

Two New Species of *Kalligramma* Walther (Neuroptera: Kalligrammatidae) From the Middle Jurassic of China

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ABSTRACT Two new fossil species of *Kalligramma* Walther (Neuroptera: Kalligrammatidae) are described from the Middle Jurassic locality at Daohugou, Inner Mongolia, China: *Kalligramma elegans* n. sp. and *Kalligramma albifasciatum* n. sp. The subcosta anterior wing vein is found in both species. *K. albifasciatum* n. sp. is remarkable by its forewing color pattern in having the broad white transverse fascia through wing, hitherto unknown in the genus. *Kalligramma turatanovae* Martynova is transferred to *Huiyingogramma* Liu et al., n. sit. A new diagnosis of the genus *Kalligramma* is provided (amended from Panfilov 1968).

KEY WORDS Neuroptera, Kalligrammatidae, Jurassic, Daohugou, China

The remarkable insects of the Mesozoic family Kalligrammatidae are large, butterfly-like neuropterans. They are assumed to have fed on pollen of the generative organs of gymnosperms (Zherikhin 1978, 1980; Rasnitsyn 1980) or possibly even on plant fluids (secretions and nectar accessible from reproductive organs, ovulate cones), judging from their long-proboscid siphonate mouthparts (Labandeira 2010). However, some authors consider them to have been predators (e.g., Fang et al. 2010).

Nineteen kalligrammatid genera (excluding *Kalligrammina* Panfilov, 1980) and 41 species have been described from the Middle Jurassic to Early Cretaceous of Eurasia (China, Mongolia, Kazakhstan, Germany, and the United Kingdom) and Brazil (Walther 1904; Handlirsch 1906–1908, 1919; Martynova 1947; Panfilov 1968, 1980; Ponomarenko 1984, 1992; Lambkin 1994; Ren and Guo 1996; Jarzembowski 2001; Ren and Oswald 2002; Ren 2003; Zhang 2003; Zhang and Zhang 2003; Engel 2005; Makarkin et al. 2009; Yang et al. 2009, 2011; Jepson et al. 2012; Liu et al. 2014; Yang et al. 2014). In addition, unnamed kalligrammatids have been reported from the Early Cretaceous of the United Kingdom (Jepson et al. 2009, 2012), Transbaikalian Russia (Makarkin 2010), and China (Yang et al. 2014), and the Middle Jurassic of China (Yang et al. 2014).

Kalligramma Walther, 1904 is the type genus of the family and most speciose kalligrammatid genus. Hitherto,

it contained 10 species described from the Middle Jurassic to Early Cretaceous of Eurasia (however, *Kalligramma? roycrowsoni* Jarzembowski is only tentatively assigned). The only diagnosis of the genus was provided by Panfilov (1968), but it is obsolete for the most part and was written in Russian. Here, we describe two new species from the Middle Jurassic of Daohugou, Inner Mongolia, China, and provide a new diagnosis of the genus. The beautifully preserved forewings of both of these specimens show the presence of the subcosta anterior vein, hitherto unknown in the genus. The other new species, *Kalligramma albifasciatum* n. sp., is remarkable for its distinctive forewing color pattern, with a broad white transverse fascia across the wing, hitherto unknown in the genus.

Materials 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; Dong Ren, Curator). These insect-bearing beds are here considered as belonging to the Jiulongshan Formation and dated Middle Jurassic, Bathonian to Callovian (Yang et al. 2012).

Specimens were examined using a Leica MZ12.5 dissecting microscope (Leica Microsystems, Wetzlar, Germany), and illustrated with the aid of a drawing tube and software CorelDraw 12 (Corel Cooperation, Ottawa, Canada) and Adobe Photoshop CS3 (Adobe Systems Inc., San Jose, CA). Specimens were photographed by Nikon D100 digital camera (Nikon, Tokyo, Japan), and a Leica M165C stereomicroscope (Leica Microsystems, Wetzlar, Germany) was used to resolve details.

