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A new gigantic lacewing species (Insecta: Neuroptera) from the Lower Cretaceous of Brazil confirms the occurrence of Kalligrammatidae in the Americas

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ABSTRACT

Makarkinia kerneri sp. nov. is described from the Lower Cretaceous Crato Formation of Brazil, based on an incomplete but very well-preserved hind wing (Neuroptera: Kalligrammatidae). The previously presumed attribution of the genus is confirmed, based on the diagnostic characters of its wing venation (e.g., dense crossvenation; the anteriorly directed branches of MP) and the presence of a distinct eye-spot on the wing. *Makarkinia* is the only American representative and youngest known genus of Kalligrammatidae. With an estimated wing length of 100–160 mm, it has the largest wings amongst all fossil and extant Neuroptera.

1. Introduction

The large, butterfly-like Kalligrammatidae represent a remarkable family of Mesozoic Neuroptera. Their long-proboscid siphonate mouthparts allowed them to feed on plant fluids (secretions and nectar accessible from reproductive organs) just like modern Lepidoptera (Labandeira, 2010).

Seventeen genera and 46 species of Kalligrammatidae have been described from the Middle Jurassic to the Lower Cretaceous of Eurasia (Engel, 2005; Handlirsch, 1906–1908, 1919; Jarzembowski, 2001; Jepson, Makarkin, & Coram, 2012; Lambkin, 1994; Liu et al., 2014, Liu, Khramov, & Zhang, 2015; Makarkin, Ren, & Yang, 2009; Martynova, 1947; Panfilov, 1968; Ponomarenko, 1992; Ren, 2003; Ren & Guo 1996; Ren & Oswald, 2002; Walther, 1904; Yang, Makarkin, & Ren, 2011, 2014a; Yang, Wang, Labandeira, Shih, & Ren, 2014b; Yang, Zhao, & Ren, 2009; Zhang, 2003; Zhang & Zhang, 2003). Bechly (1998) mentioned a putative first record of Kalligrammatidae from the Lower Cretaceous Crato Formation of Brazil based on a large hind wing (SMF B63) deposited in Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (Frankfurt am Main, Germany). However, its venation and colour pattern show that it is probably conspecific with *Putzneura parcimoniosa* Martins-Neto in Martins-Neto et Rodrigues, 2010 also from the Crato Formation, and it most likely belongs to Osmylopsychopidae (cf. upper figure on p. 98 in Bechly, 1998, and fig. 7C in Martins-Neto & Rodrigues, 2010). The listing of Kalligrammatidae among the neuropterid taxa recorded from the Crato Formation by Martins-Neto, Heads, and Bechly (2007) was based on this erroneous determination. *Makarkinia adamsi* (Martins-Neto, 1992) was originally described as a member of Panfiloviidae, and subsequently attributed to a separate family Makarkiniidae by Martins-Neto (1997, 2000). However, the fragmentary nature of the single known specimen (see below) made its true affinities difficult to determine. Several later authors (Liu et al., 2015; Makarkin & Archibald, 2003; Makarkin et al., 2009; Makarkin, Yang, Peng, & Ren, 2012) suggested that it may be a kalligrammatid, however the latest revision of the family (i.e., Yang et al., 2014b) did not mention any American representatives. The discovery of a new specimen of the genus *Makarkinia* Martins-Neto, 1997 from the same locality clearly confirms its attribution to Kalligrammatidae, which now comprises eighteen genera and 48 species. This specimen is described herein as a new species.

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2. Material and methods

The specimen described herein was collected at an unknown locality near Nova Olinda in the Araripe Basin, northeastern Brazil (Fig. 1), most probably from the Nova Olinda Member.

The fossil is lying directly on the split surface of the lithographic limestone, so that no further preparation was necessary. The specimen was studied using a Leica M80 stereo-microscope. The drawing was created digitally with Adobe Photoshop™ CS5, using a transparent layer over a scan of the fossil. The scan was made using a Canon Canoscan 4200F flatbed scanner at 1600 dpi resolution. Macro photos were taken using a Sony A65 digital camera and Sigma 105 mm F2,8 EX macro lens. Microphotographs were taken using a Leica Z-16-Apoope and Leica DFC490 digital camera. The Leica Application Suite software v.3.8.0 was used for focus stacking.

