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# New Aetheogrammatidae (Insecta: Neuroptera) from the Lower Cretaceous Yixian Formation, China

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ABSTRACT

Two new genera and three new species of the Mesozoic family Aeotheogrammatidae are described from the Lower Cretaceous of Yixian Formation (Liaoning Province, China): *Cyclicogramma rotundum* gen. et sp. nov. and *Aetheogramma bistriatum* sp. nov. from Huangbanjigou, and *Curtogramma ovatum* gen. et sp. nov. from Dawangzhangzi. The hind wing of *Cyclicogramma rotundum* gen. et sp. nov. differs from that of other species by its smaller size, its overall shape, RP bearing only two oblique radial branches, and its configurations of CuP, AA1, and AA2. *Aetheogramma bistriatum* sp. nov. is closely related to *A. speciosum* Ren and Engel, 2008, but distinguished from the latter by its distinctive configuration of RP1, and the narrower and longer AA2 space in the hind wing. *Curtogramma ovatum* gen. et sp. nov. is distinguished from all other species of the family by the forewing with M forking very far from the wing base.



## 1. Introduction

The Mesozoic family Aetheogrammatidae is one of most specialized within the Neuroptera. It is closely related to another highly specialized Mesozoic family, the Kalligrammatidae. Adults of both families have long-proboscid siphonate mouthparts allowing them to presumptively feed on gymnosperm fluids and pollen (Zherikhin, 1978; Rasnitsyn, 1980; Labandeira, 2010; Yang et al., 2012, 2014b). Hitherto, aetheogrammatids were known from only three species from the Middle Jurassic to the Lower Cretaceous of China and Kazakhstan: *Aetheogramma speciosum* Ren and Engel, 2008, *Ectopogramma kalligrammoides* Engel et al., 2011 and *Kalligrammina areolata* Panfilov, 1980 (Ren and Engel, 2008; Engel et al., 2011). However, the family placement of the latter genus and species was rather unclear as it is represented by a single incomplete hind wing. *Kalligrammina* was originally assigned to Kalligrammatidae by Panfilov (1980), but according to Ren and Engel (2008) and Engel et al. (2011), it "may be best classified in Aetheogrammatidae" (Engel et al., 2011, p. 318). Yang et al. (2011) considered this genus in Kalligrammatidae, and thought that similar character states of *Kalligrammina* Panfilov, 1980 and *Aetheogramma* Ren and Engel, 2008 "may have arisen independently, although this seems to be less plausible than they are indeed nearly related" (Yang et al., 2011, p. 65). Recently, the genus was tentatively assigned to the kalligrammatid subfamily Kalligrammatinae (Yang et al., 2014b). Based on the data presented here from the new fossils, we believe that *Kalligrammina areolata* belongs to Aetheogrammatidae.

Herein, we describe two new genera and three new species of Aetheogrammatidae from two Early Cretaceous localities of Yixian Formation, Huangbanjigou and Dawangzhangzi, in the Liaoning Province, northeastern China, and analyse the composition and characters of this family.

## 2. Material and methods

This study is based on three specimens, two collected near Huangbanjigou Village, Shangyuan County, the other one near Dawangzhangzi Village, Lingyuan City, both from the Liaoning Province, China (Fig. 1). 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). Both localities belong to the Yixian Formation; the Huangbanjigou locality is dated as early Aptian to late Barremian, and the Dawangzhangzi locality as early Aptian (Yang et al., 2007; Wang and Zhou, 2008; Makarkin

