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RAPID COMMUNICATION

The first Triassic 'Protodonatan' (Zygophlebiidae) from China: stratigraphical implications

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Abstract

The clade Triadophlebioptera within the Odonatoptera greatly diversified and became widely distributed worldwide during the Triassic. Although abundant insect fossils have been reported from the Triassic of China, no Triassic dragonflies have been recorded. In this paper, *Zygophlebia tongchuanensis* sp. nov., the first species of Zygophlebiidae discovered outside the Madygen Formation of Kyrgyzstan, is described from the Middle–Upper Triassic Tongchuan Formation of Shaanxi Province, northwestern China. The discovery extends the distribution of the family Zygophlebiidae in Asia, indicating a high diversity of Triadophlebioptera during Middle–Late Triassic times. Combined with the palaeontological and geochronological evidence, the age of the Tongchuan Formation is considered to be Anisian – Early Carnian, and the insect-bearing layers are considered to be Ladinian.

Keywords: Odonatoptera, Triadophlebiomorpha, Zygophlebiidae, Tongchuan Formation, Ladinian, China.

1. Introduction

After the Late Permian extinction event, the entomofauna greatly diversified during the Middle Triassic (Labandeira & Sepkoski, 1993; Béthoux, Papier & Nel, 2005; Ponomarenko, 2006; Shcherbakov, 2008*a*, *b*). The Odonatoptera were renewed by new taxa during the Middle and Late Triassic (Béthoux, Papier & Nel, 2005): Geroptera and 'Meganisoptera' did not survive the Permian–Triassic crisis, and the clade Odonatoclada emerged during the Permian but diversified in the Triassic with the clade Pandiscoidalia comprising the Permian Protanisoptera (and Permian Lapeyriidae (Nel, Gand & Garric, 1999)), true Odonata, and Triadophlebioptera. The last clade emerged in the Permian, greatly diversified during the Triassic and apparently vanished at the end of the Triassic Period without Jurassic representatives (Nel *et al.* 2001). It seems, however, to have been distributed worldwide as it is known from France (Middle–Upper Triassic), Germany (Middle Triassic), Kyrgyzstan (Middle–Upper Triassic), Russia (Upper Permian), Spain (Middle Triassic) and Australia (Middle Triassic) (Nel *et al.* 2001; Béthoux *et al.* 2009; Béthoux & Beattie, 2010).

In China, abundant dragonfly fossils have been reported from the Middle Jurassic – Lower Cretaceous (Fleck & Nel, 2002; Ren *et al.* 2012; Zhang *et al.* 2013; Zheng *et al.* 2015), and the oldest record is from the Lower Jurassic of Xinjiang (Zheng *et al.*, unpub. data). Although abundant insect fossils have been discovered in the Middle–Upper Triassic strata of China (Lin, 1978, 1992; IGCAGS, 1980; Lin & Mou, 1989; Zhang, 1996; Hong, 2007, 2009; Li, Hong & Yang, 2007; Sun & Hong, 2011), dragonflies have not previously been recorded from these assemblages. Qishuihe is a very important locality in Shaanxi Province, northwestern China, from which seven orders of insects (Blattaria, Coleoptera, Glosselytrodea, Hemiptera, Mecoptera, Miomoptera and Orthoptera) have been reported in the Middle–Upper Triassic Tongchuan Formation (IGCAGS, 1980; Hong, 2007, 2009; Li, Hong & Yang, 2007; Sun & Hong, 2011). Very recently, about 30 families in 12 orders were unearthed at this locality, adding to the insect diversity: here we describe the first Chinese Triassic 'Protodonate' from the Tongchuan Formation of the Qishuihe outcrop. The discovery confirms the wide distribution of the Triadophlebiomorpha during the Middle Triassic and provides evidence towards the age constraints on the Tongchuan Formation.

2. Geological setting

The specimen described herein was collected from the top of the lower part of the Tongchuan Formation in the Qishuihe outcrop, Hejiafang Village, Jinsuoguan Town, Tongchuan City, Shaanxi Province, China (Fig. 1; 28° 17′ 24″ N, 117° 52′ 32″ E).