We use the wing venation terminology of Kukalová-Peck and Lawrence (2004) in the interpretation of Yang, Makarkin, Winterton, Khramov, and Ren (2012) and Yang et al. (2014a). Terminology of wing spaces and details of venation (e.g., subcostal veinlets, traces) follow Oswald (1993). We designate all RP branches successively from the wing base: RP1 is the most proximal branch of RP; RP2 is the second branch of RP.

Abbreviations: AA1, first anterior anal vein; C, Costa; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; RA, anterior radius; RP, posterior sector; ScP, subcosta posterior.

Institutional abbreviation: SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

3. Systematic palaeontology

Order: Neuroptera Linnaeus, 1758.
Family: Kalligrammatidae Handlirsch, 1906.
Genus *Makarkinia* Martins-Neto, 1997.

1997 *Makarkinia* Martins-Neto, p. 74 (Panfiloviidae: Makarkiniinae).
2000 *Makarkinia*; Martins-Neto, pp. 99, 100 (Makarkiniidae).
2003 *Makarkinia*; Makarkin and Archibald, p. 176 (strong affinity with Kalligrammatidae).
2009 *Makarkinia*; Makarkin et al., p. 964 (assumed to be Kalligrammatidae).

Type species. *Panfilovia adamsi* Martins-Neto, 1992, by original designation.

Revised diagnosis. Large kalligrammatids (presumable forewing about 160 mm long); all subcostal veinlets strongly inclined towards apex, shallowly forked; their posterior traces with one to four short pectinate branches in both wings; MP with four anteriorly directed pectinate branches in hind wing; eye-spot present at least in hind wing; its central spot flat, and three dark rings closely spaced.

Species included. *Makarkinia adamsi* and *M. kerneri* sp. nov., both from the Lower Cretaceous (upper Aptian) Crato Formation of Brazil.

Remarks. The large size, configuration of subcostal veinlets, and the structure of the eye-spot are the most characteristic features of this genus.

The presence of subcostal veinlets that are strongly inclined towards the apex with their posterior traces possessing short pectinate branches do not occur in any other genera of the family. This configuration is slightly similar to that which occurs in the forewings of *Kalligramma* Walther, 1904, however their hind wing subcostal veinlets are mostly simple or only once deeply forked (see Panfilov, 1968, figs. 3 and 4; Ren & Guo, 1996, fig. 4; Zhang & Zhang, 2003, fig. 1). Subcostal veinlets in the hind wing of the majority of the other members of Kalligrammatidae are mostly simple (e.g., *Limnogramma* Ren, 2003, *Oregramma* Ren, 2003, *Abrigramma* Yang et al., 2014b) or deeply forked (e.g., *Kallihemerobius* Ren & Oswald, 2002).

The structure of the eye-spot is rather unusual compared with other kalligrammatids, with its central spot being flat, lacking any embossments, without any small pale ('glass') spots, and having three closely spaced dark rings. A combination of all these features is characteristic only for this genus. Moreover, one character state (i.e., the closely spaced three dark rings) is an autapomorphy of this genus.

Makarkinia kerneri sp. nov.
Figs. 2–5.

Derivation of name. From the surname of Mr. Andreas Kerner (Sparta, NJ, USA), who kindly donated this specimen from his private collection to SMNS.