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We use the venational terminology of Kukalová-Peck and Lawrence (2004) in the interpretation of Yang et al. (2012). Terminology of anal veins in general follows that applied to other Neoptera (see details in Discussion). Below, we provide a comparative list of abbreviations used by us and in the traditional terminology (*sensu* Wootton 2003) because our terminology is unknown to many entomologists, who deal primarily with extant taxa. Terminology of wing spaces and details of venation (e.g., subcostal veinlets, traces) follow Oswald (1993). Further, we use the "oblique radial branches" (ORB) concept of Oswald (1993) to designate several branches of the radius posterior (RP) that independently originate from the radius in the forewing of Kalligrammatidae, Hemerobiidae, and some other Neuroptera families. We designate all RP branches successively from the wing base: RP1 (=ORB1) is the proximal-most branch of RP; RP2 is the second branch of RP (and the proximal-most branch of ORB2); CuA1 is the proximal-most branch of CuA.

Venational abbreviations (those used in the traditional terminology in parentheses): AA1 to AA3 (=1A to 3A, first to third anal veins), first to third anterior anal veins; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; RA (=R1, first branch of radius), anterior radius; RP (=Rs, radial sector), posterior radius; RP1 (=Rs1), proximal-most branch of RP (=Rs); RP2 (=Rs2), branch of RP distad RP1 (=Rs1); ScA, subcosta anterior (no analog in the traditional terminology); ScP (=Sc, subcosta), subcosta posterior.

Systematic Paleontology

Order Neuroptera L., 1758

Family Kalligrammatidae Handlirsch, 1906

Genus *Kalligramma* Walther, 1904

Type Species. *Kalligramma haeckeli* Walther, 1904, by monotypy.

Diagnosis. (Amended from Panfilov 1968.) May be separated from other kalligrammatid genera by combination of following wing character states: one eye spot present in both fore- and hind wings (absent in *Sophogramma* Ren et Guo, 1996; *Protokalligramma* Yang et al., 2011); in forewing, humeral veinlet not recurrent, simple (strongly recurrent, branched in *Sophogramma*, *Protokalligramma*, *Huiyingogramma* Liu et al., 2014); subcostal veinlets mainly forked (all simple in *Oreogramma* Ren, 2003, *Abriogramma* Yang et al., 2014); two ORBs (numerous ORBs in *Kallihemero-bius* Ren et Oswald, 2002, *Apochrysogramma* Yang et al., 2011); branches MP pectinate anteriorly directed (dichotomous in *Sophogramma*; *Protokalligramma*; *Huiyingogramma*); in hind wing, ScP and RA fused apically (separated in *Sinokalligramma* Zhang, 2003); CuP forked distally (proximally, near its origin in *Limnogramma* Ren, 2003; *Abriogramma*, *Sinokalligramma*).

Species Included. Eleven to 12 species: *Kalligramma jurarchegonium* Zhang et Zhang, 2003 from the Middle Jurassic of Yujiagou (China, Liaoning Province); *Kalligramma paradoxum* Liu et al., 2014, *Kalligramma brachyrhynchum* Yang et al., 2014, *Kalligramma circularium* Yang et al., 2014, *Kalligramma elegans* n. sp., and *K. albifasciatum* n. sp. from the Middle Jurassic (Bathonian–Callovian) of Daohugou (China, Inner Mongolia Province); *Kalligramma haeckeli* from the Late Jurassic (early Tithonian) of Solnhofen (Germany); *Kalligramma multinerve* Panfilov, 1968, *Kalligramma flexuosum* Panfilov, 1968, and *Kalligramma sharovi* Panfilov, 1968 from the Late Jurassic (Oxfordian–Kimmeridgian) of Karatau (Kazakhstan); *Kalligramma liaoningense* Ren et Guo, 1996 from the Early Cretaceous (Barremian) of Huangbanjigou (China, Liaoning Province; Yixian Formation); *Kalligramma?* *roycrowsoni* Jarzembowski, 2001 from the Early Cretaceous (Wealden) of Tonbridge (Kent, the United Kingdom) (Walther 1904, Panfilov 1968, Ren and Guo 1996, Jarzembowski 2001, Zhang and Zhang 2003, Liu et al. 2014, Yang et al., 2014).