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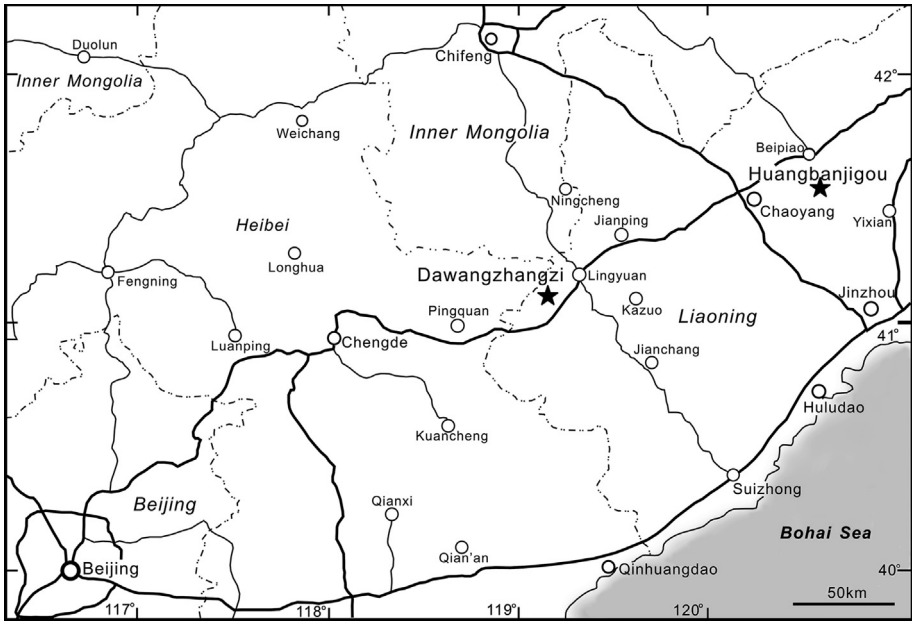


**Fig. 1.** Map showing the location of the Yixian Formation localities Huangbanjigou (41.365376N, 120.500491E) and Dawangzhangzi (41.114244N, 119.130391E) (based on the map in Kopylov and Zhang, (2015)).

et al., 2012; Yao et al., 2014). Also, we examined the holotype of *Aetheogramma speciosum* (deposited in CNUB), and detailed photographs of *Ectopogramma kalligrammoides* (deposited in the Nanjing Institute of Geology and Palaeontology, China).

Specimens were examined using a Leica MZ12.5 dissecting microscope. Line drawings were prepared with the CorelDraw 12 graphics software and with the aid of Adobe Photoshop CS3. Photographs were taken with a Nikon SMZ1000 stereomicroscope, and a Nikon D100 digital camera.

We use the venational terminology of Kukalová-Peck and Lawrence (2004) in the interpretation of Yang et al. (2012, 2014a). We treat all anal veins as branches of the anterior analis (AA1 to AA3), in general as applied to other Neoptera (e.g., Béthoux, 2005; Béthoux and Jarzembowski, 2010; Béthoux et al., 2011). Terminology of wing spaces and venation details follow Oswald (1993). We use the 'oblique radial branches' (ORB) concept of Oswald (1993) to designate more than one branch of the radius posterior that independently originate from the radius in some families of Neuroptera. The homology of individual ORB's and individual branches of RP ('Rs') follows Makarkin and Wedmann (2009).

Wing venation abbreviations used in the text and figures are as follows: AA1 to AA3, first to third anterior anal veins; CuA, cubitus anterior; CuP, cubitus posterior; MA, media anterior; MP, media posterior; ORB1, proximal-most 'oblique radial branch'; ORB2, 'oblique radial branch' distad ORB1; RA, radius anterior; RP, radius posterior; RP1, proximal-most branch of RP or ORB1; RP2, branch of RP distad RP1. ScA, subcosta anterior; ScP, subcosta posterior.

## 3. Systematic palaeontology

Order: Neuroptera Linnaeus, 1758
Family: Aetheogrammatidae Ren and Engel, 2008
Genus *Aetheogramma* Ren and Engel, 2008

*Type species*. *Aetheogramma speciosum* Ren and Engel, 2008, by original designation.

*Emended diagnosis.* In forewing, crossveins between subcostal veinlets absent [present in *Ectopogramma* Engel et al., 2011]; branches of RP, MP strongly curved [slightly curved in *Ectopogramma*]; M forked relatively close to wing base [very far from wing base in *Curtogramma* gen. nov.]. In hind wing, hind margin straight [convex in *Cyclicogramma* gen. nov.]; branches of ORB1 irregularly spaced, strongly curved [regularly pectinately spaced, straight in *Kalligrammina*].

*Species included*. *Aetheogramma speciosum* (Figs. 2A, 3A, B) and *A. bistriatum* sp. nov., both from the Lower Cretaceous Yixian Formation.

*Remarks.* The hind wings of *Ectopogramma* and *Curtogramma* gen. nov. and the forewings of *Kalligrammina* and *Cyclicogramma* are unknown.

*Aetheogramma bistriatum* sp. nov.
Figs. 2B, 3C, D

*Derivation of name.* From the Latin *bi-*, two, and *striatus* [*-a*, *-um*], striped, referring to two distinct white transverse fasciae at least in the hind wing.

