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The first genus and species of Orthophlebiidae sensu stricto from the Lower Cretaceous Dabeigou Formation of Northern China

XIN-NENG LIAN^{1,2,3*}

¹Institute of Palaeontology, Yunnan Key Laboratory of Earth System Science, Yunnan University, Kunming 650500, China

²State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

Southwest United Graduate School, Kunming 650092, China

³✉ xnlian@nigpas.ac.cn; <https://orcid.org/0000-0001-6680-1781>

*Corresponding author

Abstract

“Orthophlebiidae” represent the oldest known mecopterans characterized by scorpion-tail-like male genitalia. They were the dominant mecopterans during the Jurassic, but experienced a marked decline during the Cretaceous. Herein, I describe and illustrate a new genus and species of Orthophlebiidae sensu stricto from the Lower Cretaceous Dabeigou Formation in Liaoning Province, Northern China. The new species, *Sinorthophlebia weichangensis* **gen. et sp. nov.**, is characterized by an elongate abdomen with segment VIII forming a conical shape, as well as a remnant fork of M_4 , indicating a relatively derived position within the family. Our discovery may provide a valuable reference for future studies on the evolution of wing venation in Panorpoidea and, more broadly, on the evolution of the Jehol entomofauna.

Key words: Panorpoidea, scorpionflies, Mesozoic, new taxon, Jehol Biota

Introduction

Mecoptera are among the most ancient holometabolous insects, possessing significant systematic and palaeoecological importance. They are closely related to Diptera and Siphonaptera, and thus provide crucial evidence for understanding the origins of these two orders (Krzemiński & Krzemińska 2003; Huang *et al.* 2012; Misof *et al.* 2014; Tihelka *et al.* 2020). In addition, the Mesozoic long-proboscid mecopterans are regarded as potential pollinators of gymnosperms (Ren *et al.* 2009; Lin *et al.* 2019). Mecoptera were highly diverse during the Permian (e.g., Novokshonov 1997; Lian *et al.* 2023), but declined in the Triassic (e.g., Zhang *et al.* 2022; Lian *et al.* 2024). Subsequently, Mecoptera reached its second peak of diversity in the Jurassic (e.g., Lian *et al.* 2021), but experienced a marked decline in the Cretaceous (e.g., Bashkuev & Jarzembowski 2023; Jouault *et al.* 2023; Kaczmarek *et al.* 2024; Ross 2024). In the Cenozoic, Mecoptera were mainly characterized by the diversification of the Panorpoidea (Archibald *et al.* 2013). Nevertheless, compared with their Jurassic flourishing, Mecoptera underwent a pronounced decline.

The polyphyletic “Orthophlebiidae”, which includes the families Orthophlebiidae Handlirsch, 1906, Protorthophlebiidae Soszyńska-Maj, Krzemiński & Kopeć, 2019, and Worcestobiidae Soszyńska-Maj, Krzemiński, Kopeć & Coram, 2017, was a megadiverse group flourished during the Jurassic, with more than one hundred species reported worldwide (Zhang *et al.* 2023). “Orthophlebiidae” has been regarded as the stem group of Panorpoidea Latreille, 1805 (Willmann & Novokshonov 1998; Krzemiński *et al.* 2017), characterized by their rostrate mouthpart, upturned and bulbous male genitalia, and comb-like branches of Rs_1 (Archibald 2005; Archibald *et al.* 2013). Panorpoidea have been the dominant mecopteran lineage since the Mesozoic. Panorpidae and Panorpoididae are the only two remnant families of Panorpoidea that survived through geological deep time. Panorpidae consist of more than 500 species worldwide (Wang & Hua 2022), accounting for five-eighths of the total extant mecopterans.

Fossil records indicate that several species of “Orthophlebiidae” were already present in the late Middle Triassic, as reported from the Tongchuan entomofauna (Hong *et al.* 2002; Hong 2009). The latest occurrences of

“Orthophlebiidae” are known from the mid-Cretaceous Burmese amber (Soszyńska-Maj *et al.* 2022; Zhang *et al.* 2023). Since the Cretaceous, “Orthophlebiidae” experienced a marked decline and were replaced by other Panorpoidea (e.g., Austropanorpidae, Holcorpidae, Dinopanorpidae, Eorpidae, Panorpidae, and Panorpodidae) in the Eocene, when the diversity of Panorpoidea culminated in the so-called “Eocene apex” (Archibald *et al.* 2013).