Comments. "*Kalligramma*" *turutanovae* Martynova, 1947 from the Late Jurassic of Karatau is currently considered to belong this genus (Liu et al. 2014, Yang et al. 2014). Earlier, we assumed that this species and an unnamed species from same locality illustrated under this name (Ponomarenko 2002, Fig. 254) belong to some other (undescribed) genus (Yang et al. 2011). Subsequently, the monotypic genus *Huiyingogramma* was described from the Middle Jurassic locality of Daohugou (Liu et al. 2014); all main character states of these Karatau species are well-concordant with those of *Huiyingogramma*, i.e., the well-developed recurrent veinlet is present; MP, CuA, CuP, and AA1 are dichotomously branched; and RP1 originates from RP (not R before the origin of RP). Therefore, we consider "*K.*" *turutanovae* as belonging to this genus: *Huiyingogramma turutanovae* (Martynova 1947), n. comb.

The generic affinity of *K.?* *roycrowsoni*, known from a small wing fragment containing an eye spot (Jarzembowski 1984, 2001), is provisional.

Key to Species of the Genus *Kalligramma*

(*K.?* *roycrowsoni* is not included because of its fragmentary nature)

1. Forewings (ovate wing; CuA convex) . . . 2
Hind wings (wide subtriangular wing;
CuA concave) 8
- 2.(1). White transverse band (fascia) through
wing present *K. albifasciatum*
White transverse band absent 3
- 3.(2). Proximal part of intracubital space (between
CuA and CuP) very narrow,
nearly as wide as mediocubital space
(between CuA and MP) *K. haeckeli*
Proximal part of intracubital space broad,
conspicuously wider than mediocubital
space 4



Fig. 1. *Kalligramma elegans* n. sp., holotype CNU-NEU-NN-2013005PC (part). Scale bar, 10 mm.

- 4.(3). MP with two branches originating proximal to CuP1; proximal part of wing very dark *K. multinerve*
MP with three to five branches originating proximal to CuP1 5
- 5.(4). One gray ring around central dark spot in eye spot *K. brachyrhynchum*
Two–three gray rings around central dark spot in eye spot 6
- 6.(5). Distance between inner and outer gray rings proximal eye spot great, approximately equal to diameter of central dark spot *K. circularium*
Distance between inner and outer gray rings proximal eye spot very small, much less than diameter of central dark spot 7
- 7.(6). Distance between three gray rings distad eye spot approximately equal to their widths *K. elegans*
Distance between three gray rings distad eye spot much greater than their widths *K. paradoxum*
- 8.(1). Length of wing along posterior trace of MP considerably less than its width from apex to hind margin (perpendicular to posterior trace of MP) *K. sharovi*
Length of wing along posterior trace of MP at least not less than its width from apex to hind margin (perpendicular to posterior trace of MP) 9
- 9.(8). Costal margin in distal part clearly convex; length of wing along posterior trace of MP and its width from apex to hind margin (perpendicular to posterior trace of MP) approximately equal. *K. jurarchegonium*
Costal margin in distal part straight or concave; length of wing along posterior trace of MP greater than its width from apex to hind margin (perpendicular to posterior trace of MP) 10

- 10.(9). Costal margin in distal part clearly concave *K. flexuosum*
Costal margin in distal part straight 11
- 11.(10). Proximal branch of MP dichotomously branched *K. liaoningense*
Proximal branch of MP pectinately branched *K. haeckeli*

***Kalligramma elegans* n. sp.**

(Figs. 1, 2A, and 3A)

Holotype. CNU-NEU-NN-2013005PC (part, counterpart), housed in the collection of CNUB, China. An incomplete, beautifully preserved forewing. Daohugou locality, Inner Mongolia, China; Middle Jurassic (Jiulongshan Formation).

