Cretaceous Research 115 (2020) 104564

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Short communication

New species of green lacewings (Insecta, Neuroptera) from the Lower Cretaceous of China

Tianwei Zhang [a], Chaosheng Luo [a], Chaofan Shi [a, *], Qiang Yang [b, **], Dong Ren [c]

[a] School of Earth Sciences and Engineering, Guangdong Provincial Key Lab of Geodynamics and Geohazards, Guangdong Provincial Key Laboratory of Mineral Resources & Geological Processes, Sun Yat-sen University, No. 135, Xingang Xi Road, Guangzhou 510275, China
[b] School of Life Sciences, Guangzhou University, #230 Waihuanxi Road, Guangzhou Higher Education Mega Center, Guangzhou 510006, PR China
[c] College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Xisanhuanbeilu 105, Haidian District, Beijing 100048, PR China

ARTICLE INFO

Article history:
Received 5 March 2020
Received in revised form
26 June 2020
Accepted in revised form 5 July 2020
Available online 11 July 2020

Keywords:
Limaiinae
Mesypochrysa
Mesozoic
Yixian Formation
Jehol Biota

ABSTRACT

Two new species of green lacewings from the Lower Cretaceous of China, *Mesypochrysa binervis* sp. nov. and *Mesypochrysa pusilla* sp. nov., are described. Both new species are assigned to the extinct Chrysopidae subfamily Limaiinae. *Mesypochrysa* represents the majority of Limaiinae, containing nearly 20 species from the Jurassic and Cretaceous. The two new species share more characters with the Cretaceous species of the genus, which are discussed in detail in this study. In addition, *Mesypochrysa* is compared briefly with the other genera of the subfamily.

1. Introduction

Chrysopidae, commonly known as green lacewings, are a diverse family of Neuroptera (Engel et al., 2018). About 1416 species in 82 genera of extant green lacewings have been described worldwide (Brooks and Barnard, 1990; Garzón-Orduña et al., 2018; Winterton et al., 2019). The extant chrysopids are divided into three subfamilies, i.e. Apochrysinae, Chrysopinae, Nothochrysinae, although the phylogenetic relationships among the three subfamilies remain controversial (Brooks and Barnard, 1990; Garzón-Orduña et al., 2018; Winterton et al., 2019). In addition, a fourth extinct subfamily Limaiinae belongs to the family Chrysopidae, which includes most Mesozoic green lacewings and a few from the Cenozoic (Archibald et al., 2014; Khramov et al., 2016; Khramov, 2017).

Chrysopidae have a fossil record dated back to the Middle Jurassic (Khramov et al., 2016). Twenty six genera with over 60 species have been reported from Asia, Europe, North America and South America (Martins-Neto and Vulcano, 1988; Yang and Hong, 1990; Ponomarenko, 1992; Makarkin, 1994, 1997; Ren and Guo, 1996; Martins-Neto, 1997, 2003; Nel et al., 2005; Jepson et al., 2012; Makarkin and Archibald, 2013; Khramov, 2017; Lu et al., 2018; Makarkin et al., 2018). To date, seven genera have been recorded from the Mesozoic. Among them, three are considered as subfamily *incertae sedis*, while the other four are all assigned to the extinct subfamily Limaiinae (Martins-Neto and Vulcano, 1988; Makarkin, 1997; Nel et al., 2005; Khramov et al., 2016; Khramov, 2017). The Cenozoic green lacewings mostly belong to the extant subfamilies Nothochrysinae and Chrysopinae, but one genus from the Eocene, *Protochrysa*, is assigned to Limaiinae (Willmann and Brooks, 1991; Makarkin and Archibald, 2013; Makarkin et al., 2018). Based on current knowledge, this genus represents the most recent occurrence of Limaiinae in geological history (Makarkin and Archibald, 2013).

Among the total five genera of Limaiinae, *Mesypochrysa* is the dominant genus, which has been reported from the Middle Jurassic to Lower Cretaceous of China, Kazakhstan, Russia, England, Mongolia and Brazil (Martynov, 1927; Panfilov, 1980; Martins-Neto and Vulcano, 1988; Ponomarenko, 1992; Makarkin, 1997; Martins-Neto, 1997, 2003; Nel et al., 2005; Jepson et al., 2012; Khramov

* Corresponding author.
** Corresponding author.
E-mail addresses: shichf5@mail.sysu.edu.cn (C. Shi), yq11_1984@126.com (Q. Yang).

https://doi.org/10.1016/j.cretres.2020.104564
0195-6671/

et al., 2016; Khramov, 2017). The Cretaceous genera *Lembochrysa*, *Limaia*, *Drakochrysa* were considered as synonyms of *Mesypochrysa* by Khramov et al. (2016); thus the genus includes nearly 20 species (Khramov et al., 2016; Khramov, 2017). But the monophyly and synapomorphies of the genus still need further study. Herein, two new species of *Mesypochrysa* are described from the Lower Cretaceous Yixian Formation of northeastern China. The new species showed distinctive forewing venational characters, such as forked subcostal veinlets and the presence of two subcostal crossveins in *Mesypochrysa binervis* sp. nov., forked 1A on both new species; however, they exhibited many similarities with other species from the same formation.

