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New mecopteran insects from the Middle Jurassic Yangshuzhuang Formation of Jiyuan Basin, China

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Abstract

The Middle Jurassic Yangshuzhuang Formation in the Jiyuan Basin is rich in fossil insects; however, mecopterans have not been previously reported from this formation. Herein, we describe and illustrate five new species and two new genera of the 'Orthophlebiidae' *sensu lato* from the Yangshuzhuang Formation: *Protorthophlebia gracilis* **sp. nov.**, *Protorthophlebia curvata* **sp. nov.**, and *Jiyuanphlebia incompleta* **gen. et sp. nov.** of Protorthophlebiidae, as well as *Orthophlebia picta* **sp. nov.**, and *Quadrivena jiyuanensis* **gen. et sp. nov.** of Orthophlebiidae. Additionally, four new specimens are assigned to *Orthophlebia quadrimacula* Lin, 1982, as they share same coloured markings and similar venational pattern. Ten hindwing specimens of 'Orthophlebiidae' are also described and illustrated, representing eight distinct wing forms. Seven forewings and one possibly forewing of incompletely preserved are illustrated as at least five wing forms of 'Orthophlebiidae'. A fragmentary specimen is assigned to Mesopsychidae, although it can only be identified at familial level. Our findings indicated that the 'Orthophlebiidae' *sensu lato* were diverse in Jiyuan Basin during the Middle Jurassic, increasing the palaeodiversity of this group during the Jurassic. Moreover, the discovery of the same species in both the Yangshuzhuang Formation and the Zhiluo Formation suggests a potential stratigraphic correlation between these two formations.

Key words: Mecoptera, taxonomy, gen. et sp. nov., biostratigraphy

Introduction

'Orthophlebiidae' are extinct scorpionflies (Mecoptera: Panorpoidea) bearing a scorpion tail-like genital segment. Encompassing over 120 species (Soszyńska-Maj *et al.* 2020, 2022; Zhang *et al.* 2023), the polyphyletic group 'Orthophlebiidae' (including Orthophlebiidae and Protorthophlebiidae) is one of the most diverse mecopteran groups during the Jurassic period (Handlirsch 1939; Bode 1953; Zhang 1996; Willmann & Novokschonov 1998; Qiao *et al.* 2012). However, most orthophlebiids have been established based solely on isolated wings (many are hindwings). The lack of preserved body structures poses challenges for taxonomic studies. The 'Orthophlebiidae' serve as an evolutionary 'link' between the late Permian-Triassic Parachoristidae and the modern Panorpoidea, Panorpidae and Panorpodidae.

Some species with body structures reveal that Orthophlebiidae had evolved non-genital clamping systems as early as the Late Jurassic. *Orthophlebia heidemariae* Willmann & Novokshonov, 1998 exhibits a pair of small notal and postnotal organs along with a long falcate anal horn on abdominal segment V. Similarly, *Burmorthophlebia multiprocessa* Soszyńska-Maj *et al.*, 2022, preserved in mid-Cretaceous Burmese amber, possesses small notal and postnotal organs and a pair of relatively large anal horns. The swollen first metatarsal segments of Jurassic male 'Orthophlebiidae' are believed to have been used for sexual display (Zhang *et al.* 2021). These non-genital clamping organs likely functioned to stabilize and control females during copulation, thereby prolonging mating time and facilitating the transfer of more sperm (Soszyńska-Maj *et al.* 2022). Additionally, *Burmorthophlebia macularis* Zhang *et al.*, 2023, also from Burmese

amber, reveals that at least some Orthophlebiidae shared mouthparts with a prolonged clypeus and subgenae, closely resembling those of Panorpidae (Zhang *et al.* 2023).

The Yangshuzhuang Formation, located in the Jiyuan Basin, consists of lacustrine deposits characterized by greygreenish mudstone. This formation is abundant in fossil insects, including reported taxa such as Odonata, Hemiptera, and Diptera (Huang *et al.* 2018b, 2023; Fu & Huang 2020a, b; Liu & Huang 2020, 2021; Fu *et al.* 2023; Xu *et al.* 2023). However, Mecoptera have not previously been documented from this formation. Herein, we describe and illustrate some material of mecopterans from the Middle Jurassic (Callovian) Yangshuzhuang Formation, Jiyuan City, Henan Province, China.

Material and methods

The specimens were preserved in the brown-greenish mudstone, all collected from the top of the Middle Jurassic Yangshuzhuang Formation, Jiyuan City, Henan Province, China. Some specimens were prepared using sharp knives under a microscope. Photographs were captured with a digital camera attached to a Zeiss AxioZoom V16 stereomicroscope and later enhanced for contrast using Adobe Photoshop CC 2019. Line drawings were drafted in Adobe Illustrator 2019. All specimens are stored in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

The wing venation nomenclature generally follows Minet *et al.* (2010) and partial adoption of Bashkuev and Sukatsheva (2021). Venational abbreviations are as follows: C, costa; Sc, subcosta; h, humeral vein; R_1 , first branch of the radius; Rs, radial sector; M, media; CuA, anterior cubitus; CuP, posterior cubitus; A, anal vein; m-cua, crossvein between media and anterior cubitus

Systematic palaeontology

Order Mecoptera Packard, 1886

Family Protorthophlebiidae Soszyńska-Maj, Krzemiński & Kope, 2019

Protorthophlebia gracilis sp. nov.

Figure 1 urn:lsid:zoobank.org:act:2E1893B3-E5D8-4F3D-9684-E1580A0BE056

Material. Holotype: NIGP206317, a nearly complete forewing without a small apical part, measuring 10.7 mm in length and 3.0 mm in width, with a length-to-width ratio of 3.6. Paratype: NIGP206318, a forewing without apical part.

Etymology. The specific name is derived from the Latin *gracilis*, meaning 'slender', in reference to the slender wing.

Diagnosis. Forewings slender; costa area narrow; Sc run parallel to costa, with Sc₁ and Sc₂ well distant; two m-cua present between M_{ab} and CuA.

