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Two interesting new genera of Kalligrammatidae (Neuroptera) from the Middle Jurassic of Daohugou, China

QIANG YANG[1], VLADIMIR N. MAKARKIN[1,2,3] & DONG REN[1]

[1]*College of Life Sciences, Capital Normal University, Beijing, 100048, China. E-mail: rendong@mail.cnu.edu.cn*
[2]*Institute of Biology and Soil Sciences, Far East Branch of the Russian Academy of Sciences, Vladivostok, 960022, Russia*
[3]*Corresponding author. E-mail: vnmakarkin@mail.ru*

Abstract

Two new genera and species of Kalligrammatidae (Neuroptera) *Apochrysogramma rotundum* **gen. et sp. nov.** and *Protokalligramma bifasciatum* **gen. et sp. nov**. are described from the Middle Jurassic of Daohugou, Inner Mongolia, China. The forewing of *Protokalligramma* **gen. nov.** is characterized by the generalised structure of MP, CuA, CuP and 1A, relatively scarce crossveins, absence of an eye-spot, and dense, long spinules ('microtrichia') occurring on its wing membrane. *Apochrysogramma* **gen. nov.** is the second genus in the subfamily Kallihemerobiinae, whose forewing easily differs from that of the type genus by the more rounded shape, much more numerous and closely spaced subcostal veinlets, branches of Rs and MP, less dense crossveins, and differently constructed eye-spot.

Key words: Kallihemerobiinae, Jurassic, fossil, lacewing

Introduction

The extinct family Kalligrammatidae attracts special attention from investigators due to their large size and presumably bright coloration. Many species possess eye-spots similar to those observed on the wings of some butterflies and large moths. It is this feature which has given them the name of the 'butterflies of the Jurassic' (Engel 2005). Other characteristics of most Kalligrammatidae are dense crossveins throughout the wing, hairs covering the entire wing membrane, pectinate MP with branches directed anteriorly, and elongate palpi. All these features make the family one of most advanced neuropteran groups to have existed during the Jurassic. Hitherto, twelve genera (29 species) of Kalligrammatidae are known from the Jurassic to the Early Cretaceous (Walther 1904; Handlirsch, 1906–1908, 1919; Martynova 1947; Panfilov, 1968, 1980; Ponomarenko 1984, 1992; Ren & Guo 1996; Jarzembowski 2001; Ren & Oswald 2002; Ren 2003; Zhang 2003; Zhang & Zhang 2003; Engel 2005; Makarkin *et al*. 2009; Yang *et al*. 2009; Makarkin 2010). Detailed taxonomic treatment and phylogenetic analysis of the family are needed.

More than 60 specimens of Kalligrammatidae have been collected at the Middle Jurassic locality of Daohugou (Province of Inner Mongolia in China) (unpubl. data). Up to now, however, only three species have been described, i.e., *Kallihemerobius pleoneurus* Ren *et* Oswald, 2002 (based on an isolated forewing), *Limnogramma mirum* Ren, 2003, and *Sinokalligramma jurassicum* Zhang, 2003 (both known by isolated hind wings). In the present paper we describe two new genera whose wing venation is quite remarkable compared with other kalligrammatid genera. The forewing of *Apochrysogramma rotundum* **gen. et sp. nov.** is largely rounded with numerous branches of Rs separately originating from R. This is the second species in the subfamily Kallihemerobiinae. It can not be assigned to the type genus, *Kallihemerobius* Ren *et* Oswald, 2002, as it differs considerably from the latter by the more rounded forewing, differently constructed (i.e. embossed) eye-spot, and a number of characters in the venation (e.g., much more numerous and closely spaced subcostal veinlets, branches of Rs and MP, considerably less dense crossveins). The other species (*Protokalligramma bifasciatum* **gen. et sp. nov.**) belongs to a remarkable new genus of the family. It easily differs from other known genera by the generalised structure of MP, CuA, CuP and 1A (all are dichotomously branched), the absence of an eye-spot, and scarce crossveins.

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Material and methods

This study is based on two specimens collected near Daohugou Village (Shantou Township, Ningcheng County, Inner Mongolia, China) and 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). These insect-bearing beds are considered to belong to the Jiulongshan Formation and dated as Bathonian (Middle Jurassic) (Gao & Ren 2006). Specimens were examined using a Leica MZ12.5 dissecting microscope. Line drawings were prepared with CorelDraw 12 graphics software with the aid of Adobe Photoshop CS3, and photographed by SMZ1000 stereomicroscope and Nikon SMZ1000. We use the traditional venational terminology of Comstock (1918) (*sensu* Wootton 2003) following the recent interpretations of Oswald (1993) and Archibald & Makarkin (2006). Each branch of Rs originating separately from R is named here the oblique radial branch (for detail see Oswald 1993; Makarkin & Wedmann 2009). Venation abbreviations: 1A–3A, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; M, media; MA, media anterior; MP, media posterior; R1, first branch of radius (R); ORB, oblique radial branch; Rs, radial sector; Rs1–Rs4, first (proximal-most) to fourth branch of Rs; Sc, subcosta.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Kalligrammatidae Handlirsch, 1906

Subfamily incertae sedis

Genus *Protokalligramma* gen. nov.

Type species. *Protokalligramma bifasciatum* **gen. et sp. nov.**

Etymology. Proto- (from the Greek *protou*, before) + -kalligramma (from *Kalligramma*, a genus-group name), in reference to the taxonomic affinity of the genus as an isolated ('primitive') taxon in Kalligrammatidae. Gender neuter (ICZN, 1999: Article 30.1.2).