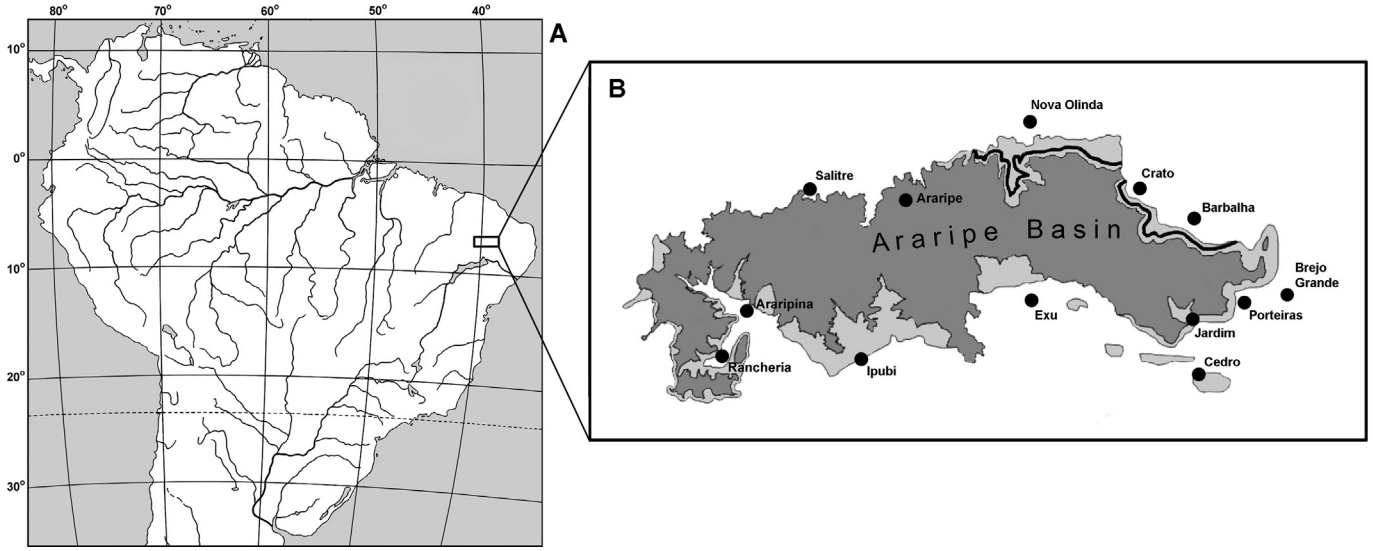

Fig. 1. Location of the Araripe Basin (Chapada do Araripe) in Brazil (A), and its simplified geological map (after Martill, 2007) (B). The Exu Formation is shown in dark grey; the combined outcrop of the Santana, Ipubi, Crato and Rio da Batateiras formations in light grey, and the extent of the fossil-bearing Nova Olinda Member in black.

Fig. 2. *Makarkinia kerneri* gen. et sp. nov., holotype SMNS 70287, specimen as preserved. Scale bar represents 10 mm.