Cretaceous representatives of “Orthophlebiidae” were reduced compared with those of Jurassic. Notable examples include *Burmorthophlebia multiprocessa* Soszyńska-Maj, Krzemiński & Wang, 2022, *Burmorthophlebia macularis* Zhang, Lin, Shih & Ren, 2023 from the mid-Cretaceous Burmese amber (Soszyńska-Maj *et al.* 2022; Zhang *et al.* 2023), *Orthophlebia liaoningensis* Ren, 1997 from the Lower Cretaceous Yixian Formation of Northern China (Ren 1997), *Orthophlebia fangshanensis* Ren *et al.* 1995 from the Lower Cretaceous Lushangfen Formation of Northern China (Ren *et al.* 1995), *Orthophlebia yaojiashanensis* (Lin 1980) from the Lower Cretaceous Laocun Formation of Eastern China (Lin 1980), *Protorthophlebia brooksorum* Jarzembowski & Soszyńska-Maj, 2017 from the Lower Cretaceous Weald Clay Formation of England (Jarzembowski & Soszyńska-Maj 2017), and *Orthophlebia bifurcata* Giebel, 1856 and several unnamed specimens from the Lower Cretaceous Durlston Formation of England (Coram & Jepson 2012). *Choristopanorpa drinnani* Jell & Duncan, 1986 is distinct in having both forewing and hindwing armed with five-branched M, which obviously should not be assigned to Orthophlebiidae *sensu stricto* (following the definition of Soszyńska-Maj *et al.* 2019, hereafter referred to as Orthophlebiidae *s. str.*). A representative of “Orthophlebiidae” was illustrated from the Lower Cretaceous Crato Formation of Brazil, although its exact taxonomic placement remains uncertain (Bechly 2007). In addition, several specimens referable to Orthophlebiidae *s. str.* were also reported from the Lower Cretaceous Khasurty locality in Siberia (Kopylov *et al.* 2020).

The Jehol Biota is well known for its exceptionally preserved fossils, which provide crucial and direct evidence for several major evolutionary events, including the origin and early evolution of birds and feathers, as well as the origin of angiosperms. Insects of the Yixian Formation are the best known, with more than 500 species reported (Zhang & Zhang 2003). In contrast, only a few insects have been reported and described from the Dabeigou Formation (Zhang *et al.* 2010). Herein, I describe and illustrate the first species of Orthophlebiidae *s. str.* from the Lower Cretaceous Dabeigou Formation in Northern China.

Material and methods

The specimen was collected from the grayish-white tuff of the Dabeigou Formation near Fengjiadian Village, Banjieta Township, Weichang County, Hebei Province (detail map see Liao *et al.* 2020: fig. 1). Two beetle larvae of *Coptoclava* Ping, 1928 and a Diptera fragment are preserved on the same slab (Fig. 1A). *Coptoclava* is among the earliest reported fossil insects from China and one of the representative insects of the Jehol entomofauna (Ping 1928; Huang 2015; Zhao *et al.* 2018). The Dabeigou Formation, composed of volcanoclastic sedimentary rocks, contains fossil-bearing beds mainly in the lower parts of tuffaceous shales and is commonly dated to the Early Cretaceous based on paleontological evidence (Qin *et al.* 2018; Li & Li 2019; Liao *et al.* 2020; Lin & Li 2021; Lin *et al.* 2022). Many authors have conducted radiometric dating on the Dabeigou Formation. The upper part of the formation yields an age of 130.7 ± 1.2 Ma (He *et al.* 2006), whereas the lower part yields an age of 134.1 ± 1.0 Ma (Yu *et al.* 2022). In addition, the underlying Zhangjiakou Formation has an age of 135.2 ± 2.3 Ma (Zhang *et al.* 2005). Thus, the Dabeigou Formation is approximately 135 to 130 Ma in age, corresponding to the Valanginian–Hauterivian stages.

