



Research article

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A new griffenfly genus and species from the Early Pennsylvanian of the Xiaheyan locality (Ningxia, China) (Insecta: Odonatoptera)

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Abstract. The erasipterid *Sinoerasipteron xiaheyanensis* Nel & Huang gen. et sp. nov. from the Moscovian Tupo Formation in Xiaheyan locality (China), is described and illustrated. It is the sixth species of the odonopteran griffenflies from this locality. This new discovery confirms the high diversity of these flying predators in the insect assemblage.

Keywords. Insecta, Erasipteridae, gen. et sp. nov., diversification.

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Introduction

The odonopteran griffenflies are well-known because some of them have reached the most important wing sizes among the Pterygota. They are called ‘giant’ insects, even if their bodies are comparable in size with those of the largest extant phasmids or beetles. Their remains are generally rare. Nevertheless, they are quite frequent and diverse in some outcrops like the Gzhelian of Commeny or the Middle Permian of Lodève in France (Nel *et al.* 2009). If these insects are present in the earliest part of the Late Carboniferous, they remain generally infrequent during this period. For instance, only two specimens of the large griffenfly species *Gallotupus oudardi* Nel *et al.*, 2008 were found in the very rich Moscovian outcrop of Avion (France) (Nel *et al.* 2008; Prokop *et al.* 2014). With no less than five described species, the Moscovian outcrop of Xiaheyan (Fig. 1) is a counterexample of higher diversity and abundance in

griffenflies (Li *et al.* 2013). These are *Shenzhousia qilianshanensis* Zhang & Hong, 2006 (in Zhang *et al.* 2006), *Oligotypus huangheensis* (Ren *et al.*, 2008), *Tupus orientalis* (Zhang, Hong & Su, 2012) (in Su *et al.* 2012), *Erasipterella jini* (Zhang, Hong & Su, 2012) (in Su *et al.* 2012), *Aseripterella sinensis* Li, Béthoux, Pang & Ren, 2013 and *Sylphalula laliquei* Li, Béthoux, Pang & Ren, 2013.

Here we describe a new genus and species of griffenfly from the same locality, confirming the impressive diversity of these flying predators in this insect assemblage.

Material and methods

One specimen was collected from the black shale of the Tupo Formation (= Yanghugou Formation) at the Xiaheyan locality, Zhongwei County, Ningxia Hui Autonomous Region. The age of the Pennsylvanian Tupo Formation is somewhat uncertain, Trümper *et al.* (2020) suggested it could be the latest Bashkirian to middle Moscovian, while Wang *et al.* (2022) approximately assigned it to the Moscovian. The fossil was carefully prepared using a sharp awl. Photographs were taken using a digital camera attached to a Zeiss Discovery V20 microscope and combined by using Photoshop ver. 10 software. The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Nanjing, China.

We follow the wing venation nomenclature of Riek & Kukalová-Peck (1984) as modified by Nel *et al.* (1993, 2009) and Jacquelin *et al.* (2018). We follow the classification of Bechly (2016), as modified by Petrulevičius & Gutiérrez (2016).



Fig. 1. Map of fossil locality. Red triangle = fossil locality; grey dotted line = limits of regions; continuous double line = secondary road; black and white dotted lines = main roads. Scale bar = 10 km.

Institutional abbreviations

CAS = Chinese Academy of Sciences, Nanjing, China

NIGP = Nanjing Institute of Geology and Palaeontology, Nanjing, China

Abbreviations for morphological terms

Arc = arculus

C = Costa

CuA = anterior cubitus

CuP = posterior cubitus

IR1, IR2 = intercalary radial veins

MA = anterior median

MP = posterior median

RA = anterior radius

RP = posterior radius

ScP = posterior subcosta

Results

Taxonomy

Class Insecta Linnaeus, 1758

Superorder Odonoptera Martynov, 1932

Clade Neodonoptera Bechly, 1996

Clade ‘Eomeganisoptera’ Rohdendorf, 1962

Family Erasipteridae Carpenter, 1939

Genus *Sinoerasipteron* Nel & Huang gen. nov.

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Type species

Sinoerasipteron xiaheyansensis Nel & Huang gen. et sp. nov.