2. Material and methods

The specimens documented in this study were collected near Huangbanjigou Village, Beipiao City, Liaoning Province, China (41°22′ N, 120°30′ E). The insect-bearing beds of the Huangbanjigou locality are considered to belong to the Yixian Formation, dated as Barremian to Aptian (Zhou, 2006, 2014; Li and Batten, 2007; Yang W et al., 2007; Yang Q et al., 2015; Ren et al., 2019). The Yixian formation is mainly composed of massive volcanic rocks interbedded with several fossil-bearing lacustrine sedimentary layers (Ren et al., 1995). Various categories of fossils, such as dinosaurs, early birds, insects, mammals and early angiosperms etc. have been reported from the stratum, which is renowned as the Jehol Biota (Ren et al., 1995; Ren, 1998; Gao et al., 2013; Yang et al., 2014; Yao et al., 2014; Shi et al., 2015; Ren et al., 2019). The type specimens are housed in the fossil insect collection of the Key Laboratory of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator).

The specimens were examined using a Zeiss Discovery V20 stereomicroscope, illustrated with the aid of a drawing tube, and photographed with an Axiocam 506 color digital camera attached to the stereomicroscope (both instruments Carl Zeiss Light Microscopy, Göttingen, Germany). The final line drawings were prepared with the aid of Adobe Illustrator CS6 and Adobe Photoshop CS6.

The terminology for morphological structures follows Makarkin and Archibald (2013). Abbreviations: 1A-3A, first to third anal veins; C, costa; c_1, first intracubital cell; c_2, second intracubital cell; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; *dcc*, distal cubital cell; *im*, basal intramedian cell; M, media; MA, anterior media; MP, posterior media; Psc, pseudocubitus; Psm, pseudomedia; R, radius; R1, first branch of R; Rs, radial sector; Sc, subcosta.

3. Systematic palaeontology

Order Neuroptera Linnaeus, 1758
Family Chrysopidae Schneider, 1851
Subfamily Limaiinae Martins-Neto and Vulcano, 1988

Genus *Mesypochrysa* Martynov, 1927
Type species: *Mesypochrysa latipennis* Martynov, 1927

Mesypochrysa binervis sp. nov. Zhang, Shi et Ren (Fig. 1A–D).
urn:lsid:zoobank.org:act:9573BBF2-7347-48CC-8EBD-2EA5211BFD3A

Etymology. The specific name is derived from the Latin prefix of *bi-* meaning two, and *-nervis* meaning vein, in reference to the two crossveins in subcostal space of the new species.
Holotype. CNU-NEU-LB2018001, a nearly complete, well-preserved specimen in ventral view.
Type locality and horizon. Huangbanjigou Village, Beipiao City, Liaoning Province, China. Yixian Formation, Lower Cretaceous.
Diagnosis. Forewing possessing two forked subcostal veinlets in the basal and middle area, two subcostal crossveins in the basal part, basal most r1-rs crossvein proximal to the separation of the first Rs branch, Rs with 10–11 branches, cell *im* longer than cell *2im*, MP and CuA coalescing shortly near the posterior margin before MP forks, 1A dichotomously forked.
Description. Forewing: Wing length 22.9 mm, width 8.0 mm. Pterostigma conspicuous (Fig. 1A and B). Trichosors present around the apex of forewing margin. Costal space slightly dilated proximally, tapering toward wing apex. Subcostal veinlets relatively sparsely arranged, most simple, two forked in the basal and middle part. One basal subcostal veinlets deeply forked on left forewing. Sc ending undetected. Two subcostal crossveins present. The crossvein 1sc-r1 slightly beyond the origin of the Rs and 2sc-r1 opposite the separation of MA and MP. R1 long, entering margin near wing apex. Rs with 11 branches. Most branches dichotomously forked. The seventh to ninth branches with multiple marginal twiggings. Crossveins between R1 and Rs sparsely arranged, the basal most one positioned proximal to the separation of the first Rs branch. MA and MP separated between the origins of Rs and first branch of Rs. Both dichotomously forked. Cell *im* long, enclosed by MA, MP and 1ma-mp. Cell *im* longer than *2im* (length ratio: 1.3:1). Crossvein rs-ma slightly oblique. Two complete gradate series present. Psm and Psc zigzag. CuA and CuP separated near wing base, proximal to Rs origin. CuA with four simple branches, CuP deeply forked, with two branches. Cell *2m-cu* formed by MP, CuA and crossvein 2m-cu. The length ratio of *2m-cu* and *im* approach 1:3. The length of cell c_2 almost equal to *dcc*, both longer than c_1 (length ratio of c_1:c_2:*dcc*: 1:2.5:2.7). 1A and 2A long and forked, 3A arched. Two cross-veins between anal veins: 1a-2a short; 2a-3a long and oblique (Fig. 1C). Hindwing: Wing length c. 20.3 mm, width 6.5 mm. Costal space narrow. Subcostal veinlets simple. Subcostal space with no crossvein detected. Rs with about ten to eleven forked branches. The distal branches with multiple marginal twiggings (Fig. 1D).