The specimen was prepared using a fine and sharp knife. Photographs were taken with a Zeiss Plan Apo Z $0.5\times / 0.125$ (FWD 114 mm) objective mounted on a Zeiss Discovery V16 microscope, with the specimen immersed in 75% ethanol to enhance contrast. Line drawing was made using Adobe Illustrator 2019 graphic software (San Jose, California). The specimen is housed in the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, China.

The venation terminology primarily follows the scheme proposed by Minet *et al.* (2010) and partly follows Bashkuev & Sukatsheva (2021).

Systematic palaeontology

Order Mecoptera Packard, 1886

Superfamily Panorpoidea Latreille, 1805

Family Orthophlebiidae Handlirsch, 1906

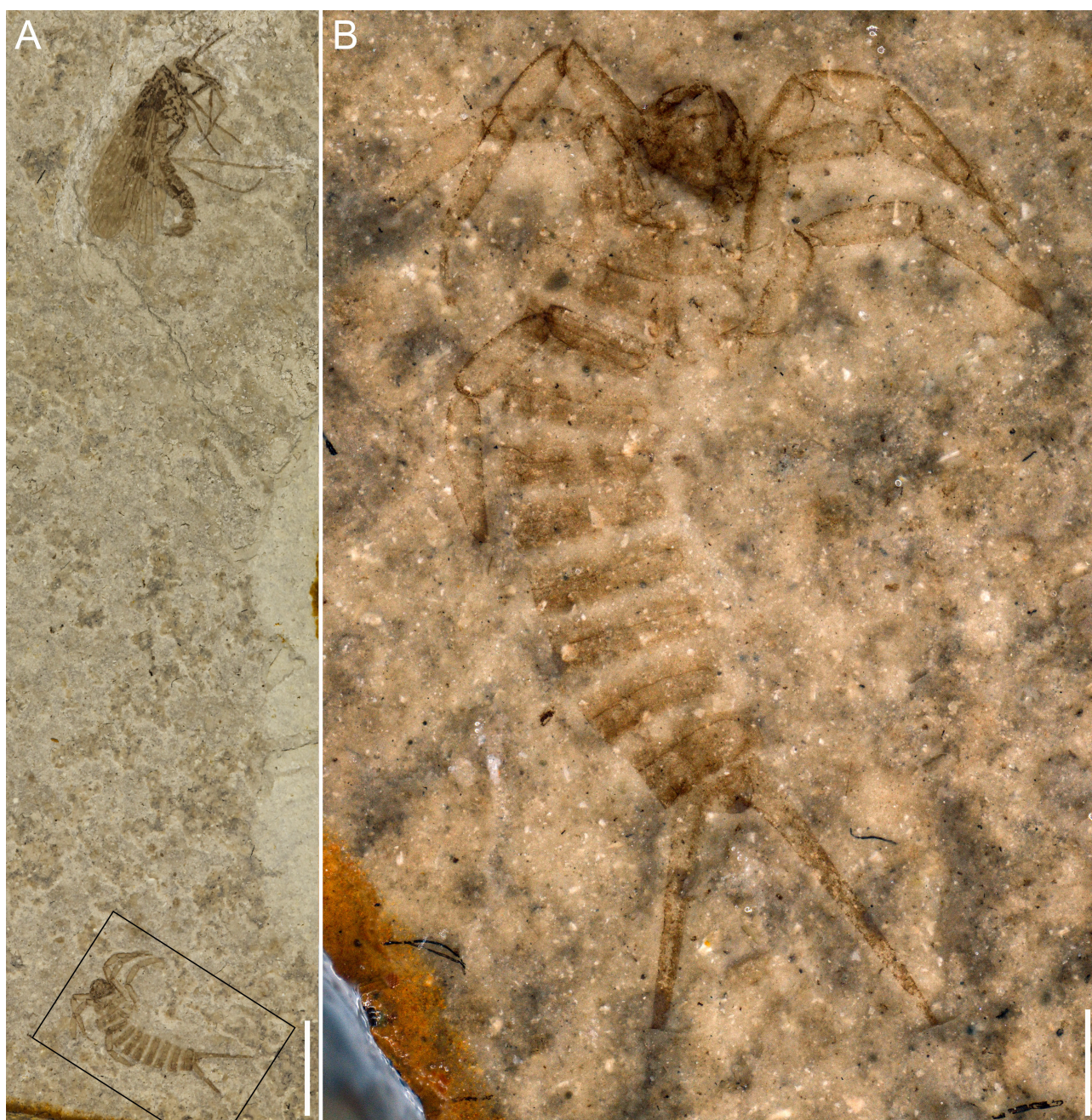


Figure 1. Photographs of holotype (NIGP209527) from the Lower Cretaceous Dabeigou Formation. **A**, *Coptoclava* sp. co-preserved with *Sinorthophlebia weichangensis* **gen. et sp. nov.** **B**, Enlargement of *Coptoclava* sp. Scale bars: 5 mm in **A** and 1 mm in **B**.

Genus *Sinorthophlebia* gen. nov.

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Etymology. The genus name is derived from *Sino-* (the Latinized prefix for “China”) and the genus *Orthophlebia*.

Type and Included species. *Sinorthophlebia weichangensis* **gen. et sp. nov.**

Diagnosis. Abdomen segment VIII short and conical shape in lateral view, Rs_{1+2} and Rs_{3+4} fork relatively late, M_4 fork small, and two m-cua crossveins.

Remarks. *Sinorthophlebia* **gen. nov.** and *Burmorthophlebia* are the only two genera of Orthophlebiidae that share a five-branched Rs . *Sinorthophlebia* differs from *Burmorthophlebia* in having a shorter rostrum, an abdomen without any non-genital grasping structures, a short and conical-shaped abdominal segment VIII, lacking ascending branches of Rs_1 , and forewing with M_4 bearing a small fork. It can be readily distinguished from *Protorthophlebia* (Protorthophlebiidae), which also has a five-branched Rs , by the much more distally positioned forks of Rs_{1+2} and

