

# New early griffenfly, *Sinomeganeura huangheensis* from the Late Carboniferous of northern China (Meganisoptera: Meganeuridae)

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New griffenfly *Sinomeganeura huangheensis* gen. n., sp. n. (Meganeuridae) is described from Upper Carboniferous (Namurian) of the Tupo Formation in northern China (Ningxia Hui Autonomous Region). This taxon exhibits unique structure of the wing venation pattern. It is highly interesting in reference to the Namurian age known for the occurrence of two meganeurids until present (*Namurotypus* Brauckmann & Zessin, 1989 and *Shenzhousia* Zhang & Hong, 2006) as well as the palaeogeographical position of the locality far from all sites in Laurussia. We demonstrate that meganeurids with relatively small wings already co-existed with large species in the Namurian, as for the Stephanian and the Late Permian. Thus, *Sinomeganeura* demonstrates that the meganeurid diversity and wing venation disparity were comparable during the Namurian and the Stephanian, suggesting that this group already had a long history in the Early Carboniferous. Odonatoptera were probably the main, if not unique predators of the flying insects during the Late Paleozoic.

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## Introduction

The Namurian is the earliest stage of the Late Carboniferous with sudden occurrence of apparently diverse winged insects (see e.g., Brauckmann et al. 2003). Because of the scarcity of the insect fossil record during this stage and in the Late Devonian to Early Carboniferous, we cannot estimate the time of origin of the pterygote insect groups (Engel & Grimaldi 2004, Prokop et al. 2005). The Namurian insect deposits are currently known from a few localities entirely located in the Euro-American region such as the Upper Silesian Coal Basin in the Czech Republic and Poland, Hagen-Vorhalle in Ruhr area (Germany), Charleroi Coal Basin in Belgium, South Limburg coalfield in the Netherlands and Manning Canyon Shale in Utah (USA) (Hennig 1981, Brauckmann et al. 1996, Rasnitsyn & Quicke 2002). Outside of

this territory, a new insect fauna known as 'Qilianshan entomofauna' was recently discovered from the Namurian C of Qilianshan Mountains in northern China (Hong 1998). This locality is representing the first Namurian deposits with fossil insects from the Far East. Its distant palaeogeographical situation from the other Carboniferous insect localities and occurrence in low latitudes suggests a rather long earlier history for the Pterygota (Rasnitsyn & Quicke 2002). First insect taxonomy studies were provided by Peng et al. (2005) and Zhang et al. (2006) and concerning the descriptions of a new family *Sinonamuropteridae* Peng, Hong & Zhang, 2005 (currently considered as *Grylloblattida sensu* Storozhenko 2002), and a new genus of 'giant dragonfly' *Shenzhousia* Zhang & Hong, 2006 (Odonatoptera, Meganeuridae): Prokop & Ren (2007) described new palaeodicty-

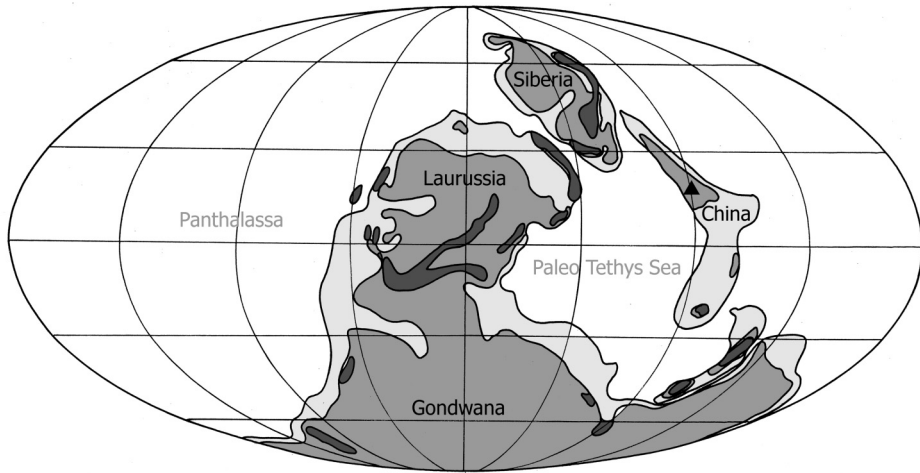


Fig. 1. Palaeogeographical world map of the Upper Carboniferous with approximate position of the locality in Zhongwei County, Ningxia Hui Autonomous Region (China) indicated by black triangle, after Scotese (2005, modified).

opterid family Namuronigxiidae bearing mosaic of characters diagnostic for several “palaeopteran” families. In addition the frequent occurrence of archaeorthopterid wing fragments (e.g., *Sinopteron huangheense* Prokop & Ren, 2007) forming up to 40 percent of all insect specimens demonstrate high abundance of this group in early Late Carboniferous ecosystems.

