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A new damsel-dragonfly (Odonata: Anisozygoptera: Campterophlebiidae) from the earliest Jurassic of the Junggar Basin, northwestern China

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A new genus and species of campterophlebiid damsel-dragonfly, *Jurassophlebia xinjiangensis* gen. et sp. nov., is described from the Lower Jurassic Badaowan Formation in the Junggar Basin, northwestern China. *Jurassophlebia* differs from all other campterophlebiid genera in having PsA in the same orientation as the distal branch of AA, and in its uniquely open subdiscoidal cell with very acute apical angle in the hind wing. The new discovery adds to the Asian diversity of damsel-dragonflies in the earliest Jurassic.

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CAMPTEROPHLEBIIDAE have a worldwide distribution from the Late Triassic (*Sogdophlebia singularis* Pritykina, 1970, Rhaetian of Kyrgyzstan) to the Early Cretaceous, but particularly flourished in the Early Jurassic of Central Asia (Pritykina 1970, Kelly & Nel 2018). In China, campterophlebiids are the dominant odonatans in the Early–Middle Jurassic, being highly diversified in the Middle Jurassic Daohugou biota but rarely recorded in the Lower Jurassic of the Junggar Basin, the Middle Jurassic of Shanxi, and the Lower Cretaceous of Inner Mongolia and Hebei (Li *et al.* 2012a, 2012b, Zheng *et al.* 2016, 2017, 2018). Although over a thousand insect fossils have been collected by the present researchers from the Lower Jurassic Tuziakeneigou outcrop of the Junggar Basin, odonatans are quite rare, with only two records described to date—*Dorsettia sinica* Zheng *et al.*, 2016 and *Honghea xui* Zheng *et al.*, 2018.

Here, we report a new campterophlebiid damsel-dragonfly from the Tuziakeneigou outcrop, and

attribute it to a new genus and species. This discovery adds to the diversity of the Campterophlebiidae, and aids evaluation of the evolution and radiation of Campterophlebiidae during the earliest Jurassic.

Material and methods

The specimen described herein was collected from the middle of the Badaowan Formation as exposed in the Tuziakeneigou outcrop, Karamay City, Xinjiang, northwestern China (locality indicated by Zheng *et al.* 2016, fig. 1). The Badaowan Formation is about 182 m thick at this site, and considered latest Rhaetian to Sinemurian in age (Sha *et al.* 2015). Lithologically, the unit is mainly composed of grey and greyish-green sandstone, siltstone and mudstone, interbedded with thin conglomerate, coal and sideritic bands. Abundant bivalves, gastropods, spinicaudatans, insects, miospores and macroplant remains are found within fine-grained clastic rocks throughout this unit. The layers in which the insect fossils have been recovered are composed of brown coal and white laminated tuff. Species of five insect orders have been described to date, including

Odonata, Coleoptera, Mecoptera, Orthoptera, and 'homopteran' Hemiptera (Zhang 1996a, 1996b, 1997a, 1997b, Zhang *et al.* 2003, Zheng *et al.* 2016). However, more than one thousand insect fossils, representing 10 orders, have been unearthed from this locality, with the entomofauna dominated by Mecoptera and Coleoptera collected mainly from the tuff layers. Some upright in-situ woody stems are also preserved in the tuff, which contains clasts of pebbles and volcanic ash, reflecting boggy, peaty and volcanic depositional conditions. This collection of depositional environments probably contributes to the dominance of Mecoptera and Coleoptera in the assemblage, and may partially explain the rarity of odonatans (Larel & Danks 2006).