*Type material.* Holotype, CNU-NEU-LB2014008, a very fragmentary thorax with one leg, and a well-preserved overlapped fore- and hind wing.

*Type locality and horizon*. Huangbanjigou, Beipiao City, Liaoning Province, China; Lower Cretaceous (Yixian Formation).

*Diagnosis.* In forewing, ORB2 originating in distal part of wing [in proximal part in *A. speciosum*]; in hind wing, AA2 space narrow, long [relatively broad, short in *A. speciosum*]; inner white fascia distinct [indistinct in *A. speciosum*].

*Description.* Mid-leg (?): tibial spurs absent; basitarsus nearly as long as next three tarsomeres together; claws poorly preserved, probably relatively small.

Forewing 53.4 mm long, 21.8 mm wide (as preserved). Preserved costal space moderately broad, slightly dilated in proximal part, gradually narrowed toward base, apex. Humeral veinlet slightly bent to wing base, not recurrent. Subcostal veinlets simple (one forked), slightly inclined to apex; no costal

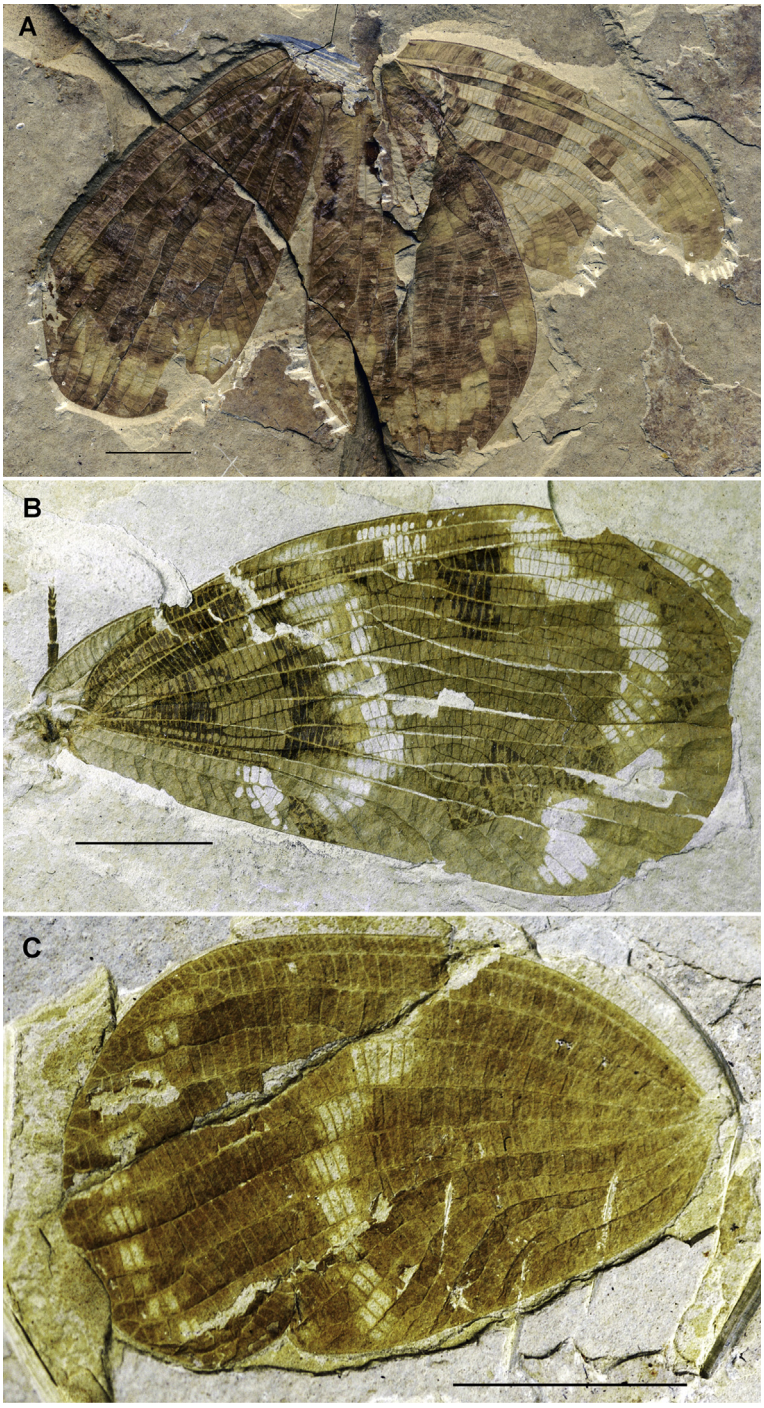


**Fig. 2.** Specimens of *Aetheogramma* Ren and Engel, 2008 and *Cyclicogramma* gen. nov. as preserved. A, *A. speciosum* Ren and Engel, 2008, holotype CNU-NEU-LB2001001 (part). B, *A. bistriatum* sp. nov., holotype CNU-NEU-LB2014008. C, *C. rotundum* gen. et sp. nov., holotype CNU-NEU-LB2014009. Scale bars represent 10 mm.

crossveins. Pterostigmal area not preserved. ScP long, almost parallel to RA for entire wing length, entering margin at or just before wing apex. Subcostal space