The first Late Triassic Chinese triadophlebiomorphan (Insecta: Odonatoptera): biogeographic implications

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The clade Triadophlebiomorpha represents a morphological 'link' between the Paleozoic griffenflies (Meganisoptera) and the modern taxa. Nevertheless they are relatively poorly known in the body structures and paleobiogeography. The Triassic dragonfly is extremely rare in China with only one previously recorded. A new family, Sinotriadophlebiidae Zheng, Nel et Zhang fam. nov., for the genus and species Sinotriadophlebia lini Zheng, Nel et Zhang gen. et sp. nov., is described from the Upper Triassic Baijiantan Formation of Xinjiang, northwestern China. It is the second Chinese Triassic odonatopteran and the second largest Mesozoic representative of this superorder in China. The discovery provides new information for the clade Triadophlebiomorpha during the Late Triassic and expands its distribution and diversity in Asia. The find reflects a close relationship between the two Triassic entomofaunas from Kyrgyzstan and the Junggar Basin, and provides a Carnian age constraint on the lowermost part of the Baijiantan Formation.

In China, Mesozoic dragonflies have been largely found in Middle Jurassic to Lower Cretaceous strata but are little known from the Triassic although a fragmentary "protodonate" (Zygophlebiidae) has been recently described from the Middle–Upper Triassic Tongchuan Formation of Shaanxi Province, China1. In the Junggar Basin of Xinjiang, northwestern China, a few insect fossils have been previously unearthed from Triassic strata2,3. Ten insect orders have been recently recorded from the Lower Jurassic of the Tuziakeneigou outcrop in Karamay City including a damsel-dragonfly Dorsettia sinica Zheng et al., 2016, which reflects a weak influence of the end-Triassic extinction on damsel-dragonflies or a quick dispersal of damsel-dragonflies during the earliest Jurassic4. In addition, four orders of insect fossils have been unearthed from the Upper Triassic Baijiantan Formation of the Shendiou outcrop in Karamay City, somewhat enhancing the distribution and diversity of the insect fauna during the Late Triassic. The clade Discoidalia is divided into two subclades: the Stigmoptera (including the modern Odonata) and Triadophlebiomorpha (Zygophlebiida + Triadophlebiida)5. The clade Triadotyromorpha is more widespread than the clade Triadophlebiomorpha as the former occurs in Kyrgyzstan, western Europe (France, Germany and Spain) and Australia6,7. All members of the clade Triadophlebiida are known from the Madygen Formation of southwestern Kyrgyzstan8.

Here we describe a new family Sinotriadophlebiidae attributable to the clade Triadophlebiida from the Upper Triassic Baijiantan Formation of the Shendiou outcrop, Karamay City, Xinjiang, northwestern China (Fig. 1A,B, 45° 44′ N, 85° 0′ E). The Baijiantan Formation unconformably underlies the Lower Jurassic Badaowan Formation in the Shendiou outcrop (Fig. 1C). It consists of grey-white or grey-yellow mudstone and silty mudstone interbedded with sideritic bands, yielding

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insects, kazacharthrans, fishes, plants and sporopollen and representing a lake facies. It has a total thickness of about 7.7 mm and is considered to be Carnian–Rhaetian (~237–201 Ma) in age in the present paper (see below).

Material

Systematic palaeontology

Order Odonatoptera (sensu Brauckmann & Zessin, 1989)
Clade Pandiscoidalia Nel, 2001
Clade Discoidalia Bechly, 1996
Clade Triadophlebiomorpha Pritykina, 1981
Clade Triadophlebiida Bechly, 1996
Family Sinotriadophlebiidae Zheng, Nel et Zhang fam. nov.
Genus Sinotriadophlebia Zheng, Nel et Zhang gen. nov.
Type species: Sinotriadophlebia lini Zheng, Nel et Zhang sp. nov. (Figs 2 and 3).

Diagnosis. AA with numerous parallel posterior branches towards wing margin; ScP crossing N and obliquely reaching wing margin distally with crossveins beneath it; RP and MAa sharing long common basal stem in basal Arc; Sn extremely prolonged and with several crossveins beneath it; CuA with numerous parallel posterior branches.

Etymology. The genus name is after Triadophlebia and Sina, Latin name for China. The species is named after Dr Lin Qibin, a Chinese palaeontologist.

Holotype. Specimen NIGP163160, a slightly damaged wing (part and counterpart), deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Locality and horizon. Shendigou outcrop, Karamay City, Xinjiang, China; Baijiantan Formation, Late Triassic (Carnian–Rhaetian).