Diagnosis. The new genus may be distinguished from other kalligrammatid genera by the following combination of forewing character states: costal space strongly narrowed towards apex; simply (generalised) constructed MP, not pectinately branched [pectinate anteriorly directed branches in most other genera], cross venation relatively scarce [dense in most other genera], eye-spot absent [shared with *Sophogramma* Ren *et* Guo, 1996; present in other genera], CuP and 1A relatively short, not running parallel to hind margin [CuP, 1A long, running nearly parallel to hind margin in most other genera].

Comments. *Protokalligramma* **gen. nov.** is unusual among Kalligrammatidae as the forewing venation strongly differs from those of most other known genera. Nonetheless, this genus may not be treated as a representative of a new family (or assigned to another family) because its venation is generally concordant with that of Kalligrammatidae. Moreover, it is similar to that of the specimen from the Late Jurassic of Karatau named '*Kalligramma turutanovae*' Martynova by Ponomarenko (2002: Fig. 254) (which itself likely represents a new genus). *Protokalligramma bifasciatum* **gen. et sp. nov.** shares with '*K. turutanovae*' a similar generalised structure of MP, CuA, CuP and 1A. In the latter, however, a well-developed eye-spot is present, cross venation is dense, CuA and CuP are longer, running almost parallel to the hind margin for considerable distance.

The presence of dense short hairs on the membrane found in the wing of *Protokalligramma* **gen. nov.** is characteristic of many Kalligrammatidae. Panfilov (1968) mentioned them to be present in the genera *Kalligramma* Walker, 1904, *Meioneurites* Handlirsch, 1906, and *Kalligrammula* Handlirsch, 1919. However, the membrane of the wings of other genera (e.g., *Sophogramma*, *Apochrysogramma* **gen. nov.**) lacks hairs. These hairs are most probably spinules (long 'microtrichia'), i.e., non-cellular, non-innervated, non-socketed, and non-articulated cuticle processes, not true sensilla (Vshivkova & Makarkin 2010). Minute true spinules ('microtrichia') occur on the wing membrane of some extant neuropteran families (e.g., Hemerobiidae, Ithonidae, Dilaridae), but they are usually invisible (or hardly visible) in fossils. The only exception is the presence of rather long hairs (probably spinules) on

part of the hind wing membrane in the Early Eocene ithonid *Palaeopsychops setosus* Archibald *et* Makarkin (Archibald & Makarkin 2006: Fig. 17).

***Protokalligramma bifasciatum* sp. nov.**
Figs. 1–3

Etymology. From the Latin *bi*, double, and *fasciatus*, striped, in references to the forewing color pattern of the holotype.

Holotype. Specimen No. CNU-NEU-NN2009026, deposited in CNUB. An incomplete, well-preserved forewing.

Type locality and horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Middle Jurassic (Bathonian, Jiulongshan Formation).

Description. Forewing broad, round-ovate, 60 mm long (as preserved; estimated complete length >70 mm), 38 mm wide (as preserved; estimated complete width about 40 mm). Entire wing membrane densely covered with short hairs, longest in basal part of costal space (in region of humeral veinlet), long in anterior portion (Fig. 3B), and short to very short in other regions. Trichiation on veins relatively short. Trichosors not visible due to dense, short trichiation on and near margins, probably absent. Costa stout. Costal space most dilated at 1/4 proximal length; slightly narrowed towards wing base, narrowed towards apex. All subcostal veinlets in proximal half dichotomously branched, connected by 2-4 crossveins forming 3-4 irregular costal series. Humeral veinlet well-developed, recurrent and branched; two unknown vein-like structures in antehumeral space (one shown in Fig. 3A, labeled *vs*). Subcostal space relatively narrow, with rather widely spaced crossveins. R1 space narrow; strongly narrowed basally. Rs originating close to base of wing, with seven preserved branches; origin of Rs1 close to origin of Rs, forked near its origin; Rs2-Rs4 profusely dichotomously forked. M and R clearly separated basally. Fork of M rather close to base of wing; MA and MP similarly constructed, both with few (dichotomous) branches distally. Cu divided into CuA and CuP very close to base of wing. CuA relatively short, with five distal pectinate branches, at least proximal-most branch deeply forked. CuP few-branched, forked twice in distal half. 1A profusely dichotomously branched. 2A pectinate, each branch dichotomously branched. 3A short, poorly preserved. Main area of wing posterior to R filled with regularly and widely spaced crossveins (compared with most other Kalligrammatidae); crossveins apparently rare in area of marginal twigging. Jugal lobe not detected, apparently absent. Wing membrane fuscous, blackish in costal space, paler in distal and posterior portion of wing, with color pattern consisting of two transverse blackish bands, and several small dark brown or blackish patches basally and near hind margin.

