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New Parachoristidae and "Orthophlebiidae" from the Tongchuan entomofauna and their implications on the early evolution of Panorpoidea

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Abstract

The Panorpoidea are among the most diverse groups of Mecoptera throughout geological time and the present day, commonly known as scorpionflies for their bulbous and upturned male genitalia resembling scorpion tails. The Mesozoic "Orthophlebiidae" and the Permian–Triassic Parachoristidae, representing basal lineages of Panorpoidea, are closely related and share several similar wing characters, thus hindering our understanding of their evolutionary history. Although the "Orthophlebiidae" were highly diverse during the Jurassic, their Triassic record remains limited. Herein, eight new species belonging to two genera of Parachoristidae and two new species belonging to two genera of "Orthophlebiidae" are described and illustrated from the Middle Triassic Tongchuan entomofauna, greatly expanding the known palaeodiversity of these families during the Triassic. The newly described species renders the Tongchuan entomofauna the most diverse entomofauna of Parachoristidae known worldwide. *Protorthophlebia prajna* **sp. nov.** and *Orthophlebia xiangyu* **sp. nov.** represent the earliest unambiguous "Orthophlebiidae" erected based on forewings, prompting a thorough revision of Triassic "Orthophlebiidae" and some coeval parachoristids exhibiting overlapping characters. Two previously established species of "Orthophlebiidae" from the Tongchuan entomofauna are redescribed based on new material.

Keywords: scorpionflies, parachoristid, new taxa, Yanchang Formation, Ordos Basin

Introduction

The superfamily Panorpoidea (sensu Willmann, 1987), commonly known as scorpionflies, is characterized by forewings with an Rs_{1+2} bearing pectinate branches, a rostrate mouthpart, and scorpion tail-like male genitalia. It has been considered to comprise the Triassic–Cretaceous "Orthophlebiidae" (comprising Orthophlebiidae, Protorthophlebiidae, and Worcestobiidae), the Jurassic Muchoriidae, the Jurassic–Eocene Austropanorpidae, the Jurassic–Eocene Holcorpidae, the Eocene Dinopanorpidae, the Eocene Eorpidae, the Jurassic?–Recent Panorpidae, and the Eocene–Recent Panorpodidae (Archibald *et al*., 2013; Willmann, 1987, 1989). The Parachoristidae, though closely related, were largely neglected by many subsequent authors. While fossils of the "Orthophlebiidae" were overwhelmingly dominant among Mecoptera during the Jurassic, it was during the Eocene that the Panorpoidea achieved their greatest family-level diversity, marking the Eocene as the apex of panorpoid scorpionflies (Archibald *et al*., 2013).

Since the Mesozoic, Panorpoidea have represented a dominant lineage within Mecoptera. The Late Permian–Late Triassic clade Parachoristidae are considered to give rise to "Orthophlebiidae", which subsequently replaced the former and reached their greatest diversity during the Jurassic (Novokshonov, 1997). Parachoristidae are closely related to the "Orthophlebiidae" in both wing venation and body structures, and were prevalent during the Middle–Late Triassic (Novokshonov, 1997, 2001; Lian *et al*., 2023a). Parachoristidae generally differ from the "Orthophlebiidae" by having a long and oblique Sc_2 and a forked M_2; however, these characters are not invariant, rendering that the boundary between the two groups unclear. "Orthophlebiidae" were subsequently replaced by other Eocene panorpoids, including Austropanorpidae, Holcorpidae, Dinopanorpidae, Eorpidae, Panorpidae, and Panorpodidae (Archibald *et al.*, 2013). Panorpidae and Panorpodidae, the only mecopteran families surviving today, include more than 500 species primarily in the Holarctic and Oriental regions, accounting for roughly five-eighths of all extant species (Wang & Hua, 2022). Although just over 120 species of "Orthophlebiidae" have

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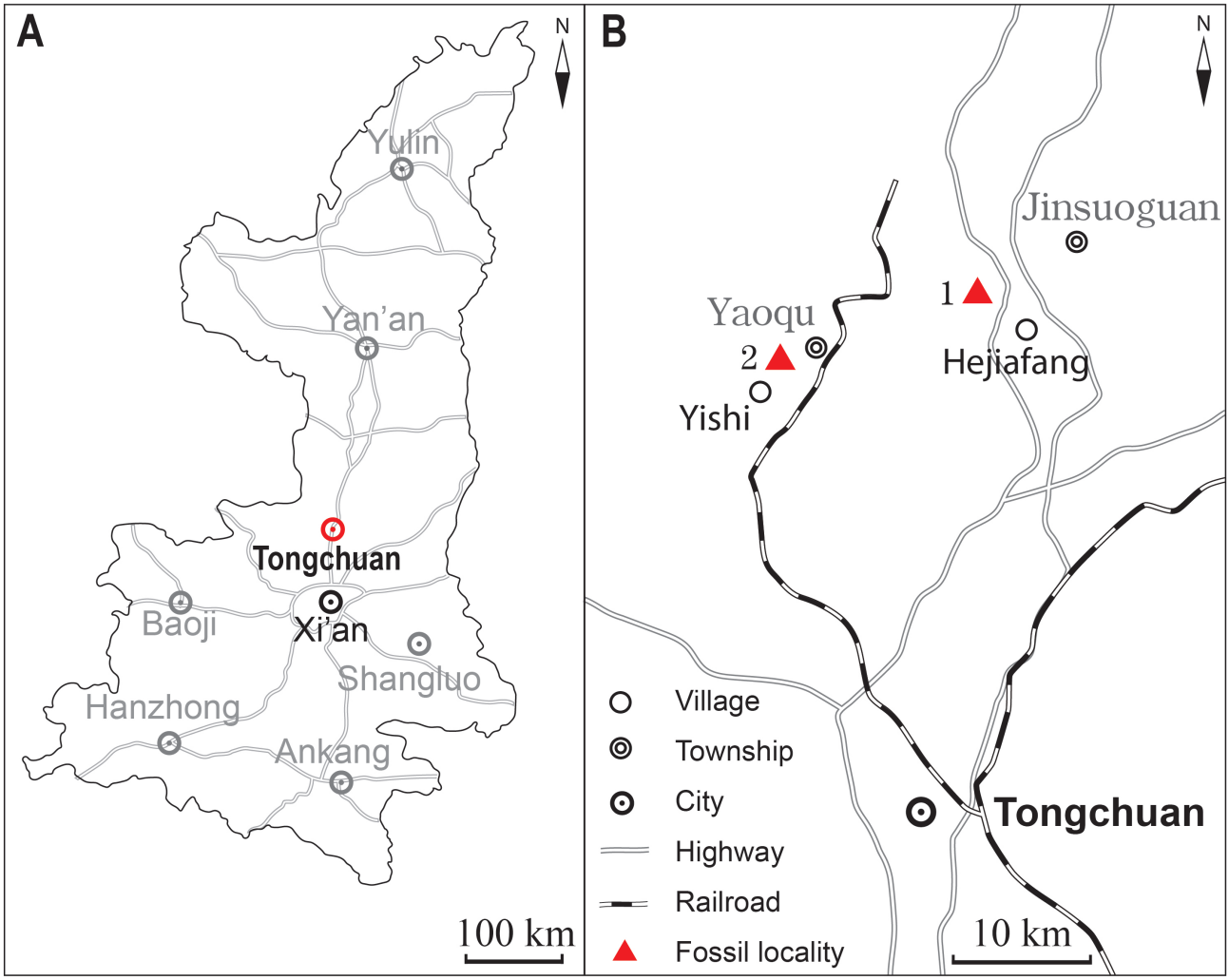

FIGURE 1. Geographic maps of fossil localities. **A**, Map of Shaanxi Province. **B**, Map of fossil localities: 1, fossil locality near Hejiafang Village, Jinsuoguan Township; 2, fossil locality near Yishi Village, Yaoqu Township.

been described (Zhang *et al*., 2023), their wing venation shows far greater morphological disparity than that of Panorpidae and Panorpodidae, suggesting that their true species diversity was likely much higher. The fossil record of "Orthophlebiidae" from the Triassic remains limited and somewhat controversial (Hong, 2009b; Hong *et al*., 2002). Therefore, unambiguous orthophlebiid fossils from the Triassic would play a crucial role in elucidating the early evolution of Panorpoidea.

Insects from the Ladinian Tongchuan entomofauna have been studied since the 1980s (Hong, 1980). Despite the diverse Mecoptera described from the Tongchuan entomofauna (Zhang *et al*., 2022), many species were inaccurately described and illustrated, and therefore require careful revision (Bashkuev, 2011). This has hindered a comprehensive understanding of the mecopterans from this entomofauna. In recent years, studies on Mecoptera from the Tongchuan entomofauna have been renewed, with several families, including Permochoristidae, Parachoristidae, Thaumatomeropidae, and the long-proboscid Mesopsychidae, being newly reported (Lian *et al*., 2021b, 2022, 2023a, b, 2024). Herein, we describe and illustrate eight new species of Parachoristidae and two new species of "Orthophlebiidae", greatly improving our understanding of the mecopteran palaeodiversity from this entomofauna.