Fossils from ‘Qilianshan biota’ include plants, insects, other invertebrates and vertebrates such as fishes. They are preserved in layers of Tupo Formation in outcrops along Qilianshan Mountains located in the Ningxia, Gansu, and Inner Mongolia regions (China). Fossil insects have been collected in the lower member of the Tupo Formation in Zhongwei County of southern Ningxia Hui Autonomous Region (Fig. 1), representing the oldest known entomofauna from China so far (Hong 1998). The paralic development of the Tupo Formation is formed by alternated beds of terrestrial and marine facies dated to stage C<sub>2</sub>t (Bashkirian – Moscovian) as equivalent of the European Namurian B-C (Peng et al. 2005). The palaeoecological analysis based on fish fossils indicates a near shore palaeoenvironment with possible role of secondary transportation (Lu et al. 2002).

Paleozoic odonopteran order Meganisoptera (so-called ‘Protodonata’) represents the stem group to true Odonata. However, the members of Meganisoptera differ from Odonata by absence of

nodus and pterostigma in wing venation, as well as males lacking secondary genitalia and females with well-developed ovipositor (Bechly et al. 2001). Above all, this group well known for the insects with largest wingspan that have ever lived such as *Meganeuropsis permiana* Carpenter, 1939 from Early Permian of Kansas reached wingspan more than 700 mm (Carpenter 1939, 1947).

### Materials and methods

The fossil specimen was observed under stereomicroscopes Olympus SZX-9 & Leica MZ 12s in dry state and under ethyl alcohol. The venation pattern line drawing was drawn directly using stereomicroscope by camera lucida and finally readjusted to the photograph scale using of graphic software (Adobe Photoshop). Photographs were made by digital camera Nikon 4500 in the highest contrast as possible by single sided cross-light pre-exposure.

Type material referred to as ‘CNU’ housed at the Key Lab of Insect Evolution & Environmental Changes, the College of Life Science, Capital Normal University, Beijing, China (CNU; Ren Dong, Curator).

We use the wing venation nomenclature of Nel et al. (1993), and Bechly (1996). Systematic and divisions follows the concept of higher phylogenetic classification of Odonoptera proposed by Bechly (1996, 2005).

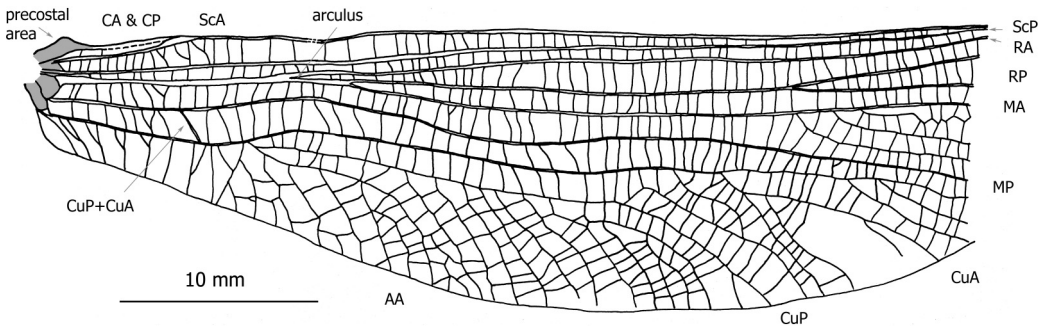


Fig 2. *Sinomeganeura huangheensis* gen. n., sp. n. (Holotype specimen No. CNU-NX2006003, Capital Normal University coll., Beijing), drawing of fore wing venation.

The venational symbols used here specified as follows: symbols in capitals denote the longitudinal veins (CA / CP – costal anterior / posterior, ScA / ScP – subcostal anterior / posterior, RA / RP – radial anterior / posterior, MA / MP – medial anterior / posterior, CuA / CuP – cubital anterior / posterior, AA – anal anterior).

**Superorder Odonatoptera Martynov, 1932**  
**Order Meganisoptera Martynov, 1932**  
 (= **Protodonata Brongniart, 1893**)  
**Family Meganeuridae Handlirsch, 1906**

**Subfamily Meganeurinae Handlirsch, 1906**  
**Genus *Sinomeganeura* Prokop, Nel & Ren, gen. n.**

*Type species.* – *Sinomeganeura huangheensis* Prokop, Nel & Ren, sp. n. by present designation and monotypy.