Rs_{3+4} , and by M_4 having a small fork rather than a deep one. The new genus resembles *Jurassipanorpa* Ding, Shih, Bashkuev, Zhao & Ren, 2014 (assigned to Panorpidae, though possibly not) in the venation pattern of Sc and Rs, but it differs the latter by its forewing having a single R_1 instead of a forked R_1 , a forked M_4 instead of a single M_4 , and two crossveins between M_4 and CuA rather than one (Ding *et al.* 2014).

***Sinorthophlebia weichangensis* sp. nov.**

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(Figs. 1–3)

Material. Holotype, NIGP209527, a nearly complete insect. Three wings (two hindwings and one forewing) overlapping, venation intricate, hardly discernible.

Etymology. The specific name is derived from the fossil locality, Weichang County.

Diagnosis. As for the genus.

Type locality and horizon. A locality near Fengjiadian Village, Weichang County, Hebei Province; Dabeigou Formation (Valanginian–Hauterivian).

Description. Male, body 10.4 mm long (from head to wing apex), abdomen longer than wings.

Head. 2.0 mm long, rostrum length twice as long as its maximal width; compound eye oval, small, long axis 0.5 mm; maxillary palps large, with four apical palpomeres visible, palpomeres length more than twice as wide; antennae filiform, pedicel drum-shaped, slightly wider than flagellomeres; flagellomeres length more than $1.5\times$ length of width, with 13 segments preserved.

Thorax. Pronotum narrow, 0.3 mm long, mesonotum 1.1 mm long, metanotum 0.6 mm long, all covered with sparse long setae; anterior margin of mesonotum with an elevated ridge.

Legs. Slender and long; femur robust, twice wider than tibia; tibia covered with random long setae, not arranged in ring, swelling at apex; tarsus pentamerous, the first tarsomere longer than the total length of the last three tarsomeres; the fifth tarsomere ended with a pair of bifid claws; tarsomeres 1–4 ventrally covered with two rows of long setae. Measurement of midleg: coxa 0.4 mm long; femur 1.7 mm long; tibia 2.0 mm long; the first tarsomere 1.2 mm long, the second tarsomere 0.6 mm long, the third tarsomere 0.4 mm long, the fourth tarsomere 0.3 mm long, and the fifth tarsomere 0.3 mm long. Measurement of hindleg: coxa 0.4 mm long, femur 1.9 mm long; tibia 3.2 mm long; the first tarsomere 1.3 mm long, the second tarsomere 0.8 mm long, and the third tarsomere 0.5 mm long.