moderately broad, slightly dilated basally; with dense crossveins. ScP apically not fused with RA. RA entering margin nearly at wing apex. RP consists of five ORB's: (1) ORB1 (RP proper) originated near wing base, long, with three long branches (RP1–RP3); RP1 originated near origin of ORB1, very long, sigmoid, simple; RP2, RP3 long, originating at approximately mid-point of wing, only distally shallowly branched; (2) ORB2 to ORB5 (RP4–RP7) originated in distal part of wing; ORB3 abnormally shortened, not reaching margin, other ORB's shallowly forked distally. M dividing into MA, MP near wing base, distad origin of ORB1. MA sigmoid, dichotomously branched only near margin. Posterior trace of MP sigmoid, with three pectinate, arched, anteriorly directed branches; proximalmost branch of MP deeply forked, with two pectinate branches, other two very shallowly forked distally. Stem of Cu not preserved; CuA, CuP incompletely preserved; sigmoid, dichotomously branched in distal parts. Anal veins not preserved. Crossveins very dense over entire wing. Forewing hidden under

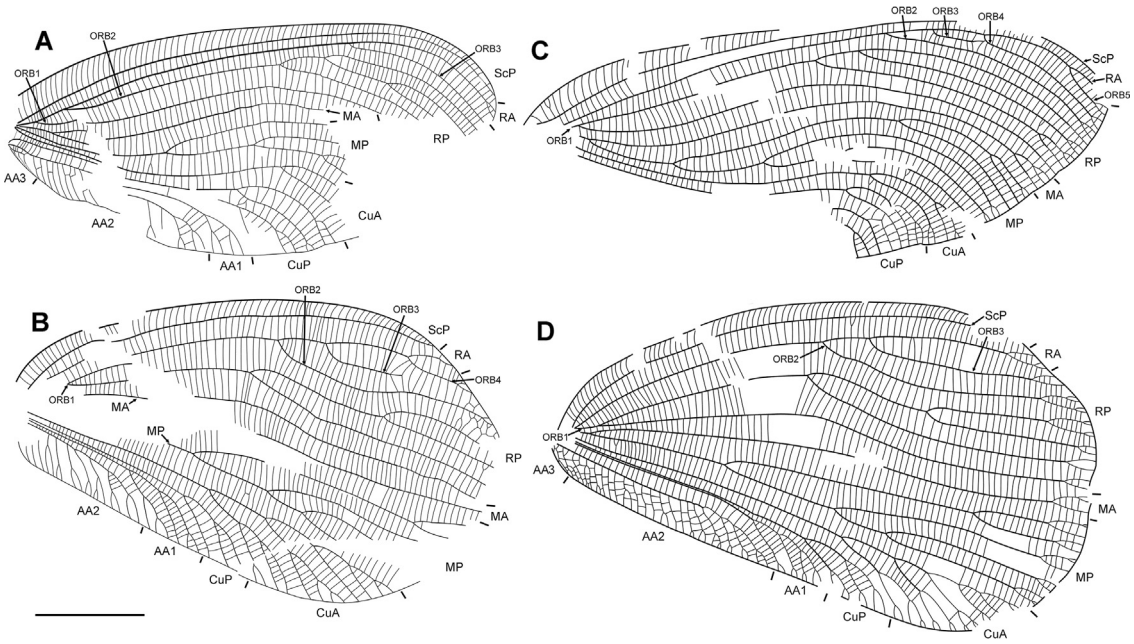


**Fig. 3.** Wing venation of *Aetheogramma*. A, *A. speciosum* Ren and Engel, 2008, holotype CNU-NEU-LB2001001, right forewing. B, same, right hind wing. C, *A. bistriatum* sp. nov., holotype CNU-NEU-LB2014008, forewing. D, same, hind wing. Scale bar represents 10 mm (all to scale).

hind wing, its colour pattern unclear, with fuscous and pale areas. Membrane setae not detected.