Type locality and horizon. Anyao Village, Jiyuan City, Henan Province, China; Middle Jurassic Yangshuzhuang Formation (Callovian).

Description. A slender forewing; costal area narrow, Sc long, run parallel to costa, terminated at level of R_{s_1} fork, with an anterior small branch; humeral short; R_1 curved apically, two crossveins present between Sc and R_1 ; pterostigma covering the apical Sc₁ and R_1 , with a vein-like bottom boundary; Rs with five branches, Rs_1 two branched, stem Rs_{1+2} 1.5 times as long as stem Rs_{3+4} , one long crossvein connecting apical stem Rs_{1+2} and R_1 ; M with five branches, stem M_{1+2} four times as long as stem M_{3+4} , stem M_4 smooth, thyridium present at fork of M; two m-cua present between M_{4b} and CuA; CuA and CuP fused basally, two crossveins linking M stem at basal part of CuA, one crossvein present between CuA and CuP; three anal veins present; one crossvein present between CuP and A_1 , A_1 and A_2 ; numerous crossveins located at apical branches of Rs and M.

Remarks. The new species, *Protorthophlebia gracilis* **sp. nov.**, differs from the specimen NIGP70076 of *Protorthophlebia latipennis* Tillyard, 1933 from the Lower Jurassic Shiti Formation in South China by its wing slenderer, costal area much narrower, Sc₂ forking earlier, R_1 distinctly curved at apex instead of rather straight, and A_3 much longer. It also differs from *Orthophlebia shartegica* Novokshonov & Sukatecheva, 2003 from the Upper Jurassic of Mongolia by its wing slenderer, costal area narrower, stem M_4 shorter, and anal veins with three branches.



Figure 1. *Protorthophlebia gracilis* **sp. nov.**, Middle Jurassic Yangshuzhuang Formation. **A**, Holotype, NIGP206317. **B**, Paratype, NIGP206318. **C**, Line drawing of holotype. **D**, Line drawing of paratype. Scale bars = 1 mm.

Protorthophlebia curvata sp. nov.

Figure 2 urn:lsid:zoobank.org:act:4328BDB5-6580-4E2A-AD52-4867184AFAC7

Material. Holotype: NIGP206319, a nearly complete forewing, 10.2 mm long (nearly complete), 3.6 mm wide. Paratype: NIGP206320, a strongly deformed forewing fragment.

Etymology. The specific name is derived from the Latin *curvata*, meaning 'curved', referring to the curved apex of R₁.

Diagnosis. Moderately rounded; costal area nearly as broad as subcostal area; Sc_1 relatively short; R_1 strongly curved at apex, and base of M_{4b} and M_{4a} desclerotized.

Type locality and horizon. Anyao Village, Jiyuan City, Henan Province, China; Middle Jurassic Yangshuzhuang Formation (Callovian).

Description. Forewing with wing base slightly shrunken; costal area moderately broad, Sc short, Sc₁ not reached R₁ fork; R₁ strongly curved after entering pterostigma; pterostigma covering apical Sc₁, with a vein-like bottom boundary; Rs with five branches, stem Rs₁₊₂ 1.5 times as long as stem Rs₃₊₄, Rs₁ forking into two branches, basal stem Rs₃₊₄ desclerotized; M with five branches, stem M₁₊₂ 3.7 times as long as stem M₃₊₄; base of M_{4a}, M_{4b} and fork of M desclerotized; stem M₃₊₄ short, two m-cua crossveins present between M_{4b} and CuA; CuA and CuP fused near wing base, CuA connected M stem by an oblique crossvein; two straight anal veins preserved; numerous thin crossveins present between each branches of Rs and M.





Figure 2. *Protorthophlebia curvata* **sp. nov.**, Middle Jurassic Yangshuzhuang Formation. **A**, Holotype, NIGP206319. **B**, Line drawing of Holotype. Scale bars = 1 mm in **A** and **B**.

Remarks. The new species, *Protorthophlebia curvata* **sp. nov.**, is similar to *P. gracilis* **sp. nov.**, but differs from the later by the combination of following characters: the wing is broader, with costal area nearly as broad as subcostal area (rather than distinctly narrower than the subcostal area); Sc terminates before Rs_1 fork instead of beyond Rs_1 fork; and basal portion of M_{4a} and M_{4b} desclerotized.

Genus Jiyuanphlebia gen. nov.

urn:lsid:zoobank.org:act:E04FB870-524F-4E14-B861-E4FABFF1761E

Etymology. The generic name is derived from the type locality, Jiyuan City, and the Greek word *phlebia*, meaning 'vein'.

Diagnosis. Forewing characters, Sc with a deep apical fork, Sc, long, more than half as long as Sc₁.

Remarks. The well-developed and elongate Sc_2 is absent in the group 'Orthophlebiidae', where Sc_2 typically appears as a short, crossvein-like structure. The relatively deep fork at the apical Sc is a typical character of Parachoristidae, a group that thrived during the Late Permian and Triassic periods. And the deep fork of Sc is an unique character of *Juraphlebia* within 'Orthophlebiidae', and an M vein with five branches further distinguishes it from Parachoristidae.



Figure 3. *Jiyuanphlebia incompleta* **gen. et sp. nov.**, Middle Jurassic Yangshuzhuang Formation. **A**, **B**, Holotype, NIGP206321a, b, part and counterpart. **C**, Paratype, NIGP206322. **D**, Line drawing of holotype. **E**, Line drawing of paratype. scale bars =1 mm.

Jiyuanphlebia incompleta gen. et sp. nov.

Figure 3 urn:lsid:zoobank.org:act:4380A619-C342-4E34-9CC9-37F4A30BDE23

Material. Holotype: NIGP206321, with part and counterpart, a forewing without basal portion, measuring 6.9 mm long (as preserved), 2.8 mm wide. Paratype: NIGP206322, a forewing without apical and posterior parts.