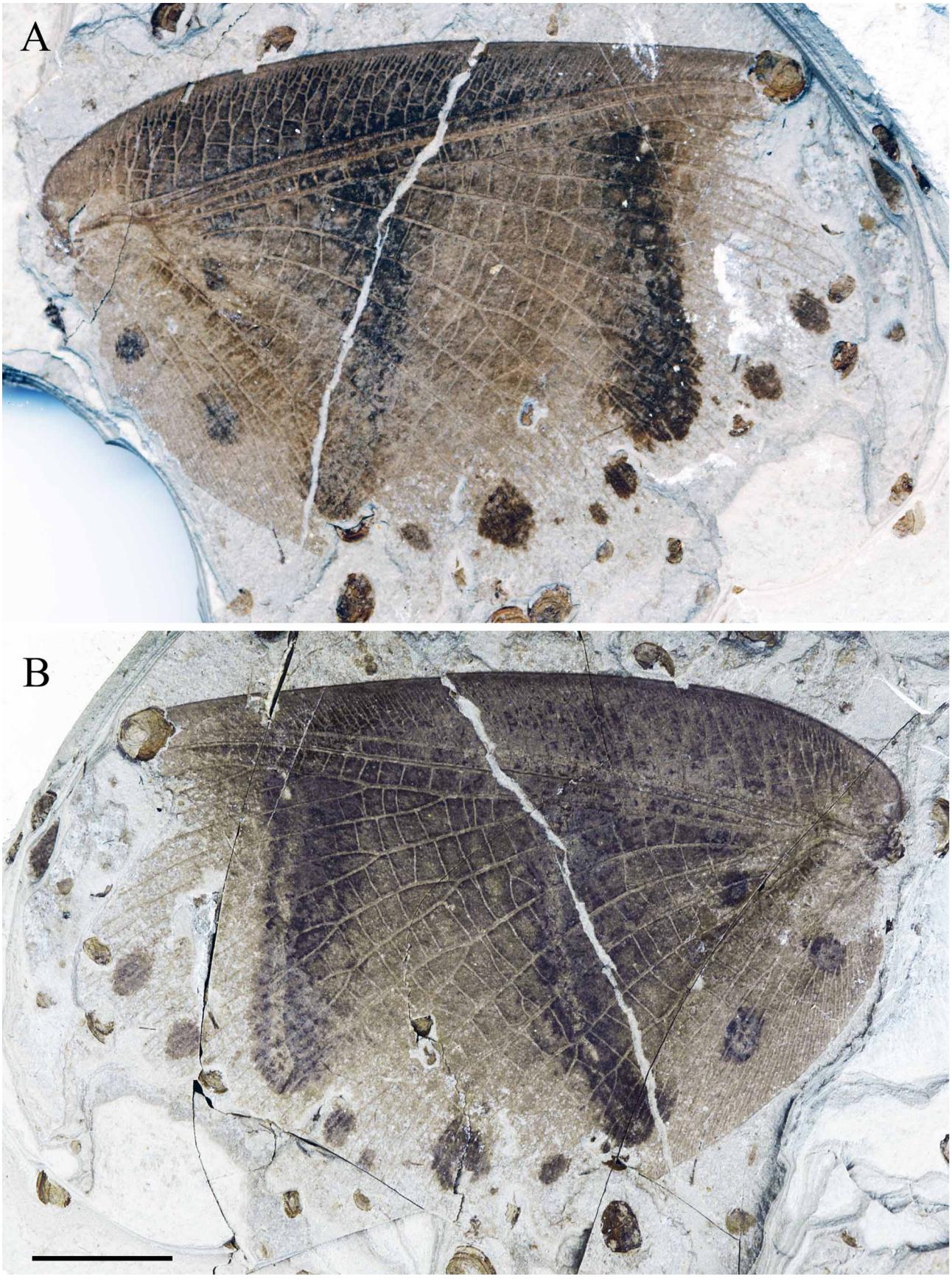
Subfamily Kallihemerobiinae Ren et Engel, 2008

Type genus. *Kallihemerobius* Ren *et* Oswald, 2002.

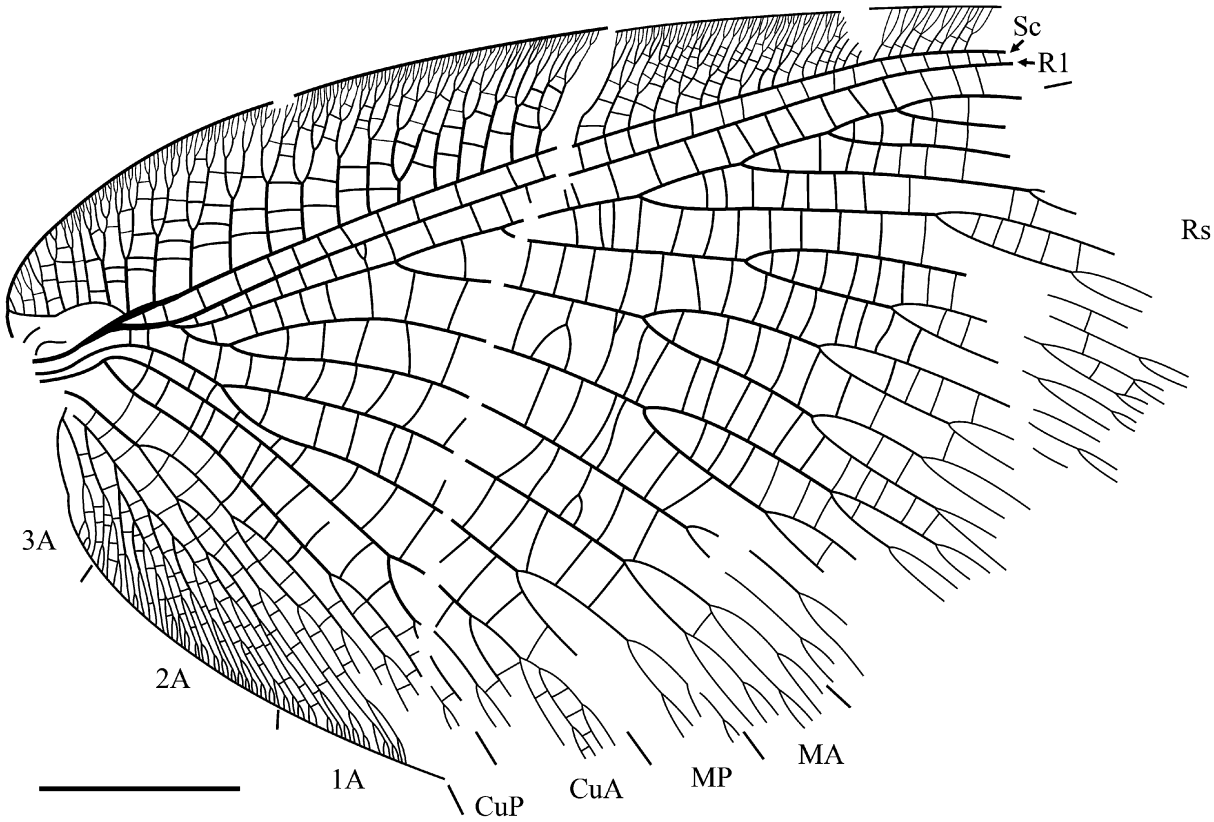
Diagnosis (modified after Ren & Engel 2008). Forewing having (1) costal space very broad; (2) numerous, regularly spaced ORBs; (3) anteriorly directed pectinate branches of MP; (4) long closely-spaced marginal veinlets all around wing (except basally) lacking crossveins between them; (5) well-developed eye-spot.