Material and methods

All specimens were collected from the yellowish green shale of the lower part of the Middle-Upper Triassic Yanchang Formation in Tongchuan City. Nearly all of them were collected from the locality near Hejiafang Village, Jinsuoguan Township, except for one specimen (NIGP209395) from Yishi Village, Yaoqu Township (Fig. 1). The fossil-bearing beds are named Chang-7 Member in the division of oil reservoirs, which is equivalent to the unit referred to as the Tongchuan Formation by some palaeontologists (*e.g*., Hong *et al*., 2002; Zheng *et al*.,

2018). Our specimens were collected from the shale in the upper part of oil shale within the Chang-7 Member at Hejiafang Village, whereas the fossils collected by Youchong Hong come from the shale in the lower part of the same oil shale.

Specimens were carefully prepared using a sharp knife. Photographs were taken with a digital camera mounted on a Zeiss Discovery V16 microscope, and some specimens were immersed in 75% ethanol to enhance contrast. Line drawings were produced using Adobe Illustrator 2019 (San Jose, California, USA). All specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing, China.

The terminology of wing venation follows Bashkuev (2022). The cubito-median Y-vein, defined by Tillyard (1919), refers to the configuration in which M_5, CuA base, and CuA form a Y-shaped structure.

Systematic palaeontology

Order Mecoptera Packard, 1886
Superfamily Panorpoidea Latreille, 1805
Parachoristidae Handlirsch, 1937
***Parachorista* Tillyard, 1926**

***Parachorista pulchra* sp. nov.**
(Figs 2, 3)

Material. Holotype, NIGP209381a, b, part and counterpart, with two forewings and one hindwing preserved.

Etymology. The species name derived from the Latin word *pulchra*, referring to the beautiful wings.

Diagnosis. Forewing with five coloured strips vertically aligned; Sc with a narrow symmetrical fork; Rs with six branches, and Rs_{1+2} half as long as Rs_{3+4}. Hindwing with a deep R_1 fork at the level of Rs_1 fork.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. Forewing 17.7 mm long, 6.7 mm wide, tongue-shaped, gradually tapering from wing apex to wing base, widest at 4/5 of the wing length; five coloured strips vertically aligned; Sc long, extending into pterostigma, forking into two narrow and symmetrical branches; Sc fork distinctly proximal to Rs fork; humeral vein oblique; R_1 single, curved after entering pterostigma; a crossvein connected the middle Sc_1 and R_1; pterostigma stained with coloured markings and covered with dense, tiny nodules, with a vein-like boundary marking its lower margin; Rs with six branches, Rs_1 with three branches, Rs_2, Rs_3, and Rs_4 single; Rs_{1+2} half as long as Rs_{3+4}; M with six branches, M_2 and M_4 forked, crossvein m-cua connected CuA and basal M_{4b}; CuA curved apically, cubito-median Y-vein well-developed, M_5 relatively short, CuA base horizontal; CuP single and straight; four anal veins detected, A_3 short and forking into two branches near its base; one crossvein between branches of A_3, A_1 and A_2, and CuA and CuP, respectively; two crossveins between A_2 and A_3; numerous crossveins between branches of Rs and M.

Hindwing slightly smaller than forewing; Sc short and single, ending at the level of Rs_1 fork, R_1 forking into two branches at level of Sc termination, connected to Sc by a crossvein; an oblique crossvein connected the fork of R_1 and Rs_1; Rs with six branches, Rs_{1+2} as long as Rs_{3+4}; M with four branches, M_{1+2} 3.3× length of M_{3+4}; M fused with CuA for a long distance, CuP and A_1 detected; other details obscured by overlapping forewing.

Remarks. The new species closely resembles *Triasoparachorista huaxiaensis* Hong, 2009, from the Tongchuan entomofauna, but differs from the latter by its forewings with Sc_2 much longer, Sc fork narrower, only one crossvein between Sc and R_1 (*vs*. two), M_{1+2} 3.3× length of M_{3+4} (*vs*. 2.5×), and A_3 two-branched (*vs*. single); differs from *P. asiatica* Novokshonov, 1997, by its smaller forewing (length 17.7 mm *vs*. 23.0 mm), broader wing apex, the costal area without a basal crossvein, and much slender coloured strips; differs from *P. immota* Novokshonov, 2001, by its larger forewing (length 17.6 mm *vs*. 11.0 mm), narrower wing base relative to apex, and sparser crossveins. The hindwing of *Parachorista pulchra* **sp. nov.** differs from *P. splendida* Tillyard, 1926, (established based on hindwing) by its deeper R_1 fork, and Rs with six branches instead of five.

***Parachorista libaii* sp. nov.**
(Figs 4, 5)

Material. Holotype, NIGP209382, a forewing and a hindwing overlapping. Paratypes: NIGP209383a, b, part and counterpart, a complete forewing; NIGP209384a, b, part and counterpart, a forewing missing anal veins; NIGP209385a, b, part and counterpart, a nearly complete forewing, apex deformed; NIGP209386a, b, part and counterpart, a nearly complete forewings with a small part of wing base missed; NIGP209387, a hindwing preserved with only anterior part.

Etymology. The species name *libaii* is dedicated to the famous Chinese poet Li Bai.

Diagnosis. Forewing relatively small; Sc_1 more than twice as long as Sc_2; Rs with five branches, Rs_{1+2} shorter than Rs_{3+4}, and Rs_1 longer than its branches.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of Middle-Upper Triassic Yanchang Formation, Ladinian.

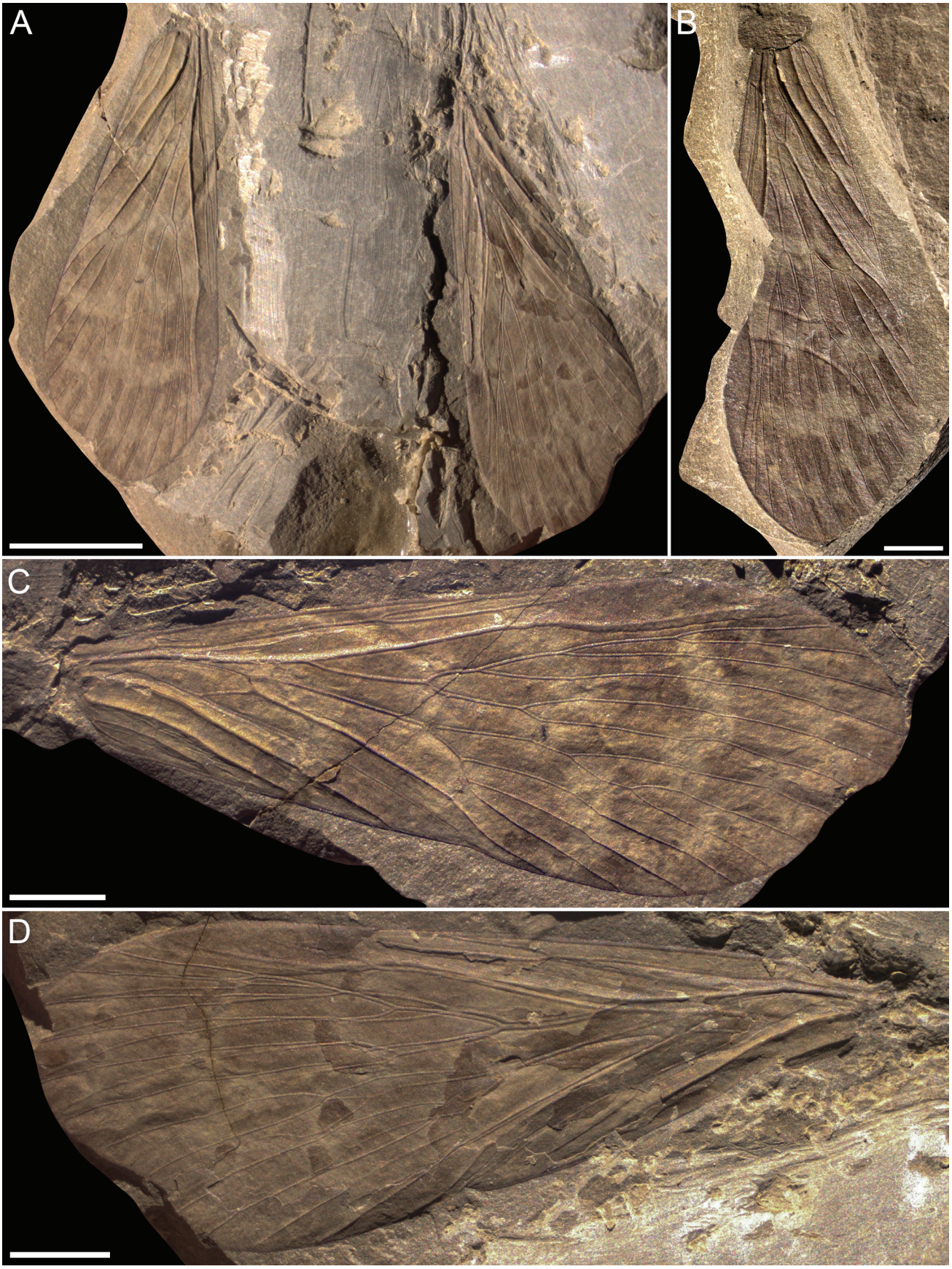

FIGURE 2. *Parachorista pulchra* **sp. nov.**, holotype, NIGP209381. **A**, NIGP209381a. **B**, NIGP209381b. **C**, Enlargement of the right forewing from **A**. **D**, Enlargement of the left forewing and hindwing from **A**. Scale bars: 5 mm in **A**, 2 mm in **B**–**D**.