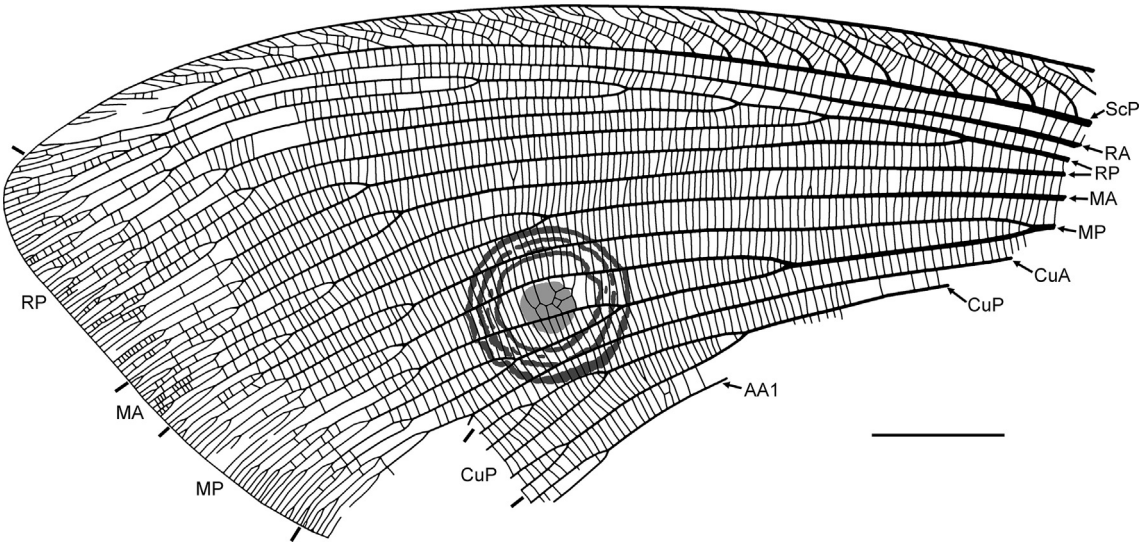

Fig. 3. Drawing of hind wing venation of *Makarkinia kerneri* gen. et sp. nov., holotype SMNS 70287. Scale bar represents 10 mm.

Type material. Holotype, SMNS 70287, deposited at SMNS. A well-preserved distal two thirds of a hind wing.

Type locality and horizon. Vicinity of Nova Olinda (precise outcrop is unknown), Araripe Basin, Ceará, NE Brazil. Lower Cretaceous, Aptian (ca. 115 mya), Crato Formation (Martill & Heimhofer, 2007). The specimen stems from the unweathered grey limestones of the Crato Formation, which often show preservation of colour pattern in fossil insects, contrary to the more common oxidated yellowish limestones from the same formation.

Diagnosis. Wing markedly smaller than that of *M. adamsi*, ca. 100–120 mm long (estimated) [larger, ca. 140–160 mm (estimated) in *M. adamsi*]; costal margin smoothly convex in distal two thirds [strongly convex in *M. adamsi*]; MP with at least four branches directed anteriorly [simple or at most once deeply forked in *M. adamsi*]; eye-spot distinct [not detected in *M. adamsi*].

Description. Hind wing 78 mm long, 39 mm wide as preserved (estimated complete length ca. 100–120 mm, width ca. 45 mm). Costa basally stout becoming narrower towards wing apex, thin along outer margin. Costal space moderately broad, narrowed continuously towards apex. Subcostal veinlets relatively widely spaced, strongly inclined towards apex, shallowly forked with their posterior traces possessing one to four short pectinate branches, connected to each other with many crossveins. Subcostal space rather broad, slightly narrowed apicad. ScP and RA distally fused quite abruptly; veinlets of ScP + RA not preserved, probably few. RP with six branches; dichotomously branched distally, especially greatly RP1, RP2; distal branches running nearly parallel to stem of RP, proximal branches running at acute angle. MA rather shallowly dichotomously branched, but deeper than branches of RP. MP pectinately branched, with four branches directed anteriorly; all branches dichotomously branched distally. CuA concave, probably dichotomously branched distally (incompletely preserved). CuP

Fig. 4. Eye-spot of *Makarkinia kerneri* gen. et sp. nov., holotype SMNS 70287. Scale bar represents 5 mm.