The Tongchuan Formation conformably underlies the Upper Triassic Yanchang Formation and overlies the Lower–Middle Triassic Ermaying Formation. The lower part of the Tongchuan Formation consists of greyish green or red

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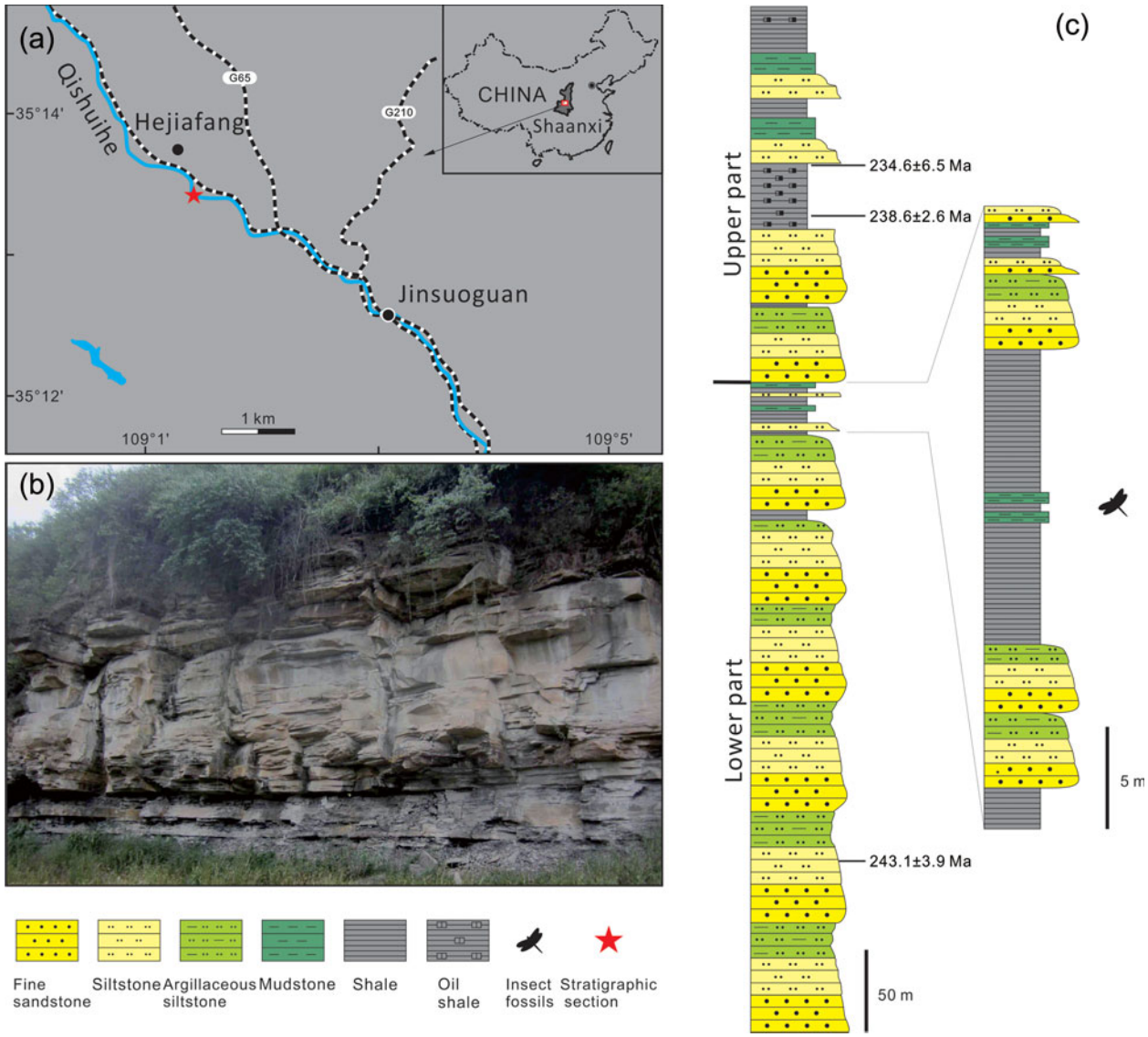

