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An exceptionally well-preserved fossil Kalligrammatid from the Jehol Biota

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A new species of Neuroptera, *Sophogramma lii* sp. nov. is described and illustrated in this paper. This new species is assigned to *Sophogramma* Ren of Kalligrammatidae, mainly based on its humeral recurrent veins, the basal cell present between posterior branch of media at base of wing, etc. The new species is distinguished from all other *Sophogramma* species on the difference of wing venation. This exceptionally well-preserved specimen is recovered from the Yixian Formation, Huangbanjigou, located near Beipiao City, in western Liaoning Province. The genus diagnosis has been emended based on new characters shown in this new species. Based on a summary of localities, distribution and geological ages of all genera and species of the Kalligrammatidae, we suggest that Kalligrammatids might have originated in Eastern Asia, especially in China. Function of the wing pigmentation is discussed briefly.

Kalligrammatidae, Neuroptera, new species, Insecta, Jehol Biota, China

The Kalligrammatidae is an extinct family within Neuroptera. They are a group of rather large neuropterans, and only known by compression fossils from the Middle Jurassic to Early Cretaceous. This paper describes and illustrates a remarkable, new kalligrammatid species from the Yixian Formation, located in Huangbanjigou, Beipiao City, in western Liaoning Province, China. This exceptionally well-preserved specimen with detailed venations of four wings and some body parts provides valuable information to enhance our understanding of kalligrammatids.

Up to now, twelve extinct genera (*Angarogramma* Ponomarenko[1]; *Kalligramma* Walther[2]; *Kalligrammina* Panfilov[3]; *Kalligrammula* Handlirsch[4]; *Lithogramma* Panfilov[5]; *Meioneurites* Handlirsch[6]; *Palparites* Handlirsch[6]; *Sophogramma* Ren & Guo[7]; *Kallihemerobius* Ren & Oswald[8]; *Oregramma* Ren[9]; *Limnogramma* Ren[9]; *Sinokalligramma* Zhang[10]) have been reported from Europe (Germany, Great Britain) and Asia (Kazakstan, Mongolia, Russia and China) (Scudder, 1886[11]; Walther, 1904[2]; Handlirsch, 1906-08, 1919[4,6]; Cockerell, 1928[12]; Martynova, 1947, 1962[13,14]; Panfilov, 1968, 1980[3,5]; Ponomarenko, 1984, 1992[1,15]; Whalley, 1988[16]; Carpenter, 1992[17]; Lambkin, 1994[18]; Ren & Guo, 1996[7]; Jarzenmbowski, 2001[19]; Ren & Oswald, 2002[8]; Ren, 2003[9]; Zhang, 2003[10]; Zhang & Zhang, 2003[20]; Engel, 2005[21]).

The age of the Yixian Formation is still being debated, with the following three opinions presented: (1) the Late Jurassic (Ren et al., 1997[22]; Zheng et al., 2003[23]); (2) transition from the Late Jurassic to Early Cretaceous (Chen et al., 2004[24]; Wang et al., 2005[25]); (3) the Early Cretaceous (Swisher et al., 1999[26]; Zhou et al., 2003[27]). At present, we cannot draw a definite conclusion about its certain age solely based on our current fossil data, because only three *Sophogramma* species were reported from the Yixian Formation (Ren et al., 1996[7]). Here, we tentatively consider it as the Late Ju-

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rassic to Early Cretaceous.

1 Material and methods

The specimen described here was collected from the Yixian Formation. The specimen was examined under a Leica MZ 7.5 dissecting microscope and illustrated with the aid of a drawing tube attachment. Partially magnified images of the specimens were taken under a Nikon SMZ1000. Line drawings were prepared with CorelDraw 12 graphics software. The photographs were taken by Epson Perfection 1650. The holotype (part and counterpart) is deposited in the Key Lab of Insect Evolution and Environmental Changes, College of Life Science, Capital Normal University, Beijing, China (CNUB; Ren Dong, Curator).