Abdomen. Genitalia bulbous and upturn; abdominal segments tapering in width from I to VIII; I–V length distinctly shorter than wide, sternites and tergites separated; sternites and tergites of VI and VII incompletely fused: VI with a distinct seam between the tergite and sternite, and VII with a faint seam, whereas in VIII the tergites and sternites fully fused; segment VI with length slightly longer than wide; VII with length distinctly longer than wide, with terminal upper margin concave; VIII conical-shaped, terminal portion wide, longer than length; gonocoxite bulbous, gonostylus sickle-shaped, with a pointed terminal.

Wing. Forewing elongate, 8.4 mm long, and 2.5 mm wide; Sc moderately long, terminating beyond Rs_{1+2} fork, with one crossvein-like crossvein Sc_2 near fork of Rs; R_1 single, apically curved; Rs with five branches; Rs_{1+2} and Rs_{3+4} long, Rs_{1+2} 1.6 mm long, Rs_{3+4} 1.9 mm long; M with five branches, M_{1+2} $4.3\times$ length of M_{3+4} , M_4 with a apical small fork; two m-cua crossveins connecting M_4 and CuA; m-cua₁ connecting basal M_4 and CuA, aligned with crossvein cua-cup; M_5 reduced to a transverse strut; CuA and CuP single, CuA slightly sinuous near apex; two single anal veins visible; several crossveins located between branches of Rs and M.

Discussion

The genus *Protorthophlebia* was originally included within Orthophlebiidae s. str., characterized by the presence of a five-branched Rs. Soszyńska-Maj *et al.* (2019) elevated *Protorthophlebia* to family rank (Protorthophlebiidae), mainly based on its male abdomen being shorter than the wings, the shorter rostrum, while retaining the five-branched Rs in the wings as a diagnostic character. It is worth noting, however, that a five-branched Rs is also shared by the mid-Cretaceous genus *Burmorthophlebia* (Soszyńska-Maj *et al.* 2022; Zhang *et al.* 2023), which is armed with long rostrum and abdomen. Therefore, the number of Rs branches alone is clearly insufficient for distinguishing Protorthophlebiidae from Orthophlebiidae s. str. However, in both Orthophlebiidae s. str. and Protorthophlebiidae, the majority of species are known only from wing characters, and the taxonomy of many of these species is inevitably confused. In this paper, I tentatively follow the viewpoint of Soszyńska-Maj *et al.* (2019) in treating Protorthophlebiidae as a valid family.