Diagnosis

ScP shortened, only reaching 30% of wing length; RA distally fused with C into a strong costal vein distad level of RP2; base of IR2 quite distant from that of RP3/4 (situated seven cells distally); MA with seven long posterior branches; seven posterior branches of CuA; CuP with a long stem, seven-eight branches, and three rows of cells between it and posterior margin of wing; anal area with two rows of cells.

Etymology

Named after ‘*Sinica*’, Latin name for China and the genus name *Erasipteron*. Gender neutral.

Sinoerasipteron xiaheyansensis Nel & Huang gen. et sp. nov.

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Figs 2–3

Diagnosis

As for the genus, by monotypy.

Etymology

Named after the Xiaheyan locality (Ningxia, China).

Material examined

Only one specimen collected from the black shale of the Tupo Formation at Xiaheyan locality, without counterpart.

Holotype

CHINA • imprint of a forewing, with extreme base missing and apex folded; Xiaheyan, Muscovian Tupo Formation; stored at Nanjing Institute of Geology and Palaeontology; NIGP202927; CAS.

Description

Imprint of moderately well preserved forewing (for justification see below), nearly complete, with extreme base missing; wing elongate not triangular-shaped; preserved length 68.1 mm, maximum width 10.8 mm; anterior wing margin and ScP straight; ScP reaching anterior wing margin opposite fork between RP1/2 and RP3/4 (i.e., at 30% of wing length); RA distally fused with C into strong costal vein; area between RA and RP1 with strong oblique crossvein at point of fusion of RA with C, basad origin of IR1; arculus at ca 8.0 mm from wing base; RP+MA 2.5 mm long; stem of of RP 10.0 mm long basad fork between RP1/2 and RP3/4; three longitudinal veins in area between IR1 and RP2; RP1/RP2 fork 27.5 mm distal of fork between RP1/2 and RP3/4; IR2 with two-three posterior branches; RP3/4 simple; MA with seven posterior branches; MP simple, undulated; CuA regularly posteriorly pectinate, with seven posterior branches; CuP- and CuA-crossings difficult to identify; CuP with long stem, seven-

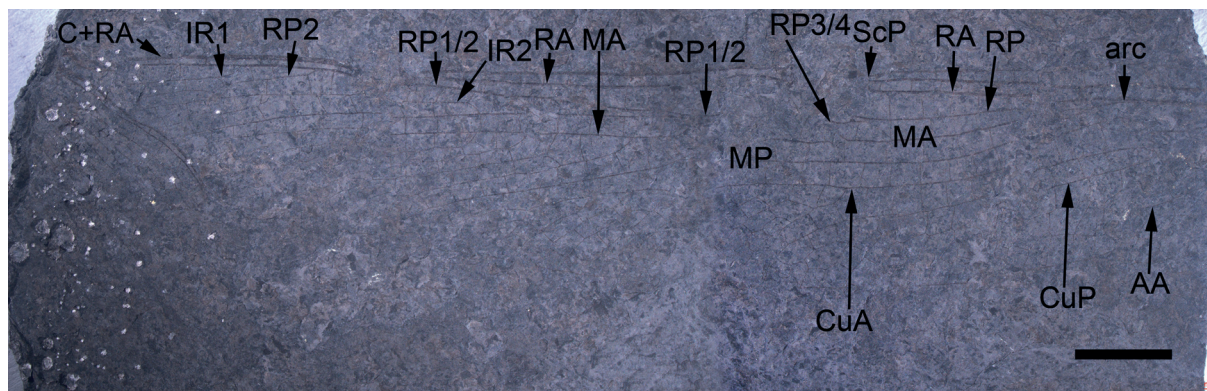


Fig. 2. *Sinoerasipteron xiaheyanensis* Nel & Huang gen. et sp. nov., holotype (NIGP202927). Photograph. Scale bar = 5 mm.