Etymology. The specific name is derived from the incomplete preservation of the specimen.

Diagnosis. Stem Rs_{1+2} nearly twice as long as stem Rs_{3+4} ; stem M_{1+2} more than four times as long as stem M_{3+4} .

Type locality and horizon. Anyao Village, Jiyuan City, Henan Province, China; Middle Jurassic Yangshuzhuang Formation (Callovian).

Description. Holotype: wing moderately broad, with costal area half as broad as subcostal area; Sc forked into two branches at apex, Sc₁ more than twice as long as Sc₂; R₁ single, distinctly curved near apex, a crossvein connected Sc and R₁; pterostigma lentoid, coloured, with a vein-like bottom boundary, covered the apical Sc₁ and R₁; Rs with five branches, stem Rs₁₊₂ 1.7 times as long as stem Rs₃₊₄, stem Rs₁₊₂ slightly longer than stem Rs₁; M with five branches, stem M₁₊₂ 4.6 times as long as stem M₃₊₄, stem M₄ short, M_{4b} curved at an angle close to 90 degrees at its base, where the crossvein m-cua arises; thyridium present at fork of M; two m-cua crossveins connected M_{4b} and CuA; CuA curved near apex, CuP single; numerous thin crossveins connected each branches of Rs and M.

Paratype: costal area narrow and fold, Sc with a deep fork at apex; Rs preserved with five branches, apical part missed; stem Rs_{1+2} 1.6 times as long as stem Rs_{3+4} ; M preserved only the stem M_{1+2} and M_{3+4} ; CuA and CuP single, fused near wing base, one crossvein connected stem M and CuA; thyridium present at the fork of M; three anal veins, one crossvein connected apical A_1 and A_2 , A_2 and A_3 , respectively; one crossvein connected stem Sc and R_1 , R_1 and stem Rs_{1+2} , respectively.

Family Orthophlebiidae Handlirsch, 1906 Orthophlebia Westwood, 1845

Orthophlebia quadrimacula Lin, 1982 Figure 4

Description of new material. NIGP206323, a forewing lost apical part, 1.5 mm long (as preserved), 0.6 mm wide. Wing preserved with three coloured bands and several basal coloured spots; Sc with one anterior small branch, costal area relatively narrow; crossvein sc-r₁ oblique, stem Rs_{1+2} longer than Rs_{3+4} ; M with five branches, stem M_{1+2} four times as long as stem M_{3+4} , stem M_{4a+b} short, thyridium present at fork of M; M_{4b} curved at an angle close to 90 degrees at its base, where the crossvein m-cua arises; CuA and CuP fused near wing base; three anal vein present, A₃ forked into two small branches; two crossveins present between M and Rs, M_{4b} and CuA, and CuA and CuP, respectively; stem M linked CuA by a crossvein at basal part; one crossvein connected apical A₁ and A₂, and basal A₂ and A₄, respectively.

NIGP206324 (Figs. 4B, E), a forewing preserved with apical part, 0.9 mm long, 4.5 mm wide; NIGP206325 (Fig. 4C), a forewing preserved with apical part, 0.8 mm long, and 4.9 mm wide. Both specimens preserved with three apical coloured bands; Sc terminated distad the Rs₁ fork, nearly parallelled to costa; R₁ curved apically, pterostigma margin unclear, mixed with the coloured pterostigmal band; Rs with six branches, stem Rs₁₊₂ longer than stem Rs₃₊₄; apical wing covered with dense numerous unpigmented crossveins; M with five branches. Additional specimens, NIGP206326, a fragment of apical forewing; NIGP206327, a fragment of middle forewing.

Remarks. These new specimens from the Yangshuzhuang Formation are assigned to *Orthophlebia quadrimacula* Lin, 1982, as they share nearly identical coloured patterns, which serve as valuable diagnostic features for distinguishing species. Additionally, the wing size of these specimens is comparable to that of the holotype. The Rs with six branches, and the ratios of stem Rs_{1+2} to stem Rs_{3+4} , stem M_{1+2} to stem M_{3+4} , as well as the position of the crossvein sc-r₁, are all highly similar to those of the holotype. Although the relative length of Rs, stem Rs_{1+2} , and stem Rs_{3+4} are slightly different, we do not consider these differences as significant enough for specific differentiation.



Figure 4. New material of *Orthophlebia quadrimacula* Lin, 1982, Middle Jurassic Yangshuzhuang Formation. **A**, NIGP206323; **B**, NIGP206324; **C**, NIGP206325; **D**, Line drawing of NIGP206323. **E**, Line drawing of NIGP206324. Scale bars = 1 mm.

Orthophlebia picta sp. nov.

Figure 5

urn: lsid: zoobank.org: act: 6A0855E7-8A10-4E3E-88E1-FAAF67483748

Material. Holotype, NIGP206328, a nearly complete forewing lacking a small part of base, 8.9 mm long, 3.3 mm wide. Paratype: NIGP206329a, b, with part and counterpart, the specimen without apical part and anal area, 9.1 mm long (as preserved), 3.7 mm wide; NIGP206330a, b, with part and counterpart, only preserved with apical wing, 6.5 mm long (only preserved a half), 3.2 mm wide. Additional specimens: NIGP206331 and NIGP206332.

Etymology. The specific name is derived from the Latin *picta*, meaning 'coloured', indicating the species is full covered by coloured markings.

Diagnosis. Moderately broad forewings nearly fully covered with coloured markings, with pale lines and spots aligned along the crossveins. Stem Rs_{1+2} distinctly longer than stem Rs_{3+4} , stem Rs_1 more than twice as long as stem Rs_{1a+b} . Stem M_{1+2} more than four times as long as stem M_{3+4} .



Figure 5. *Orthophlebia picta* **sp. nov.**, Middle Jurassic Yangshuzhuang Formation. **A**, Holotype, NIGP206328. **B**, **C**, Paratype, NIGP206329a, b, part and counterpart. **D**, Line drawing of holotype. Scale bars = 1 mm.