Venation abbreviations[28,29]: Wing nomenclature and abbreviations used in the text and figures are as follows: 1A-3A, anal veins; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; f, frenulum; M, media; MA, anterior branch of media; MP, posterior branch of media; R, radius; R1, first branch of radius; Rs, radial sector; pt, pterostigma; C, costa; Sc, subcosta.

2 Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus,1758

Family Kalligrammatidae Handlirsch, 1906

Genus *Sophogramma* Ren, 1996

Type species. *Sophogramma papilionacea* Ren, 1996

Included species. *Sophogramma plecophlebia* Ren, 1996, *Sophogramma eucalla* Ren, 1996, and *Sophogramma lii* sp. nov. described below, all from the Yixian Formation, China.

Revised diagnosis. Forewing eye-spot absent. Humeral recurrent veins (Vr) present. All costal veinlets sinuate and forked. R_s with about 12—15 primary branches, many of them deeply forked. MA with 5 parallel pectinate branches. A basal cell (bc) present between MP_1 and MP_2 at base of wing. MP with basal fork far proximal and with no additional forkings before vicinity of wing margin. CuA pectinately forked and terminated at posterior margin of wing. CuP single, with a few branches near wing margin. 1A running parallel to CuP for a long distance and with numerous branches.

Hind wing S_c and R_1 both curved posteriorly. R_1 simple; R_s with no less than 14 branches, and each sequentially forked. MA forked earlier than all branches of R_s. MP dichotomously forked near middle of wing, with two pectinately forked branches, no basal cell (bc) between MP_1 and MP_2. CuA with about 4 branches. CuP approximately parallel with CuA at posterior part of wing, with no less than 8 dichotomous pectinate branches. 1A with at least 8 pectinate branches; 2A dichotomously forked.

Remarks. The new species *Sophogramma lii* sp. nov. can be attributed to the genus *Sophogramma* based on the above-mentioned characters (Ren, 1996[7]).

Sophogramma lii sp. nov. (Figures 1—4)

Etymology. The specific name of *lii* is dedicated to Mr. Li Shichang for his discovery of this specimen and his contribution to fossil research.

Holotype. A well-preserved part and counterpart with complete forewings, hind wings and incomplete body (with gender unknown), registration No. CNU-NEU-LB2008001P and C (Figure 1).

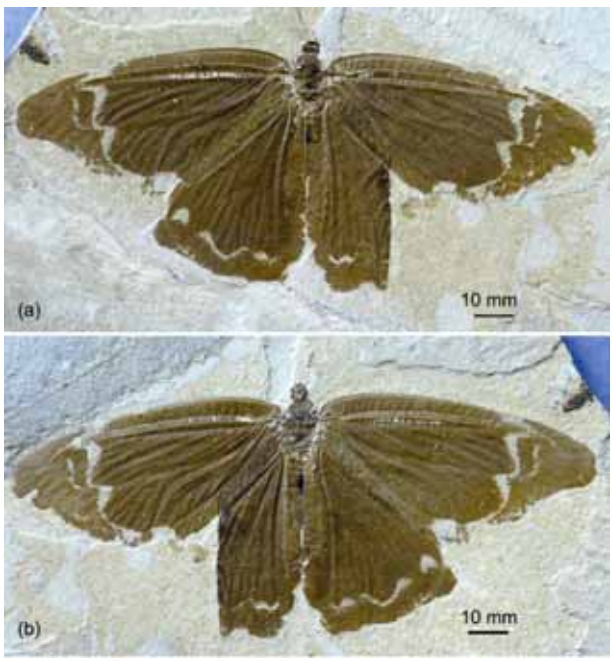

Figure 1 *Sophogramma lii* sp. nov., holotype: (a) and (b), photograph of part and counterpart, No. CNU-NEU- LB2008001P and C.

Type locality and horizon. Yixian Formation, the Late Jurassic to Early Cretaceous, Huangbanjigou, Beipiao City, Liaoning Province, China.