Description. Wing hyaline, quite elongate, preserved length 99.53 mm, estimated complete length 101–102 mm, width at level of N 10.6 mm, maximum width 16.13 mm; distance from wing base to base of Arc 5.79 mm, and from base of Arc to N 19.95 mm. Nodal structures well preserved (Fig. 3D), showing nodal furrow,
the peculiar pattern of branching of IR2 and IR1 on RP2 in Zygophlebioidea \textsuperscript{8, 10} sensu Zygophlebioidea Pritykina, 1981 (MP, unlike in the Triadotypomorpha. Within the Triadophlebiomorpha, the affinity of the new genus with the long and oblique. It also shares a characteristic of this clade in the presence of numerous posterior branches of cells basally inbetween, and strongly divergent distally. CuP long, slightly curved, and somewhat parallel to CuA basally. AA with numerous parallel posterior branches, directed towards wing base, with distal part reaching posterior wing margin opposite base of RP3/4. MP slightly curved with several posterior branches. Postdiscoidal area between MAa and MP narrow and converging distally (Fig. 3G). MAa simple. RP3/4 nearly straight, aligned with oblique Sn, with numerous posterior branches between MAa and RP3/4. IR2 simple and probably separated from RP1 at 16.43 mm distal of base of RP3/4 (Fig. 3F) with two posterior branches. Base of IR1 not clear; one row of cells between IR1 and RP1; IR1 without posterior branches but a series of secondary longitudinal veins present between IR1 and RP2. No Pt present. Numerous postnodal crossveins present between C and RA, not aligned with numerous postsubnodal crossveins between RA and RP1.

Discussion

\textit{Sinotriadophlebia} gen. nov. has a highly developed N with a kink in ScP, obvious nodal furrow, aligned Cr and Sn, and a typical odonatoid DC basally open but distally delimited by a characteristically oblique vein MAb between MA and MP. These characters are apomorphies of the Discoidalia Bechly, 1996. It should be noted that Bechly\textsuperscript{10} assigned the two subclades Triadophlebiomorpha Pritykina, 1981 and Triadotypomorpha Bechly, 1996 to the clade Triadophlebioptera Bechly, 1996, considering that Triadotypomorpha also has a typical odonatoid DC closed distally by MAb. However, MAb is in fact absent from \textit{Triadotyptus guillaumei} Grauvogel and Laurentiaux, 1952, the type genus of the Triadotyptidae Grauvogel and Laurentiaux, 1952 within Triadotypomorpha\textsuperscript{11}. In addition, Bechly\textsuperscript{12} put the Piroutetiidae Nel, 1989 in the Triadotypomorpha, and here we restore it in its original position. A further difference between \textit{Sinotriadophlebia} and \textit{Triadotypus} is that MP is simple in the latter but it has numerous posterior branches in the former.

\textit{Sinoriadophlebia} has the following synapomorphies of the Triadophlebiomorpha: petiole very long and of unique shape (not formed by a fusion of CuA + CuP + AA with the anal margin as in other odonates with petiolated wings); MP distinctly curved distal of its origin at the distal angle of DC; and discoidal vein MAb very long and oblique. It also shares a characteristic of this clade in the presence of numerous posterior branches of MP, unlike in the Triadotypomorpha. Within the Triadophlebiomorpha, the affinity of the new genus with the Zygophlebioidea Pritykina, 1981 (\textit{Triadotypus} sensu Bechly, 1996) can be excluded because \textit{Sinotriadophlebia} does not share the peculiar pattern of branching of IR2 and IR1 on RP2 in Zygophlebioidea\textsuperscript{8, 10}. \textit{Sinotriadophlebia} also has the following synapomorphies of the Triadophlebiida Bechly, 1996 (Mitophlebiidae Pritykina, 1981 + Triadophlebioidea Pritykina, 1981): CuA + CuP + AA fused with MP and Sn very oblique. The Mitophlebiidae can be excluded from consideration by Sn not being concavely curved in \textit{Sinotriadophlebia}. The Triadophlebioidea comprises Pauroplophlebiidae Bechly, 1996 and Triadophlebiidae Pritykina, 1981. The absence of the fusion of ScP with RA from the base to N in \textit{Sinotriadophlebia} excludes affinity with Pauroplophlebiidae and Triadophlebiidae can also be excluded by the following differences: RP3/4 unforked in \textit{Sinotriadophlebia} but forked in Triadophlebiidae;
many antensubnodal crossveins present in the former but only one in the latter; and vestige of stem of media not suppressed or completely fused with the hind margin in the former. Sinoriadophlebia, however, shares with Triadophlebiidae the secondary fusion of the common stem of MP + Cu + AA with the hind margin of the wing.

In conclusion, Sinotriadophlebia can be attributed to neither the Mitophlebiidae nor the Triadophlebiomorpha (Fig. 4). A new family is proposed based on the following combined differences: large size with wing length reaching up to 100 mm (within the Triadophlebiida, all species are less than 80 mm except Neritophlebia longa Pritykina, 1981 being 120–125 mm in length); distal part of ScP crossing N very obliquely with crossveins beneath it; CuA with numerous parallel posterior branches (a character also present in Triadotypus, but more developed than in Sinotriadophlebia); RP and MAa fused into a long basal stem (a character also present in Triadotypus, but not in all other Triadophlebiida); Sn extremely oblique and very elongate, with several crossveins beneath it (a character shared with the Neritophlebiinae).