Figure 1. (Colour online) Fossil locality in the Qishuihe outcrop of Jinsuoguan Town, Tongchuan City, Shaanxi Province, China. (a) Geographical sketch map of Jinsuoguan Town; (b) photograph of the Qishuihe outcrop yielding the fossil insects; (c) stratigraphic column of the Tongchuan Formation (based on the data of IGCAGS, 1980; Li, Hong & Yang, 2007; Liu, Li & Li, 2013).

sandstone, with the top interbedded with shale and mudstone. The upper part is composed of greyish green or red fine sandstone and siltstone, interbedded with greyish green or black shale with black oil-shale at the top. The Tongchuan Formation yields bivalves, spinicaudatans, ostracods, insects, tadpole shrimps, fish, reptiles, sporopollen and plants (IGCAGS, 1980; Wu, Liu & Li, 2001; Hong, 2007, 2009; Li, Hong & Yang, 2007; Sun & Hong, 2011), and has a total thickness of *c.* 596 m. The layers bearing the insect fauna are considered to be Ladinian in age while the Tongchuan Formation is assigned an Anisian – early Carnian age in the present paper (see below).

3. Materials and methods

The specimen was examined dry and under alcohol using a Nikon SMZ1000 stereomicroscope. Observation was augmented by temporary wetting with laboratory alcohol which improved the contrast between the fossil and the matrix, eliminating the surface irregularity of the latter. Photographs were prepared using a Canon 5D digital camera and the line drawings were prepared from photographs using image-editing software (CorelDRAW X7 and Adobe Photoshop CS6). The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

The higher classification of the clade Triadophlebioptera, as well as family and generic characters followed in the present work, are based on the phylogenetic system proposed by Bechly (1996; unpub. data, 2016: https://dl.dropboxusercontent.com/u/13756162/Website/odonata/system.htm) and in part by Nel *et al.* (2001). All measurements are given in mm. The nomenclature of the dragonfly wing venation used in this paper is based on the interpretations of Riek (1976) and Riek & Kukalová-Peck (1984), as modified by Nel *et al.* (1993) and Bechly (1996). Vein abbreviations are as follows: AA, anterior anal; AP, posterior anal; Arc, arculus; Ax0, Ax1, Ax2, primary antenodal cross-veins; C, costal margin; CP, posterior costa; Cr, nodal cross-vein; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; DC, discoidal cell; MA, anterior median; MP, posterior median; N, nodus; R, radius; RA, anterior radius; RP, posterior radius; ScA, anterior subcosta; ScP, posterior subcosta; Sn, subnodal cross-vein.

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Figure 2. (Colour online) Photographs of *Zygophlebia tongchuanensis* sp. nov., holotype. (a) Part (NIGP162226a) of the wing; (b) counterpart (NIGP162226b) of the wing. Scale bars = 5 mm.

4. Systematic palaeontology

Order ODONATOPTERA *sensu* Brauckmann & Zessin, 1989
Clade TRIADOPHLEBIOPTERA Bechly, 1996
Subclade TRIADOPHLEBIOMORPHA Pritykina, 1981
Family ZYGOPHLEBIIDAE Pritykina, 1981
Genus *Zygophlebia* Pritykina, 1981

Type species Zygophlebia ramosa Pritykina, 1981

Zygophlebia tongchuanensis sp. nov.
Figures 2–4

Holotype. NIGP162226a (Fig. 2a) and NIGP162226b (Fig. 2b), a basally well-preserved wing (part and counterpart), deposited in NIGPAS.

Locality and Horizon. Qishuihe outcrop, Hejiafang Village, Jinsuoguan Town, Tongchuan City, Shaanxi Province, China; Tongchuan Formation, Anisian – lower Carnian (Fig. 1).

Diagnosis. Wing characters only. Complete wing 60 mm long (as estimated); four rows of cells between MP and CuA just below Sn; CuP slightly zigzagged basally; ScP basally curved and extremely close to RA before Arc.

Etymology. Named after the city of Tongchuan where the Qishuihe outcrop is located and which yielded the holotype.