Etymology. The specific epithet is derived from the Latin *elegans*, elegant, graceful, fine.

Diagnosis. Most closely related to *K. paradoxum*, but may be separated from it (and other species of *Kalligramma*) by structure of the eye spot: distance between inner and outer gray rings proximal eye spot much less than diameter of central dark spot, and distance between three gray rings distad eye spot approximately equal to their widths.

Description. Forewing 75 mm in length, 41.5 mm in width as preserved (estimated complete length ≈90 mm; width ≈42–42.5 mm). Costal space moderately broad; slightly narrowed basally. ScA well-developed, strongly curved terminating on ScP (Fig. 3A). Humeral veinlet simple, not recurrent (apical part only slightly curved to wing base), stout. Two basal subcostal veinlets stout; other conspicuously thinner, strongly inclined to wing apex; most subcostal veinlets once to twice forked, connected by numerous crossveins. Subcostal space moderately broad; with dense crossveins, but more widely spaced than in radial space. RA space markedly narrower than subcostal space; with dense crossveins. RP originates near wing base, with two ORBs: ORB1 (RP1) rather deeply forked (within eye spot); ORB2 (RP proper) with 12 preserved branches, dichotomously

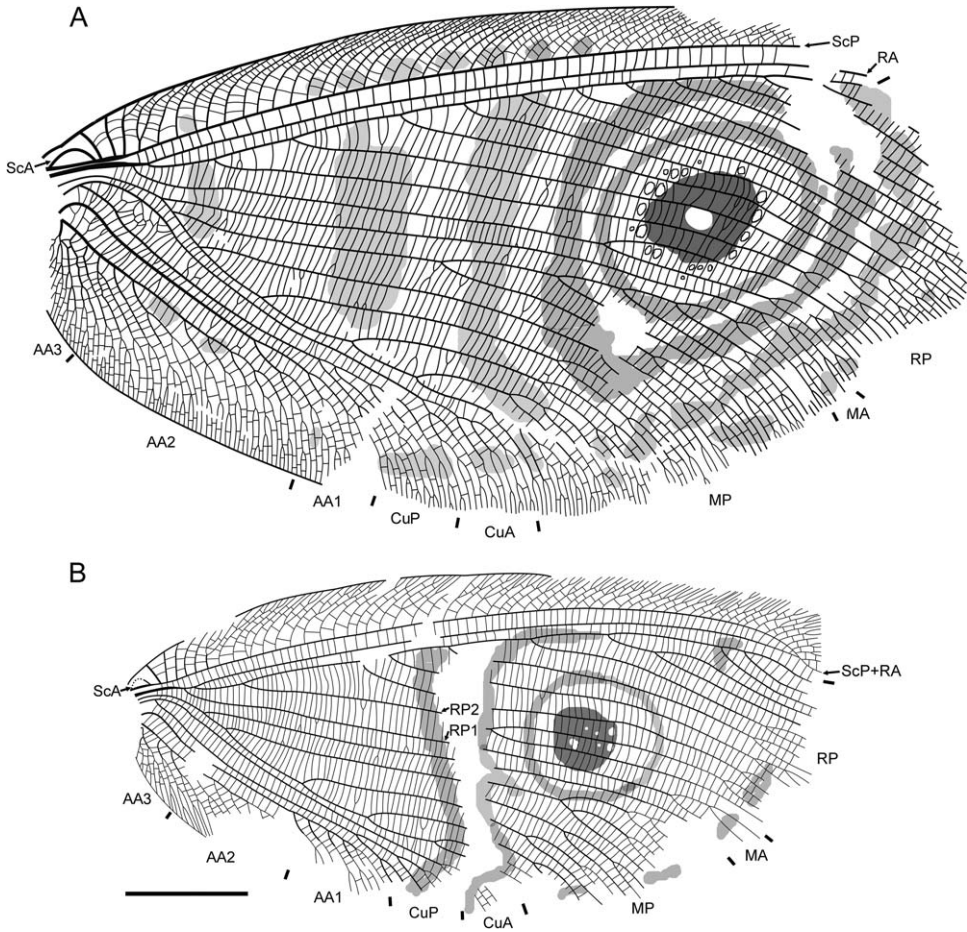


Fig. 2. Drawings of *Kalligramma* forewings. (A) *K. elegans* n. sp., holotype CNU-NEU-NN-2013005PC. (B) *K. albifasciatum* n. sp., holotype CNU-NEU-NN-2013006PC. Scale bar, 10 mm (both to scale).