Sinotriadophlebia lini is the second largest Mesozoic odonatopteran from China, being slightly smaller than the damselfly Hsiufua chaoi (107.6 mm wing for forewing length) from the Middle-Upper Jurassic of Inner Mongolia. In addition, the Triassic Iverya averyi Béthoux & Beattie, 2010 is currently considered within Triadophlebiomorpha but not in Triadotypidae, showing combined characters of Triadotypidae and Triadophlebiomorpha. It shares the characters present in the Triadophlebiomorpha but not in Triadotypus: oblique MAa, well separated RP and MAa, and long petiole. However, it also shares with Triadotypus a CuA with numerous posterior branches and a simple MP, unlike in Triadophlebiomorpha. The discovery of much better preserved specimens is necessary to determine its exact position.
Numerous fossils including insects, kazacharthrans, fishes, plants and sporopollen have been unearthed from the Baijiantan Formation of the Shendigou outcrop in Xinjiang\textsuperscript{13, 14}. The sporopollen assemblage in the Baijiantan Formation is mostly inherited from that of the upper part of the Karamay Formation\textsuperscript{13} and the megaspore assemblage resembles that of the Upper Triassic Haojiagou Formation in the southern Junggar Basin\textsuperscript{15}, all indicating a Late Triassic age. The Baijiantan Formation is found in the northwestern Junggar Basin and can be correlated with the Huangshanjie-Haojiagou formations in the southern and eastern basin (Fig. 5). The Huangshanjie and Haojiagou formations are considered to be Carnian\textsuperscript{16} and Norian–Rhaetian in age\textsuperscript{17, 18}, separately. Therefore, the age of the Baijiantan Formation is probably Carnian–Rhaetian.

The clade Triadophlebiida were previously only recorded from the Madygen Formation of southwestern Kyrgyzstan\textsuperscript{8}. The age of the Madygen Formation is considered to be Ladinian–Carnian\textsuperscript{19–21}. The discovery of Sinotriadophlebia therefore points to a Carnian age for the lowermost part of the Baijiantan Formation. The relatively short distance between the Madygen fossil site and northwestern Xinjiang suggests a close relationship between the two insect faunas.

![Figure 4.](image_url) Hypothetical position of Sinotriadophlebiidae in Pandiscoidalia. The line drawing is made by D.-R.Z. using CorelDRAW X7 (Version number: 17.0.0.491, URL link: http://www.corel.com/cn/).

| System | Series | Stage | Age (Ma) | Junggar Basin |
|--------|--------|-------|----------|---------------|
|        |        |       |          | Northwestern Part | Southern Part | Eastern Part |
| Triassic | Upper | Rhaetian | ~209 | Baijiantan Fm. | Haojiagou Fm. | Haojiagou Fm. |
|         | Norian |       | ~227 |              |               |               |
|         | Carnian |      | ~237 |              | Huangshanjic Fm. | Huangshanjic Fm. |
| Middle  | Ladinian |      | ~242 | Karamay Fm. | Karamay Fm. | Karamay Fm. |
|         | Anisian |      |       |              |               |               |
| Lower   | Olenekian | Induan | ~247 | Baikouquan Fm. | Shaofanggou Fm. | Shaofanggou Fm. |
|         |        |       | ~251 |              | Jiucayuan Fm. | Jiucayuan Fm. |

![Figure 5.](image_url) Correlation of the Triassic strata in the Junggar Basin (★ star showing the formations yielding insect fossils; Fm. = Formation). The correlation table is made by D.-R.Z. using CorelDRAW X7 (Version number: 17.0.0.491, URL link: http://www.corel.com/cn/).
Methods
The specimen was examined dry under a Nikon SMZ1000 stereomicroscope. Photographs were taken using a Canon 3D 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 nomenclature of the odonotpteran wing venation used in this paper is based on the interpretations of Riek22 and Riek & Kukalová-Peck23, as modified by Nel et al.24 and Bechly16 25. Vein abbreviations are as follows: AA, anterior anal vein; Ax, primary antenodal crossvein; Arc, arculus; C, costa; CP, posterior costa; Cr, nodal crossvein; CuA, anterior cubitus; CuP, posterior cubitus; DC, discoidal cell; IR, intercalary radial vein; MA, anterior median; MP, posterior median; N, nodus; R, radius; RA, anterior radius; RP, posterior radius; ScP, posterior subcosta; Sn, subnodal crossvein.

The higher classification of Triadophlebiidae, as well as family and generic characters followed in the present work, is based on the phylogenetic system proposed by Bechly25 and modified by Nel et al.3.

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Author Contributions
D.Z. designed the project. D.Z., A.N., S.-C.C. and H.Z. performed the analytical work and wrote the manuscript. H.W., B.W., and E.A.J. collected data. All authors discussed and approved the final manuscript.

Additional Information
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