Description. Wing hyaline (Figs 2–4). Preserved length 24.81 mm, estimated completed length 60 mm, maximum width 6.51 mm; distance from wing base to base of Arc: 7.28 mm; from wing base to N: 19.75 mm. Nodal structures well preserved, showing a nodal furrow, a slightly oblique Cr, and a slightly oblique Sn aligned with Cr (Nel *et al.* 1996, fig. 5). Primary antenodal cross-veins well preserved, Ax1 5.22 mm distal of Ax0 and aligned with base of Arc; Ax2 1.96 mm distal of Arc; Ax2 and Ax1 distinct with opposite obliquity. No secondary antenodal cross-veins present between primary antenodal cross-veins; 11 antenodal cross-veins present in first row (between C and ScP), not aligned with 11 of second row (between ScP and RA), distal of Ax2. Seven antesubnodal cross-veins present between RA and RP basal of Sn and well distal of Arc. Fifteen antefurcal cross-veins present between RP and MA basal of midfork (base of RP3/4) and distal of Arc. Six postnodal cross-veins present between C and RA, not aligned with five postsubnodal cross-veins between RA and RP1/2. ScP very close to RA basally and curved distally. Long posterior vein MAb present. Basal stem of Cu + AA rather long and separated slightly distal of Arc. AA, CuP and CuA distally separated nearly at same point, 11.35 mm from wing base. CuA closely parallel to MP at base, rather straight distally with one row of cells basally between MP and CuA and divergent distally with four rows just below N. CuP long, zigzagged basally, and parallel to CuA with only one row of cells in between. AA with one posterior branch directed towards wing base. MP closely parallel to MAa distal of Arc with only one row of cells in between, slightly narrowed distally. Midfork aligned with Sn with one or two rows of cells between RP1/2.

Remarks. The Triadophlebioptera *sensu* Bechly 1996 is currently divided into two subclades, Triadotypomorpha and Triadophlebiomorpha, but the relative positions of these clades are still unclear (Nel *et al.* 2001), with the latter subclade comprising Zygophlebiida (= Zygophlebiidae + (Xamenophlebiidae + Permophlebiidae)) and Triadophlebiida. The family Zygophlebiidae Pritykina, 1981 consists of four genera (Pritykina, 1981; Bechly,

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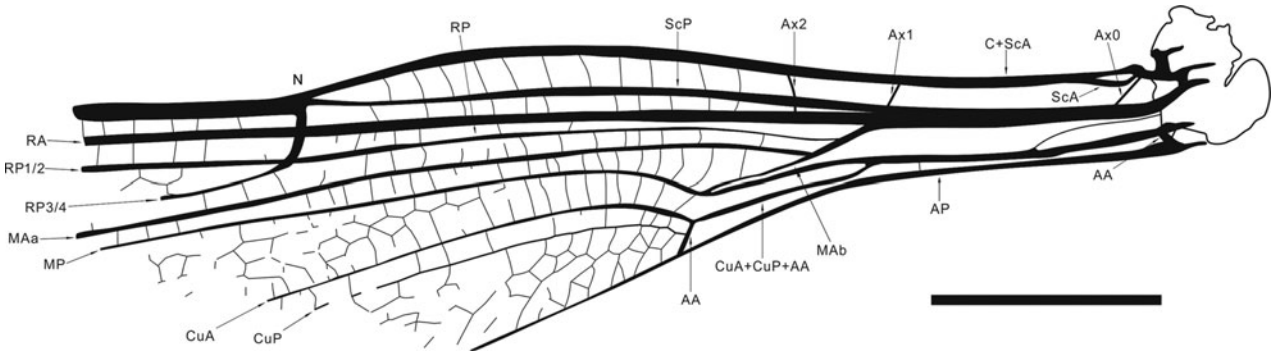

Figure 3. Line drawing of *Zygophlebia tongchuanensis* sp. nov., holotype (NIGP 162226a, b). Scale bar = 5 mm.