branched distally. M far apart from R basally; dividing into MA, MP well proximad origin of RP2. MA strongly concave, nearly straight for almost entire length, shallowly, pectinately branched distally. MP occupying relatively large area, its posterior trace with five pectinate branches directed anteriorly; proximal-most branch (MP1) with four-five pectinate branches directed posteriorly; other branches of MP rather shallowly dichotomously branched. Stem of Cu very short (Cu dividing into CuA and CuP at wing base). CuA strongly convex, with three pectinate branches distally, all dichotomously branched. CuP slightly sigmoid basally, concave, with three long pectinate branches distally, all dichotomously branched. AA1 long, dichotomously branched. AA2 long, pectinately branched, with nine long dichotomously forked branches. AA3 short, incompletely preserved. Crossveins very dense over entire wing; many crossveins abnormally forked in radial, intracubital, intraanal spaces; two crossveins abnormally fused medially (three cases) or connected by additional crossvein (five cases). Costa anteriorly covered with very short, dense hairs; thinner veins, crossveins covered with rather rare, longer hairs arranged in one line. Membrane hairs pres-

ent, very dense in costal space, sparse in other wing areas. Eye spot well-developed, consisting of blackish central structure, several smaller brown rounded structures, grayish rings. Central blackish structure ovoid in shape, 10 mm per 7 mm, with one brown spot in center (≈ 2 mm in diameter) and many (≈ 20 in number) smaller brown or pale spots differing in size (0.2 to 1 mm in diameter), forming ring around central structure. Around this structure, three ovoid grayish rings: (1) inner ring ovoid, narrow (1 to 1.5 mm in width); between its inner border and blackish structure ≈ 3 -mm distance; (2) intermediate ring broader, 2 to 3 mm anteriorly, 4 to 5 mm posteriorly; between its inner border and first ring 1 to 2 mm distance; (3) outer ring incomplete, indistinct, most broad. Rest of wing color pattern consists of several grayish patches and spots over wing.

Kalligramma albifasciatum n. sp.

(Figs. 2B, 3B, and 4)

Holotype. CNU-NEU-NN-2013006PC (part, counterpart), CNUB, China. An incomplete, rather poorly

