiinae.

Alternatively, the diversification of ants, a group closely associated with sternorrhynchans (Delabie 2001), could have had an impact on green lacewings. It is well known that there are symbiotic relationships between sternorrhynchans and many species of ants which collect sternorrhynchan sugary excreta (honeydew) in return for protection they provide against predators, including

FIG. 6. Spindle diagram and stratigraphical range of the subfamilies of Chrysopidae.



larvae of Chrysopidae (Novgorodova and Gavrilyuk 2012). For this reason, larvae of the three recent subfamilies have evolved special adaptations against aphid-tending ants (Tauber *et al.* 2014). Modern chrysopid larvae typically bear short, hooked setae on the dorsal surface of the abdomen and long setae situated on lateral tubercles of abdominal segments. This pattern of setae typically is used to attach packets of trash consisting of vegetable matter, arthropod remains or waxes from sternorrhynchan prey (Eisner *et al.* 1978, 2002). Not all species of recent taxa of Chrysopidae have trash-carrying larvae: in the Nothochrysiniae, one genus of four with larvae described is trash-carrying; in Apochrysiniae, this ratio is one of one, and for Chrysopinae, it is 23 of 36 (Tauber *et al.* 2014). Trash-carrying behaviour, where it exists, is a vital adaptation for feeding on ant-protected colonies of sternorrhynchans (Eisner *et al.* 1978). In experiments that exposed green lacewing larvae to ants, approximately 40% of larvae denuded of trash packets were killed. However, for the same species all larvae carrying trash packets on their backs survived (Hayashi and Nomura 2011).

It can be hypothesized that the nakedness of larvae is an ancestral state of Chrysopidae for two reasons. First, the majority of genera of the extant, basal, green lacewing subfamily Nothochrysiniae lack the usual morphological modifications for trash-carrying (Tauber *et al.* 2014). Second, the larvae of Hemerobiidae, the sister group of Chrysopidae (Beutel *et al.* 2010; Winterton *et al.* 2010), which also feed on sternorrhynchans (New 1975; Vidya *et al.* 2010), lack adaptations for trash-carrying and, as slender-bodied insects, rely only on their high mobility (Smith 1923). Interestingly, the larvae of the Recent genera *Brinckochrysa* Tjeder, 1966 and *Atlantochrysa* Hölzel, 1970 (Chrysopinae), which do not demonstrate trash-carrying behaviour, also move very rapidly (Duelli *et al.* 2014).

The larvae of Mesozoic Limaiinae probably lacked manoeuvrability and simultaneously retained their ancestral naked condition. The putative absence of the trash-carrying capacity in combination with slow movement was sufficient for the green lacewings living in an ant-free world during the Middle Jurassic to Lower Cretaceous.

However, when ants diversified during the Late Cretaceous to early Eocene (Moreau *et al.* 2006), it became a serious disadvantage to Limaiinae larvae. It is an unlikely coincidence that the last and rare representatives of Limaiinae are known from the early Eocene (Makarkin and Archibald 2013), when ants first become common in the fossil record (LaPolla *et al.* 2013). According to Wilson and Hölldobler (2005), the first Cretaceous ants were rare in terms of both diversity and abundance. The modern ant fauna emerged when the four most species-rich subfamilies of ants – Myrmicinae, Formicinae, Ponerinae and Dolichoderinae – underwent an adaptive radiation during the early to middle Eocene (Wilson and Hölldobler 2005). This event seems to be directly related to the disappearance of Limaiinae by the middle Eocene.

Unfortunately, green lacewing larvae are too poorly known from the Mesozoic to verify this hypothesis. Only two Mesozoic chrysopoid larvae have been described to date: *Hallucinochrysa* Pérez-de la Fuente *et al.*, 2012 from Albian Spanish amber and a first instar larva from Campanian Canadian amber (Engel and Grimaldi 2008). *Hallucinochrysa*, probably a third instar, possessed extremely long abdominal tubercles and carried dorsally a trash packet consisting of the trichomes of gleicheniacean ferns. Because of this larva's bizarre morphology unlike other recent green lacewings, Pérez-de la Fuente *et al.* (2012) refrained from assigning *Hallucinochrysa* to Chrysopidae and placed it in the superfamily Chrysopoidea, which includes, besides Chrysopidae, the several extinct families of Mesochrysopidae, Allopteridae, Tachinymphidae and Liassochrysidae (Nel *et al.* 2005). The larva from Canadian amber bore long setae on its abdomen, presumably for trash-carrying (Engel and Grimaldi 2008). Taking into account the Late Cretaceous age of Canadian amber, this specimen could represent a larva either of Limaiinae or an early Nothochrysinae. To determine whether the larvae of Limaiinae possessed any modifications for trash-carrying, it would be useful to examine a chrysopoid larva from Early Cretaceous Lebanese amber (D. Azar pers. comm.). Lebanese amber is considered to be late Neocomian – early Aptian in age (Penney and Selden, 2002; Veltz *et al.* 2013), when Limaiinae were especially abundant.

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APPENDIX: SPECIES KEY

*Key to the species of Mesypochrysa**

1 Small lacewings; Rs with 5–6 branches in forewings, Rs with 5–6 branches in hindwings.	2
Medium to large lacewings; forewings with 7–20 branches of Rs, hindwings with 7–17 branches of Rs.	4
2 MP two-branched in hindwings.	3
MP single in hindwings.	<i>M. minuta</i>
Hindwings unknown, cells of Rs wide, only slightly elongated.	<i>M. latipennis</i>
3 CuA with 4 branches in hindwings.	<i>M. reducta</i>
CuA with 2 branches in hindwings.	<i>M. miniscula</i>
4 Length ratio of 2m-cu cell to im cell in forewings 1:3.	6
Length ratio of 2m-cu cell to im cell in forewings 1:2.	8
Forewings unknown or bad-preserved.	5
5 MP single in hindwings.	<i>M. minima</i>
MP two-branched in hindwings.	<i>M. falcata</i>
Hindwings unknown, branches of Rs extensively branched terminally in forewings.	<i>M. polyclada</i>
6 Rs with 9–11 branches in forewings.	7
Rs with 19–20 branches in forewings.	<i>M. magna</i>
7 The number of unforked branches of CuA and MP in forewings is 5.	<i>M. chrysopa</i>
The number of unforked branches of CuA and MP in forewings is 8.	<i>M. criptovenata</i>
8 The number of unforked branches of CuA and MP in forewings is 3 or 4.	9
The number of unforked branches of CuA and MP in forewings is 6 or 7.	11
9 The number of unforked branches of CuA and MP in forewings is 4.	10
The number of unforked branches of CuA and MP in forewings is 3.	<i>M. sinica</i>
10 Cells of Rs narrow in forewings.	<i>M. chrysopoides</i>
Cells of Rs wide in forewings.	<i>M. polyneura</i>
11 The number of unforked branches of CuA and MP in forewings is 7.	12
The number of unforked branches of CuA and MP in forewings is 6.	<i>M. intermedia</i>
12 Rs with 13 branches, their terminal forks small.	<i>M. angustialata</i>
Rs with 9 branches, their terminal forks large.	<i>M. curvimedia</i>

**M. confusa* is not included in the Key because of its poor original description.