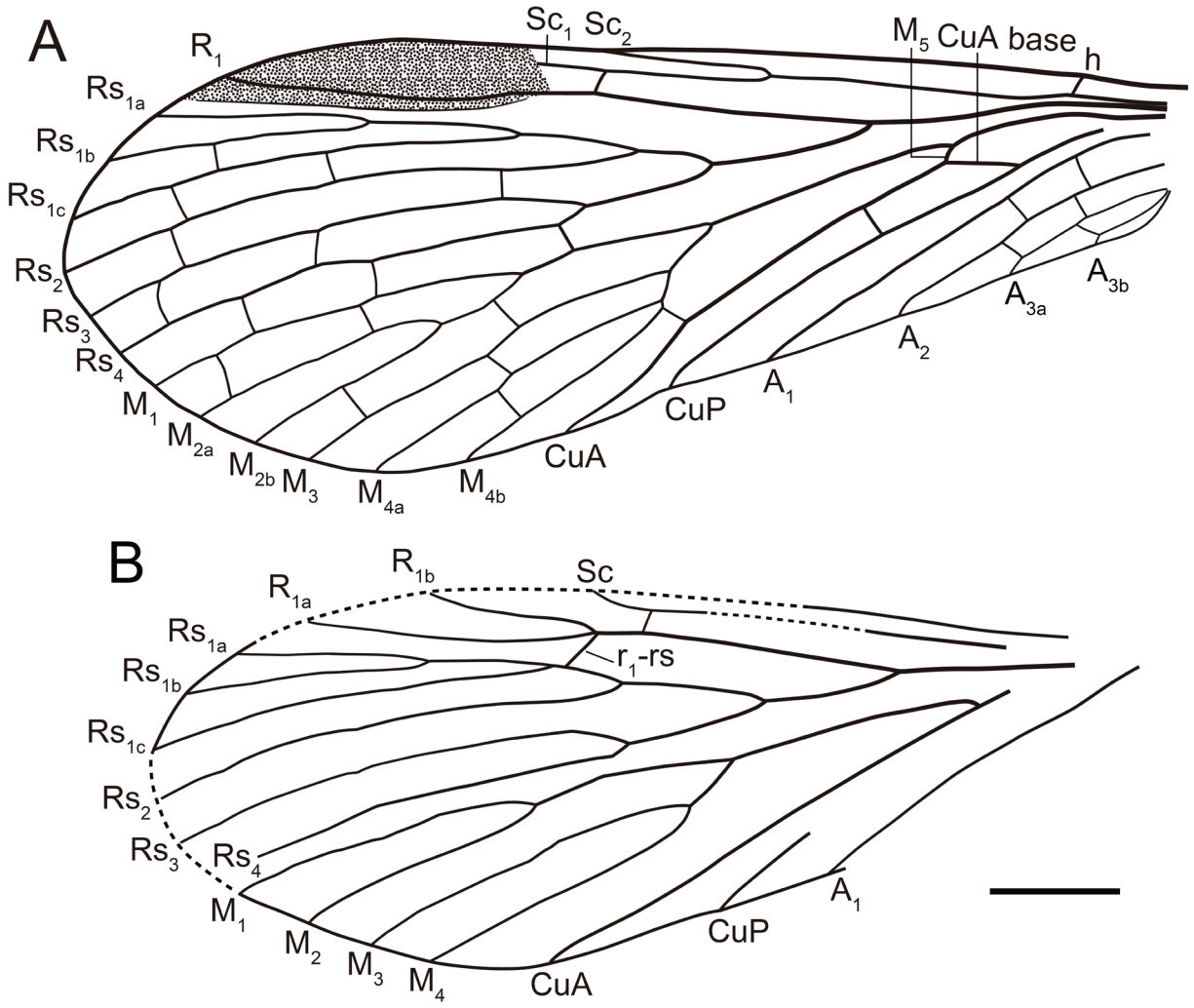

FIGURE 3. Line drawings of *Parachorista pulchra* **sp. nov. A**, Forewing. **B**, Hindwing. Scale bars: 2 mm.

Description. Holotype, NIGP209382. Forewing: 10.0 mm long (as preserved), 3.5 mm wide; Sc two-branched, Sc_2 moderately long, Sc_1 sharply bent after the crossvein sc-r_1; pterostigma pigmented, boundary unclear; Rs with five branches, Rs_1 with two branches, Rs_{1+2} slightly shorter than Rs_{3+4}, Rs_1 nearly twice as long as Rs_{1a}; M with six branches, M_2 and M_4 forked, M_{1+2} 2.6× length of M_{3+4}; crossvein m-cua connected middle of M_4 and CuA; CuA bent apically, cubito-median Y-vein well-developed, M_5 developed, CuA base and M_4 curved; CuP straight, a crossvein connected CuA and CuP; two anal veins detected; several crossveins distributed at branches of Rs and M.

Hindwing slightly smaller than forewing, Sc single and long, apical part missing; a crossvein connected apical Sc and apical R_1; R_1 deeply forked into two branches, R_1 fork proximal to the level of Rs_{1+2} fork, an oblique crossvein connected posterior branch of R_1 and Rs_1; Rs with five branches, Rs_1 with two apical branches, Rs_{1+2} slightly longer than Rs_{3+4}; M with four branches, M_{1+2} more than twice as long as M_{3+4}; CuA and CuP single and straight, a crossvein connected CuA and CuP; only A_1 detected; several crossveins at the branches of Rs and M.

Paratypes: NIGP209383, a relatively slender forewing, 12.1 mm long, 4.4 mm wide, length/width ratio 2.8; gradually narrowing to wing base; Sc with two branches, Sc_1 long and faint after entering pterostigma, at least twice as long as Sc_2; Sc fork at the same level as Rs fork; R_1 single, curved downwards after entering pterostigma, a crossvein connected mid-Sc_1 and R_1; pterostigma lentoid, pigmented, with vein-like lower boundary; Rs with five branches, Rs_1 two-branched, Rs_{1+2} slightly shorter than Rs_{3+4}, Rs_1 twice as long as Rs_{1+2}, Rs_1 distinctly longer than Rs_{1a}; M with seven branches, M_2 with two branches, M_4 with three branches, M_{4b} and M_{4c} relatively short, M_{1+2} 3.2× length of M_{3+4}; crossvein m-cua connected CuA with M_{4b+c}; CuA and CuP single, cubito-median Y-vein well-developed, a crossvein connected middle part of CuA and CuP; A with four branches, A_3 forked near its base, two closely spaced crossveins

FIGURE 4. *Parachorista libaii* **sp. nov. A**, Holotype, NIGP209382. **B**, Paratype, NIGP209386. **C**, Paratype, NIGP209383. Scale bars: 2 mm.

connected A_1 and A_2, one crossvein connected A_2 and A_3, and branches of A_3; numerous crossveins connected the branches of Rs and M.

NIGP209384, forewing 11.1 mm long, 4.1 mm wide; humeral vein oblique; Sc_1 long, faint after entering pterostigma, Sc_2 about 1/3 length of Sc_1; R_1 single, curved downwards at apex, a crossvein connected Sc_1 and R_1; pterostigma lentoid, pigmented; Rs with five branches, Rs_{1+2} slightly shorter than Rs_{3+4}, Rs_1 more than twice as long as its branches; M with six branches, M_2 and M_4 forked, M_{1+2} more than twice as long as M_{3+4}; crossvein m-cua connected basal M_{4b} and CuA; CuA and CuP single, connected by a crossvein; cubito-median Y-vein well-developed, CuA base more than twice as long as M_5; several crossveins at branches of Rs an M.