Mesypochrysa pusilla sp. nov. Zhang, Shi et Ren (Fig. 2A–D)
urn:lsid:zoobank.org:act:EEBDBCEC-34BF-4F65-9176-CBF37455AA28

Etymology. The specific name is derived from the Latin adjective of *pusillus -a*, *-um*, meaning small, in reference to the relatively small and narrow wings of the species.
Holotype. CNU-NEU-LB2018002, the specimen preserved with four wings overlapped in lateral view and partial body, male.
Type locality and horizon. Huangbanjigou Village, Beipiao City, Liaoning Province, China. Yixian Formation, Lower Cretaceous.
Diagnosis. Forewing all subcostal veinlets simple, basal most r1-rs crossvein proximal to the separation of the first Rs branch, Rs with 10–11 branches, cell *im* longer than cell *2im*, 1A dichotomously forked.
Description. Forewing: Wing length 17.0 mm, width 5.7 mm. Pterostigma conspicuous (Fig. 2A and B). Trichosors present around the apical of forewing margin. Costal space slightly dilated proximally, tapering toward apex of wing. Subcostal veinlets simple. Sc ending undetected. Pterostigmal area with dense simple crossveins. Subcostal space narrow, no crossvein detected. R1 entering wing margin before the wing apex. Crossveins between R1 and Rs sparsely arranged, the basal most one proximal to the separation of the first Rs branch. Rs with 10 branches. Most Rs branches dichotomously forked except the apical branches with multiple marginal twiggings. Two complete gradate series present. Psm and Psc zigzag. MA and MP separated between the origins of Rs and first r1-rs crossvein. The crossvein 1rs-m slightly distal to the separation of MA and MP. MA and MP both dichotomously forked. Cell *im* long and narrow, about five times as long as width. Cell *im* longer than *2im* (length ratio: 1.9:1). Cell *2m-cu* distinctly shorter than *im*,