Hind wing shaped as half-circle, with costal, outer margins strongly arched and hind margin straight, 49.5 mm long, 29.3 mm wide. Costal space narrower than in forewing, equally moderately broad along nearly entire length. Pterostigma absent. All subcostal veinlets simple, slightly inclined to apex; no costal crossveins. ScP much shorter than in forewing. Subcostal space very broad, slightly broadened toward apex, with dense crossveins. ScP apically not fused with RA. RA entering margin before wing apex. RP consists of three ORB's (or four ORB's if branch of RA treated as ORB4): ORB1 (RP proper) originated near wing base, its anterior trace pectinately branched with three branches shallowly forked distally: proximal-most branch (RP1) originated near origin of ORB1, arched; next branch (RP2) originated nearly at wing mid-point, distal-most branch (RP3) originated at distal 1/3 wing length; ORB2, ORB3 originated from distal part of radius, both forked near wing margin. M dividing into MA, MP near wing base; MA slightly sinuate, nearly simple, forked only near wing margin; posterior trace of MP with three pectinate, anteriorly directed branches; proximal-most branch of MP dichotomously branched rather far from wing margin; other two branches shallowly forked. Stem of Cu not preserved, probably dividing into CuA and CuP at wing base; CuA with five distal pectinate branches, each dichotomously forked; CuP dichotomously branched before origin of proximal branch of CuA. AA1 long, very close to CuP nearly for entire length, with three pectinate branches distally. AA2 long, running parallel to hind margin for long distance, with about 20 pectinate branches (many forked), connected with each other by two-six crossveins; AA3 very short. Crossveins very dense over entire wing. Wing fuscous, with two white broad transverse interrupted fasciae (distal one along outer margin; proximal one slightly proximad mid-point of wing), and white patch between these fasciae anteriorly; eye-spot absent. Membrane setae not detected.

*Remarks.* The venation, wing shape and size of *Aetheogramma bistriatum* sp. nov. are very similar to those of *A. speciosum*, but it is distinguished from the latter as indicated in the *Diagnosis*. We re-examined its holotype CNU-NEU-LB2001001PC (Figs. 2A, 3A, B), and found that some character states were incorrectly figured on the original description (Ren & Engel, 2008, figs. 3, 4).

Genus *Cyclicogramma* gen. nov.

Type and only species. *Cyclicogramma rotundum* gen. et sp. nov.

*Derivation of name.* From the Latin *cyclicus* [*-a*, *-um*] (from the Greek *kuklikos*), circular, round, and *gramma*, a traditional ending of generic names in Kalligrammatidae and related families (from the Greek *gramma*, mark, drawing, letter), referring to the circular shape of the hind wing. Gender neuter.

*Diagnosis.* Hind wing less than 30 mm long [ca. 50 mm long in *Aetheogramma*]; two ORB's [three-four ORB's in *Aetheogramma*, *Kalligrammina*]; anterior traces of CuP, AA1, AA2 sigmoid [proximally straight, distally smoothly arched in *Aetheogramma*, *Kalligrammina*]; hind margin convex [straight in *Aetheogramma*, *Kalligrammina*].

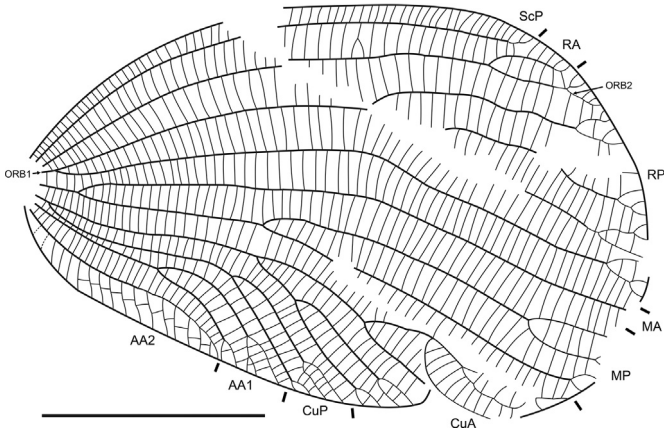


**Fig. 4.** Hind wing venation of *Cyclicogramma rotundum* gen. et sp. nov., holotype CNU-NEU-LB2014009 (converted to standard right view). Scale bar represents 10 mm.