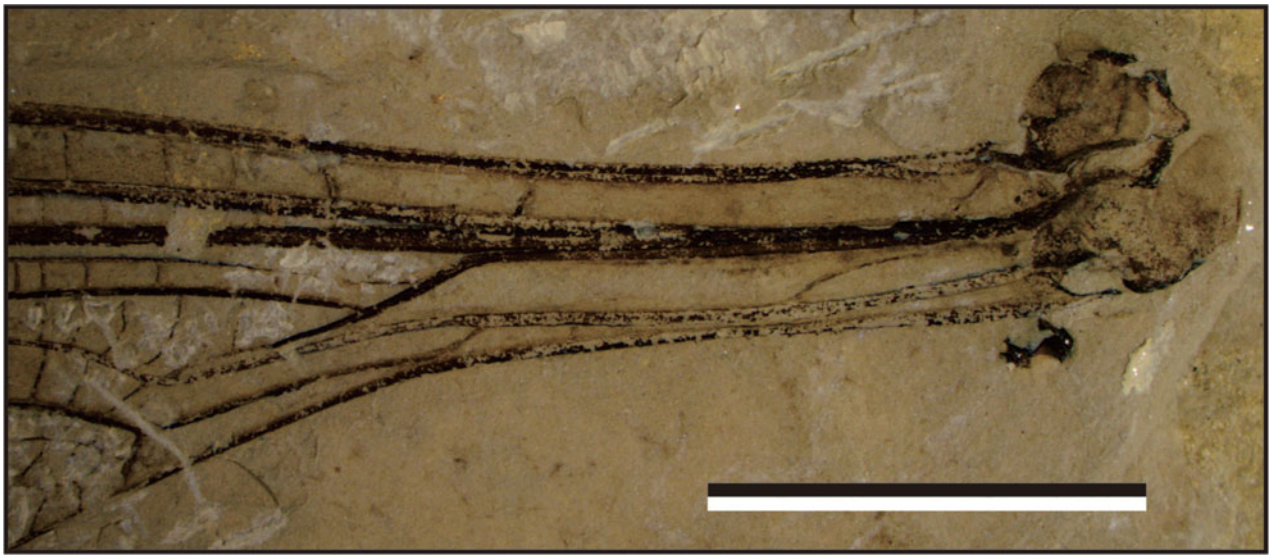

Figure 4. (Colour online) Wing base of *Zygophlebia tongchuanensis* sp. nov., holotype (NIGP162226a). Scale bar = 5 mm.

1996; Nel *et al*. 2001): *Zygophlebia* Pritykina, 1981, *Zygophlebiella* Pritykina, 1981, *Mixophlebia* Pritykina, 1981 and *Cyrtophlebia* Pritykina, 1981 (a poorly known taxon of uncertain affinities) from the Middle Triassic Madygen Formation of Kyrgyzstan.

The new specimen can be attributed to the subclade Triadophlebiomorpha Pritykina, 1981 by the following autopomorphies (Bechly, 1996): wing with a very long petiole; a unique type of petiole (MP and Cu basally separated, and distally fused together with AA; more distally, CuA + CuP + AA separated from MP); MP distinctly curved distal of its origin at distal angle of DC; very long and oblique discoidal vein MAb present.

The lack of information concerning the distal half of the wing renders the attribution of this specimen to a precise superfamily uncertain. Nevertheless, some characters including Cr and Sn being perpendicular to C, ScP and R, and the apical anal vein AA reduced to an oblique cross-vein between the posterior wing margin and CuP, are apomorphies supporting an attribution to the superfamily Zygophlebioidea (Bechly, 1996).

Within this clade, affinities with the Xamenophlebiidae Pritykina, 1981 are excluded because the midfork (basal division of RP into RP1/2 and RP3/4) is below Sn instead of shifted basally. In fact, the new specimen can be attributed to the family Zygophlebiidae by the closely parallel CuA and CuP with only one row of cells in between. Regarding the genera of the Zygophlebiidae, the new specimen can be excluded from *Zygophlebiella* Pritykina, 1981 because in the latter only two or three rows of cells are present in the area between CuP and the posterior wing margin, and CuA is more zigzagged than in *Zygophlebia* Pritykina, 1981 and *Mixophlebia* Pritykina, 1981 (in preserved part). Affinity with *Mixophlebia* can be excluded by MAb, CuP + AA and AA not being aligned. Due to absence of the basal wing half in *Cyrtophlebia* Pritykina, 1981 and the apical wing half in the new specimen, it is not easy to compare it with the former. However, Bechly (unpub. data, 2016: https://dl.dropboxusercontent.com/u/13756162/Website/odonata/system.htm) suggested that *Cyrtophlebia* could be related to Xamenophlebiidae, unlike the new fossil which actually shares a series of important characters with the genus *Zygophlebia*: CuA not zigzagged; wing broad with many cells (but less than in *Mixophlebia*); and numerous rows of cells in the area between CuP and the posterior wing margin (even if the exact number cannot be absolutely determined due to incomplete preservation: five or six rows can be observed).