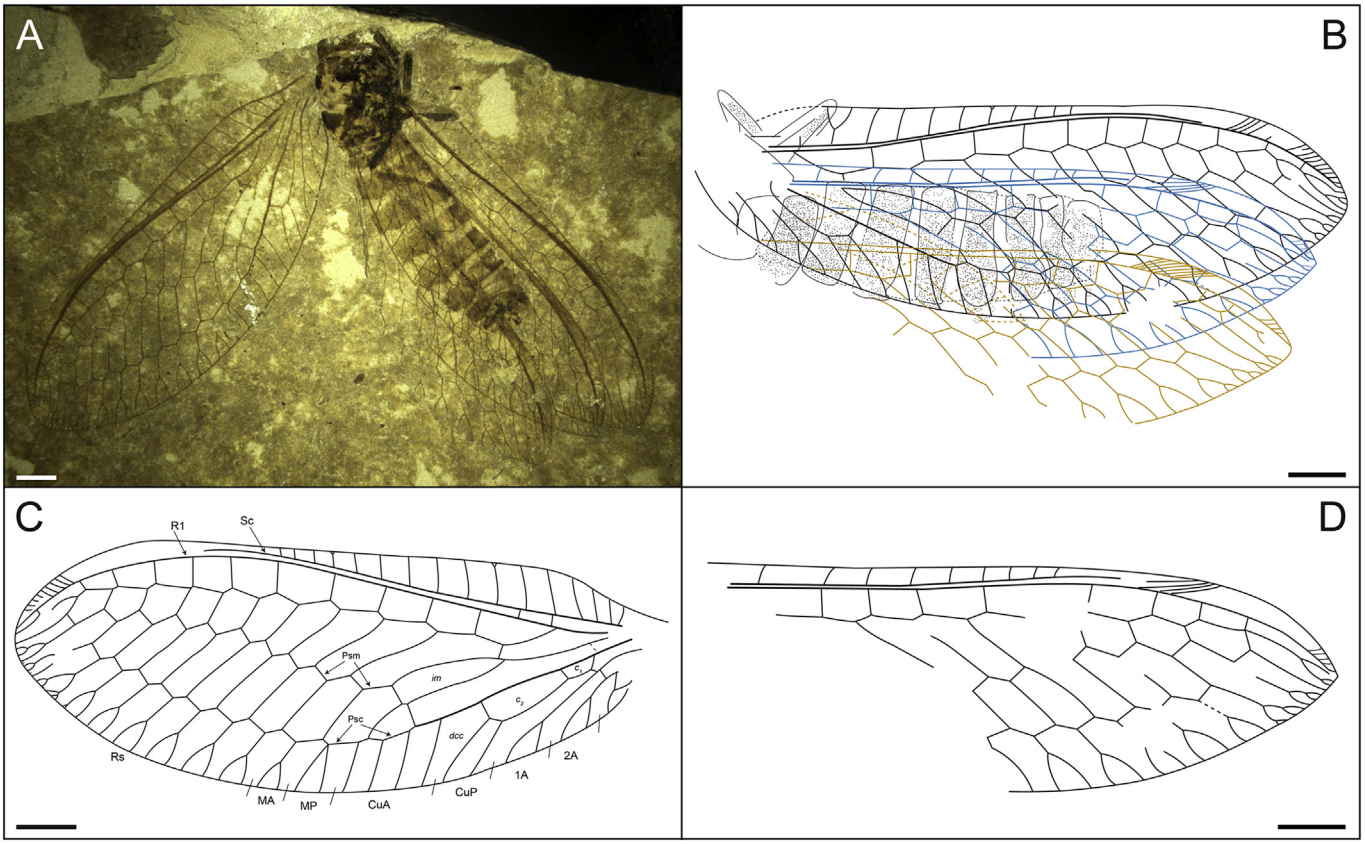

Fig. 1. *Mesypochrysa binervis* sp. nov., holotype CNU-NEU-LB2018001. A, photo of holotype; B, line drawings left forewing and both hind wings; C, line drawing of right forewing; D, line drawing of left hind wing; scale bars: 2 mm.