Genera included. *Kallihemerobius* and *Apochrysogramma* **gen. nov.** (both from the Middle Jurassic of Daohugou, China).

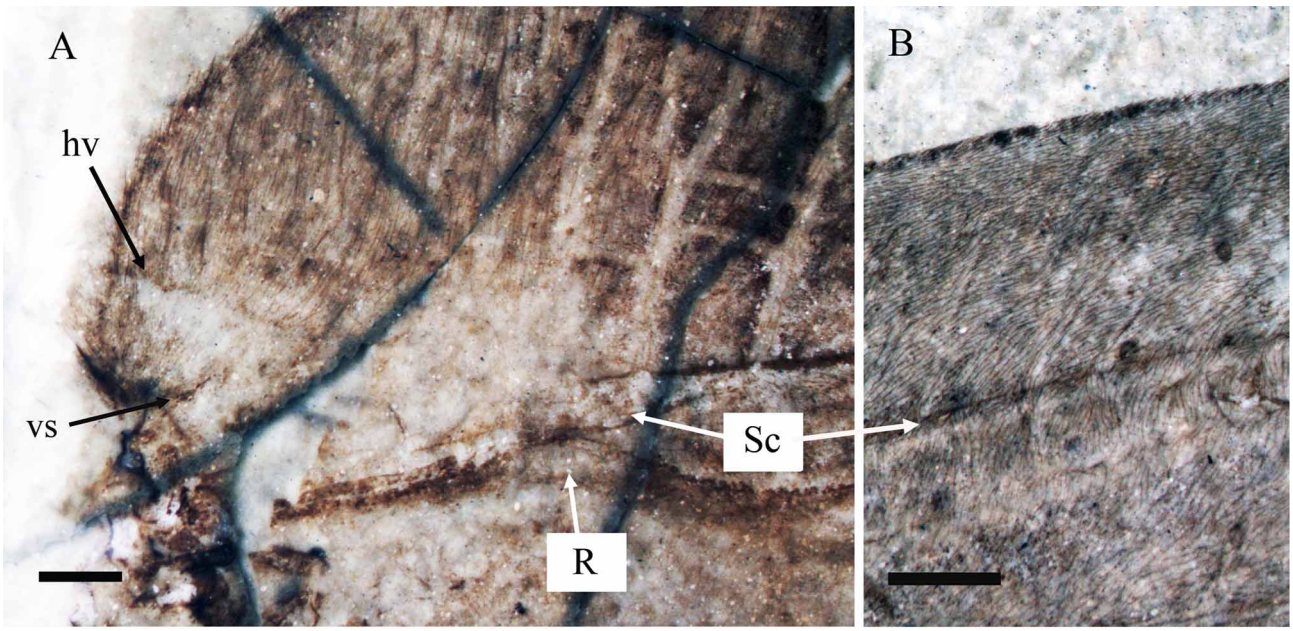
Comments. The presence of more than one ORB is known in Hemerobiidae, Ithonidae, Dilaridae, Kalligrammatidae (Kallihemerobiinae and the genus *Kalligrammina* Panfilov, 1980), and Aetheogrammatidae (the single genus *Aetheogramma* Ren *et* Engel, 2008) (Panfilov 1980; Ren & Engel 2008; Winterton & Makarkin 2010). This is obviously an apomorphic state in the order, and most probably it has evolved independently at least in the three former families because of a distant relationship with Kalligrammatidae (see Grimaldi & Engel 2005: Fig. 9.4; Engel & Grimaldi 2008: Table 3). Of the kalligrammatid-like taxa, *Kalligrammina* and *Aetheogramma* have a similarly constructed Rs-system in the hind wing with 5 ORBs: ORB1 is simple, originating close to the wing base; ORB2 is pectinate, originating close to the wing base, with four regular branches (*Kalligrammina*) or with two branches originating far distally (*Aetheogramma*); the distal ORB3 to ORB5 are simple (the forewing of



FIGURES 1. *Protokalligramma bifaciatum* **gen. et sp. nov**. Holotype No. CNU-NEU-NN2009026, general view of the specimen. A, part. B, counterpart. Scale bar = 10 mm.



FIGURES 2. *Protokalligramma bifaciatum* **gen. et sp. nov**. Holotype CNU-NEU- NN2009026, composite drawing of the forewing venation. Scale bar = 10 mm.