Description. Head partially preserved in dorsal view. Only left antenna partly preserved with 9 mm, probably filiform, at least 28 segments preserved, scape and pedicel missing. There are two distinct torulus, left compound eyes visible. The exterior of its cervix and

thorax blurry. Part of abdomen missing, only 4 segments discernable. Thoracic legs absent, only prothorax coxa can be seen. Both forewings and hind wings almost complete, and with undulating lighter-colored stripes on the four wings. Wing span at least 153 mm. Forewing length 74 mm, width 33 mm (estimated). Hind wing about 52 mm long, 39 mm wide (at wing mid-point). Line drawing of the holotype is shown in Figure 2.

Right forewing: approximately obtuse triangular. Inner margin and outer margin partly missing, no eye-spot markings. Vr obviously present, most of costal crossveins curving and forking, pterostigma remarkable from the first crossvein. S_c and R_1 fused apically and thence curved posteriorly to enter margin before wing apex. R_s with 12 original branches, except for the first one, the other branches forked deeply, the first and the second branches (R_{S1}, R_{S2}) forked later than MA. MA with 3 flexual and pectinate branches, the forked region expansive and forked deeply. MP forked near the wing base, MP_1 and MP_2 forming a loop or cell (bc) basally. CuA pectinately forked, with 4 main branches at least, twig partly absent. CuP simply bifurcated apically. 1A running parallel to CuP for a long distance and with 8 pectinately branches. 2A appearing dichotomously forked. 3A simple. Right forewing venation is shown in Figure 3.

Left hind wing: short and broad, nearly acute triangular. Wing outer margin more or less absent, most costal margin overlapped by forewing's anal region. C, S_c and crossveins between them poorly determinable. Anal veins overlapped with body, borderline unclear. S_c and R_1 both curved posteriorly, and then respectively entering wing margin. R_1 simple, only with two branches. R_s with no less than 14 branches, and each sequentially

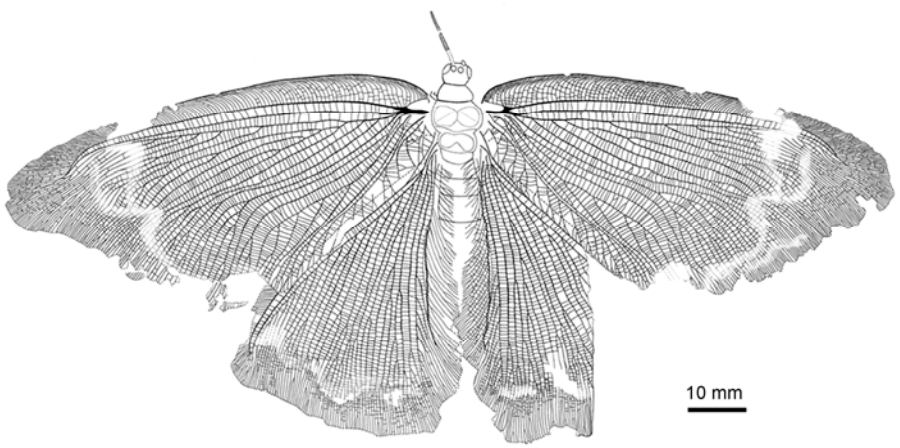

Figure 2 *Sophogramma lii* sp. nov., line drawing of holotype, No. CNU-NEU-LB2008001P.