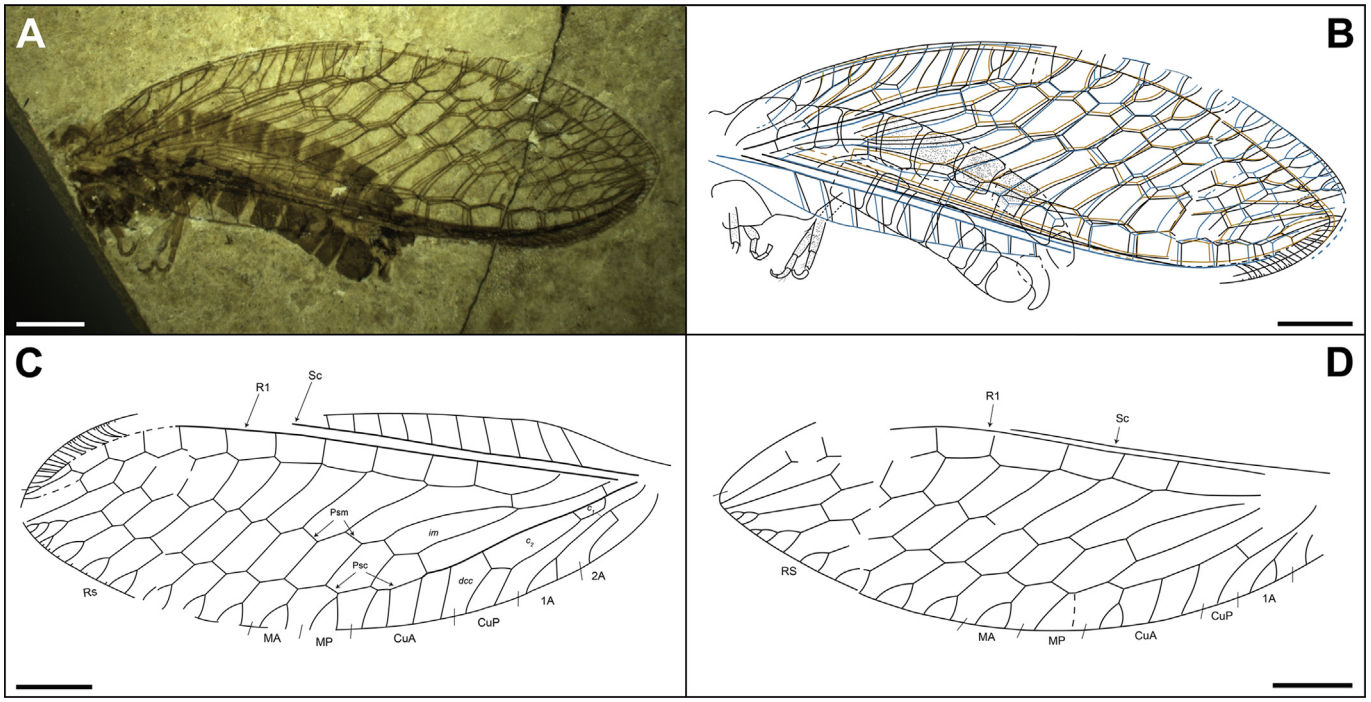

Fig. 2. *Mesypochrysa pusilla* sp. nov., holotype CNU-NEU-LB2018002. A, photo of holotype; B, line drawings of preserved body part and overlapping four wings; C, line drawing of left forewing; D, line drawing of left hind wing; scale bars: 2 mm.

nearly half the *im* length. Two m-cu crossveins present. Crossvein 1m-cu short, slightly proximal to the separation of CuA and CuP. Crossvein 2m-cu longer than 1m-cu. CuA with four simple branches. CuP dichotomously forked. Cell c_2 longer than *dcc*, *dcc* longer than c_1 (length ratio of c_1:c_2:*dcc*: 1:2.9:2.2). 1A forked (Fig. 2C).

Hindwing: Wing length c. 15.4 mm, width 4.9 mm. Rs with 7–8 branches, distal Rs branches with multiple marginal twiggings. CuA with three branches, distal branch forked. CuP simple. 1A forked (Fig. 2D).

4. Discussion

Both new species are assigned to Limaiinae based on forewing characters such as Sc short, R1 terminated near wing apex, inner gradate series continuous with Psm, Psc well developed, cell *im* long and narrow, proximally tapering, crossvein 2m-cu located in the distal part of cell *im* (Makarkin, 1997; Nel et al., 2005; Makarkin and Archibald, 2013). The species are assigned to *Mesypochrysa* based on characters of crossveins in pterostigmal area simple, two complete gradate series, developed but zigzag Psm and Psc, CuP dichotomously forked. *Mesypochrysa* was the majority of limaiines in Mesozoic, with nearly twenty species, although the generic status of some species are still questionable (Martins-Neto and Vulcano, 1988; Yang and Hong, 1990; Ren and Guo, 1996; Martins-Neto, 1997; Khramov et al., 2016; Khramov, 2017). Here we tentatively follow the species composition of the genus in Khramov et al. (2016) and Khramov (2017). *Mesypochrysa* can be distinguished from the other four genera of Limaiinae mainly by forewing characters, although the phylogeny of the subfamily as well as synapomorphies need further study. *Mesypochrysa* differ from *Baisochrysa* and *Parabaisochrysa* by two gradate series, while the latter two genera have three gradate series (Makarkin, 1997; Khramov et al., 2016; Lu et al., 2018). *Aberrantochrysa* is distinguished from *Mesypochrysa* by irregularly arranged crossveins in radial area, a weakly developed Psm, and MP, CuA, CuP with more branches (Khramov, 2017). *Protochrysa* is differentiated from the other limaiines by forked crossveins in pterostigmal area (Willmann and Brooks, 1991; Rust, 1999; Makarkin and Archibald, 2013; Zhang et al., 2020).