The specimen was examined dry 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 taken using a Canon 5D digital camera and line drawings were prepared from these photographs using image-editing software (CorelDraw X8 and Adobe Photoshop CS6). The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

The higher classification of fossil and extant Odonoptera is based on the phylogenetic system of Bechly (1996), with the dragonfly wing venation nomenclature used in this paper based on the interpretations of Riek (1976) and Riek & Kukalová-Peck (1984), as modified by Nel *et al.* (1993) and Bechly (1996). Venation abbreviations are as follows: AA—anterior anal; AP—posterior anal; Arc—arculus; Ax—primary antenodal crossvein; C—costa; Cr—nodal crossvein; CuAa—distal branch of anterior cubitus; CuAb—proximal branch of anterior cubitus; CuP—posterior cubitus; DC—discoidal cell; IR—intercalary radial vein; MAa—anterior branch of anterior media; MAb—posterior branch of anterior media; MP—posterior media; N—nodus; 'O'—oblique vein; PsA—pseudo-anal vein; Pt—pterostigma; RA—anterior radius; RP—posterior radius; Sn—subnodal crossvein; ScP—posterior subcostal; SdC—subdiscoidal cell. All measurements are given in millimetres.

Systematic palaeontology

Order Odonata Fabricius, 1793

Clade ISOPHLEBIOPTERA Bechly, 1996

Subclade ISOPHLEBIIDA Bechly, 1996

Superfamily ISOPHLEBIOIDEA Handlirsch, 1906

Family CAMPTEROPHLEBIIDAE Handlirsch, 1920

Type genus: *Campterothlebia* Bode, 1905

Jurassophlebia Zheng, Nel & Zhang gen. nov.

Type species. Jurassophlebia xinjiangensis Zheng, Nel & Zhang sp. nov.

Etymology. Named for the Jurassic period and the Greek word 'phlebia' (meaning 'veins').

Diagnosis. Male hind-wing characters only, body unknown. Subelliptical brown membrane along anal triangle, divided into two parts; anal area triangular in shape; Ax1 and Ax2 parallel, hypertrophied and of same obliquity; subdiscoidal cell posteriorly open, narrow and transverse and divided by two crossveins in its posterior part, with a length/width ratio >3:1; area between MP and CuA broad, but less than twice width of postdiscoidal area in basal part; postdiscoidal area with two or three rows of cells before level of N, distally constricted by an opposed curvature of related veins.

Jurassophlebia xinjiangensis Zheng, Nel & Zhang sp. nov. (Figs 1, 2)

Etymology. Named after Chinese province of Xinjiang, where the type species was found.

Diagnosis. CuA parallel with MP before reaching wing margin; CuAa with five well-defined posterior branches; Pt elongate, not braced.

Holotype. NIGP163294a,b, part and counterpart of a well-preserved male hind wing (Figs 1A, 2A).

Locality and age. Tuziakeneigou outcrop, Karamay City, Xinjiang, China; Lower Jurassic (uppermost Rhaetian–Sinemurian) Badaowan Formation.

Description. Single hind wing with apex missing (Fig. 1). Wing with short petiole (Fig. 2B,C); preserved length 54.74 mm, width at level of N 15.76 mm; distance from wing base to Arc 4.84 mm, from Arc to N 24.39 mm, and from N to Pt 16.04 mm. Primary antenodal crossveins strongly developed, with Ax0 near wing base (Fig. 2C), Ax1 3.67 mm distal of Ax0, and Ax2 4.65 mm distal of Ax1; Ax1 and Ax2 distinctly oblique, hypertrophied and roughly parallel (Fig. 2D). No secondary antenodal crossveins present between C and ScP; 11 secondary antenodal crossveins present between ScP and RA distal of Ax2. Fourteen antesubnodal crossveins present between RA and RP, extending from Arc to Sn. Mid-fork 9.2 mm distad of Arc, closer to Arc than to N. Five antefurcal crossveins present between RP and MA basal of mid-fork. Base of IR2 4.84 mm distad of mid-fork. DC basally closed (Fig. 2B), free of crossveins, length of proximal side 0.84 mm, length of anterior side 2.85 mm, length of distal side (MAb) 2.38 mm, and length of posterior side 3.04 mm. MAb well aligned with distal free part of CuA, and not orientated in single transverse plane with 'gaff'.