Type locality and horizon. Anyao Village, Jiyuan City, Henan Province, China; Middle Jurassic Yangshuzhuang Formation (Callovian).

Description. Relatively broad forewing, wing nearly fully covered with coloured markings, the crossveins area usually lucking pigment, wing base exhibit more unpigmented spots; costal area relatively narrow, subcostal area about twice as broad as costal area; Sc long, terminated the level of Rs₁ fork, run parallel to costa, with one short anterior crossvein-like branch; R₁ single, apical part strongly curved; pterostigma with a vein-like bottom boundary, with its coloured blending seamlessly with the wing markings, making it difficult to be distinguished; Rs with six branches, Rs₁ three branched, stem Rs₁₊₂ 1.5 times as long as stem Rs₃₊₄, stem Rs₁ twice as long as stem Rs_{1a+b}; M with five branches, stem M₁₊₂ more than five times as long as stem M₃₊₄, stem M_{4a+b} short, smoothly curved, two m-cua crossveins present; CuA and CuP single and fused near base, CuA connected M stem by an oblique crossvein; two anal vein preserved; numerous crossveins present between each branch of Rs and M, with the uncoloured lines and spots usually aligned along the crossveins.

Remarks. The preservation of coloured markings varies depending on conditions, as seen in our specimens NIGP206329a and NIGP206329b—while one part retains the coloured markings well, the counterpart does not. For specimens where coloured markings are absent or poorly preserved, classification should be approached with caution.

The new species, *Orthophlebia picta* **sp. nov.**, resembles *Orthophlebia diminuta* Bode, 1953, but differs from the latter (based on the drawing of Willmann, 1984: Fig. 1c) by wing relatively broader at base, stem M_{1+2} much shorter, and the space between A_1 and CuP moderately broad instead of narrow.

Subfamily Gigaphlebiinae Soszyńska-Maj & Krzemiński, 2018

Genus Quadrivena gen. nov.

urn:lsid:zoobank.org:act:DB3558BF-20E0-4274-B7D4-48AC9777FF1A

Type species. Quadrivena jiyuanensis gen. et sp. nov.

Etymology. The new genus name *Quadrivena* is derived from the Latin words *quadri*- meaning 'four' and *vena* meaning 'vein'. This name refers to the characteristic presence of four crossveins between Sc and R_1 , which distinguishes this genus within Gigaphlebiinae.

Diagnosis. The new genus differs from the other genera of Gigaphlebiinae by having four distinctive crossveins between Sc and R_1 .

Quadrivena jiyuanensis gen. et sp. nov.

Figure 6 urn:lsid:zoobank.org:act:D9A0BF85-5444-4685-A152-D13DF0180A3E

Material. Holotype, NIGP206333, a nearly complete forewing, measuring 30.8 mm (nearly complete) in length and 8.7 mm in width, with a length-to-width ratio slightly more than 3.5. Paratype, NIGP206334, a forewing only preserved with its apical part.

Etymology. The specific name is named after Jiyuan City, where the specimen was collected.

Diagnosis. Forewing characters, Sc with one anterior branch; four crossveins present between Sc and R_1 ; stem M_{4b+c} long, A_3 with an apical fork.

Type locality and horizon. Anyao Village, Jiyuan City, Henan Province, China; Middle Jurassic Yangshuzhuang Formation (Callovian).

Description. Holotype, forewing, elongate; wing fully covered with coloured markings, with some areas covered by rocks or broken with departed rocks; costal area with basal part and distal part moderately broaden; Sc long, with one anterior branch, forking at 7/10 of Sc; Sc₁ short, oblique, apical Sc₁ with an extra small vein that not reach to wing margin; four crossveins evenly located between middle part of Sc and R₁; R₁ single, apical part curved downwards; Rs ten branched, pectinate, stem Rs₁₊₂ distinctly longer than stem Rs₃₊₄; Rs₁ seven branched, Rs₂ single; Rs₃₊₄ fork not preserved, departed with rock; stem Rs longer than stem Rs₃₊₄; M six branched, M fork not preserved, M₁₊₂ long, M₃₊₄ four branched, stem M_{4b+c} long; M fork distinctly distad Rs fork; CuA and CuP single, CuA connected basal M with a crossvein, fused with CuP near wing base, two crossveins present between CuA and CuP; four anal veins present, A₁ and A₂ single, A₃ apically forked into two branches, crossvein a₁-a₂, a₂-a₃ present.

Remarks. The new species, *Quadrivena jiyuanensis* gen. et sp. nov., can be confidently placed within the subfamily Gigaphlebiinae based on its forewing with large size, Rs with nine to ten branches, and M with six branches. The four crossveins between Sc and R_1 are strong and distinctive in the holotype. Furthermore, all reported specimens of Gigaphlebiinae are in well-preserved condition (Soszyńska-Maj et al. 2018; Lian et al. 2021), but none have been reported with four crossveins between Sc and R_1 . Therefore, we confidently argue that the presence of these four crossveins is a unique character of the new species, justifying the establishment of a new genus based on this character.

Quadrivena jiyuanensis gen. et sp. nov. can be distinguished from related taxa by the following characters. It differs from *Gigaphlebia palmaris* (Martynova, 1948) in having Sc with two branches instead of three, Rs with ten or nine branches instead of eight branches, M_{4b+c} much longer, and present of four crossveins between Sc and R_1 . It differs from *Gigaphlebia grandis* (Martynova, 1927) by stem Rs_{1+2} longer than stem Rs_{3+4} instead of stem Rs_{1+2} shorter than stem Rs_{3+4} , Rs longer than Rs_{3+4} instead of shorter, stem M_{4b+c} long, present of four crossveins between Sc and R_1 , and A_3 with two branches instead of one; differs from *Gigaphlebia riccardii* (Petrulevičius & Ren, 2012) in having Sc with two branches instead of three, stem Rs longer than stem R_{3+4} instead of shorter, stem R_{3+4} instead of shorter, stem Rs_{1+2} longer than stem Rs_{1+2} longer than stem Rs_{3+4} instead of three, stem Rs longer than stem R_{3+4} instead of shorter, stem Rs_{1+2} longer than stem Rs_{1+2} longer than stem Rs_{1+2} longer than stem Rs_{3+4} instead of three, stem Rs longer than stem R_{3+4} instead of shorter, stem Rs_{1+2} longer than stem Rs_{3+4} instead of shorter, stem Rs_{3+4} instead of shorter.