*Etymology.* – Generic name is from *Sino* (after Latin name for China) and generic name *Meganeura*. Gender feminine.

*Diagnosis.* – Forewing characters only. ScA rather long; stems of CuP and CuA fused to a single oblique vein between [M & Cu] and AA; no small crossveins ending on oblique vein CuA+CuP; short distance between point of fusion of CuA+CuP with AA and their distal separation; narrow anal and cubital areas; no narrowing of the area between MP and CuA; first posterior branch of MA opposite base of RP3/4; wing relatively small (compared to the ‘giant’ meganeurids).

*Included species.* – Type species only.

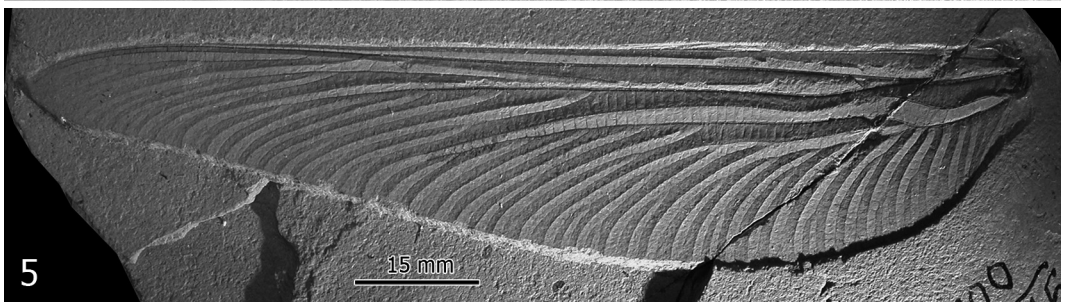
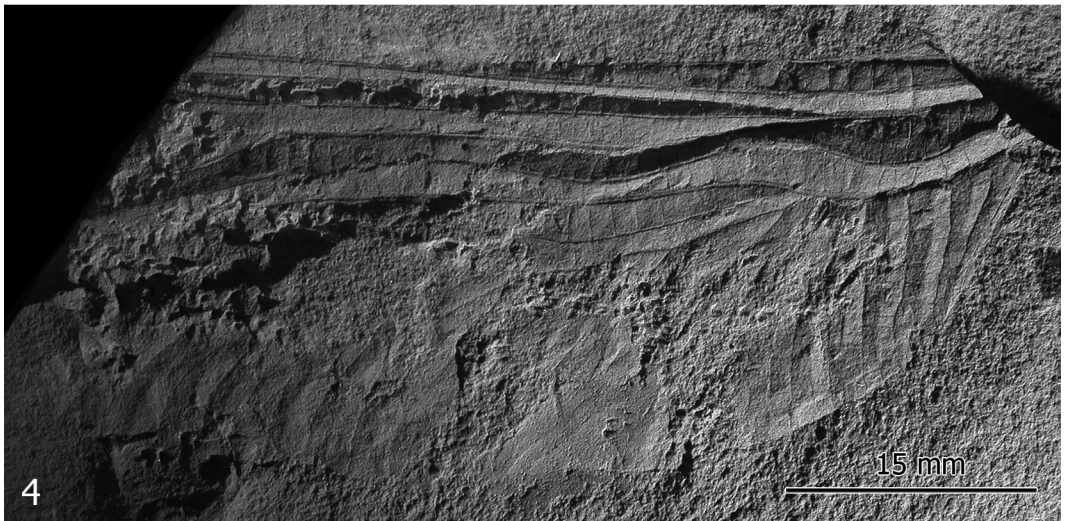
***Sinomeganeura huangheensis* Prokop, Nel & Ren, sp. n.**

(Figs 2-3)

*Type material.* – Holotype. Specimen CNU-NX2006003, housed in Capital Normal University coll., Beijing; nearly complete and well-preserved fore wing, apical part of wing missing; Xiaheyuan Village of Zhongwei County, Ningxia Hui Autonomous Region, China; Upper Carboniferous, Namurian B – C, Tupo Formation.

*Etymology.* – Species name is after the Huanghe River, next to the type outcrop.