NIGP209385, forewing 9.8 mm long, 3.5 mm wide, length/width ratio 2.8; humeral vein oblique, Sc_1 long, more than twice Sc_2; R_1 single, curved downwards near its

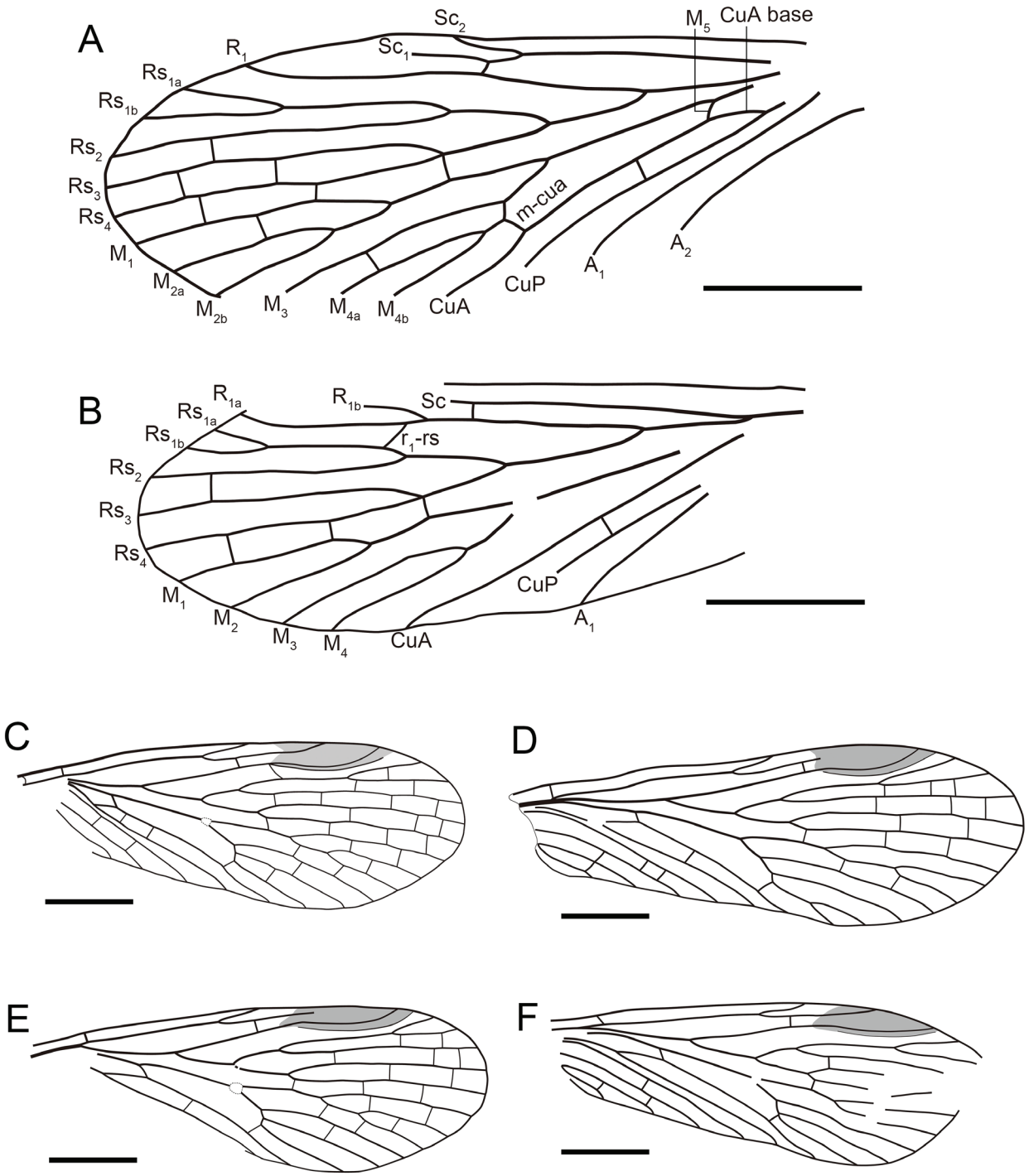

FIGURE 5. Line drawings of *Parachorista libaii* **sp. nov. A**, Holotype, NIGP209382, forewing. **B**, Holotype, NIGP209382, hindwing. **C**, Paratype, NIGP209386. **D**, Paratype, NIGP209383. **E**, Paratype, NIGP209384. **F**, NIGP209385. Scale bars: 2 mm.

apex, a crossvein connected basal Sc_1 and R_1; pterostigma lentoid, pigmented, with a vein-like lower boundary; Rs with five branches, Rs_{1+2} distinctly shorter than Rs_{3+4}, Rs_1 nearly twice as long as Rs_{1a}; M with six branches, M_2 and M_4 forked, M_{1+2} more than twice as long as M_{3+4}; crossvein m-cua connected M_4 fork and CuA; CuA and CuP single, CuA slightly sinuous near apex, cubito-median Y-vein distinct, CuA base more than twice as long as M_5; A with four branches, A_3 forked into two branches near its base; many crossveins between branches of M and Rs; a crossvein between A_1 and A_2, A_2 and A_3, and branches of A_3, respectively.

NIGP209386, forewing 10.0 mm long (as preserved), 3.8 mm wide; humeral vein present; Sc_1 long, reached into the pigmented pterostigma, and more than twice as long as Sc_2; R_1 single, curved downwards at apex, a crossvein connected Sc_1 and R_1, and a long and oblique crossvein connected R_1 and Rs_1; Rs with five branches, Rs_{1+2} distinctly shorter than Rs_{3+4}, Rs_1 1.5× length of Rs_{1a}; M with six branches, M_2 and M_4 forked, M_{1+2} 2.4× length of M_{3+4}; crossvein m-cua connected basal M_{4b} and CuA; CuA and CuP single, CuA with a sinuous apex; cubito-median Y-vein well developed, CuA base distinctly longer than M_5; three anal veins preserved; two crossveins between CuA and CuP, and A_1 and A_2, respectively; numerous crossveins at branches of Rs and M.

NIGP209387, hindwing 11.8 mm long; Sc single and entering pterostigma, pterostigma covered with dense nodules; R_1 forked into two branches near its apex, a crossvein connected Sc and R_1, a very oblique crossvein connected R_1 fork and basal Rs_1; Rs with five branches, Rs_{1+2} longer than Rs_{3+4}, Rs_1 longer than its branches.

Remarks. The new species, *Parachorista libaii* **sp. nov.**, is represented by seven specimens, all sharing a relatively short Sc_2 and the two-branched Rs_1 with a long stem. Although NIGP209383 has a three-branched M_4, the extra branch is short and considered intraspecific variation.

P. libaii **sp. nov.** differs from *P. religiosa* Novokshonov, 2001 by its broader forewings, and absence of hyaline spots along the crossveins; differs from *P. comica* Novokshonov, 1997 by its broader forewings, longer stem Rs_{1+2}, and deeper fork of M_4. The hindwing differs from *P. pulchra* **sp. nov.** by its smaller size, R_1 fork proximal rather than distal to Rs_{1+2} fork, five-branched Rs instead of six, and Rs fork nearly at same level rather than distinctly proximal to M fork.

***Parachorista ruga* sp. nov.**
(Fig. 6)

Material. Holotype, NIGP209388, a forewing missing a small part of the wing apex, preserved part of the thoraces and legs.

Etymology. The species name is derived from the Latin word *ruga*, referring to the wrinkled wing.

Diagnosis. Forewing small; Sc_2 short, two crossveins connect Sc_1 with R_1; Rs with five branches, Rs_{1+2} twice as long as Rs_{3+4}, and Rs_1 distinctly longer than its branches.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. Thorax and legs partly preserved; leg pubescence arranged in rings.

Forewing 8.6 mm long, 3.3 mm wide; Sc long, extending into pterostigma, forked into two branches; Sc fork distal to Rs fork, Sc_2 short, Sc_1 more than 4× as long as Sc_2; R_1 single, initially straight and then bent after entering pterostigma; Rs with five branches, Rs_1 with two branches, Rs_1 much longer than its branches and twice as long as Rs_{1+2}, Rs_{1+2} more than twice as long as Rs_{3+4}; M with six branches, M_2 and M_4 forked, M_2 fork small, M_{1+2} five times as long as M_{3+4}, M_4 sharply curved; crossvein m-cua connected CuA with the curved point of M_4; CuA curved apically, cubito-median Y-vein well-developed, CuP straight; three anal veins detected, crossveins at cubito–anal area distinct, a crossvein between CuA and CuP, and A_2 and A_3; two adjacent crossveins between A_1 and A_2.

Remarks. The new species, *P. ruga* **sp. nov.**, resembles *P. libaii* **sp. nov.** in wing size, but differs from the latter by the combination of the following characters: Sc_2 much shorter, two crossveins between Sc_2 and R_1 instead of one, stem Rs_{1+2} twice as long as stem Rs_{3+4} instead of stem Rs_{1+2} shorter than stem Rs_{3+4}, stem M_{1+2} at least four times as long as M_{3+4} instead of just over twice, and M_2 fork is small.