FIGURES 3. *Protokalligramma bifaciatum* **gen. et sp. nov**. Holotype CNU-NEU- NN2009026 (part). A, basal portion of the costal space. B, the forewing anterior portion showing dense long spinules ('microtrichia') on the membrane. hv, humeral vein; R, radius, Sc, subcosta, vs, unknown venal structure. Scale bar = 1 mm (for A, B).

Aetheogramma has a similar Rs-system; that of *Kalligrammina* is unknown). Ren & Engel (2008) suggested that *Kalligrammina* "should be transferred to Aetheogrammatidae" (p. 166), but did not formally transfer it because of

the fragmentary nature of the specimen (an incomplete hind wing is only known). It is possibly that this peculiar character state in these two kalligrammatid-like genera may have arisen independently, although this seems to be less plausible than they are indeed nearly related. Configuration of ORBs in Kallihemerobiinae is different from that of these genera in many respects, e.g., ORBs are more numerous (>9), regularly spaced, and all relatively similarly constructed. It is quite probably that the character state of more than one ORB in Kallihemerobiinae and *Kalligrammina* has evolved independently.

Genus *Apochrysogramma* gen. nov.

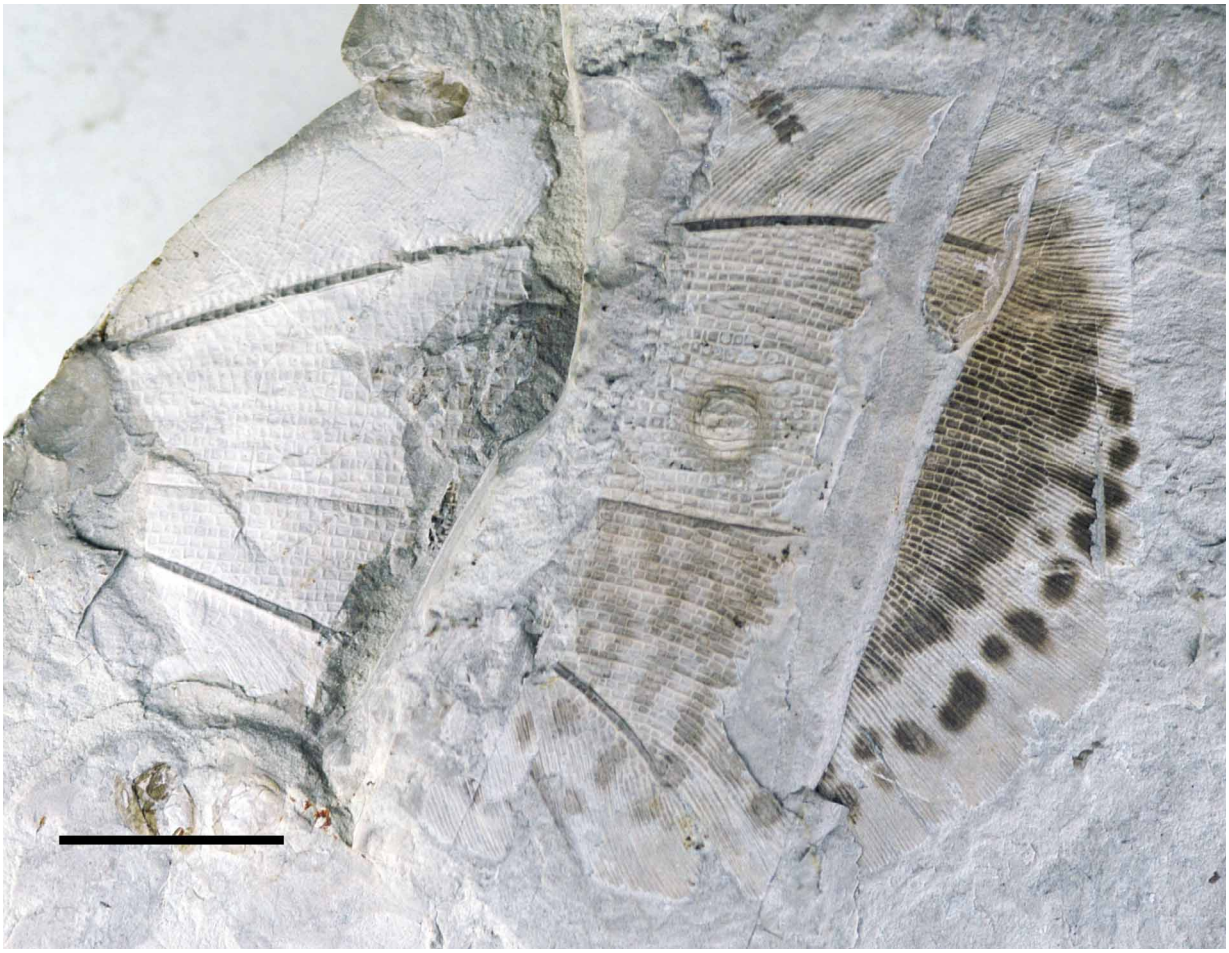
Type species. *Apochrysogramma rotundum* **gen. et sp. nov.**

Etymology. Apochryso– (from *Apochrysa*, a genus-group name), and –gramma (a traditional ending of generic names in Kalligrammatidae, from the Greek *gramma*, drawing, letter), in reference to the superficial resemblance to Apochrysinae genera (Chrysopidae). Gender neuter (ICZN, 1999: Article 30.1.2).

Diagnosis. The new genus clearly differs from *Kallihemerobius* by the more numerous and closely spaced subcostal veinlets, ORBs, and branches of MP; broader costal space; fewer crossveins; and differently constructed eyespot.

***Apochrysogramma rotundum* sp. nov.**
Figs. 4–6

Etymology. The specific name is derived from the Latin *rotundus*, round, in reference to the rounded shape of the forewing of the holotype.