The two new species share characters such as costal space dilated proximally, the basal most r1-rs crossvein proximal to the separation of the first Rs branch, Rs with 10–11 branches, most dichotomously forked, but the distal branches with multiple marginal twiggings, MA, MP with two branches, CuA with four branches, cell *im* longer than cell *2im*, cell c_2 about 2–3 times c_1 in length, CuP and 1A not touching near base, both dichotomously forked. They differ from *M. magna*, *M. falcata*, *M. angustialata*, *M. intermedia*, *M. sinica*, *M. cannabina*, *M. latipennis*, *M. miniscula*, in which forewing basal most r1-rs positioned posterior to the separation of the first Rs branch (Martynov, 1927; Panfilov, 1980; Ren and Guo, 1996; Makarkin, 1997; Khramov et al., 2016; Khramov, 2017). Additionally, *M. magna*, *M. falcata*, *M. angustialata*, *M. intermedia* have more than 15 Rs branches on forewing, while *M. latipennis* have only seven Rs branches, which is different from the two new species (Martynov, 1927; Panfilov, 1980; Makarkin, 1997). The two new species are distinct from *M. criptovenata* and *M. confuse* in which Rs branches are mostly simple (Martins-Neto and Vulcano, 1988). The length ratio of cell c_1 to c_2 is greater in *M. magna*, *M. chrysopa*, *M. naranica* (1:0.5–1.5), but extremely small in *M. intermedia* and *M. cannabina* (1:4–4.7), which is distinct from the two new species (Panfilov, 1980; Makarkin, 1997; Khramov, 2017). In *M. miniscula* and *M. polyneura*, CuP and 1A touch shortly after CuP separation, which is different from the new species, although the touching CuP and 1A might alternatively be due to the not well preserved situation of type specimens (Ren and Guo, 1996). The forked 1A on forewing that is shared by *M. binervis* sp. nov. and *M. pusilla* sp. nov. is not common in *Mesypochrysa*; it is only found in four other species, i.e. *M. chrysopoides*, *M. naranica*, *M. polyneura* and *M. cannabina*. However, it is noteworthy that in many specimens, the wing base is poorly preserved (Ponomarenko, 1992; Ren and Guo, 1996; Khramov, 2017). However, this character is common in extant chrysopids. Almost all the genera in Chrysopinae and Apochrysinae and some in Nothochrysopinae have the forewing 1A forked (Brooks and Barnard, 1990; Makarkin et al., 2018).

The two new species differ from each other by two forked subcostal veinlets in the basal and middle area, two subcostal crossveins in the basal part, MP and CuA coalescing shortly near the posterior margin before MP forks in *M. binervis* sp. nov. vs. all subcostal veinlets simple, no subcostal crossvein, MP and CuA not fusing or touching in *M. pusilla* sp. nov. In *M. chrysopoides*, *M. magna*, *M. intermedia*, one basal subcostal crossvein is present, which is different from either *M. binervis* sp. nov. or *M. pusilla* sp. nov. (Panfilov, 1980; Ponomarenko, 1992; Makarkin, 1997).

M. binervis sp. nov. possesses two characters which are distinct from most other *Mesypochrysa* species, that is, the occurrence of a few terminal forked subcostal veinlets in the proximal and middle area and presence of two sc-r1 crossveins in the basal part on forewing. *M. curvimedia* from the Lower Cretaceous of Russia possesses one forked subcostal veinlets midway on the wing, but differs from *M. binervis* sp. nov. by costal space not notably dilated proximally, subcostal space without crossvein, Rs basal branches, MA, MP and cell *im* curved, CuA with five branches, 1A simple. In contrast, *M. binervis* sp. nov. has the costal space dilated proximally, subcostal space with two crossveins in the basal part, Rs branches, M branches and cell *im* not distinctly curved, CuA with four branches, 1A forked (Makarkin, 1997). *M. binervis* sp. nov. most resembles *M. miniscula* and *M. polyneura* which were from the same formation, sharing characters like dilated costal space in proximal part, two sc-r1 crossveins in basal subcostal space, 1A forked (Ren and Guo, 1996; Khramov et al., 2016). But the new species can be differentiated from *M. miniscula* and *M. polyneura* by having a few forked subcostal veinlets, MP and CuA coalescing shortly near the posterior margin before MP forked, CuP connected with 1A by a short crossvein near wing base. In contrast, the latter two genera possessing all simple subcostal veinlets, MP and CuA not coalescing or touching, CuP touching 1A shortly after the separation of CuP from CuA (Ren and Guo, 1996). *M. binervis* sp. nov. also differs from *M. miniscula* by its basal most r1-rs crossvein proximal to the separation of the first Rs branch, distal Rs branches with multiple marginal twiggings; whereas in *M. miniscula* the basal most r1-rs crossvein is posterior to the separation of the first Rs branch, and the distal Rs branches are simple. Besides, *M. binervis* sp. nov., as well as *M. pusilla* sp. nov., possessed more r1-rs crossveins than *M. miniscula* and *M. polyneura* (Ren and Guo, 1996).

Acknowledgements

Our thanks go to editors and two anonymous reviewers for helpful suggestions on this paper. This study was supported by National Natural Science Foundation of China (grant nos. 31501881, 31711530649, 41602014, 41688103), Program for Changjiang Scholars and Innovative Research Team in University (grant no. IRT-17R75), Support Project of High-level Teachers in Beijing Municipal Universities (IDHT20180518), and The Basic Work Special Project of the National Ministry of Science and Technology of China (2013FY111500), Scientific Research Foundation of Guangzhou University (2900603133).