*Remarks*. The hind wings of *Ectopogramma* and *Curtogramma* gen. nov. are unknown. However, all main character states of their forewing venation indicate that their hind wing venation should be significantly different from that of *Cyclicogramma* gen. nov.

*Cyclicogramma rotundum* sp. nov.
Figs. 2C, 4
2002 *Sophogramma plecophlebia* (non Ren and Guo, 1996): Wu, fig. on p. 27.
2012 Aetheogrammatidae: Makarkin et al., fig. 4B.

*Derivation of name.* From the Latin *rotundus* [*-a*, *-um*], round, referring to the shape of the hind wing.

*Type material.* Holotype, CNU-NEU-LB2014009, a complete, well-preserved hind wing.

*Type locality and horizon*. Huangbanjigou, Beipiao City, Liaoning Province, China; Lower Cretaceous (Yixian Formation).

*Description.* Hind wing broadly oval, 28.1 mm long, 18.3 mm wide. Trichosores not detected. Costal space very narrow basally, gradually slightly dilated towards apex. Humeral veinlet crossvein-like. All subcostal veinlets simple, nearly straight, not connecting by crossveins. Pterostigma absent. ScP relatively short. Subcostal space much broader than costal space; with dense crossveins. ScP distally not fused with RA. RA simple. RP consists of two ORB's (or one if distal ORB is treated as posterior branch of terminal fork of RA): ORB1 originated very near wing base, pectinate, with two branches: proximal branch (RP1) originated from ORB1 near its origin, arched, forked distally; distal branch (RP2) originated from ORB1 slightly distad wing mid-point, deeply forked; ORB2 (=RP3) very short. M dividing into MA, MP distad origin of RP1 (proximal branch of ORB1). MA concave, simple, slightly arched. MP deeply forked somewhat proximad wing mid-point; anterior branch deeply forked, posterior branch shallowly forked. Cu dividing into CuA, CuP near wing base, proximad fork of M. CuA slightly sinuate, with four pectinate branches; proximal branch deeply dichotomously forked, other probably simple (distal portion crumpled). CuP sigmoid, dichotomously branched slightly proximad proximal-most branch of CuA. AA1 close to CuP proximally, dichotomously branched similarly to branching of CuP. AA2 long, slightly sigmoid, with many short simple branches connected with each other by one crossvein, forming one series of gradate crossveins (eleven crossveins detected). AA3 not detected, probably very short. Crossveins very dense over entire wing. Wing fuscous, with two white transverse interrupted fasciae (one near middle, other near wing margin) (Fig. 2C). Membrane setae not detected.

Genus *Curtogramma* gen. nov.

*Type and only species. Curtogramma ovatum* gen. et sp. nov.

*Derivation of name.* From the Greek *kurtos*, curved, arched, and *gramma*, a traditional ending of generic names in Kalligrammatidae and related families (from the Greek *gramma*, mark, drawing, letter), referring to strongly arched shape of all principal veins. Gender neuter.

*Diagnosis.* Forewing M forking very far from wing base [relatively close from wing base in *Aetheogramma*, *Ectopogramma*]; MA strongly arched [sigmoid or nearly straight in *Aetheogramma*, *Ectopogramma*].

*Remarks.* Although the forewing of *Kalligrammina* is unknown, its hind wing venation allows concluding that *Curtogramma* gen. nov. is distantly related to *Kalligrammina*.

*Curtogramma ovatum* gen. et sp. nov.
Figs. 5, 6

*Derivation of name.* The specific name is from the Latin *ovatus* [*-a, -um*], oviform, referring to the shape of the forewing.

*Type material.* Holotype, CNU-NEU-LL2014001, a complete, well-preserved forewing.

*Type locality and horizon*. Dawangzhangzi, Lingyuan City, Liaoning Province, China; Lower Cretaceous (Yixian Formation).