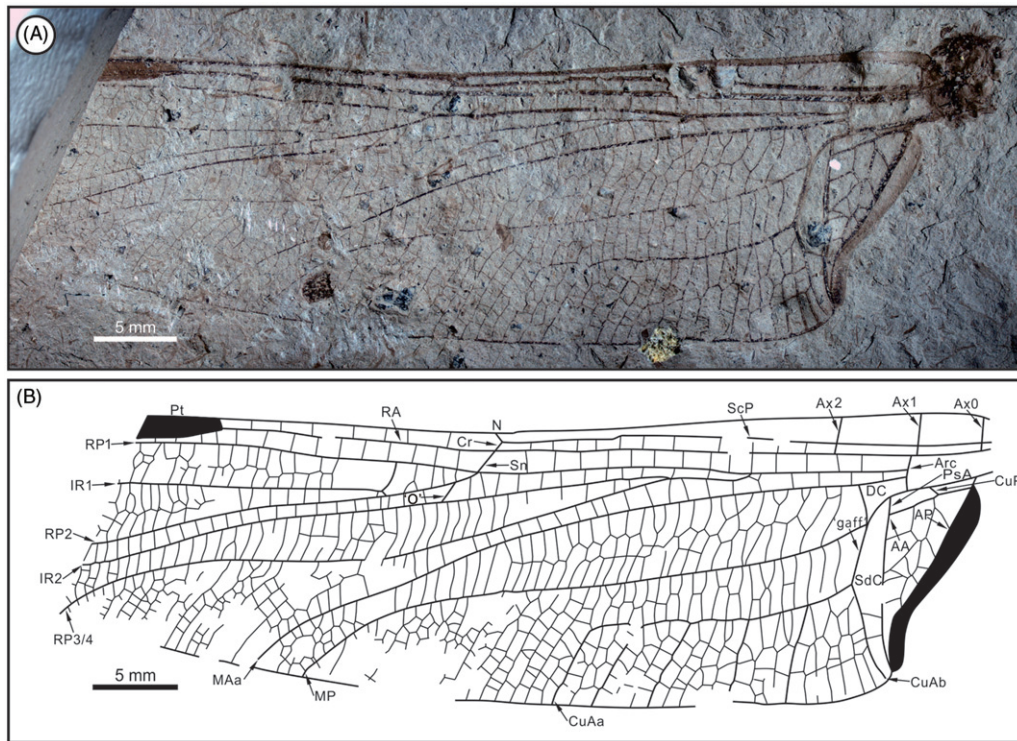


Fig. 1. *Jurassophlebia xinjiangensis* Zheng, Nel & Zhang, gen. et sp. nov.: **A**, Photograph of holotype part (NIGP163294a); **B**, Line drawing showing interpreted wing venation, based on part and counterpart.

MP nearly straight basally, curved distally, ending on posterior wing margin 40.51 mm from wing base. CuA separates from MP 8.25 mm from wing base and directed towards posterior wing margin, distally dividing into CuAa and CuAb; CuAa short and zigzagged, parallel with MP before bending towards posterior wing margin, ending on posterior margin basal of N, 17.6 mm from wing base; CuAb short, directed towards wing base but not meeting main branch of AA, thus SdC open. SdC transverse, with acute apical angle; 10.7 mm long and 1.8 mm wide; divided by two crossveins in its posterior part, with length/width ratio >3:1. Medial area free of crossveins; submedial area containing only CuP. PsA in same orientation as distal branch of AA, separating submedial and subdiscoidal areas. Anal area broad (Fig. 2B), 10.78 mm long and 5.11 mm wide; some irregular cells between AA and AP. Anal angle obvious (male specimen), with a subelliptical brown membrane rimming its proximal edge (hairy AP). AA without basal posterior branch; main branch of AA distally bent strongly towards posterior wing margin.

Nodal structures well preserved; Sn oblique and well aligned with Cr (Fig. 2E). Seven postnodal crossveins present between C and RA, not aligned with ten crossveins between RA and RP1. Pt not braced (Fig. 2F), sclerotized, preserved length 5 mm and maximum 1.23 mm wide. Four crossveins present between RA and RP directly below Pt. RP2 aligned with Sn. IR1 straight, separated from base of RP2 by five cells or 4.75 mm. Single 'O' present, separated by two cells or 1.3 mm from base of RP2. Twelve crossveins in space between