References

Archibald, S.B., Makarkin, V.N., Greenwood, D.R., Gunnell, G.F., 2014. The red queen and the court jester in green lacewing evolution: bat predation and global climate change. PALAIOS 29, 185–191.

Brooks, S.J., Barnard, P.C., 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). Bulletin of the British Museum (Natural History). Entomology 59, 117–286.

Engel, M.S., Winterton, S.L., Breitkreuz, L.C., 2018. Phylogeny and evolution of Neuropterida: where have wings of lace taken us? Annual Review of Entomology 63, 531–551.

Gao, T.P., Shih, C.K., Rasnitsyn, A.P., Xu, X., Wang, S., Ren, D., 2013. New transitional fleas from China highlighting diversity of Early Cretaceous Ectoparasitic insects. Current Biology 23 (13), 1261–1266.

Garzón-Orduña, I.J., Winterton, S.L., Jiang, Y., Breitkreuz, L.C.V., Duelli, P., Engel, M.S., Penny, N.D., Tauber, C.A., Mochizuki, A., Liu, X., 2018. Evolution of green lacewings (Neuroptera: Chrysopidae): a molecular supermatrix approach. Systematic Entomology 44, 499–513.

Jepson, J.E., Makarkin, V.N., Coram, R.A., 2012. Lacewings (Insecta: Neuroptera) from the Lower Cretaceous Purbeck Limestone Group of southern England. Cretaceous Research 34, 31–47.

Khramov, A.V., 2017. A new assemblage of Early Cretaceous green lacewings (Chrysopidae: Neuroptera) from Transbaikalia. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 107, 195–202.

Khramov, A.V., Liu, Q., Zhang, H., Jarzembowski, E.A., 2016. Early green lacewings (Insecta: Neuroptera: Chrysopidae) from the Jurassic of China and Kazakhstan. Papers in Palaeontology 2, 25–39.

Li, J.G., Batten, D.J., 2007. Palynological evidence of an Early Cretaceous age for the Yixian Formation at Sihetun, western Liaoning, China. Cretaceous Research 28, 333–338.

Linnaeus, C., 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, tenth ed., pp. 1–824 Salviae, Holmiae.

Lu, X.M., Wang, B., Ohl, M., Liu, X.Y., 2018. The first green lacewing (Insecta: Neuroptera: Chrysopidae) from the mid-Cretaceous amber of Myanmar. Zootaxa 4399, 563–570.

Makarkin, V.N., 1994. Upper Cretaceous Neuroptera from Russia and Kazakhstan. Annales de la Société Entomologique de France 30, 283–292.

Makarkin, V.N., 1997. Fossil Neuroptera of the Lower Cretaceous of Baisa, East Siberia, Part 3, Chrysopidae. Spixiana 20, 107–118.

Makarkin, V.N., Archibald, S.B., 2013. A diverse new assemblage of green lacewings (Insecta, Neuroptera, Chrysopidae) from the early Eocene Okanagan Highlands, western North America. Journal of Paleontology 87, 123–146.

Makarkin, V.N., Wedmann, S., Weiterschan, T., 2018. The first green lacewings from the late Eocene Baltic amber. Acta Palaeontologica Polonica 63 (3), 527–537.

Martins-Neto, R.G., 1997. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. X – descrição de novos táxons (Chrysopidae, Babinskaiidae, Myrmeleontidae, Ascalaphidae e Psychopsidae). Revista Uniersidade de Guarulhos, Série Ciências Exatas e Tecnológicas 2 (4), 68–83.

Martins-Neto, R.G., 2003. The Santana Formation Paleoentomofauna reviewed, Part I: Neuropteroida (Neuroptera and Raphidioptera): systematic and phylogeny, with description of new taxa. Acta Geologica Leopoldensia 25 (for 2002), 35–66.

Martins-Neto, R.G., Vulcano, M.A., 1988. Neurópteros (Insecta: Planipennia) da Formacão Santana (Cretáceo inferior), Bacia do Araripe, Nordeste do Brasil. I: Familia Chrysopidae. Anais da Academia Brasileira de Ciencias 60 (2), 189–201.

Martynov, A.V., 1927. Jurassic fossil insects from Turkestan. Order Neuroptera. Izvestia Akademii Nauk SSSR 21, 764–768.

Nel, A., Delclòs, X., Hutin, A., 2005. Mesozoic chrysopid-like Planippenia: a phylogenetic approach (Insecta: Neuroptera). Annales de la Société Entomologique de France 41, 29–68.