***Parachorista triassica* sp. nov.**
(Fig. 7)

Material. Holotype, NIGP209389, a forewing and a hindwing overlapping.

Etymology. The species name is derived from the Triassic period.

Diagnosis. Forewing elongate; pterostigma elongate; Rs with five branches; M_{3+4} extremely short.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. Forewing slender, 17.0 mm long, 4.9 mm wide (L/W ratio = 3.5); Sc long, two-branched, Sc fork distal to Rs fork, Sc_1 faint after entering pterostigma; R_1 single, curved downwards after entering pterostigma; pterostigma lentoid, elongated, basal part nearly reaching the level of Rs_{1+2} fork, bottom bounded by a vein-like boundary; Rs with five branches, Rs_{1+2} slightly shorter than Rs_{3+4}, Rs_1 nearly as long as its branches; M with six branches, M_2 and M_4 forked, M_{3+4} very short; crossvein m-cua faint, connected CuA with basal M_{4b}; CuA single, curved apically; cubito-median Y-vein well-developed, CuA base curved; CuP single, two crossveins connected distal CuA and CuP; anal veins with four branches, A_1 and A_2 single, A_3 forked, A_{3b} close to wing margin; a crossvein connected A_1 and A_2, and A_2 and A_3, respectively.

Hindwing partially preserved; crossvein r_1–rs connected basal R_1; Rs with five branches, similar to forewing; M with four branches; CuA and CuP single, A_1 straight.

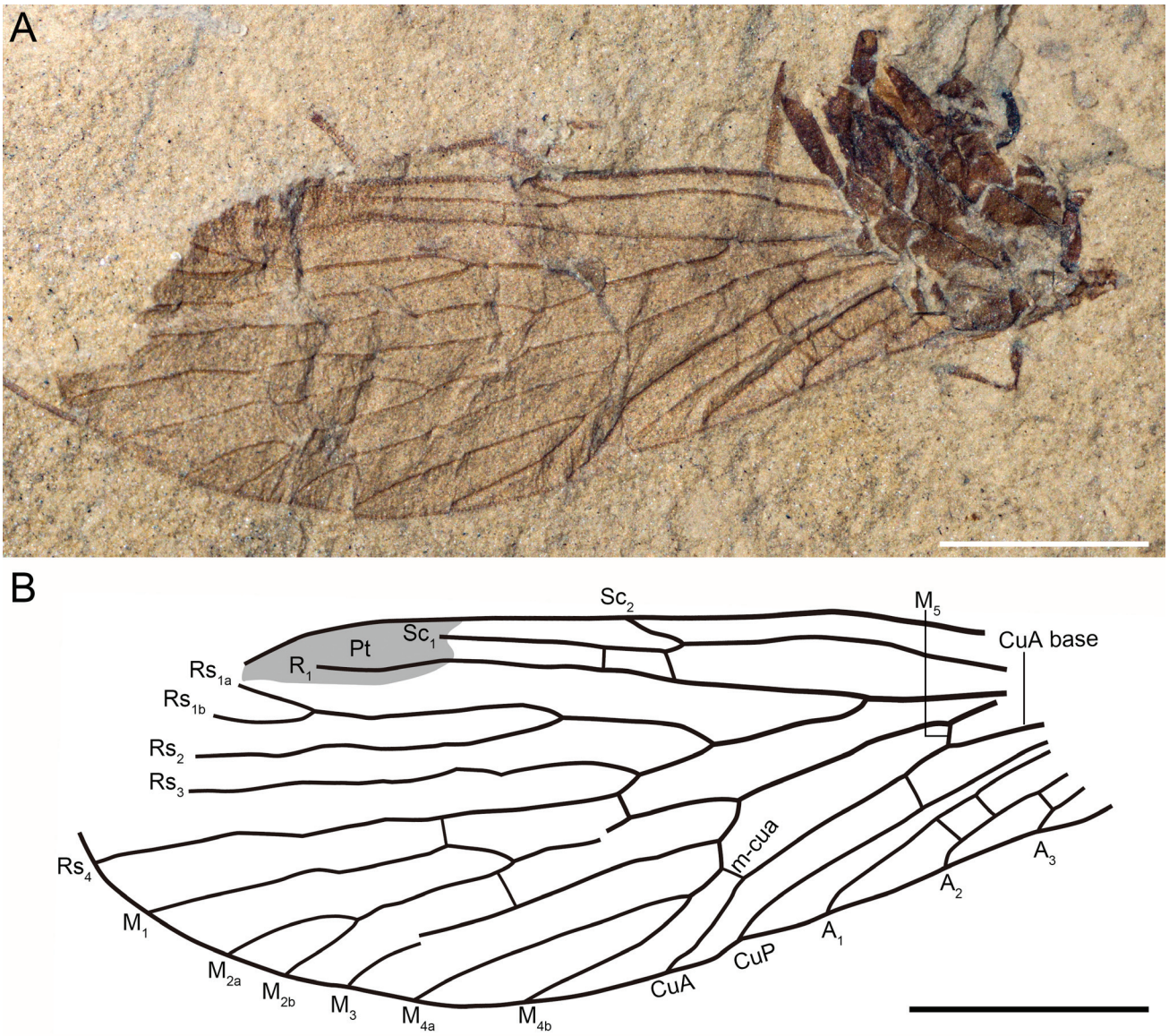

FIGURE 6. *Parachorista ruga* **sp. nov.**, holotype, NIGP209388. **A**, Photograph. **B**, Line drawing. Scale bars: 2 mm.

Remarks. The new species, *Parachorista triassica* **sp. nov.**, can be readily distinguished from the other congeneric species by its elongate wing and distinctly short M_{3+4}.

***Parachorista elegantula* sp. nov.**
(Figs 8, 9)

Material. Holotype, NIGP209390, a completely preserved wing with a fine wing base. Paratypes, NIGP209391a, b, part and counterpart, a nearly complete forewing; NIGP209392a, b, with part and counterpart, a forewing lacking posterior apex; NIGP209393, an incomplete forewing missed one-third of wing base; NIGP209394, an incomplete forewing, with only wing base preserved.

Etymology. The species name is derived from the Latin *elegantula*, diminutive of *elegans*, meaning "elegant", referring to the delicate wings.

Diagnosis. Forewing moderately large; Sc_2 long, more than half of Sc_1; Rs with five branches, Rs_1 shorter than its branches.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. Holotype: forewing 14.2 mm long, 5.2 mm wide, length/width ratio 2.7; apex rounded and slowly tapering to wing base, some light-coloured patches covered the wing; Sc with two branches, both long and somewhat curved, Sc_1 reaching pterostigma, faint after entering pterostigma, Sc fork proximal to Rs fork, a crossvein connected Sc_1 and R_1; humeral crossvein present; R_1 somewhat straight, slightly curved near apex; pterostigma lentoid and pigmented; Rs with five branches, Rs_1 with two branches, Rs_{1+2} 0.7× length of Rs_{3+4}, Rs_1 distinctly shorter than its branches; M with six branches, M_2 and M_4 forked, M_{1+2} 2.3× length of M_{3+4}, M_4 sharply