*Description.* Forewing broadly oval, 59.4 mm long, 32.3 mm wide. Trichosores not detected. Costal space moderately broad proximally, strongly narrow distally; most dilated at proximal 1/6, gradually narrowed toward base. Humeral veinlet probably crossvein-like. All subcostal veinlets simple, closely spaced, straight; in proximal half slightly inclined to apex, in distal part perpendicular to ScP. No costal crossveins. Pterostigma absent. ScP long, entering margin near wing apex. Subcostal space broad nearly for entire length, somewhat narrowed distally; with dense crossveins. ScP not fused with RA apically. RA distally forked, entering margin at wing apex. RP consists of three ORB's: ORB1 (RP proper) originated very near wing base, with four pectinate branches: proximal-most branch (RP1) originated near origin of ORB1, strongly arched in distal half, shallowly forked distally; other three branches (RP2 to RP4) originated in distal part of wing, slightly arched, dichotomously branched near margin (RP2), other two shallowly forked distally; ORB2, ORB3 originated in distal 3/4 part of wing, shallowly forked distally. M dividing into MA, MP very far from wing base. MA concave, strongly arched, shallowly forked distally. MP strongly arched, with three pectinate, anteriorly directed branches parallel to posterior trace of MP, all distally forked. Stem of Cu not preserved, probably dividing into CuA, CuP at wing base. Both CuA, CuP strongly arched in distal parts, deeply dichotomously branched. AA1 long, strongly arched in distal part, deeply dichotomously branched. AA2 long, parallel to hind margin, pectinate, with ca. 20 mostly simple branches, all connected with each other by one crossvein proximally, two-three crossveins distally. Presumed AA3 short, relatively stout, simple. Crossveins very dense over entire wing. Wing colour pattern unclear, consisting of grey and rust-brown patches for entire wing; eye-spot absent. Membrane setae not detected.

## 4. Discussion

We consider Aetheogrammatidae to include the following five genera from the Mesozoic of Asia: *Ectopogramma* from the Middle Jurassic of Daohugou, China; *Kalligrammina* from the Upper Jurassic of Karatau, Kazakhstan; and *Aetheogramma*, *Cyclicogramma* gen. nov. and *Curtogramma* gen. nov. from the Lower Cretaceous of the Yixian Formation, China. Also, a nearly complete specimen of a new, undescribed taxon possessing long-proboscid siphonate mouthparts is known from the Yixian Formation (see Wu, 2002, fig. on p. 26; Zhang, 2007, fig. on p. 104).

The venation of Aetheogrammatidae is most similar to that of Kalligrammatidae, but distinguished from the latter by the following character states: (1) ScP and RA are widely separated distally (fused in Kalligrammatidae), (2) the distal branches of RP are translocated onto RA in both wings (no branches translocated in most genera of Kalligrammatidae except for a few genera of Kallihemerobiinae in which all branches are translocated), and (3) the costal margin of the hind wing is strongly arched (not or slightly arched in Kalligrammatidae). Aetheogrammatidae share other character states with all or some genera of Kalligrammatidae. The loss of trichosores might also be a diagnostic feature of Aetheogrammatidae. Trichosores are absent in the Early Cretaceous taxa with certainty, and not detected in the Jurassic *Ectopogramma* and