Panfilov, D.V., 1980. New Representatives of Lacewings (Neuroptera) from the Jurassic of Karatau. In: Topachevskiy, V.A. (Ed.), Mesozoic fossil insects. Nauka Dumka, Kiev, pp. 82–111 (in Russian).

Ponomarenko, A.G., 1992. New lacewings (Insecta, Neuroptera) from the Mesozoic of Mongolia. In: Grunt, T.A. (Ed.), New Taxa of Fossil Invertebrates of Mongolia. Nauka Press, Moscow, pp. 101–111 (in Russian).

Ren, D., 1998. Flower-associated brachycera flies as fossil evidence for Jurassic angiosperm origins. Science 280 (5360), 85–88.

Ren, D., Guo, Z.G., 1996. On the new fossil genera and species of Neuroptera (Insecta) from the Late Jurassic of northeast China. Acta Zootaxonomica Sinica 21, 461–479.

Ren, D., Lu, L.W., Guo, Z.G., Ji, S.A., 1995. Faunae and Stratigraphy of Jurassic-Cretaceous in Beijing and the Adjacent Areas. Seismic Publishing House, Beijing, pp. 1–233.

Ren, D., Shih, C.K., Gao, T.P., Wang, Y.J., Yao, Y.Z., 2019. Rhythms of Insect Evolution: Evidence from the Jurassic and Cretaceous in Northern China. Wiley Blackwell, New York, pp. 1–728.

Rust, J., 1999. Biologie der Insekten aus dem Ältesten Tertiär Nordeuropas. Habilitationsschrift zur Erlangung der venia legendi für das Fach Zoologie. Biologische Fakultät der Georg-August-Universität Göttingen, Göttingen, pp. 1–482.

Schneider, W.G., 1851. Symbolae ad Monographiam Generis Chrysopae, Leach. Hirt, Vratislaviae, pp. 1–178.

Shi, C.F., Winterton, S.L., Ren, D., 2015. Phylogeny of split-footed lacewings (Neuroptera, Nymphidae), with descriptions of new Cretaceous fossil species from China. Cladistics 31 (5), 455–490.

Willmann, R., Brooks, S.J., 1991. Insekten aus der Fur-Formation von Dänemark (Moler, ob. Paleozän/unt. Eozän?). 6. Chrysopidae (Neuroptera). Meyniana 43, 125–135.

Winterton, S.L., Gillung, J.P., Garzón-Orduña, I.J., Badano, D., Breitkreuz, L.C.V., Duelli, P., Engel, M.S., Liu, X.Y., Machado, R.J., Mansell, M., Mochizuki, A., 2019. Evolution of green lacewings (Neuroptera: Chrysopidae): an anchored phylogenomics approach. Systematic Entomology 44, 514–526.

Yang, C.K., Hong, Y.C., 1990. *Drakochrysa*, an Early Cretaceous new genus of Chrysopidae (Insecta: Neuroptera) from Laiyang Basin, Shandong province. Geoscience 4, 15–26.

Yang, W., Li, S.G., Jiang, B.Y., 2007. New evidence for Cretaceous age of the feathered dinosaurs of Liaoning: zircon U-Pb SHRIMP dating of the Yixian Formation in Sihetun, northeast China. Cretaceous Research 28, 177–182.

Yang, Q., Wang, Y.J., Labandeira, C.C., Shih, C.K., Ren, D., 2014. Mesozoic lacewings from China provide phylogenetic insight into evolution of the Kalligrammatidae (Neuroptera). BMC Evolutionary Biology 14 (1), 126.

Yang, Q., Makarkin, V.N., Shih, C.K., Ren, D., 2015. New Aetheogrammatidae (Insecta: Neuroptera) from the Lower Cretaceous Yixian Formation, China. Cretaceous Research 55, 25–31.

Yao, Y.Z., Cai, W.Z., Xu, X., Shih, C.H., Engel, M.S., Zheng, X.T., Zhao, Y.Y., Ren, D., 2014. Blood-feeding true bugs in the early Cretaceous. Current Biology 24 (15), 1786–1792.

Zhang, Tianwei, Shi, Chaofan, Pang, Hong, Ren, Dong, 2020. New species of *Protochrysa* (Neuroptera: Chrysopidae) from the Early Cretaceous of China. Journal of Environmental Entomology 42 (2), 506–510. https://doi.org/10.3969/j.issn.1674-0858.2020.02.32.

Zhou, Z.H., 2006. Evolutionary radiation of the Jehol Biota: chronological and ecological perspectives. Geological Journal 41 (3–4), 377–393.

Zhou, Z.H., 2014. The Jehol Biota, an Early Cretaceous terrestrial Lagerstätte: new discoveries and implications. National Science Review 1 (4), 543–559.