*Description.* – Part and counterpart of an elongate forewing with apex missing, no trace of coloration preserved; broadest part at about midwing; pre-costal area of CA and CP enlarged, but rather short; vein ScA reaching anterior wing margin about 7.8 mm from wing base; simple concave ScP nearly parallel to anterior wing margin, and reaching it in apical part of wing, 48 mm from wing base; stem of radial veins dividing 13.8 mm from wing base forming the “arculus”, RA strong, simple, parallel to ScP, and ending probably in apex; R and MA fused in their basal parts; RP basally attached to MA separating about 3.4 mm from arculus, RP bifurcating into RP1+2 and RP3+4 in distal part of wing; nearly straight MA with distal posterior pectinate branches, first at the level of bifurcation between RP1+2 and RP3+4; simple corrugated MP basally fused with Cu, ending on posterior wing margin near wing apex; CuA+CuP emerging from MP about 8.5 mm from wing base, and forming a single strong oblique crossvein in area between MP and AA (a slightly oblique crossvein is present two cells distal of



Figs 3-5. 3, *Sinomeganeura huangheensis* gen. n., sp. n. (Holotype specimen No. CNU-NX2006003, Capital Normal University coll., Beijing), photograph of imprint; 4, *Arctotypus sinuatus* Martynov, 1932 (Holotype specimen No 2334/6; Paleontological Institute of Russian Academy of Sciences coll., Moscow) photograph counter-imprint; 5, *Arctotypus sylvaensis* Martynov, 1932 (Holotype specimen No 1700/3245; Paleontological Institute of Russian Academy of Sciences coll., Moscow), photograph of counter-imprint.

CuA+CuP, but it is as weak as the other crossveins of the area, thus it cannot correspond to CuA); slightly corrugated CuA attached with CuP and AA divides from them 2.5 mm from basal connection of oblique vein CuA+CuP, and terminating distally with six main branches; separation of CuP from AA 0.6 mm distal of point of separation between CuA and CuP+AA; CuP pectinated with nine main simple posterior branches; distal part of AA forming a relatively small anal area with six main posterior branches (forewing structure); simple short AP reaching posterior wing margin near wing base.

*Dimensions.* – Length of forewing fragment about 48.6 mm, probable total length about 70 mm (wingspan about 150 mm); wing width about 14.5 mm.

## Discussion

Despite of the lack of the main synapomorphy of the Meganeuridae ('characteristical oblique vein between RA and RP near the base of RP2'), *Sinomeganeura* gen. n. can be attributed to this group as it has the typical synapomorphy of the subfamily Meganeurinae Handlirsch, 1906, viz. 'stems of CuP and CuA fused to a single oblique vein between [M & Cu] and AA, distinctly stronger than the crossveins of this area'. *Sinomeganeura* has a relatively small forewing, not exceeding 70 mm long, instead of wing lengths above 250 mm of the well-known giant *Meganeura* Brongniart, 1885 and *Meganeuropsis* Carpenter, 1939. *Meganeuropsis* differs from *Sinomeganeura* in the very long distance between the point of fusion of CuA+CuP with AA and their distal separation, the very broad anal and cubital areas, and the distinct narrowing of the area between MP and CuA (Carpenter 1947). *Meganeura* differs from *Sinomeganeura* in the presence of numerous crossveins in area between MP(+Cu) and AA, longer fusion of AA with CuP and CuA, broader anal area, with about ten rows of cells, instead of one or two in basal part of wing (Carpenter 1943).

Bechly (1996) followed the list of Meganeuridae of Brauckmann & Zessin (1989). Note that Bechly (2007, internet site <http://www.bernstein.naturkundemuseum-bw.de/odonata/system.htm>) maintained the Kargalotypidae Zessin, 1983 (previously considered as a subfamily of the Mega-

neuridae), as a family of Meganisoptera and ignored its recent revision that transferred it into the Triadophlebiomorpha (Nel et al. 2001).

The phylogeny and classification of the Meganeuridae remains in great part unresolved, as no known synapomorphy characterizes the subfamily Tupinae Handlirsch, 1919 (Bechly 1996). Also *Carpentertypus* Zessin, 1983 (type genus of the Carpentertypinae Zessin, 1983, one species *C. durhami* (Carpenter, 1960)) is based on very incomplete fossil wing apices, hardly comparable with *Sinomeganeura* (Carpenter 1960, Zessin 1983). The structure of the veins CuA and CuP is unknown in the Carpentertypinae. Bechly (1996) characterized this subfamily after the branches of main veins more or less zigzagged, and the branching of vein MA reduced. First character is not present in *Sinomeganeura*, but second is unknown in *Sinomeganeura*.