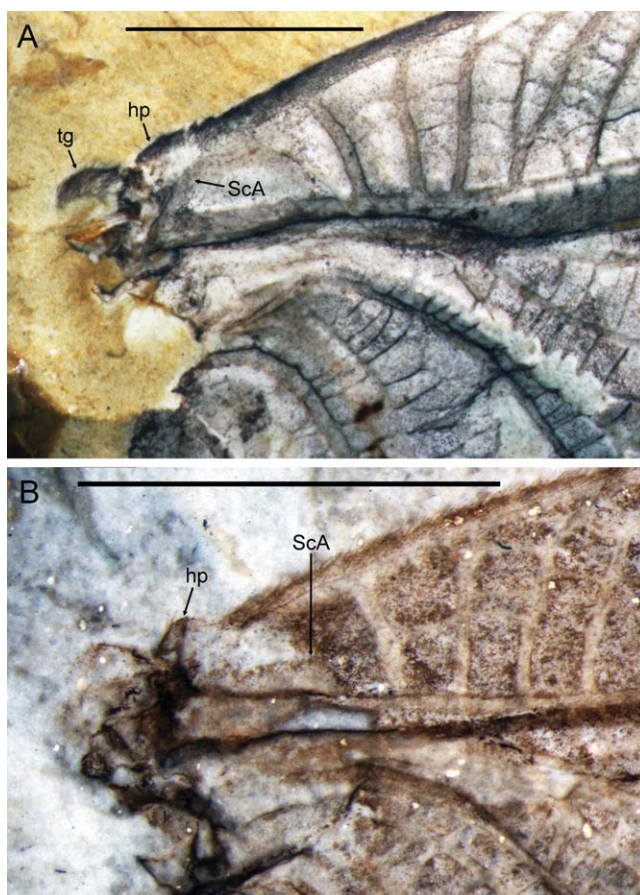


Fig. 3. Basal part of *Kalligramma* forewings. (A) *K. elegans* n. sp., holotype CNU-NEU-NN-2013005PC. (B) *K. albifasciatum* n. sp., holotype CNU-NEU-NN-2013006PC. Scale bars, 5 mm. Abbreviations: hp, humeral plate; tg, tegula. (Online figure in color.)

preserved forewing, Daohugou locality, Inner Mongolia, China; Middle Jurassic (Jiulongshan Formation).

Etymology. The specific epithet is derived from the Latin *albus* (-a, -um), white, and *fasciatus* (-a, -um), banded, striped, referring to the white transverse band (fascia) in the forewing.

Diagnosis. May be separated from other species of the genus by its white transverse fascia across most of forewing mid-length.

Description. Forewing 57 mm in length, 28 mm in width as preserved (estimated complete length ≈ 62 –63 mm; width ≈ 29 mm). Costal space moderately broad; narrowed basally. ScA poorly preserved, configured as strongly curved vein terminating on ScP (Fig. 3B). Humeral veinlet simple, not recurrent, stout. Basal subcostal veinlets stouter than other, strongly inclined to wing apex; most subcostal veinlets once to twice forked (except four basal-most), connected by numerous crossveins. Subcostal space moderately broad; with closely spaced crossveins. ScP, RA fused distally. RA space markedly narrowed than subcostal space; with dense crossveins. RP origins near wing base, with two ORBs: ORB1 (RP1) simple

for most length, only distally branched; ORB2 (RP proper) with eight branches proximal to fusion of ScP, RA; RP2 rather deeply forked proximad eye spot; RP7 very deeply forked; other branches of RP not forked until marginal dichotomous branching. M far apart from R basally; dividing into MA, MP well proximad origin of RP2. MA nearly straight for almost entire length. MP occupying relatively large area, its posterior trace with four pectinate branches directed anteriorly; three proximal branches (MP1–MP3) dichotomously branched at level of central blackish structure of eye spot. Stem of Cu very short (Cu dividing into CuA, CuP at wing base). CuA strongly convex, with few distal branches. CuP slightly incurved, with three long pectinate branches distally, proximal-most deeply forked. AA1 long, pectinately branched with five branches. AA2 long, pectinately branched, with at least seven long branches; three proximal-most branches dichotomously forked. AA3 short, dichotomously branched. Crossveins very dense over entire wing; eight of these in radial, intramedial spaces abnormally forked. Costa at anterior margin covered with comparatively long, dense hairs; hairs on ScP, RA short, dense; on thinner veins, cross-