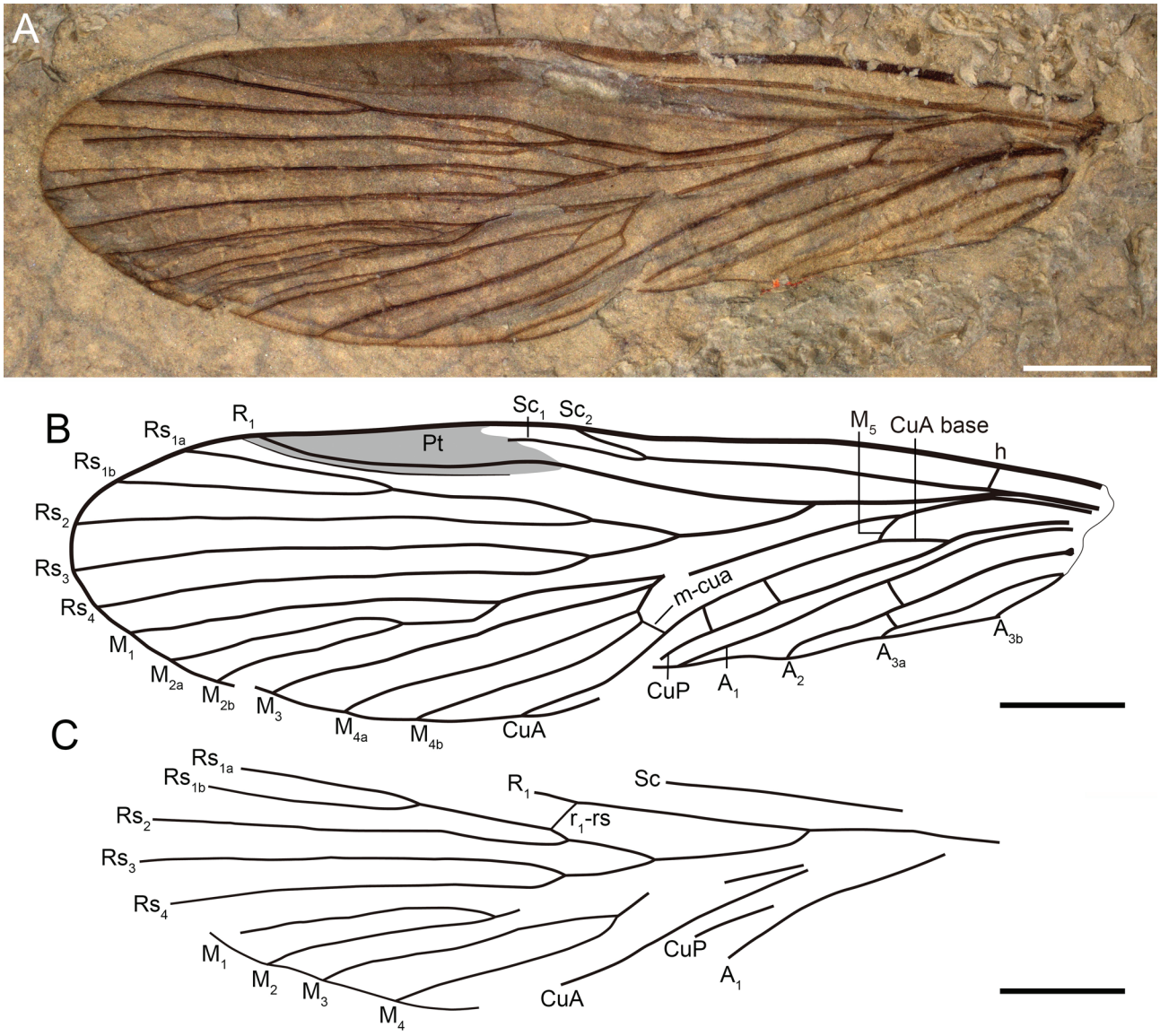

FIGURE 7. *Parachorista triassica* **sp. nov.**, holotype, NIGP209389. **A**, Photograph. **B**, Line drawing of forewing. **C**, Line drawing of hindwing. Scale bars: 2 mm.

curved near base, crossvein m-cua faint and connected the curved point of M_4 with CuA; CuA curved after the connection with m-cua; cubito-median Y-vein well-developed, M_5 half as long as CuA base; CuP straight; A with four branches, A_3 forked near its base; a crossvein connected A_1 and A_2 near wing base, two crossveins connected the middle of A_2 and A_3; one crossvein between the two branches of A_3; crossveins at branches of Rs and M usually faint.

Paratypes: NIGP209391, forewing rather slender, 13.1 mm long (nearly complete), 3.2 mm wide, length/width ratio 4.1; Sc forked into two long branches, Sc_1 1.8× length of Sc_2, Sc_1 reached to pterostigma; a crossvein connected Sc_1 and R_1; R_1 curved downwards after entering pterostigma; pterostigma lentoid, covered with dense tiny nodules and pigmentation; Rs with five branches, Rs_1 with two branches, Rs_{1+2} slightly shorter than Rs_{3+4}, Rs_1 distinctly shorter than its branches; M with six branches, M_2 and M_4 forked, M_{1+2} 2.7× length of M_{3+4}, M_4 sharply curved; crossvein m-cua faint, connected curved point of M_4; Rs fork and M fork almost at same level; CuA curved apically, cubito-median Y-vein conspicuous, M_5 twice as long as CuA base; CuP straight; A with four branches, A_3 forked near base; a crossvein connected middle of CuP and CuA, basal part of A_1 and A_2, apical branches of A_3, two crossveins connected A_3 and A_2; crossveins between the branches of Rs and M usually faint.

NIGP209392, forewing length preserved 13.9 mm, width preserved 5.0 mm; Sc two-branched, Sc fork slightly proximal to Rs fork; Sc_1 long, faint after entering pterostigma; R_1 single, curved downwards after entering pterostigma, a crossvein connected basal part of Sc_1 and R_1; Rs with five branches, Rs_1 with two branches, Rs_{1+2} 0.7× length of Rs_{3+4}; Rs_{3+4} forking asymmetrically; the

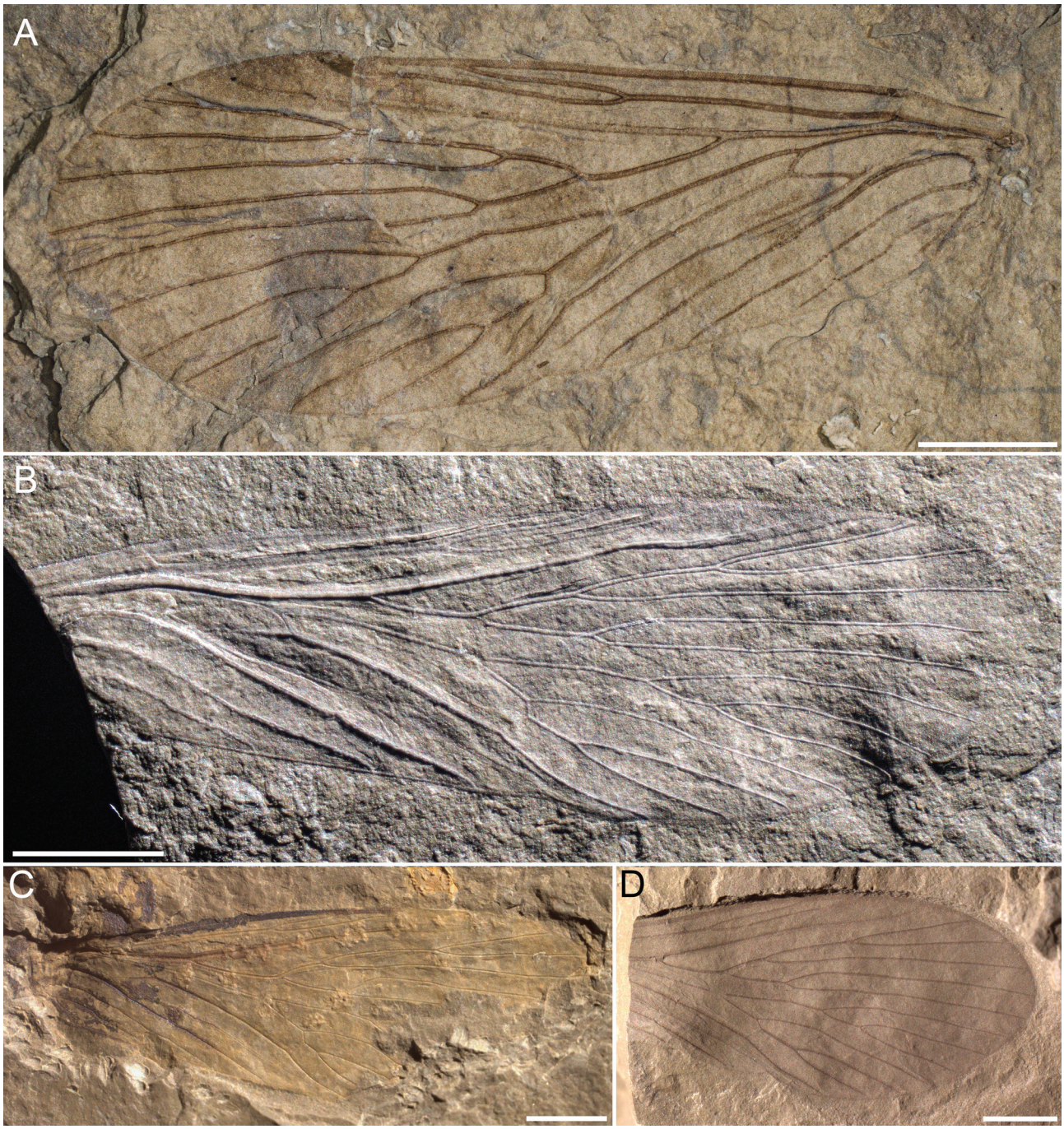

FIGURE 8. *Parachorista elegantula* **sp. nov. A**, Holotype, NIGP209390. **B**, Paratype, NIGP209391b. **C**, Paratype, NIGP209392a. **D**, Paratype, NIGP209393. Scale bars: 2 mm.

apex of M_{1+2} branches missing, M_{3+4} preserves three branches, M_4 two-branched, M_{1+2} twice as long as M_{3+4}; M fork proximal to Rs fork; two m-cua crossveins present; CuA single, apically curved, CuP single; cubito-median Y-vein distinct, CuA base more than twice as long as M_5; A with four branches, A_3 forked near its base; a crossvein connected the middle of CuA and CuP, A_2 and A_3, and the branches of A_3, two crossveins connected A_1 and A_2.