The unique specimen shares nearly all the characters of the basal half of the wing with the type species *Zygophlebia ramosa* Pritykina, 1981, viz. AA reduced to an oblique cross-vein between the posterior wing margin and the branching of Cu + AA into CuA and CuP; CuA not zigzagged and without a posterior branch; CuA and CuP

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closely parallel with one row of cells in between; CuP + AA strongly zigzagged between point of separation of CuA from CuA + CuP + AA and point of separation between CuP and AA; CuA + CuP + AA fused to MP, but separated basal of base of Arc; and Cr and Sn perpendicular to ScP and RA. However, the new fossil is different from *Z. ramosa* in the following characters: wing larger, possibly 60 mm long (*c.* 40 mm in *Z. ramosa*); four rows of cells between MP and CuA just below Sn instead of one row; CuP slightly zigzagged basally; ScP basally more curved and extremely close to RA before Arc. These differences are sufficient to establish a new species.

5. Stratigraphic implications

The Tongchuan Formation was established in the Qishuihe outcrop of Shaanxi Province, northwestern China, by IGCAGS (1980), yielding abundant fossils. The age of the Tongchuan Formation was traditionally considered to be either Middle Triassic or Middle–Late Triassic (IGCAGS, 1980; Wu, Liu & Li, 2001; Hong, 2007, 2009; Li, Hong & Yang, 2007; Sun & Hong, 2011). In this formation, both the bivalve and plant assemblages indicate a Middle Triassic age, and the sporopollen assemblage resembles that in the underlying Lower–Middle Triassic Ermaying Formation (IGCAGS, 1980). The Ermaying Formation yields the reptiles *Shaanbeikannemeyeria* and *Sinokannemeyeria* (Sun, 1980) and is dated at 245.9 ± 3.2 Ma in its upper part (Anisian; Cohen *et al*. 2013; Liu, Li & Li, 2013), indicating a Middle Triassic age for the lower part of the Tongchuan Formation. The upper part of the Tongchuan Formation bearing the reptile *Yonghesuchus sangbiensis* was considered to be early Late Triassic in age (Wu, Liu & Li, 2001). Abundant insect fossils have been reported from the lower part of the Tongchuan Formation in the Qishuihe outcrop (IGCAGS, 1980; Hong, 2007, 2009; Li, Hong & Yang, 2007; Sun & Hong, 2011) and were regarded as Ladinian by Hong (2007, 2009). The lower part of the Tongchuan Formation in Shanxi Province was dated as 243.1 ± 3.9 Ma and the upper part as 234.6 ± 6.5 Ma, indicating a Middle – early Late Triassic age for the whole formation (Anisian – early Carnian (Cohen *et al*. 2013; Liu, Li & Li, 2013)), which could be supported by the above palaeontological evidence. The insect fauna was unearthed several hundred metres above the dated level ~243.1 Ma and c. 100 m below the dated level ~238.6 Ma (Fig. 1), indicating that the insect-bearing layers are most likely to be Ladinian in age.

All the known genera and species of the Zygophlebiidae were discovered in the Madygen Formation of Kyrgyzstan except this new Chinese species. In Kyrgyzstan, nearly 100 families in 20 insect orders have been discovered in the Madygen Formation, including ten families of Odonatoptera which mostly only appear in the Triassic (Shcherbakov, 2008*c*). The age of the Madygen Formation is considered to be Ladinian–Carnian (Shcherbakov, 2008*c*) based on the megaflora (Ladinian–Carnian (Dobruskina, 1995)) and insects (Carnian (Ponomarenko, 2002) or Ladinian (Shcherbakov, 2008*b*)). The discovery of *Z. tongchuanensis* sp. nov. in the Qishuihe outcrop supports a Ladinian age.

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