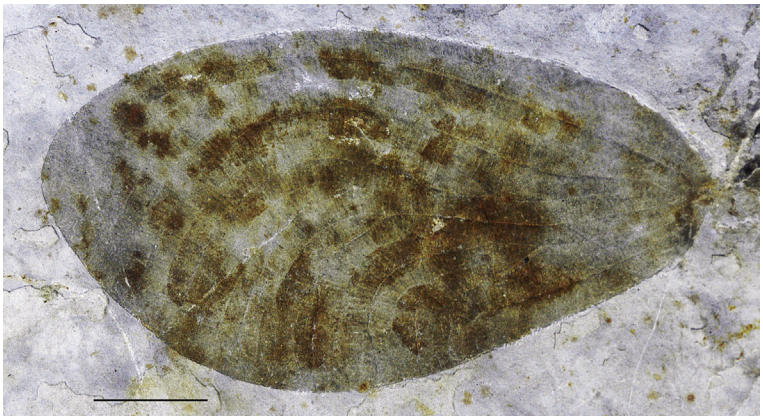

**Fig. 5.** *Curtogramma ovatum* gen. et sp. nov., holotype CNU-NEU-LL2014001 as preserved. Scale bar represents 10 mm.

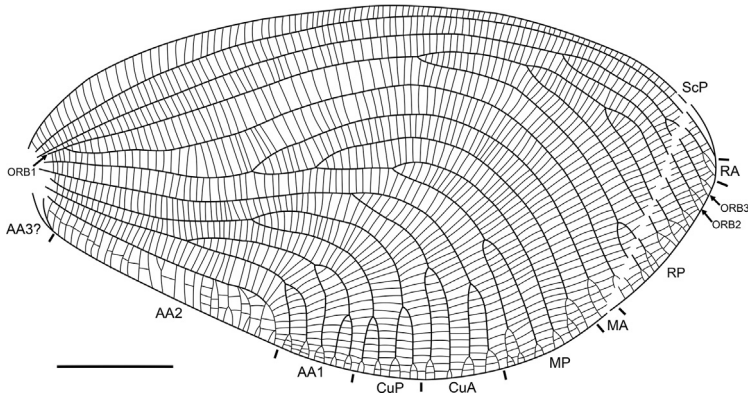


**Fig. 6.** Forewing venation of *Curtogramma ovatum* gen. et sp. nov., holotype CNU-NEU-LL2014001 (converted to standard right view). Scale bar represents 10 mm.

*Kalligrammina*. However, trichosores in Kalligrammatidae are also hardly identified. The absence of an eye-spot in wings of Aetheogrammatidae is also not a diagnostic feature of the family as it is absent in some genera of Kalligrammatidae. Moreover, there are rather clear indications of the presence of a vestigial eye-spot in *Ectopogramma* (Engel et al., 2011, fig. 1). The same pertains to the humeral veinlet: the crossvein-like humeral veinlet of Aetheogrammatidae is also not diagnostic, as such a humeral veinlet is characteristic of most genera of Kalligrammatidae.

The genus *Kalligrammina*, represented by an incomplete hind wing, possesses two diagnostic states of the Aetheogrammatidae (i.e., [1] and [2]), but its costal margin is only partly preserved.

*Ectopogramma* was placed in the separate subfamily Ectopogrammatinae within Aetheogrammatidae (Engel et al., 2011). The authors noted that diagnostic forewing character states of the subfamily are mainly plesiomorphic and widely distributed in kalligrammatid genera (e.g., the presence of distinctive end-twigging and costal crossveins; the subcostal veinlets are strongly bent to apex). Given the more ancient age of *Ectopogramma* compared with other aetheogrammatid genera, it is quite reasonable that this genus is more similar to kalligrammatids. These families are currently considered as sister (Makarkin et al., 2013, fig. 7), but Aetheogrammatidae might be only a specialized branch of Kalligrammatidae (Makarkin et al., 2012).

Recently, the family Kalligrammatidae was divided into five subfamilies: Kalligrammatinae, Kallihemerobiinae, Meioneuritinae, Oregrammatinae and Sophogrammatinae (Yang et al., 2014b).

The family Aetheogrammatidae is similar to Kallihemerobiinae in possessing more than two ORB's (i.e., more than one branch of RP independently originating from R). This phenomenon may be explained by translocations of these branches onto R (formally, the common stem RA+RP). This concept is developed by Béthoux (2007, 2012). He defines translocation as “the fusion of a vein (sector/branch) with another from the origin of the latter, so that there is no visible basal free part of the translocated vein” (Béthoux, 2007, p. 138). In particular, the translocation of the RP branches onto RA represents an example of ‘pectinate fusion’ (Shi et al., 2012). This is most characteristic of Hemerobiidae. Also, the basal-most branch of RP is translocated onto R in most Osmylopsychopidae and some Ithonidae and Dilaridae.

## 5. Conclusions

The three new species described in this paper double those known of the Aetheogrammatidae. This enigmatic family now comprises five genera and six species distributed in Asia (China and Kazakhstan) from the Middle Jurassic to the Lower Cretaceous. The wing venation of two new species of *Curtogramma* gen. nov. and *Cyclicogramma* gen. nov. is particularly remarkable, even within this family, markedly increasing its morphological diversity. In general, the venation of Aetheogrammatidae is derived relative to that of the Kalligrammatidae, indicating that both families are closely related. Given current knowledge, it is hard to determine if they are sister taxa or if the Aetheogrammatidae constitute a specialized branch of the Kalligrammatidae.

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