RP, RP2, IR2 and 'O'. Area between RP1 and IR1 with one row of cells basal of Pt, and three rows of cells distal of Pt base. Area between IR1 and RP2 progressively widening from the level of the Pt base. Area between RP2 and IR2 with one row of narrow cells at level of Pt. Area between IR2 and RP3/4 with one row of cells at base, progressively broadening to two or three cells' width below IR1 base, narrowing below Pt and broadening again along posterior wing margin. Area between RP3/4 and MAA with one row of narrow cells before base of IR1, but widening distally to encompass many cells along posterior wing margin. Postdiscoidal area between MAA and MP with one to three rows of cells before level of N, constricting to one row of cells distal of N before expanding to at least four cells along wing margin. Area between MP and CuA broad with one or two rows of large cells, less than twice width of postdiscoidal area in basal part. Area between CuAa and posterior wing margin with three to six rows of cells.

Discussion

The new specimen can be attributed to the family Campteropterygidae, rather than the Isophlebiidae, based on the following characters (Nel *et al.* 2009, Li *et al.* 2012a): hind-wing longitudinal veins (especially RP3/4) more or less undulate; no secondary antenodal crossveins between C and ScP; MAb and 'gaff' not orientated in one transverse plane; male hind-wing anal angle not rounded. Within the Campteropterygidae, *Jurassophlebia* shares its posteriorly open hind-wing