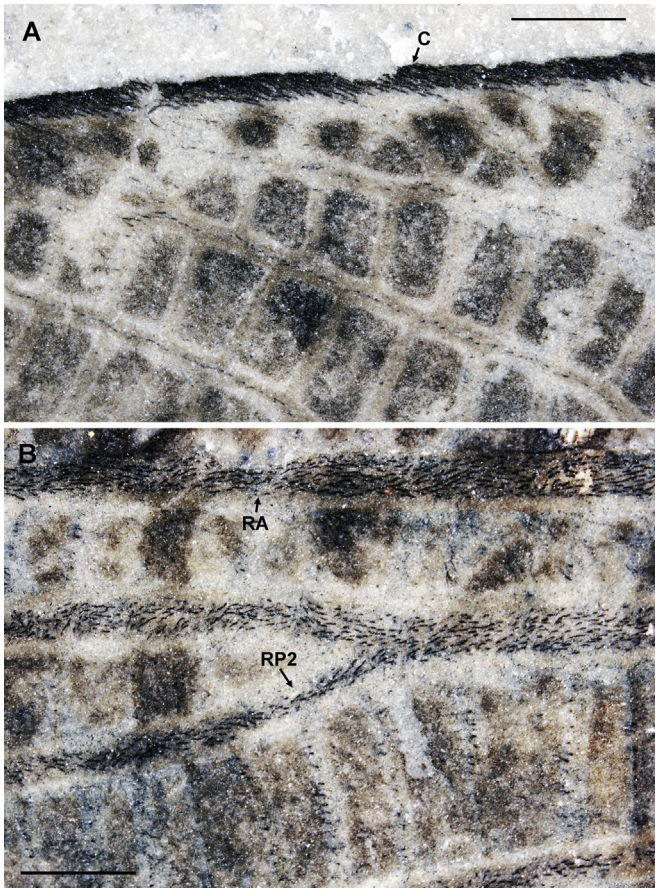

Fig. 5. Setation on veins and costal wing margin of *Makarkinia kerneri* gen. et sp. nov., holotype SMNS 70287. A, costal space near wing base. B, an area near origin of RP2. Scale bars represent 1 mm.

convex, pectinately branched with three preserved branches. AA1 fragmentarily preserved. Crossveins very dense between branches of RP to AA1; slightly scarcer in subcostal and RA spaces; scarce or absent between branches of end-twigging. Trichosors absent along anterior (costal) margin, and not visible along outer margin. Setae on C along costal margin short, very dense (Fig. 5A), becoming somewhat longer and stronger towards wing apex; setae along outer margin short, dense, fine. Setae on veins very short; dense, spaced in several irregular rows on stout veins (Fig. 5B), and arranged in single row on thin longitudinal veins, veinlets and crossveins. Membrane setae more frequent in distal quarter of wing becoming sparser or absent towards wing base. Wing membrane in general rather dark. Colour pattern consists of eye-spot, two dark interrupted stripes and numerous paler small rounded spots along outer margin, and marmorate costal and subcostal spaces. Eye-spot well-developed, rounded consisting of three dark brown closely-spaced rings and central spot. Outer dark ring widest, 11 mm in diameter. Two inner dark brown rings narrower; inner-most ring ca. 7 mm in diameter. Central spot pale brown, ca. 3 mm in diameter, flat (not embossed).

Remarks. This wing is interpreted as being a hind wing due to its concave CuA, which is a characteristic feature of hind wings in Neuroptera (Makarkin et al., 2009). This species can easily be separated from *Makarkinia adamsi*, if the latter is interpreted as a hind wing, but it may theoretically be conspecific with *M. adamsi*, if the latter is represented by a forewing. Unfortunately, the preserved wing of *M. adamsi* is even more fragmentary than that of *M. kerneri* sp. nov., and does not allow a confident determination as to whether it represents a hind or forewing. Only the slightly wider costal space and larger size of *M. adamsi* compared with those of *M. kerneri* sp. nov. suggest that *M. adamsi* might be a forewing. However, these features are not conclusive. Colour pattern and venational details of these wings distinguish them from each other enough to be treated as belonging to two different species, at least until more complete specimens of this genus are found.

4. Family affinity of *Makarkinia*

The first species of *Makarkinia* (i.e., *Panfilovia adamsi* Martins-Neto, 1992) was originally described as a new species within the family Panfiloviidae. This species is represented by a distal anterior part of a gigantic wing (Martins-Neto, 1992, fig. 9; pl. 2, fig. A). The wing is 107 mm long as preserved, and its complete length was estimated to be 200–250 mm by Martins-Neto (1992). However, its actual estimated length is markedly shorter, a maximum of ca. 160 mm.

Martins-Neto (1997) described the new genus *Makarkinia* for this species, based on its gigantic wing size and fewer branches of RP compared with *Panfilovia* Makarkin, 1990. *Makarkinia* was placed in the new monotypic subfamily Makarkiniinae within Panfiloviidae. Later, this subfamily was elevated to family level (Makarkiniidae) without providing an improved diagnosis (Heads, Martill, & Loveridge, 2005; Martill, Bechly, & Heads, 2007; Martins-Neto, 2000, 2003, 2005; Martins-Neto et al., 2007; Martins-Neto & Rodrigues, 2009, 2010). Therefore, this family remained very poorly defined.