instead of shorter, stem M_{4b+c} long, present of four crossveins between Sc and R_1 , and A_3 with two branches instead of one. It differs from *Longiphlebia stigmosa* (Qiao & Ren, 2012) by Sc fork earlier, stem Rs longer than stem R_{3+4} instead of shorter, present of three crossveins between Sc and R_1 , and A_3 with two branches instead of single. It differs from *Longiphlebia incompleta* Lian, Cai & Huang, 2021 by absent of hyaline spots, Sc with two branches instead of five branches, Rs longer than stem R_{3+4} instead of shorter, present of four crossveins between Sc and R_1 , and A_3 with two branches instead of five branches, Rs longer than stem R_{3+4} instead of shorter, present of four crossveins between Sc and R_1 , and A_3 with two branches instead of shorter branches instead of shorter.



Figure 6. *Quadrivena jiyuanensis* sp. nov., Middle Jurassic Yangshuzhuang Formation. A–C, Holotype, NIGP206333, B and C are enlargement from A. D, Paratype, NIGP206334. E, Line drawing of holotype. Scale bars: A and E = 5 mm, B-D = 2 mm.

Hindwings of 'Orthophlebiidae'

Hindwings of 'Orthophlebiidae' differ from their forewings in several distinctive characters: Sc is significantly shorter and unbranched; R_1 possesses an apical fork; M has four branches instead of five; and CuP fuses with A_1 rather than CuA. Generally, the number of Rs branches remains consistent between hindwings and forewings, which provides

a useful character for generic classification. However, the isolated hindwings of most Mecoptera are inadequate for precise taxonomic classification, as similar venation patterns may be shared across different genera. As a result, we refrain from assigning our new fossil hindwings to specific species when forewings and hindwings are preserved separately.



Figure 7. Hindwings of 'Orthophlebiidae'. A, NIGP206335. B, NIGP206336. C, NIGP206337. D, NIGP206338. E, NIGP206339. F, NIGP206340. G, NIGP206341. H, NIGP206342. I, NIGP206343. A, B, D, F, and H are hindwings of Protorthophlebiidae indet. C, E, G, and I are hindwings of Orthophlebiidae indet. Scale bars = 1 mm.

A total of ten hindwing specimens (NIGP206335–NIGP206344) were discovered from the Yangshuzhuang Formation. Among these, five specimens exhibit a five-branched Rs (Figs. 7A, B, D, F, H), and are assigned to Orthophlebiidae. Four specimens display a six-branched Rs (Figs. 7C, E, G, I), which are attributed to Protorthophlebiidae.

NIGP206335 (Figs. 7A, 8) and NIGP206336 (Fig. 7B) share considerable morphological similarities and are likely conspecific. NIGP206335 measures 7.8 mm in length and 2.6 mm in width, while NIGP206336 measures 6.7 mm in length and 2.4 mm in width. Differences between the two include the relative lengths of Sc, the comparative fork levels of Rs_{1+2} and Rs_{3+4} , the comparative fork levels of M_{1+2} and M_{3+4} , and the arrangement of certain crossveins.

NIGP206338 (Fig. 7D) is a slender wing, measures 9.5 mm in length and 2.9 mm in width, however, the deformed wing suggests it would be wider. This specimen exhibits coloured markings that are darker at the wing apex than at the base. The pterostigmal area is large, and R_{1b} is long and distinct. The fork of M_{1+2} and M_{3+4} occurs later, with the stem of M_{1+2} being twice as long as that of M_{3+4} .

NIGP206340 (Fig. 7F) measures 6.4 mm in length (as preserved) and 2.6 mm in width. Notable features include R_1 fork being distad R_{s_1} fork, stem $R_{s_{1+2}}$ being equal in length to stem R_{s_1} , branches of R_{s_1} being much longer than stem R_{s_1} , and stem M_{1+2} being about twice as long as stem M_{3+4} .

NIGP206342 (Fig. 7H) measures 8.8 mm in length (as preserved) and 2.6 mm in width. It is distinctive for its wing densely covered with coloured markings. The stem Rs_{1+2} is as long as stem Rs_1 , though the branches of Rs_1 are significantly shorter than the stem.

NIGP206337 (Fig. 7C) and NIGP206343 (Fig. 7I) are both large and exhibit distinct coloured markings. NIGP206337 is 6.3 mm wide, while NIGP206343 is 4.1 mm wide (incomplete). The two specimens represent different species, as evidenced by differences in their coloured markings and venation. NIGP206337 has markings distributed in bands, while those of NIGP206343 are not banded. Additionally, the fork levels of R_1 differ, and R_{1b} in NIGP206337 is distinctly curved.

NIGP206339 (Fig. 7E), an elongate hindwing, measures 8.9 mm in length and 2.8 mm in width. Preserved with part and counterpart, both lack coloured markings. The costal area is notably narrow, and the stem Rs_1 is long. NIGP206341 (Fig. 7G) is relatively broad and almost completely covered with coloured pigments. Its stem Rs_{1a+b} is

short. In conclusion, hindwings of mecopterans from the Yangshuzhuang Formation exhibit significant morphological diversity. The branches of Rs can be categorized into two groups: five-branched and six-branched, which distinguish Protorthophlebiidae from Orthophlebiidae. The ten specimens can be divided into eight distinct wing forms, with two

specimens assigned to the same form and one specimen being too fragile for precise classification.



Figure 8. Line drawing, NIGP206335.