FIGURES 4. *Apochrysogramma rotundum* **gen. et sp. nov**. Holotype CNU-NEU- NN2009033, general view of the specimen. Scale bar = 10 mm.

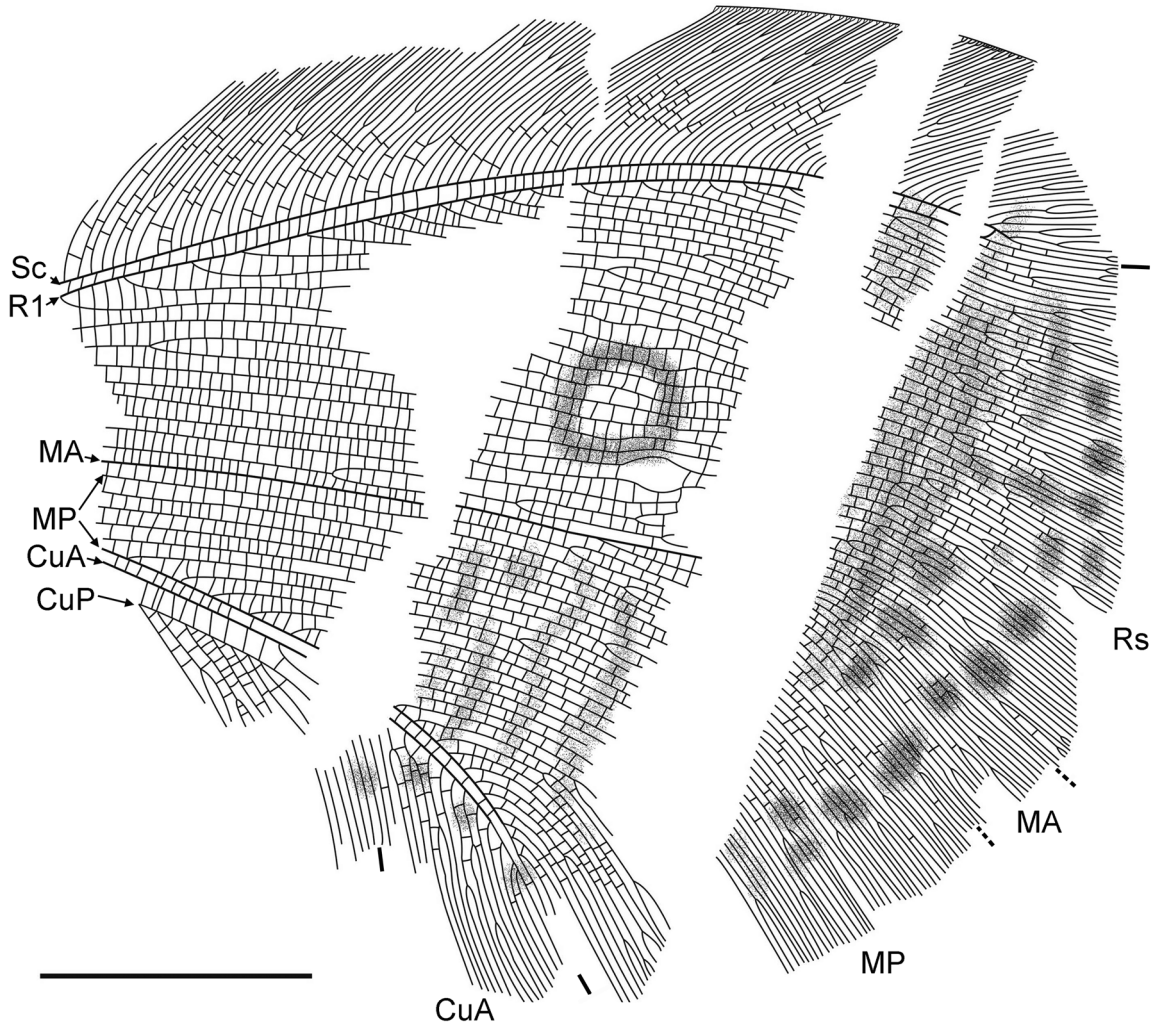


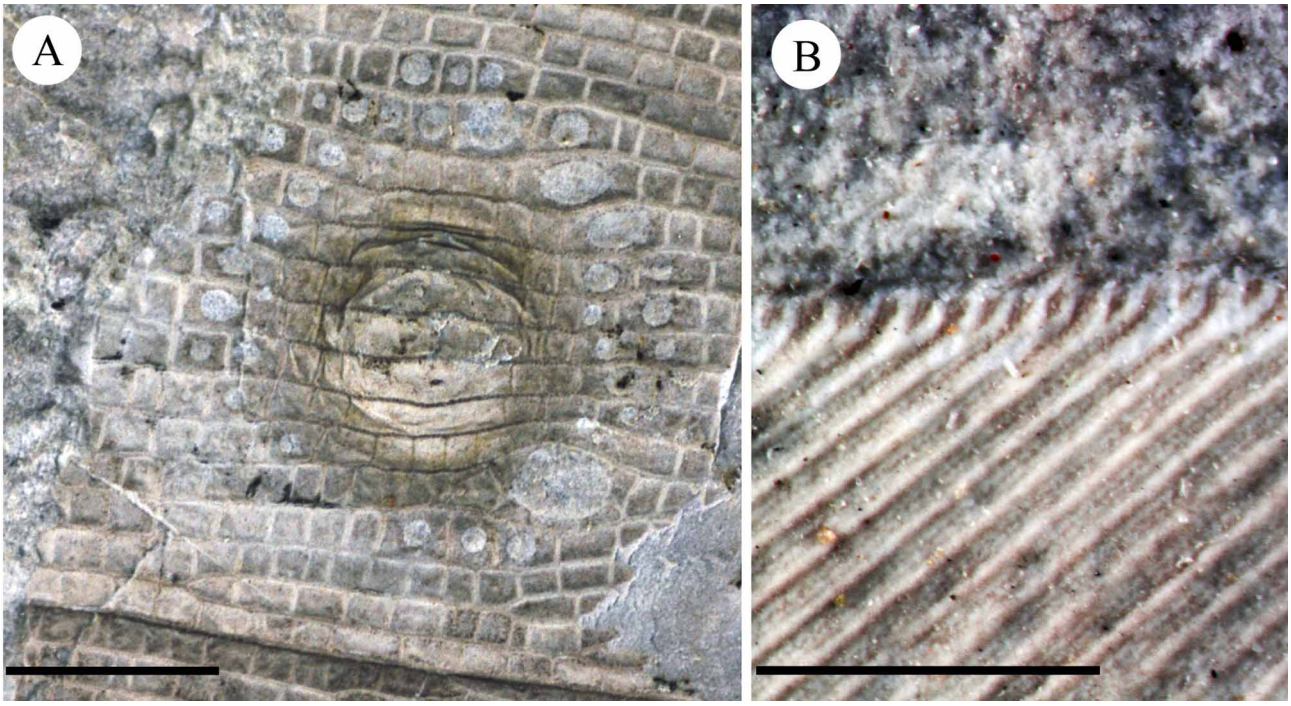
FIGURE 5. *Apochrysogramma rotundum* **gen. et sp. nov**. Holotype CNU-NEU- NN2009033. Drawing of the forewing (restored). Scale bar = 10 mm.

Holotype. Specimen No. CNU-NEU-NN2009033, deposited in CNUB. An incomplete well-preserved forewing, broken into two parts (proximal and distal) and preserved on different layers.

Type locality and horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Middle Jurassic (Bathonian, Jiulongshan Formation).

Description. Forewing rounded, with costal margin slightly convex, about 45 mm long as originally preserved (39 mm when restored; estimated complete length >55 mm), 36 mm wide. Costal space very broad, not narrowed towards wing apex. Subcostal veinlets very closely spaced, few-branched, parallel to each other, connected by irregularly spaced crossveins between their basal portions; very shallowly forked near costal margin (alternatively, the fusion of trichosors and curved veinlet terminations could form these shallow forks; Fig. 6B). Trichosors not detected. Sc concave, distally not fused with R1. R convex, parallel to Sc for long distance. Subcostal space narrow. Rs almost completely incorporated into R, with at most 26 ORBs. ORB1 (=Rs1) forked four times in middle part of wing; other ORBs sometimes forked once or twice before marginal twigging. MA strongly concave, straight for most of length, few branched distally. Stem of MP concave, curved smoothly posteriorly with numerous (approximately 25) pectinate, anteriorly directed branches. CuA strongly convex, running parallel to MP; with approximately 12 pectinate branches. CuP slightly concave, pectinate. Anal region not preserved. Crossveins numerous, dense over most of wing (subcostal to intracubital spaces), sparse between branches of CuA, CuP basally; entirely absent for long distances between closely spaced terminal veinlets of ORBs, branches of MP, CuA, CuP ('marginal twigging'). Eye-spot well developed, faintly visible, consisting of rounded central convex structure