Makarkin and Archibald (2003) mentioned that the preserved venation of *Makarkinia* suggests that it could be a Kalligrammatidae. Subsequently, the family Makarkiniidae was considered as a possible or definite synonym of Kalligrammatidae (Liu et al., 2015; Makarkin et al., 2009, 2012; Ren & Makarkin, 2009).

However, the kalligrammatid affinity of *Makarkinia*, which was based on *M. adamsi*, was not well established and only tentative. The wing of *M. kerneri* sp. nov. provides clear evidence for this attribution. It is supported by the presence of an eye-spot and the anteriorly directed branches of MP, together with other kalligrammatid character states also observed in *M. adamsi* (i.e., large size, dense crossvenation, and general characteristics of the venation). On the other hand, the venation in the costal space and dense crossvenation throughout the wing found in *Makarkinia kerneri* sp.

nov. are quite similar to those of the Jurassic panfiloviid genus *Epipanfilovia* Yang, Makarkin, & Ren, 2013. Moreover, the forewings of *Epipanfilovia oviformis* Yang et al., 2013 are also large, 60–90 mm long. But, the wings of Panfiloviidae lack the main kalligrammatid features (i.e., the presence of an eye-spot and the anteriorly directed branches of MP), and ScP and RA are not fused distally in *E. oviformis* (the only species of Panfiloviidae with completely preserved venation).

5. Palaeobiogeographical and biological implications of *Makarkinia*

The Brazilian late Aptian *Makarkinia* is the only known kalligrammatid genus in the Americas. Other genera are described from the Middle Jurassic to Lower Cretaceous of Eurasia (England, Germany, Kazakhstan, Transbaikalian Russia, Mongolia, and China). Most of the species are known from China. In general, all these Eurasian kalligrammatids are found in the territory of the Euro-Sinian floristic region extending from western and southern Europe through Central Asia and China to Japan. The climate of this region was subtropical to tropical during most of the Jurassic to Early Cretaceous (Vakhrameev, 1988). No definite kalligrammatids have been found in the territory of the Siberian floristic region. Therefore, kalligrammatids can be interpreted as thermophile insects. This climatic preference agrees well with the finding of *Makarkinia* in the equatorial area of South America.

The genus *Makarkinia* comprises the youngest known kalligrammatids. In Eurasia, the family became extinct probably slightly earlier: the youngest kalligrammatids here occur in the lower Aptian of the Chinese Yixian Formation.

This genus has the largest wings known amongst Neuroptera, both extinct and extant. The estimated complete length of *M. adamsi* (the presumable forewing) is ca. 160 mm. These wings are larger than any of the other kalligrammatids (forewing length of these ranges from 37 to 100 mm), and other neuropterans, the largest of which are found in some extant Myrmeleontidae (e.g., *Palpares* Rambur, 1842, *Echthromyrmex* McLachlan, 1867).

The presence of short setae on the wing veins (Fig. 5) suggests that adults of *Makarkinia* were diurnal and probably flew in bright sunlight just like many modern butterflies. Due to their large size, these kalligrammatids likely suffered attacks by pterosaurs and birds, which occurred in the Crato Formation (Naish, Martill, & Merrick, 2007; Unwin & Martill, 2007). This is indicated by fragmentary preserved wings of both species and the presence of a prominent eyespots used as protection devices.

6. Conclusions

The new species *Makarkinia kerneri* sp. nov. described herein confirms the attribution of the genus to Kalligrammatidae and thus the occurrence of this extinct lacewing family in the Americas. This is the only kalligrammatid genus known from an equatorial area, confirming the climatic preference of the family as thermophile insects. *Makarkinia* is also remarkable by its gigantic size and the unusual structure of an eye-spot.

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