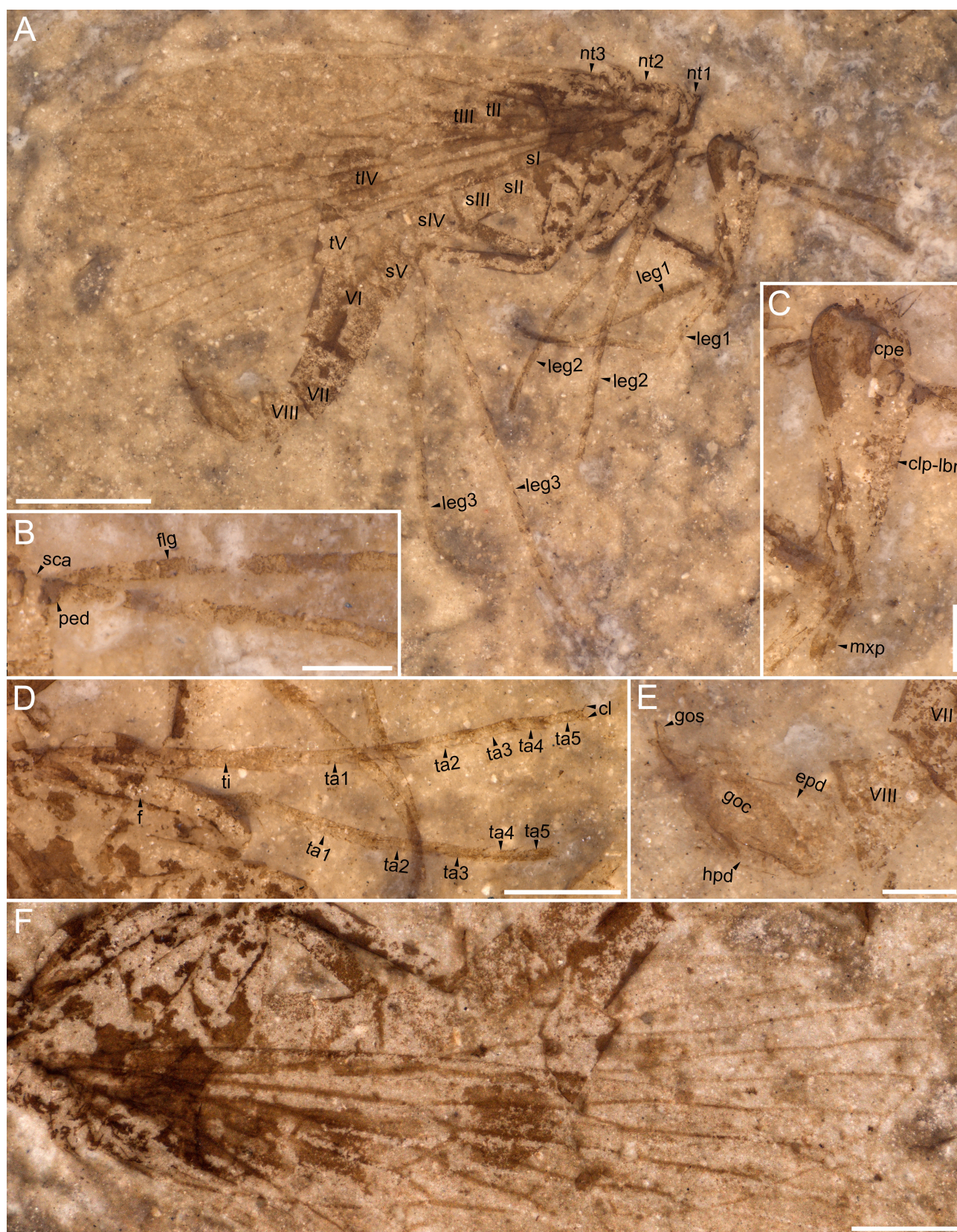


Figure 2. Photographs of holotype (NIGP209527) of *Sinorthophlebia weichangensis* **gen. et sp. nov.** from the Lower Cretaceous Dabeigou Formation. **A**, General habitus. **B**, Antennae. **C**, Head in lateral view. **D**, Midleg. **E**, Genitalia. **F**, Enlargement showing a forewing. Abbreviations: cl, claws; cpe, compound eye; epd, epandrium; f, femur; flg, flagellomere; goc, gonocoxite; gos, gonostylus; hpd, hypandrium; clp-lbr, clypeolabrum; leg1/2/3, foreleg, midleg, hindleg; nt1/2/3, proto-/meso-/metanotum; mxp, maxillary palp; ped, pedicel; ti, tibia; ta, tarsus; VI/VIII, abdominal segments VI/VIII; sI/V, sternites I/V; tII/V, tergites II/V; Scale bars = 2 mm in **A**, 1 mm in **D** and **F**, 0.5 mm in **B**, **C**, **E**.