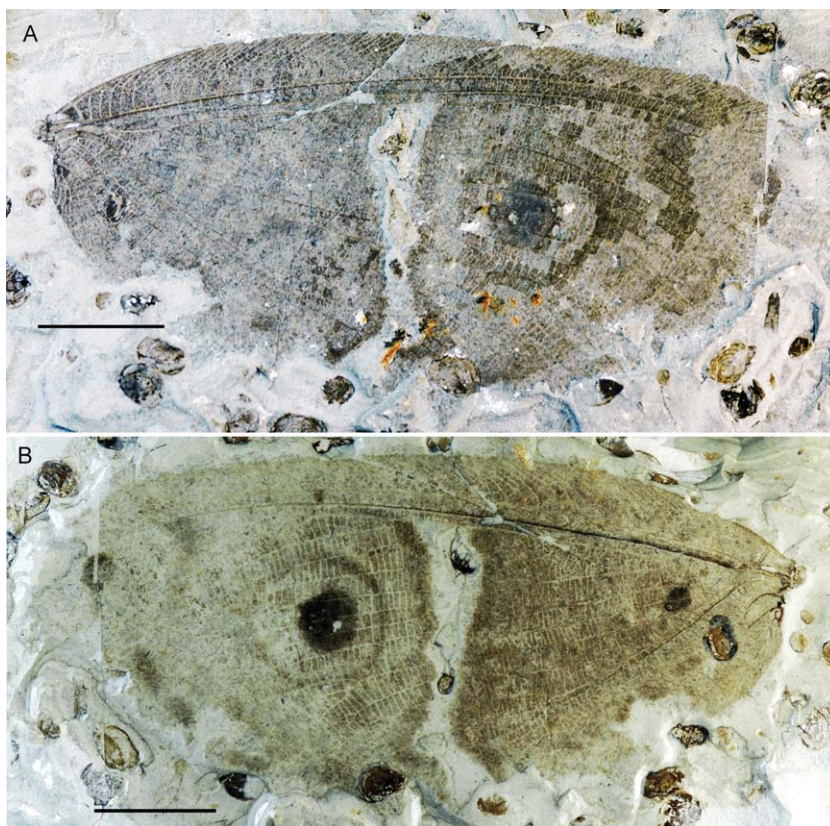


Fig. 4. *Kalligramma albifasciatum* n. sp., holotype CNU-NEU-NN-2013006PC. (A) part (dry). (B) counterpart (wetted with ethanol). Scale bars, 10 mm. (Online figure in color.)

veins hairs not detected. Membrane hairs not preserved. Wing color pattern consists mainly of white transverse band (fascia) and eye spot. Eye spot well-developed, consisting of blackish central structure and one brownish ring. Central dark structure slightly ovoid in shape (4.5 per 5 mm) with several (≈ 6 in number) smaller pale spots differing in size (0.2 to 0.8 mm in diameter) within it. Around this structure, one brownish ring nearly round in shape, ≈ 11 mm in diameter, very narrow (0.5 to 1 mm wide); between its inner border and blackish structure 2 to 4 mm distance. White transverse fascia 2 mm to 4 mm broad located almost medially, rather broadly bordered by brownish. Wing proximad fascia brownish; rest of wing color pattern consists of several brownish spots in distal part of wing.

Discussion

The beautifully preserved forewing venation of these new species of *Kalligramma* (especially *K. elegans* n. sp.) allows consideration of some of its character states in more detail, particularly with regards to homology and terminology. The relatively distinct ScA is detected in both new species of *Kalligramma* (Fig. 3). ScA is well developed only in few groups of Neuroptera, usually in those taxa which have the cos-

tal space dilated basally, e.g., Hemerobiidae, Parakse-
neuridae, the kalligrammatid genus *Protokalligramma*. However, in some Nymphidae (including the oldest known species from the Middle Jurassic), this vein is distinct, although the costal space in these nymphids is basally narrowed (Makarkin et al. 2013). The same is characteristic of these new species of *Kalligramma*. It is quite possible that ScA is present in all Kalligrammatidae; however, so far it has not been detected, or possibly simply overlooked. In all taxa of Neuroptera, the ScA (when present) is similarly configured, as a short vein structure terminating on ScP.