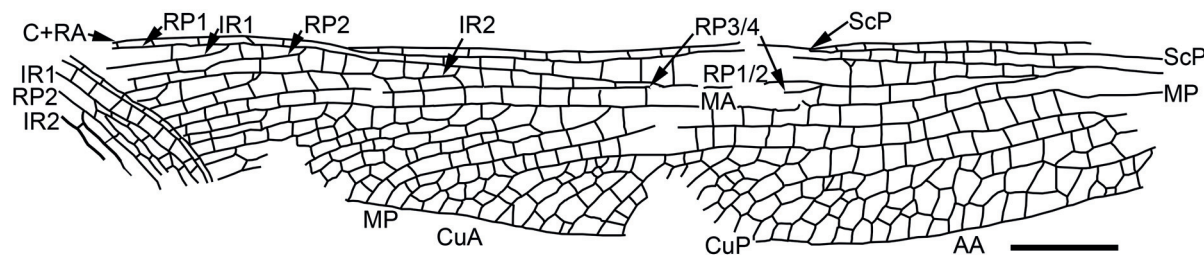


Fig. 3. *Sinoerasipteron xiaheyanensis* Nel & Huang gen. et sp. nov., holotype (NIGP202927). Reconstruction. Scale bar = 5 mm.

eight branches, and three-four rows of cells between it and posterior margin of wing; two rows of cells between AA and posterior margin of wing with four-five poorly defined posterior branches.

Age and outcrop

Tupo Formation at Xiaheyan locality, Zhongwei County, Ningxia Hui Autonomous Region, NW China; Moscovian, Pennsylvanian.

Discussion

This wing is clearly that of an Odonoptera. It is remarkable in the short vein ScP, reaching ca 30% of the total wing length. Similar shortened ScP are present in the Eugeoptera Petrulevičius & Gutiérrez, 2016, Erasipteridae Carpenter, 1939, Paralogidae Handlirsch, 1906, and the Odonatoclada Bechly, 2003, but not the other Carboniferous griffenflies in which ScP is longer, fusing with the costal margin distad midwing (Bechly 1996, 2016).

The Eugeoptera only comprise *Eugeopteron* Riek & Kukalová-Peck, 1984 and *Tupacsala* Petrulevičius & Gutiérrez, 2016. Both strongly differ from the new fossil in the distinctly broader cubito-anal area and the triangular-shaped wings (Riek & Kukalová-Peck 1984; Petrulevičius & Gutiérrez 2016). The Paralogidae strongly differ from the new fossil in the shorter stem of CuP, and quite broader cubito-anal area, with more than five-six rows of cells between CuP and posterior margin of wing, first fork of RP strongly divergent (Carpenter 1960; Nel *et al.* 2009). The Odonatoclada have a reduced branching of vein MA, unlike in the new fossil. Also, in this group, the Lapeyriidae Nel, Gand & Garric, 1999 and the Nodialata have better-defined nodal structures, with a nodal crossing and a subnodus (Nel *et al.* 1999; Nel & Huguet 2002).

The Erasipteridae currently comprise the genera *Erasipterella* Brauckmann, 1983, *Erasipteroides* Brauckmann & Zessin, 1989, *Erasipteron* Pruvost, 1933, *Rasnitsynala* Zessin, Brauckmann & Gröning, 2011, *Whalleyala* Brauckmann & Zessin, 1989, *Zessinella* Brauckmann, 1988.

The new fossil differs from *Erasipteron* in the vein MA with seven long posterior branches, and CuP with branches vs simple, and in the vein RA fused with C distad the level of RP2 (Pruvost 1933; Brauckmann 1983). *Erasipteron* is also supposed to have an ‘archedictyon’ (a net of small cells present in the larger ‘normal’ cells), a character that would need to be verified on the type material.

The type species of *Erasipterella* (*E. piesbergensis* Brauckmann, 1983) is based on incomplete wings. In particular, the apical part of ScP is not preserved, so the exact length of this vein is uncertain, although it seems to be rather short (Brauckmann 1983; Brauckmann *et al.* 1985; Brauckmann & Zessin 1989). *Erasipterella piesbergensis* has a narrower area between CuP and the posterior margin of the wing, with two rows of cells in-between. It also has a CuP with very short posterior branches, unlike in the new fossil. *Erasipterella jini* (Zhang, Hong & Su, 2012), originally placed in the genus *Sinierasiptera* Zhang, Hong & Su, 2012 and its own family Sinierasipteridae Zhang, Hong & Su, 2012 (in Su *et al.* 2012), was later transferred in the genus *Erasipterella* and the family Sinierasipteridae synonymized with the Erasipteridae (Li *et al.* 2013). These last authors indicated that it has a simple CuP, unlike the new fossil. Nevertheless, they share a vein RA fused with C distad the base of RP2. Interestingly, Li *et al.* (2013: fig. 5) figured fore- and hind wings of *E. jini* in which the general shape of hind wing shows a quite broad anal area, which is not the case in the new fossil. This suggests that the new fossil is a forewing.