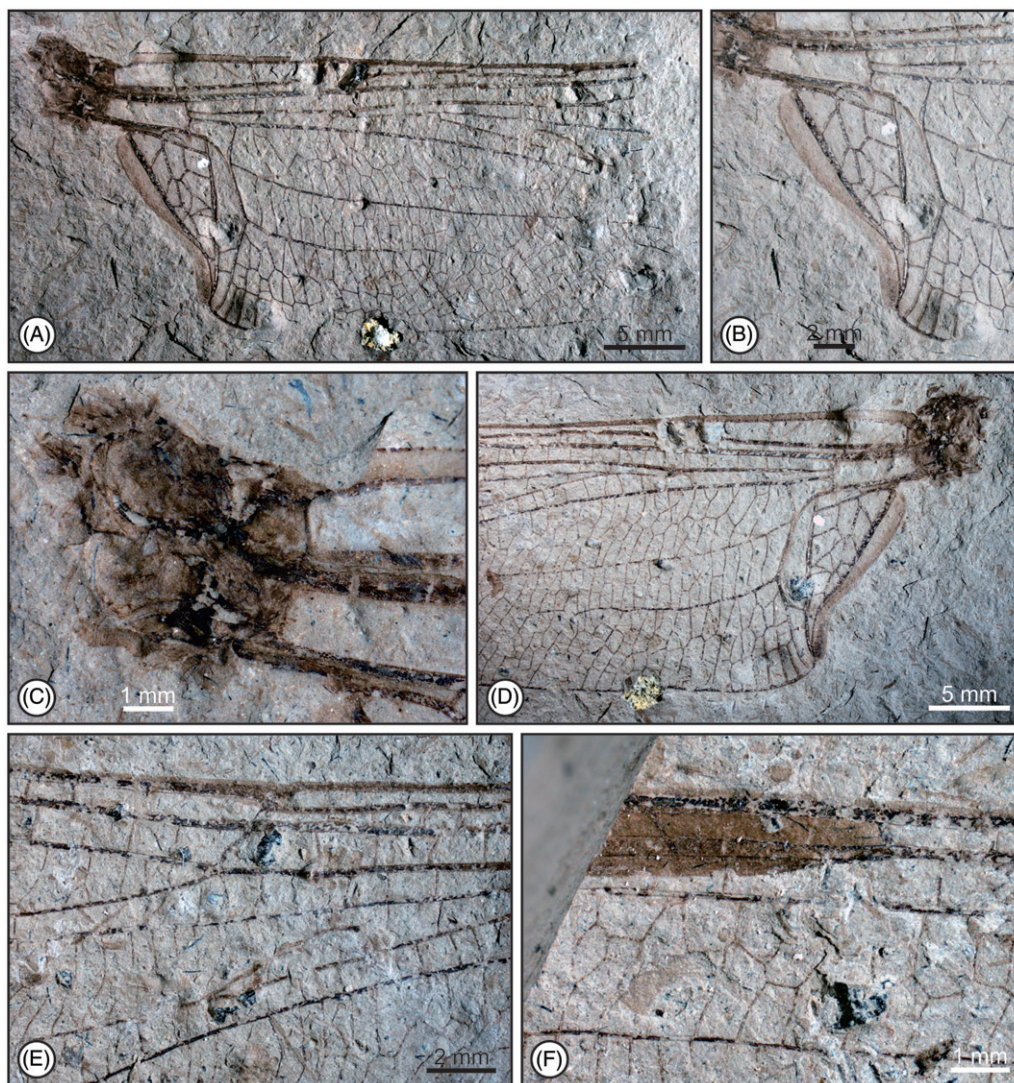


Fig. 2. *Jurassophlebia xinjiangensis* Zheng, Nel & Zhang, gen. et sp. nov., photograph of holotype (NIGP163294a,b): A, Counterpart; B–C, Wing base of counterpart; D, Basal area of part; E, nodal area of part; F, Pterostigmal area of part.

subdiscoidal cell with only eight other genera; viz., *Lateophlebia* Kelly & Nel, 2018, *Pteropteron* Pritykina, 1970, *Dorsettia* Whalley, 1985, *Oreophlebia* Pritykina, 1985, *Amnifleckia* Zhang *et al.*, 2006, *Pritykinia* Nel *et al.*, 2009, *Qibinina* Nel *et al.*, 2009 and *Gallodorsettia* Nel & Weis, 2017. *Jurassophlebia* is excluded from the genera *Pteropteron*, *Oreophlebia* and *Amnifleckia*, as it lacks a hook-like anal angle in the male hind wing.

The triangular anal area and subelliptical brown membrane along the anal triangle seen in *Jurassophlebia* are characters shared with only *Dorsettia*, *Gallodorsettia*, and probably with *Angaroneura* Pritykina, 1985, *Pteropteron*, and *Amnifleckia* (Zheng *et al.* 2016, Nel & Weis 2017). *Amnifleckia* and *Pteropteron* have already been excluded based on the absence of an anal hook in *Jurassophlebia*, and *Angaroneura* has a supplementary long vein in the subdiscoidal cell between AA and CuAb that also differs from *Jurassophlebia*. *Jurassophlebia* differs from *Dorsettia* in having two or three rows of cells

between MA and MP, and in the basal area between MP and CuAa; in the lack of parallel posterior AA branches in the anal area; and in the lack of transverse crossveins in the subdiscoidal cell (Zheng *et al.* 2016). Both *Gallodorsettia* and *Jurassophlebia* have two or three rows of cells between MA and MP, and in the basal area between MP and CuAa, and share a similarly shaped CuAa (Nel & Weis 2017); however, the former has transverse crossveins in the subdiscoidal cell, and three parallel posterior AA branches in the anal area, thereby differing from the new genus. Any similarities between *Jurassophlebia* and *Lateophlebia* can be excluded, since the former has its PsA aligned with the distal part of AA and develops a broad area between RP3/4 and IR2 at the level of the base of RP2 and the nodus, instead of this broadened region being distinctly distal of these structures as seen in *Lateophlebia*.

Within the Campterophlebiidae, *Jurassophlebia* can be easily distinguished from all other genera by the presence of PsA in the same orientation as the distal

branch of AA, and in its uniquely open subdiscoidal cell with very acute apical angle in the hind wing. It should be noted that the hairy AP and subelliptical brown membrane along the anal triangle are features seen in many Early Jurassic campteropteroidea, including *Jurassophlebia xinjiangensis* and *Dorsettia sinica* Zheng *et al.*, 2016 from China, *Dorsettia laeta* Whalley, 1985 from England, *Gallodorsettia kronzi* Nel & Weis, 2017 from Luxembourg, *Pteronopteron mirabile* Pritykina, 1970 from Kyrgyzstan and *Campteropteroidea elegans* Bode, 1905 from Germany. However, other Early Jurassic forms (e.g., *Sagulia ansinervis* Pritykina, 1970) lack this membrane.

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