Several tupine genera can be excluded because their veins CuP and CuA are not fused into a single strong oblique vein, i.e. *Stephanotypus* Zessin, 1983, *Namurotypus* Brauckmann and Zessin, 1989, *Tupus* Sellards, 1906, *Meganeurula* Handlirsch, 1906 (visible in the three species *M. selysii* (Brongniart, 1894), *M. confusa* (Handlirsch, 1919), and *M. titana* (Meunier, 1909), pers. obs.), and *Arctotypus* Martynov, 1932 (Zessin 1983, Brauckmann & Zessin 1989, Carpenter 1992) (see Figs 4-5).

Nothing is known on the structures of the CuP and CuA when crossing through the area between MP and AA for *Solutotherates* Brauckmann and Zessin, 1989 (one species *S. analis* (Carpenter, 1980)), but it seems to have a strong narrowing of area between MA and CuA, unlike *Sinomeganeura* (Carpenter 1980: fig. 1).

*Boltonites* Handlirsch, 1919 (based on *B. radstockensis* (Bolton, 1914)) had apparently a fusion of CuA + CuP, as in *Sinomeganeura* (after Bolton 1914: pl. 18, fig. 1). *B. radstockensis* is hardly comparable to *Sinomeganeura* due to its very fragmentary state. Nevertheless, its wing width at apex of AA is 40 mm, instead of 13.2 mm in *Sinomeganeura*, and it has a strong narrowing of area between MA and CuA.

*Petrotypus* Zalessky, 1950 is based on the basal two third of a hindwing, from the Kungurian of Central Ural, Russia. Zalessky (1950) did not figure nor describe it correctly, but it seems that had separated crossveins CuP and CuA, after its original photograph. *Megatypus* Tillyard, 1925 has also

its CuA and CuP fused into a single oblique vein, but it differs from *Sinomeganeura* in its very large wings and presence of several small crossveins ending on the oblique vein CuA+CuP (Carpenter 1943). *Schlechtendaliola* Handlirsch, 1919 (type species *S. nympha* Handlirsch, 1919) is based on a very fragmentary wing, poorly figured in Handlirsch (1906: 311, pl. 31, fig. 40), impossible to compare with *Sinomeganeura*. *Ephemerites* Geinitz, 1865 (type species *E. rückerti* Geinitz, 1865) is also based on a very poorly known specimen (Brauckmann & Zessin 1989: 184). *Palaeotherates* Handlirsch, 1906 (type species: *P. pennsylvanicus* Handlirsch, 1906) is based on median part of a wing, revised by Carpenter (1960: text-fig. 4). It is hardly comparable to *Sinomeganeura*, but fortunately, its first posterior branch of MA is far distal from the base of RP3/4, instead of being opposite it as in *Sinomeganeura*. The same situation occurs in *Shenzhousia* Zhang & Hong, 2006 from the same formation as *Sinomeganeura* (Zhang et al. 2006). A consistent difference between *Palaeotherates* and *Shenzhousia* is the broader area between MA and MP at level of the oblique vein between RA and RP in the latter.

## Conclusions

Up to now, the only Namurian Meganeuridae are *Namurotypus* Brauckmann and Zessin, 1989 and *Shenzhousia* Zhang & Hong, 2006. Other Namurian Odonatoptera belongs to more inclusive clades, viz. 'Erasipteridae' Carpenter, 1939 and Eugeopteridae Riek, 1984. *Namurotypus* has a less derived condition of the CuP-CuA veins than *Sinomeganeura* and the other Meganeurinae. We demonstrated that meganeurids with relatively small wings already co-existed with large species in the Namurian, as well in the Stephanian and the Late Permian (Nel pers. obs.). 'Small' and 'large' meganeurids certainly had different biology, prey, and hunting habits, as for the small and large modern dragonflies. Damselflies-like Protozygoptera were also present during the Late Carboniferous (Jarzembowski & Nel 2002). Thus, *Sinomeganeura* demonstrates that the meganeurid and odonatopteran diversity and wing venation disparity were comparable during the Namurian and the Stephanian, suggesting that this group already had a long history in the Early Carboniferous. Terrestrial vertebrates probably predated only on ground living arthropods, as the flying vertebrates

appeared circa 100 Ma later during the Triassic. The high diversity of the Carboniferous Odonatoptera as predators of flying insects suggests that their importance in the arthropod trophic chains was probably higher at this time than in the Mesozoic and the more recent periods.

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