Undetermite forewings of 'Orthophlebiidae'

We also collected some incomplete forewings from the Yangshuzhuang Formation (Fig. 9). Due to the lack of sufficient information, we have not assigned them to specific species, nor have we described new species that include them. Among these, NIGP206381 (Fig. 9H) is not identifiable as either a forewing or a hindwing because the key distinguishing

characters between the two are not preserved. However, its dense pigmented markings and the pale, elongated strip at the wing apex suggest that it is distinctive from other wings of Jiyuan Basin. Its Rs has six branches, allowing it to be placed within Orthophlebiidae. NIGP206374 (Fig. 9A) and specimen NIGP206376 (Fig. 9C) also feature an Rs with six branches, and can be assigned to Orthophlebiidae. NIGP206374 has a densely punctate membrane, while NIGP206376 has a smoother membrane surface, and there are clear differences in the relative lengths of their stem Rs₁, Rs_{1a-c}, and Rs_{1a+b}, leading to their identification as distinct wing forms. NIGP206377 (Fig. 9D) preserves an Rs with five branches, and can be placed within Protorthophlebiidae. Specimen NIGP206380 (Fig. 9G) shows distinct sparse, block-like wing spots, which clearly differentiate it from other specimens, indicating it represents a separate wing form. NIGP206375 (Fig. 9B), NIGP206378 (Fig. 9E) and NIGP206379 (Fig. 9F) lack sufficient detail in their Rs to be assigned to specific genera and species; however, NIGP206379 does have dense pigmented markings and may belong to the same wing form as NIGP206381.

In conclusion, the specimens discussed above represent at least five forewing forms, three of which can be assigned to Orthophlebiidae, one to Protorthophlebiidae, and the other one may belong to either of the two families.



Figure 9. Undetermined forewings of 'Orthophlebiidae'. **A**, NIGP206374. **B**, NIGP206375. **C**, NIGP206376. **D**, NIGP206377. **E**, NIGP206378. **F**, NIGP206379. **G**, NIGP206380. **H**, NIGP206381. Scale bars = 1 mm.

Mesopsychidae indet.

Figure 10

Specimen NIGP206345a, b, part and counterpart, incomplete forewing, deformed and twisted. Costal area nearly as broad as subcostal area, Sc with two short anterior branches, the apical anterior branch oblique, the basal one transverse; humeral vein located near wing base; a crossvein present between apical Sc and R_1 , two crossveins present between R_1 and stem Rs_{1+2} ; Rs_1 and Rs_2 only preserved with their basal parts; CuA and CuP single in visible parts, space between CuA and CuP broad, CuA base connected the fusion of M and CuA, two cua-cup crossveins present, cua-cup₂ preserved a clear base; one anal vein present.



Figure 10. Mesopsychidae indet. A, NIGP206345a, part. B, NIGP206345b, counterpart. C, Line drawing. Scale bars = 2 mm.

Despite the partial preservation of Rs and M, the specimen can be confidently assigned to the Mesopsychidae based on the combination of several characters: the broad wing, an extensive costal area, and the presence of two short anterior branches of Sc. Additionally, the space between CuA and CuP is relatively broad, the CuA base is well-developed, and the present of two cua-cup crossveins. These traits are consistent with those observed in the genus *Turbidapsyche* (Mesopsychidae) (Lian *et al.* 2024b). However, the absence of crossvein cua-cup₂ within *Turbidapsyche*, and the incomplete preservation of the M and Rs branches in our fossil, leads us to classify this specimen as Mesopsychidae indet.

Discussion

A total of 37 specimens were discovered from the Middle Jurassic Yangshuzhuang Formation in the Jiyuan Basin. The new materials predominantly belong to 'Orthophlebiidae' (encompassing Orthophlebiidae and Protorthophlebiidae). Only a single specimen can be assigned to another mecopteran family, Mesopsychidae, an extinct lineage of long-proboscid insects presumed to be pollinators of certain Mesozoic gymnosperms (Ren *et al.* 2009).

'Orthophlebiidae' represents a highly diverse and polyphyletic group during the Mesozoic (Hendlirsch 1906; Willmann 1989; Ansorge 1995; Zhang 1996; Soszyńska-Maj *et al.* 2018; Zhang *et al.* 2023). Historically, approximately twenty genera were placed within 'Orthophlebiidae', although most have since been dismissed (Hong *et al.* 2007). Currently, it is widely accepted that Orthophlebiidae comprises the following genera: *Orthophlebia*, *Gigaphlebia*, *Longiphlebia*, *Juraphlebia*, and *Burmorthophlebia* (Soszyńska-Maj *et al.* 2022). *Protorthophlebia*, once considered one of the most diverse genera within Orthophlebiidae, has been reclassified and elevated to the family Protorthophlebiidae, primarily based on abdominal characters. Similarly, *Mesopanorpa*, historically one of the three most diverse genera within Orthophlebiidae, has been synonymized with *Orthophlebia* (Willmann 1989). This study follows the opinion of Soszyńska-Maj *et al.* (2018) that all species with six or more branches of Rs should be assigned to Orthophlebiidae, while species with Rs having five branches are assigned to Protorthophlebiidae.

The forking pattern of *Jiyuanphlebia* gen. nov. is distinctive within 'Orthophlebiidae'. While 'Orthophlebiidae' typically displays a Sc single or with one short crossvein-like anterior branch, which does not form a deep fork, *Jiyuanphlebia* gen. nov. exhibits a Sc with a deep fork formed by the long Sc₁ and Sc₂, resembling that of Parachoristidae. Parachoristidae and 'Orthophlebiidae' share morphological similarities including the pectinate Rs and horse-face rostrum. Parachoristidae is distinctive for its six-branched M, with M_2 bifurcating into two branches, and a deep Sc fork, while 'Orthophlebiidae' constently have a single M₂.