(i.e. embossed) (approximately 3 mm diameter) with concave margin, and many (approximately 35 in number) smaller pale spots differing in size (0.2 mm to 1.5 mm diameter), forming ring around central spot (Fig. 6A); each pale spot located in one cell, whereas central spot occupying many cells. Rest of wing color pattern consists of several fuscous stripes in MP space, dark transverse band in radial space distal of eye-spot, and a dozen dark spots along outer margin.



FIGURES 6. *Apochrysogramma rotundum* **gen. et sp. nov**. Holotype CNU-NEU- NN2009033, forewing details. A, eye-spot. B, costal margin showing branching of the subcostal veinlets. Scale bars = 3 mm (A), 1 mm (B).

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References

Archibald, S.B. & Makarkin, V.N. (2006) Tertiary giant lacewings (Neuroptera: Polystoechotidae): revision and description of new taxa from western North America and Denmark. *Journal of Systematic Palaeontology*, 4, 119–155. [Errata: 3, 307].

Comstock, J.H. (1918) *The wings of insects*. Comstock Publication Company, Ithaca, NY, 430 pp.

Engel, M.S. (2005) A remarkable kalligrammatid lacewing from the Upper Jurassic of Kazakhstan (Neuroptera: Kalligrammatidae). *Transactions of the Kansas Academy of Science*, 108, 59–62.

Engel, M.S. & Grimaldi, D.A. (2008) Diverse Neuropterida in Cretaceous amber, with particular reference to the paleofauna of Myanmar (Insecta). *Nova Supplementa Entomologica*, 20, 1–86.

Gao, K.Q. & Ren, D. (2006) Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou Beds. *Acta Geologica Sinica*, 80, 42–45.

Grimaldi, D.A. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, Cambridge, UK, xv + 755 pp.

Handlirsch, A. (1906–1908) *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen*. W. Engelmann, Leipzig, ix+1430 pp. [Issued in 1906 (pp. 1–640), 1907 (pp. 641–1120), 1908 (pp. 1120–1430)].

Handlirsch, A. (1919) Eine neue Kalligrammide (Neuroptera) aus dem Solnhofener Plattenkalke. *Senckenbergiana*, 1 (3), 61–63.