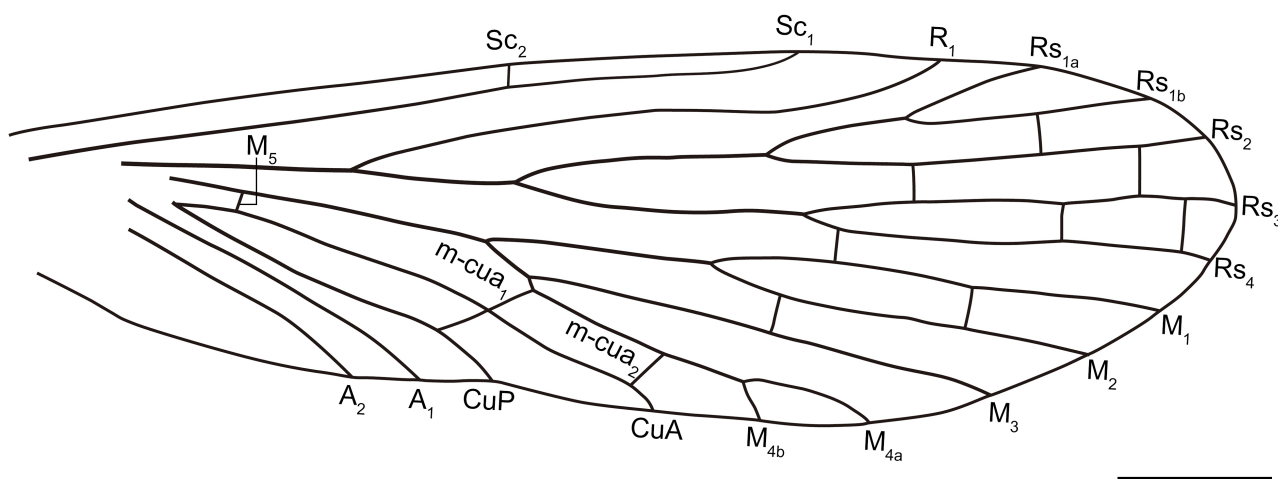


Figure 3. Line drawing of the forewing of *Sinorthophlebia weichangensis* **gen. et sp. nov.** Scale bar = 1 mm.

Sinorthophlebia weichangensis possesses an elongate abdomen exceeding the wing length and a relatively long rostrum, and is thus assigned to Orthophlebiidae s. str. (Soszyńska-Maj *et al.* 2019). The M_4 of *Sinorthophlebia* is forked near the apex, representing a derived character. In the derived lineages of Panorpoidea, such as Panorpidae and Panorpodidae, M_4 has been modified to a single vein (Wan & Hua 2022). The small fork of M_4 in *Sinorthophlebia* probably represents a transitional condition between the deep fork of basal Panorpoidea and the single M_4 typical of derived lineages (Archibald *et al.* 2013), suggesting that *S. weichangensis* may represent one of the most derived members of Orthophlebiidae s. str.

One of the most remarkable behavioral traits of scorpionflies is that males provide a nuptial gift (either a dead arthropod or a salivary mass) to females to prolong copulation (Byers & Thornhill 1983; Engqvist & Sauer 2003). An alternative strategy for males is to use grasping structures on the dorsal abdomen to control and forcibly mate with the female (Wang & Hua 2022). Studies on the extant *Neopanorpa* (Panorpidae) have shown that the length of the notal organ is closely correlated with the development of the salivary glands and mating tactics, reflecting an adaptive divergence between nuptial gifting and coercive copulation (Tong & Hua 2019). The abdomens of *Sinorthophlebia weichangensis*, as well as *Cantabra soplao* Soszyńska-Maj, Pérez-de la Fuente, Krzemiński & Wang, 2022, lack any non-genital seizing structures, suggesting that a nuptial gift strategy predominated over coercive tactics during copulation (Soszyńska-Maj *et al.* 2022).

Our discovery of *Sinorthophlebia weichangensis* **gen. et sp. nov.** represents the first scorpionfly described and illustrated from the Lower Cretaceous Dabeigou Formation, which preserves the first stage of the Jehol Biota (Zhang *et al.* 2010; Zhou *et al.* 2021). The conical-shaped abdomen VIII, the distal forks of Rs_{1+2} and Rs_{3+4} , and the distal forks of M_4 are distinctive characters within Orthophlebiidae s. str. The distal fork of M_4 suggests that *Sinorthophlebia* **gen. nov.** may represent one of the most derived members of Orthophlebiidae s. str. The new findings may provide a valuable reference for future studies on the evolution of wing venation in Panorpoidea and, more broadly, on the evolution of the Jehol entomofauna.

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