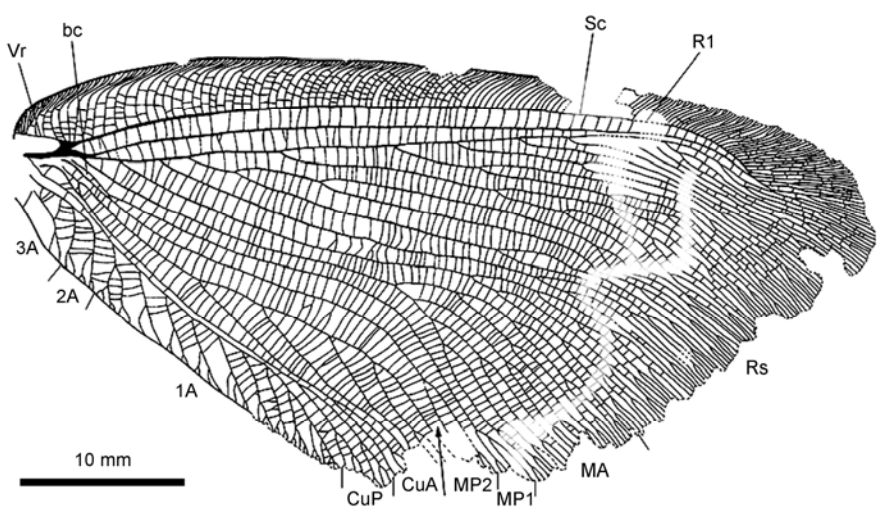

Figure 3 *Sophogramma lii* sp. nov., line drawing of right forewing.

forked. MA forked earlier than all branches of R_s, with two deeply forked branches. MP dichotomously forked near middle of wing, with two pectinately forked branches, no basal cell (bc) between MP_1 and MP_2 at base of wing. CuA with 4 branches, pectinately forked at posterior wing. CuP approximately parallel with CuA at posterior part of wing, with no less than 8 dichotomous pectinate branches. 1A unsurely with at least 8 pectinate branches; 2A distinctly dichotomous forked, basal missing; 3A missing. Left hind wing venation is shown in Figure 4.

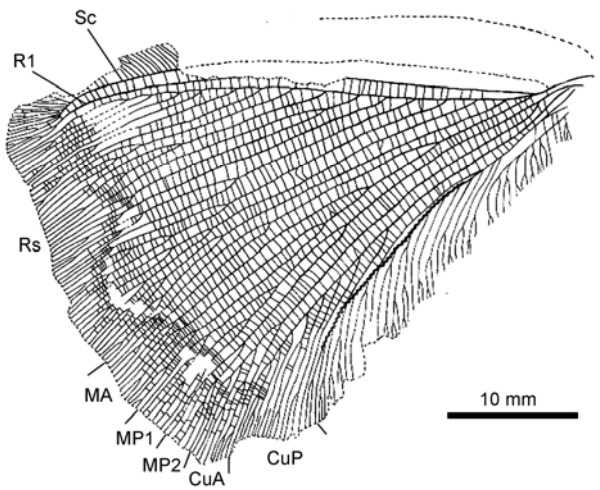

Figure 4 *Sophogramma lii* sp. nov., line drawing of left hind wing.

Comparison. The new species *S. lii* sp. nov. is similar to *S. papilionacea* in forewing (*S. papilionacea* preserved without hind wings, the same for the other two species): the new species has R_s with 12 original branches, except for the first one, all other branches forked deeply; the R_s 12 branches of *S. papilionacea* all biforked. R_{s1} and R_{s2} of the new species forked later than MA; but those of *S. papilionacea* forked at the wing basal, much earlier than MA. *S. Lii*'s 1A has 8 pectinately branches; but *S. papilionacea*'s 1A has only 6 branches.

S. lii sp. nov. resembles *S. plecophleboidis* in forewing, but the new species has pterostigma remarkable from the first crossvein; *S. plecophleboidis* pterostigma is not obvious at costal margin, only appears at the anterior part. CuA of the new species has 4 branches; but that of *S. plecophleboidis* has only one branch.

S. lii sp. nov. is allied to *S. eucalloidis* in forewing, but the new species has R_s with 12 branches; *S. eucalloidis* R_s with 15 branches. The new species R_{s1} forked later than MA; *S. eucalloidis* R_{s1} and MA forked simultaneously. The first and second branches of R_s of the new species forked lately; R_s branches of *S. eucalloidis* all forked earlier except for the first one. The new species has CuA with at least 4 branches; *S. eucalloidis* has CuA with no less than 7 pectinate branches.