ICZN (1999) *International Code of Zoological Nomenclature*. 4th edition. International Trust for Zoological Nomenclature, London, xxix + 305 pp.

Jarzembowski, E.A. (2001) A new Wealden fossil lacewing. *In*: Rowlands, M.L.J. (Ed.), *Tunbridge Wells and Rusthall Commons. A History and natural History.* Tunbridge Wells Museum and Art Gallery, Tunbridge Wells, 56–58.

Linnaeus, C. (1758) *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th ed., vol. 1*. Salvii, Holmiae, 824 pp.

Makarkin,V.N. (2010) New psychopsoid Neuroptera from the Lower Cretaceous of Baissa, Transbaikalia. *Annales de la Société Entomologique de France (N.S.)*, 46, 254–261.

Makarkin, V.N., Ren, D. & Yang, Q. (2009) Two new species of Kalligrammatidae (Neuroptera) from the Jurassic of China, with comments on venational homologies. *Annals of the Entomological Society of America*, 102, 964–969.

Makarkin V.N. & Wedmann S. (2009) First record of the genus *Sympherobius* (Neuroptera: Hemerobiidae) from Baltic amber. *Zootaxa*, 2078, 55–62.

Martynova, O.M. (1947) Kalligrammatidae (Neuroptera) from the Jurassic shales of Kara-Tau (Kazakhstanian SSR). *Doklady Akademii Nauk SSSR (N.S.)*, 58, 2055–2058. (In Russian).

Oswald, J.D. (1993) Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). *Journal of the New York Entomological Society*, 101, 143–299.

Panfilov, D.V. (1968) Kalligrammatids (Neuroptera, Kalligrammatidae) from the Jurassic deposits of Karatau. In: Rohdendorf, B.B. (Ed.), *Jurassic insects of Karatau*. Nauka Press, Moscow, 166–174. (In Russian).

Panfilov, D.V. (1980) New representatives of lacewings (Neuroptera) from the Jurassic of Karatau. *In*: Dolin, V.G., Panfilov, V.G.,, Ponomarenko, A.G. & Pritykina, L.N., *Fossil Insects of the Mesozoic*. Naukova Dumka, Kiev, 82–111. (In Russian).

Ponomarenko, A.G. (1984) Neuroptera from the Jurassic of eastern Asia. *Paleontologicheskii Zhurnal*, 1984(3), 64–73 (In Russian; English translation: *Paleontological Journal*, 1985, 18(3), 59–69).

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. Transactions of the Joint Soviet-Mongolian Paleontological Expedition, vol. 41*. Nauka Press, Moscow, 101–111. (In Russian).

Ponomarenko, A.G. (2002) Superorder Myrmeleontidea Latreille, 1802 (=Neuropteroidea Handlirsch, 1903). *In*: Rasnitsyn, A.P. & Quicke, D.L.J. (Eds.), *History of Insects*. Kluwer Academic Publishers, Dordrecht, 176–192.

Ren, D. (2002) A new lacewing family (Neuroptera) from the Middle Jurassic of Inner Mongolia, China. *Entomologia Sinica*, 9(4), 53–67.

Ren, D. (2003) Two new Late Jurassic genera of kalligrammatids from Beipiao, Liaoning (Neuroptera: Kalligrammatidae). *Acta Zootaxonomica Sinica*, 28, 105–109.

Ren, D. & Engel, M.S. (2008) Aetheogrammatidae, a new family of lacewings from the Mesozoic of China (Neuroptera: Myrmeleontiformia). *Journal of the Kansas Entomological Society*, 81, 161–167.

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. & Oswald, J. (2002) A new genus of kalligrammatid lacewings from the Middle Jurassic of China (Neuroptera: Kalligrammatidae). *Stuttgarter Beiträge zur Naturkunde*, (B), 317, 1–8.

Vshivkova, T.S. & Makarkin, V.N. (2010) Ultrastructural morphology of leg cuticle derivatives useful for phylogenetic study of Neuropterida (Insecta: Megaloptera, Neuroptera): preliminary report. *In*: Devetak, D., Lipovšek, S., Arnet, A.E. (Eds.), *Proceedings of the Tenth International Symposium on Neuropterology. Piran, Slovenia, 2008.* University of Maribor, Faculty of Natural Sciences and Mathematics, Maribor, 287–300.

Walther, J. (1904) Die Fauna der Solnhofener Plattenkalke. Bionomisch betrachtet. *Denkschriften der Medizinisch-Naturwissenschaftlichen Gesellschaft zu Jena*, 11, 133–214.

Winterton S. & Makarkin V.N. (2010) Phylogeny of moth lacewings and giant lacewings (Neuroptera: Ithonidae, Polystoechotidae) by using DNA sequence data, morphology, and fossils. *Annals of the Entomological Society of America*, 103, 511–522.

Wootton, R.J. (2003) Wings. *In*: Resh, V.H. & Carde, R.T. (Eds.), *Encyclopedia of insects*. Academic Press, London, 1186–1192.

Yang, Q., Zhao, Y.Y. & Ren, D. (2009) An exceptionally well-preserved fossil Kalligrammatid from the Jehol Biota. *Chinese Science Bulletin*, 54, 1732–1737.

Zhang, J.F. (2003) Kalligrammatid lacewings from Upper Jurassic of Daohugou Formation in Inner Mongolia, China. *Acta Geologica Sinica*, 77, 141–146. (English Edition)

Zhang, J.F. & Zhang, H.C. (2003) *Kalligramma jurarchegonium*, sp. nov. (Neuroptera: Kalligrammatidae) from the Middle Jurassic of northeastern China. *Oriental Insects*, 37, 301–308.