The subfamily Gigaphlebiinae was separated from Orthophlebiidae and is distinguished by its large wing size, which includes a greater number of Rs, and M branches. The Rs of Gigaphlebiinae typically possesses more than seven branches, while the M is characterized by six branches in forewings and five branches in hindwings. This differs from the other 'Orthophlebiidae', in which the M generally has five branches in forewings and four in hindwings. Currently, Gigaphlebiinae comprises three genera, Gigaphlebia, Longiphlebia, and Quadrivena gen. nov., encompassing five species from the Jurassic deposits of Dzhil Formation in Kyrgyzstan, the Karabastau Formation in Kazakhstan, and China (Soszyńska-Maj et al. 2018; Lian et al. 2021). Species of Gigaphlebiinae have been reported from the Middle-Upper Jurassic Haifanggou Formation of the Daohugou Biota (Qiao et al. 2012; Soszyńska-Maj et al. 2018), the Upper Jurassic Tiaojishan Formation of the Linglongta Biota (Lian et al. 2021), and a newly identified member from the Yangshuzhuang Formation in Henan Province. The new species, Quadrivena jiyuanensis gen. et sp. nov., possesses a large wing size, a Rs with night or ten branches, and an M with six branches in forewings, is undouble a Gigaphlebiinae. The age of the Zhiluo Formation in the Ordos Basin remains a subject of debate, with various authors placing it between the early Middle Jurassic and the Late Jurassic (Zhang & Liao 2006; Chen et al. 2017; Huang et al. 2018a; Huang 2019). The Zhiluo Formation also been suggested to belong to the late Middle Jurassic to early Late Jurassic, which is similar in age to the Yangshuzhuang Formation at the Jiyuan Basin and Haifanggou Formation in Yanliao area (Lian et al. 2024a). The discovery of O. quadrimacula from both Yangshuzhuang and Zhiluo Formations provides evidence of a stratigraphic correlation between these two formations. Furthermore, the Middle-Upper Jurassic Haifanggou Formation from Daohugou and the Yangshuzhuang Formation yield the same species of Hemiptera, Jurocercopis grandis Wang & Zhang, 2009, indicating a stratigraphic correlation among these units (Fu et al. 2020a). This suggests that the insects from the Yangshuzhuang Formation belong to the early assemblage of Yanliao biota. The new discovery of O. quadrimacula in the Yangshuzhuang Formation implies that the Zhiluo Formation can also be correlated with the Yangshuzhuang and Haifanggou formations, representing an early assemblage of the Yanliao biota.

Our discovery of 37 new specimens from the Middle Jurassic Yangshuzhuang Formation represents the first report of mecopterans from this formation. These findings increase the palaeobiodiversity of 'Orthophlebiidae' and provide valuable insights into the biostratigraphic correlation of the Yangshuzhuang Formation.

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References

- Ansorge J. 1995. Revision der liassischen 'Permochoristidae' (Stammgruppenvertreter der Antliophora = Mecoptera + Diptera). *Studia Dipterologica* 2(1): 21–26.
- Bashkuev A. S. & Sukatsheva I. D. 2021. New species of *Kamopanorpa* Martynov from the Permian of South Siberia with comments on the systematic position of Microptysmatidae (Protomeropina = Permotrichoptera). *Palaeoentomology* 4(5): 453–461. https://doi.org/10.11646/palaeoentomology.4.5.11

Bode A. 1953. Die Insektenfauna des ostniedersächsischen oberen Lias. Palaeontographica A 103: 1–375.

- Chen Y., Feng X. X., Chen L. L., Jin R. S., Miao P. S., Sima X. Z., Miao A. S., Tang C., Wang G. & Liu Z. R. 2017. An analysis of U-Pb dating of detrital zircons and modes of occurrence of uranium minerals in the Zhiluo Formation of northeastern Ordos Basin and their indication to uranium sources. *Geology in China* 44(6): 1190–1206. https://doi.org/10.12029/gc20170611
- Fu Y. Z. & Huang D. Y. 2020a. Jurocercopis grandis Wang & Zhang, 2009 from the Jiyuan Basin and Daohugou beds of northern China and its morphological revision (Hemiptera, Cicadomorpha, Cercopoidea). Palaeoentomology 3(1): 087–095. https://doi.org/10.11646/palaeoentomology.3.1.12
- Fu Y. Z. & Huang D. Y. 2020b. A new fossil cercopoid from the middle Jurassic Ordos and Jiyuan basins, northern China (Hemiptera, Cicadomorpha). *Historical Biology* 33(10): 2025–2030. https://doi.org/10.1080/08912963.2020.1765167
- Fu Y. Z., Xu M. M., Gao J. & Huang D. Y. 2024. The Archijassidae from the Jurassic of China (Hemiptera, Cicadomorpha, Membracoidea) and its palaeoecological significance. *Historical Biology* 36(10): 2233–2238. https://doi.org/10.1080/08912963.2023.2250109
- Handlirsch A. 1906. Die fossilen Insekten und die Phylogenie der rezenten Formen: Ein Handbuch für Paläontologen und Zoologen. Engelmann, Leipzig, Germany, 640 pp.
- Handlirsch A. 1939. Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. II. Teil. Annalen des naturhistorischen Museums in Wien 49:1–240.
- Hong Y. C. & Zhang Z. J. 2007. Reclassification of fossil Orthophlebiidae (Insecta: Mecoptera). Entomotaxonomia 29(1): 26–36.
- Huang D. Y. 2019. Jurassic integrative stratigraphy and timescale of China. Science China-Earth Sciences 62(1): 223–255. https://doi.org/10.1007/s11430-017-9268-7
- Huang D. Y., Cai C. Y., Fu Y. Z. & Su Y. T. 2018a. The Middle-Late jurassic Yanliao entomofauna. *Palaeoentomology* 1(1): 3–31. https://doi.org/10.11646/palaeoentomology.1.1.2
- Huang D. Y., Cai C. Y. & Nel A. 2018b. A new damsel-dragonfly of the small family Selenothemistidae from the Late Jurassic of China (Odonata, Isophlebioptera). *Journal of Paleontology* 92(6): 1049–1053. https://doi.org/10.1017/jpa.2018.33
- Huang D. Y., Xu M. M., Zhao Q., Gao J. & Nel A. 2023. New stem-anisopteran dragonflies in the Jurassic of China (Odonata: Epiproctophora). Zootaxa 5396(1): 26–34. https://doi.org/10.11646/zootaxa.5396.1.7
- Lian X. N., Cai C. Y. & Huang D. Y. 2021. A new orthophlebiid scorpionfly (Insecta, Orthophlebiidae) from the Late Jurassic Linglongta

biota of northern China. *Historical Biology* 33(12): 3585–3589. https://doi.org/10.1080/08912963.2021.1878512