3 Discussion

Hitherto, the new species *S. lii* sp. nov. is the most complete and beautiful kalligrammatid fossils[1–21] described, for its extended four wings and partial body. The variability between the left and right wings[30] in same kalligrammatid individual has not been recorded before. In the new species *S. lii* sp. nov., left wings and right wings do not show distinct differences, except that R_{s3} of the left forewing has more branches than those of the right forewing.

Based on current fossil evidence, Kalligrammatidae is thought to be an extinct group with unique wing venation different from other groups. By the Middle Jurassic and possibly into the Early Cretaceous, there was a remarkable increase in the diversity of this group in northeastern China. As afore-mentioned, twelve genera and twenty-six species have been described up to date and summarized in Table 1, and localities and distribution of these species are shown on a world map in Figure 5. From the distribution map, we can see that most of the fossil species, about 73% of species and 83% of genera, were found in Asia during the geological age of the Middle Jurassic to the Early Cretaceous. Europe has only five species and three genera during the geological age of the Late Jurassic or the Early Cretaceous. Only in China, 3 genera and 3 species have been described with

Table 1 Summary of localities, distribution and geological ages the Kalligrammatid genera and species

Distribution	Genus(Number of species)	Geological Age(Formation)
China	*Kalligramma* (2), *Kallihemerobius* (1), *Limnogramma* (1), *Oregramma* (1), *Sinokalligramma* (1), *Sophogramma* (4)	Middle Jurassic, Late Jurassic to Early Cretaceous (Haifanggou, Jiulongshan, Yixian)
Kazakhstan	*Kalligramma* (4), *Kalligrammina* (1), *Kalligrammula* (1), *Lithogramma* (1), *Meioneurites* (3)	Late Jurassic (Karabastau)
Germany	*Kalligramma* (1), *Kalligrammula* (1), *Meioneurites* (1), *Palparites* (1)	Late Jurassic (Solnhofen)
Russia	*Angarogramma* (1)	Late Jurassic (Uda)
England	*Kalligramma* (1)	Early Cretaceous (Wadhurst Clay)
Monglia	*Kalligrammula* (1)	Early Cretaceous (Shine-Khuduk)

Figure 5 Sketch map showing the distribution of the Kalligrammatid species.

the earliest geologic age of the Middle Jurassic. Therefore, we propose that Kalligrammatid might have originated in Eastern Asia, most likely in China.

Based on the fossils found in northeastern China, associated with some aquatic beetles, freshwater conchostracans[31], salamanders[32], dinosaurs[33], and paleobotanical data from fossil spores, pollen and plants[34], we propose that the environment of northeastern China must have been very warm and humid during that age with rich diversity of species existing in the ecosystem.

Kalligrammatids were the "butterflies-like lacewings" of the Jurassic. Their densely setose, patterned wings, bodies and long palpi gave them the superficial appearance of large moths or butterflies, despite occurring 60—90 million years before the first papilionoid fluttered. Kalligrammatids were apparently rather diverse, with numerous genera and species occurring in the Middle Jurassic to the Early Cretaceous faunas of Central Asia and Europe. The large, broad wings were sometimes marked with distinct patterns, most commonly with eyespots similar to those found on large moths and fulgoroid plant hoppers, that flash them when startled, presumably to mimic vertebrate eyes[35].

The new species has undulating lighter-colored stripes on all four wings (Figures 1—4), the same as those found on a forewing of *S. papilionacea*[7]. It should be a type of special wing pigmentation, not caused by poor preservation or weathering. It's nearly the same as wing pigmentation of living moths and butterflies. It might mimic some other poisonous or unpalatable species to avoid being eaten[36]. Also, there are many types of wing colour patterns in neuropterans which might give some indication of their living environment[37–40]. It is proposed that the stripes on the wings and outer wing margin in our fossil were used to mimic some plant growth at riparian situations or to evade natural enemies, but that wound be pure speculation[41–44]. Certainly, these hypotheses need more fossil data and studies to elucidate in the future. We hope these information could give some help to speculate the environment of the time.

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