NIGP209393, 11.0 mm long (as preserved), Sc with two long branches, Sc_1 1.5× length of Sc_2; Sc fork slightly proximal to Rs fork; R_1 single, apex slightly curved; pterostigma lentoid; Rs with five branches, Rs_1 with two branches, Rs_{1+2} 0.7× length of Rs_{3+4}, Rs_1 distinctly shorter than its branches; M with six branches, M_2 and M_4 forked, M_{1+2} 2.3× length of M_{3+4}, M_4 sharply curved near its base, crossvein m-cua connected the curved point of M_4 and CuA; CuA single, curved near apex; CuP single and rather straight; two anal veins detected; several crossveins between branches of Rs and M.

Remarks. The new species, *Parachorista elegantula* **sp. nov.**, resembles *P. religiosa* Novokshonov, 2001, but differs from the latter by its forewing covered with sparse

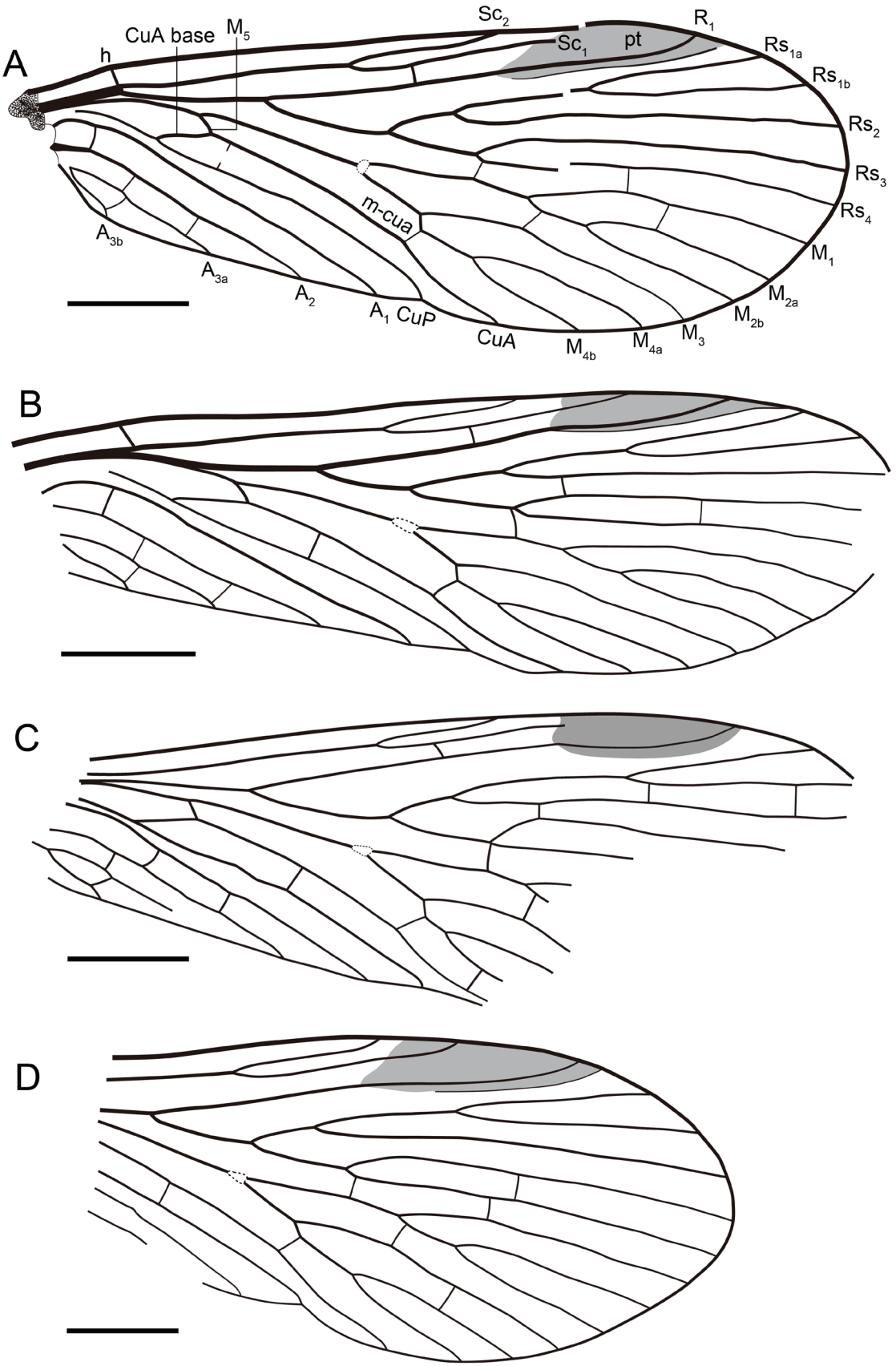

FIGURE 9. Line drawings of *Parachorista elegantula* **sp. nov. A**, Holotype, NIGP209390. **B**, Paratype, NIGP209391. **C**, Paratype, NIGP209392. **D**, Paratype, NIGP209393. Scale bar = 2 mm.

coloured markings instead of apical wings fully covered with coloured markings, longer Sc_2 (more than half length of Sc_1), and M_{1+2} just over twice as long as M_{3+4} instead of 4×.

***Parachorista hongi* sp. nov.**
(Figs 10, 11)

Material. Holotype, NIGP209395a, b, part and counterpart, a complete forewing collected from Yishi Village, Yaoqu Township. Paratype, NIGP209396, four overlapping wings, all incomplete, the specimen was collected from the locality near Jinsuoguan Village, Jinsuoguan Township.

Etymology. The species name is dedicated to the late Palaeontologist Youchong Hong.

Diagnosis. Forewing medium-sized; Rs with six branches, Rs_1 *ca.* twice as long as Rs_{1+2}.

Type locality and horizon. A locality near Yishi Village, Yaoqu Township, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. Holotype, forewing 11.6 mm long, 3.1 mm wide, length/width ratio 3.5; wing basal part shrunken, covered with small nodules; apical half of wing covered with pigments; Sc with two branches, Sc fork at the same level as Rs fork, Sc_1 more than twice as long as Sc_2, not visible after entering the pterostigma; R_1 single, curved downwards after entering pterostigma, a crossvein connected basal part of Sc_1 and R_1; pterostigma lentoid, pigmented, with small wrinkled structure, a vein-like boundary at bottom; Rs with six branches, Rs_1 with three