- Lian X. N., Wang Y. H., Cai C. Y. & Huang D. Y. 2024a. Field trips of the 9th International Conference on Fossil Insects, Arthropods, and Amber—a overview on Mesozoic palaeontology and stratigraphy of the Ordos Basin. *Palaeoentomology* 7(2): 167–175. https://doi.org/10.11646/palaeoentomology.7.2.1
- Lian X. N., Zhang Y., Cai C. Y. & Huang D. Y. 2024b. A new genus of Mesopsychidae from the late Middle Triassic Tongchuan entomofauna and its taxonomic and palaeogeographic implications. *Mesozoic* 1(2): 144–158. https://doi.org/10.11646/mesozoic.1.2.7
- Lin Q. B. 1982. Insecta, pp. 329–332. In: Palaeontology Atlas of Eastern China, III (Nanjing Institute of Geology and Mineral Resources, editor). Geological Publishing House, Beijing, 382 pp.
- Liu Y. M. & Huang D. Y. 2020. New materials of trichocerid and ptychopterid dipterans from the earliest Late Jurassic of Jiyuan Basin, China. *Palaeoentomology* 3(5): 461–465.

https://doi.org/10.11646/palaeoentomology.3.5.3

- Liu Y. M. & Huang D. Y. 2021. A new species of Crenoptychoptera Kalugina, 1985 (Diptera: Ptychopteridae) from the Middle–Late Jurassic of Jiyuan Basin, China. *Palaeoentomology* 4(1): 027–029. https://doi.org/10.11646/palaeoentomology.4.1.5
- Minet J., Huang D. Y., Wu H. & Nel A. 2010. Early Mecopterida and the systematic position of the Microptysmatidae (Insecta: Endopterygota). Annales de la Société entomologique de France 46(1–2): 262–270. https://doi.org/10.1080/00379271.2010.10697667
- Qiao X., Shih C. K. & Ren D. 2012. Two new Middle Jurassic species of orthophlebiids (Insecta: Mecoptera) from Inner Mongolia, China. Alcheringa: An Australasian Journal of Palaeontology 36(4): 469–475. https://doi.org/10.1080/03115518.2012.671689
- Ren D., Labandeira C. C., Santiago-Blay J. A., Rasnitsyn A., Shih C. K., Bashkuev A., Logan M. A. V., Hotton C. L. & Dilcher D. 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. *Science* 326: 840–847. https://doi.org/10.1126/science.1178338
- Soszyńska-Maj A., Krzemiński W., Kopeć K., Cao Y. Z. & Ren D. 2018. Large jurassic scorpionflies belonging to a new subfamily of the family Orthophlebiidae (Mecoptera). *Annales Zoologici* 68(1): 85–92. https://doi.org/10.3161/00034541ANZ2018.68.1.004
- Soszyńska-Maj A., Krzemiński W., Kopeć K., Cao Y. & Ren D. 2020. New Middle Jurassic fossils shed light on the relationship of recent Panorpoidea (Insecta, Mecoptera). *Historical Biology* 32(8): 1081–1097. https://doi.org/10.1080/08912963.2018.1564747
- Soszyńska-Maj A., Krzemińska E., Pérez-de la Fuente R., Wang J. S., Szpila K., Skibińska K., Kopeć K. & Krzemiński W. 2022. Evolution of sexual conflict in scorpionflies. *Elife* 11: e70508. https://doi.org/10.7554/eLife.70508
- Willmann R. 1984. Mecopteren aus dem Lias von Niedersachsen (Insecta, Holometabola). Neues Jahrbuch für Geologie und Paläontologie. *Monatshefte* (7): 437–448.
- Willmann R. 1989. Evolution und phylogenetisches System der Mecoptera (Insecta: Holometabola). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 544: 1–153.
- Willmann R. & Novokschonov V. 1998. New Mecoptera from the Upper Jurassic of Karatau (Kazachstan)(Insecta, Mecoptera: 'Orthophlebiidae'). *Paläontologische Zeitschrift* 72: 281–297.
- Xu M. M. & Huang D. Y. 2023. A new species of *Cicadocoris* (Hemiptera, Coleorrhyncha, Progonocimicidae) from the Middle Jurassic of the Jiyuan Basin, China. *Zootaxa* 5396(1): 35–40. https://doi.org/10.11646/zootaxa.5396.1.8
- Zhang H. C. 1996. Mesozoic insects of Orthophlebiidae (Insecta, Mecoptera) from Junggar Basin, Xinjiang, China. *Acta Palaeontologica Sinica* 35(4): 442–454.
- Zhang Y. J., Lin X. D., Shih C. K., Ren D. & Zhao Y. Y. 2023. First report of detailed mouthpart structures of Orthophlebiidae (Insecta: Mecoptera) from mid-Cretaceous amber of northern Myanmar. Cretaceous Research 144: 105443. https://doi.org/10.1016/j.cretres.2022.105443
- Zhang Y. J., Shih P. J. M., Wang J. Y., McNamara M. E., Shih C., Ren D. & Gao T. P. 2021. Jurassic scorpionflies (Mecoptera) with swollen first metatarsal segments suggesting sexual dimorphism. *BMC Ecology Evolution* 21(1): 47. https://doi.org/10.1186/s12862-021-01771-3