Erasipteroides valentini (Brauckmann, Koch & Kemper, 1985), type species of *Erasipteroides*, is based on incomplete fore- and hind wings, with only the basal third of wings preserved. Nevertheless, the CuP has at most very short apical branches, unlike in the new fossil (Brauckmann *et al.* 1985).

Rasnitsynala sigambrorum Zessin, Brauckmann & Gröning, 2011 has a very particular vein CuP, shortened and strongly similar to the posterior branches of CuA (Zessin *et al.* 2011). The distal part of ScP is not preserved, thus it is not possible to determine if its only reaches mid-wing or goes farther. Thus, its attribution to the Erasipteridae is questionable. Zessin *et al.* (2011: fig. 3) has figured a RA strongly approximating C in the distal half of wing, but not fused with it, unlike in the new fossil.

Whalleyala pennsylvanicus Brauckmann & Zessin, 1989 has a RA separated from C up to a position very close to the wing apex, a very narrow anal area, a simple CuP, and a CuA without well-defined posterior branches, unlike the new fossil (Brauckmann & Zessin 1989).

Zessinella siope Brauckmann, 1988 is based on incomplete wings. Nevertheless, it differs from the new fossil in the narrow anal area with one row of cells (Brauckmann 1988).

Li *et al.* (2013) described *Sylphalula laliquei*, a taxon they did not clearly placed, but that shares a shortened ScP with the Erasipteridae. Its CuP has only a very short distal posterior branch.

Li *et al.* (2013) also described *Aseripterella sinensis*, an ‘Erasipteridae’-like taxon from the Carboniferous of Northern China, sharing a shortened ScP with the Erasipteridae. It shares with the new fossil a RA fused with C distad the base of RP2, and the presence of distal branches of CuP. But it differs from the new fossil in the presence of only one row of cells between AA and the posterior margin of wing vs. two in the new fossil, and the presence of 10–11 posterior branches of CuA vs. only seven in the new fossil. In the new fossil, the base of IR2 is quite distant from that of RP3/4 (situated seven cells distally) vs. only two cells in *Aseripterella sinensis*. Lastly, the holotype of *Aseripterella sinensis*, a nearly complete forewing, is clearly smaller than the new fossil: max. 54 mm long and 9.4 mm wide, vs. more than 58.0 mm long (probably 61 mm) and 11.0 mm wide in the new fossil.

Li *et al.* (2013: 132–133) did not make a formal diagnosis for *Aseripterella sinensis*, but they proposed the ‘occurrence of a single row of cross-veins in the area between AA and the posterior wing margin’ as the first character to separate it from the other ‘meganisopteran Odonoptera’. As the new fossil has two such rows of cells, it would not fall in this taxon. The difference in the position of the base of IR2 is more diagnostic to separate the two taxa.

The new fossil differs from *Shenzhousia qilianshanensis* in the narrower cubital area and quite shorter ScP (Zhang *et al.* 2006; Li *et al.* 2013). *Tupus orientalis* and *Oligotypus huangheensis* also have a quite longer ScP than in the new fossil (Ren *et al.* 2008; Li *et al.* 2013).

Conclusion

Sinoerasipteron xiaheyanensis Nel & Huang gen. et sp. nov. is the sixth described species of griffenfly from the Moscovian Xiaheyan locality, confirming the impressive diversity of these insects in this rather ancient subperiod of the Late Carboniferous. The oldest known Odonoptera are Arnsbergian (Serpukhovian, 326.4–318.1 Ma) (Petrulevičius & Gutiérrez 2016), thus only 19.4 to 2.9 Ma older than the Moscovian (307.0–315.2 Ma), and they belong to much more ‘basal’ groups than those from the Xiaheyan locality. Also, representatives of the ‘Protozygoptera’, a group of Odonoptera much more ‘derived’ than the griffenflies, are known in the Moscovian of Avion (Prokop *et al.* 2014). Thus, it seems that the whole superorder Odonoptera is either much older (as supposed by Misof *et al.* 2014, among others), and/or that it knew a quick and important diversification during this rather short period.

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