The RP in this genus consists of two branches which originate separately from the radius: the first (proximal-most) branch of RP (RP1) originates proximad RP proper; RP proper is long and pectinately branched. Oswald (1993) used the term ORB to designate these separate branches of RP ("Rs"). Such a configuration of RP as found in *Kalligramma* is also characteristic of many other genera of Kalligrammatidae (e.g., *Oregramma* Ren, 2003, *Sinokalligramma* Zhang, 2003, *Sophogramma* Ren and Guo, 1996), Osmolyptochopidae, and some Ithonidae and Dilaridae. Our RP1 is identified as MA by many authors (discussed by Makarkin et al., 2009). Moreover, Shi et al. (2012) stated that our RP1 "can only be MA" (p. 623). However, the beautifully preserved forewing of *Kal-*

ligramma elegans n. sp. shows that R and M are running basally as absolutely separate veins to the wing base. This condition is characteristic of all extant Neuroptera with generalized venation (e.g., Ithonidae, Osmyliidae) irrespective of whether RP is represented by a single stem (e.g., all genera of Osmyliidae), two (e.g., *Kalligramma*) or many stems (Hemerobiidae, Aetheogrammatidae). If our RP1 is treated as MA, then the media is divided into two completely separate stems: MA fully fused with R basally and MP going as a separate vein to the wing base. This state of the media (MA and MP are completely separated having no a common stem) is sometimes hypothesized as plesiomorphic in Pterygota (e.g., Kukalová-Peck 1983, Kukalová-Peck and Lawrence 2004). However, such a primitive condition is so far not detected in any insect taxon. Moreover, the similarity of the forewing venation of basal Carboniferous Neuroptera (e.g., Béthoux and Jarzembowski 2010, Ilger and Brauckmann 2011) and the Permian Neuroptera is so obvious, that the homology of principal veins in these groups is very probable. In these and other basal Neuroptera RP1 is never considered as MA. It is necessary to emphasize that we are only considering forewing venation. The hind wing venation of Neuroptera needs further, detailed examination.

All three anal veins are convex in these species, as in all other taxa of Neuroptera. Kukalová-Peck and Lawrence (2004) considered the first anal vein AA1 (their AA1 + 2) in the hind wing to be lost in Neuropterida, and present among the Holometabola only in basal Hymenoptera (e.g., Xyelidae). We followed this point (e.g., Yang et al. 2012). Recently, Shcherbakov (2013) described the new Permian family Nanosialidae, which is supposedly ancestral to Raphidioptera. The forewing venation of this family is similar to that of Xyelidae and the Permian Parasialidae (Megaloptera). The venation of many early Permian members of Permithonidae (the single known family of Neuroptera at that time) is also similarly configured. Therefore, the homology of anal veins in basal Hymenoptera, Megaloptera, Raphidioptera, and Neuroptera is very probable. All of these taxa have three anal veins in both wings plesiomorphically (with the possible exception of the hind wing of Parasialidae), which are convex, at least in Neuropterida. We may reasonably suggest that these veins are branches of the anterior analis, assuming that branches of the posterior analis do not occur in Neuropterida. Based on these assumptions, we designate three anal veins in both wings as the first to third anterior analis (AA1 to AA3). AA2 and AA3 (and AA4 in a few taxa) may also be interpreted as branches of a single vein (AA2) as has been proposed for other Neuroptera orders (e.g., Plecoptera: Béthoux 2005). However, recognizing that this is also possible, we designate each vein separately because these anal veins in Neuroptera are never fused at the wing base. This terminology well agrees with the approach applied to other orders of Neuroptera (see e.g., Béthoux 2005; Béthoux and Jarzembowski 2010; Béthoux et al. 2011, 2012). The anal veins in Neuroptera were collectively designated as AA and

the first anal vein in both wings as AA1 by Shi et al. (2012). Generally, this approach (but not terminology!) is based on investigations of Snodgrass (1935).

The forewing color pattern of *Kalligramma albifasciatum* n. sp. is unusual for the genus. In addition to the eye spot that is characteristic of *Kalligramma*, this species possesses a broad white transverse fascia across much of the wing. Hitherto, a similar white fascia was found in both wings of all species of *Sophogramma* from the Early Cretaceous of China. However, such a transverse white fascia in *Sophogramma* is interrupted, zigzagged, and located in the distal part of wings (see Yang et al. 2009, Fig. 1), somewhat similar to the condition seen in some extant butterflies (e.g., some *Neptis* F., and *Limenitis* F.).

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