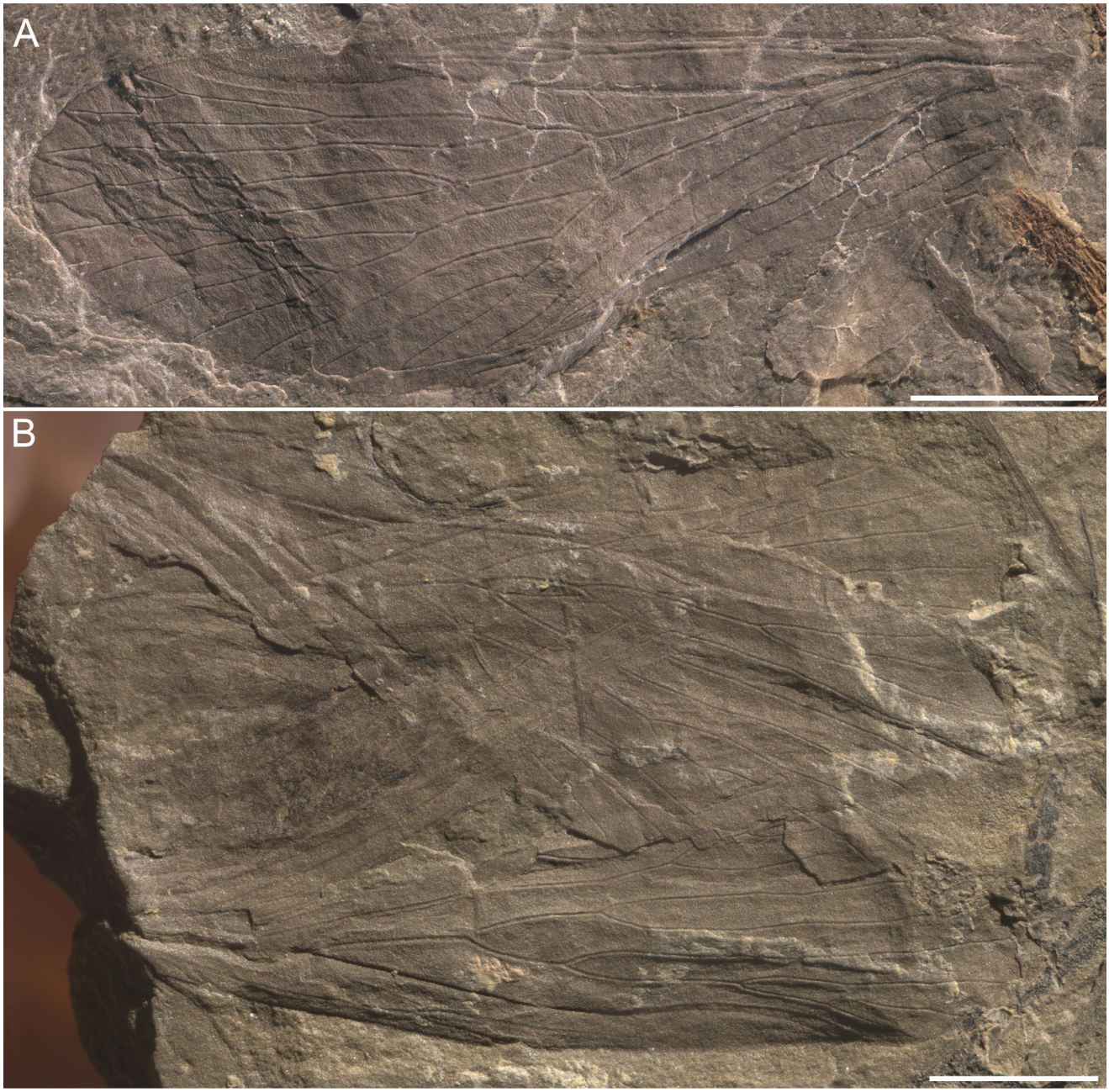

FIGURE 10. *Parachorista hongi* **sp. nov. A**, Holotype, NIGP209395b. **B**, Paratype, NIGP209396. Scale bars: 2 mm.

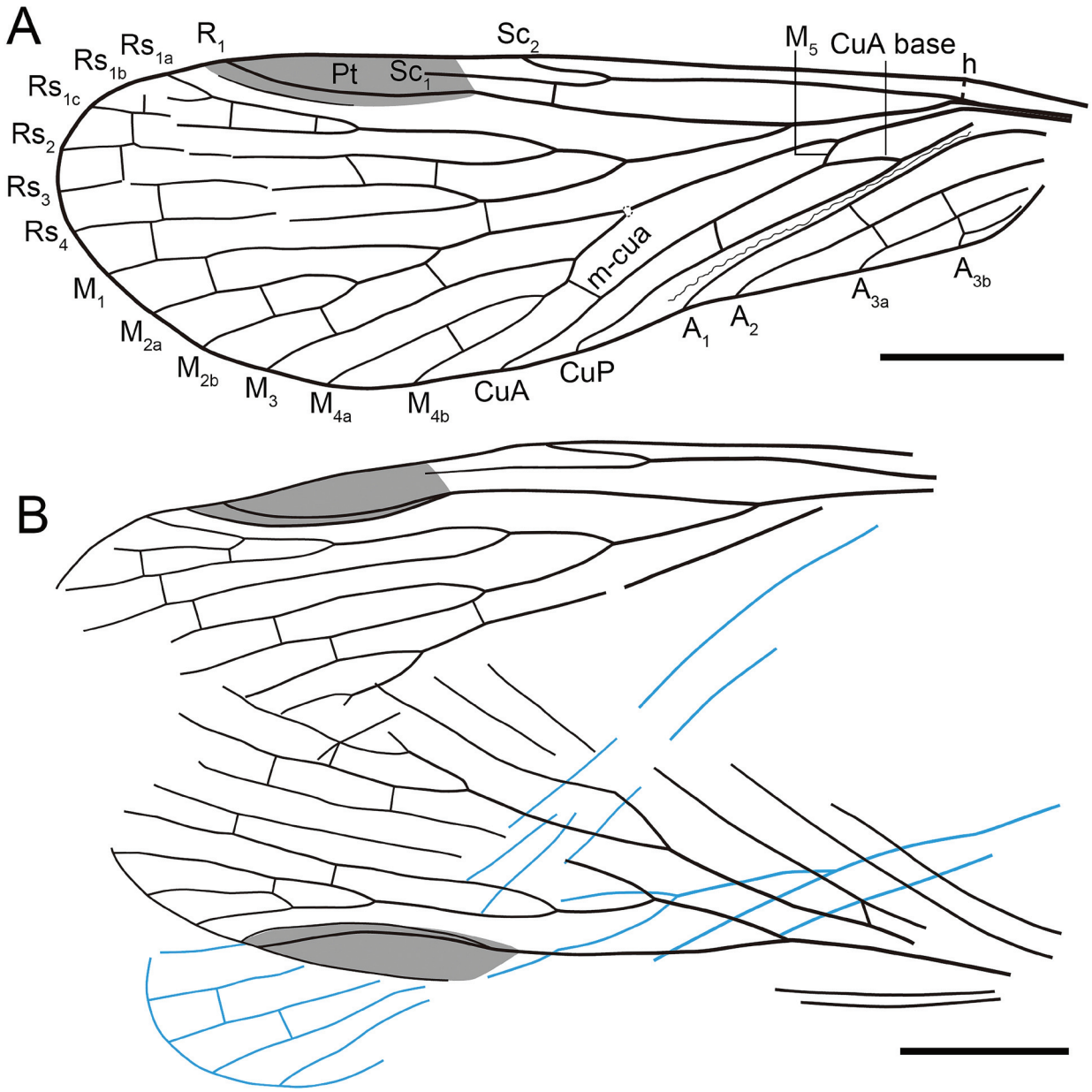

FIGURE 11. Line drawings of *Parachorista hongi* **sp. nov. A**, Holotype, NIGP209395. **B**, Paratype, NIGP209396. Scale bars: 2 mm.

branches, the apical fork of Rs_1 small, Rs_{1+2} 0.4× length of Rs_{3+4}, Rs_1 2.8× length of Rs_{1+2}; M with six branches, M_2 and M_4 forked, M_{1+2} 2.6× length of M_{3+4}, M_4 sharply bent; M fork slightly distal to Rs fork, m-cua connected the mid-M_4 and CuA; CuA single, apically curved, cubito-median Y-vein well-developed, CuP single and apically sinuous, a crossvein connected CuA and CuP; the area between CuP and CuA shrunken; anal veins with four branches, A_3 forked at its base, one crossvein connected A_1 and A_2, and apex of the two branches of A_3; two crossveins connected middle part of A_2 and A_3; many crossveins connected the branches of Rs and M.

Paratype, NIGP209396, a forewing preserved length 11.7 mm, width preserved 4.0 mm; Sc with two branches, fork of Sc relatively broad, distinctly proximal to Rs fork and at the level of middle Rs, Sc_1 at least twice as long as Sc_2, Sc_1 faint after entering pterostigma; R_1 single, curved downwards after entering pterostigma; pterostigma lentoid, a vein-like boundary limited its bottom; Rs with six branches, R_1 with three branches, Rs_{1+2} 0.7× length of Rs_{3+4}, Rs_1 1.7× length of Rs_{1+2}; basal Rs_{1b} sharply curved, and connected with Rs_{1c} by a crossvein; M with six branches, M_2 and M_4 forked into two branches, M_{1+2} 2.8× length of M_{3+4}, Rs fork and M fork nearly at the same level; CuA and CuP partly preserved; anal veins poorly preserved, only A_1 detected; many crossveins between the branches of Rs and M, but usually faint.

Remarks. The new species, *Parachorista hongi* **sp. nov.**, resembles *P. pulchra* **sp. nov.**, but differs from the latter by its broader Sc fork, Sc_1 more than twice as long

as Sc_2 (instead of less than twice), anterior branches of Rs_1 curved upwards, and Rs_1 longer than Rs_{1a+b} (instead of shorter). It differs from *Triasoparachorista huaxiaensis* Hong, 2009 in having a much longer Sc_2, the Rs fork situated at the same level as the M fork (instead of markedly proximal to it), and the anterior branches of Rs_1 curved upwards. It also differs from *P. asiatica* Novokshonov, 1997 by the smaller and broader wing, the Sc fork more distal, Sc_1 more than twice as long as Sc_2 (instead of less than twice), and the Rs fork situated at the same level as the M fork (instead of markedly proximal to it).

***Parachorista orienta* sp. nov**
(Fig. 12)

Material. Holotype, NIGP209397, a single forewing, with part of wing base missing.

Etymology. The specific name is derived from the Latin word *orienta*, oriental.

Diagnosis. Sc_1 long, sinuous near apex; Rs and M five-branched.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. Forewing, 10.5 mm long (as preserved), 4.2 mm wide, tongue-shaped, base moderately narrow; Sc with two branches, Sc_2 relatively short, Sc_1 more than four times as long as Sc_2, Sc_1 sinuous near apex, Sc fork slightly distal to Rs fork; R_1 single, curved downwards after entering pterostigma, a crossvein connected the base of Sc_1 and R_1; pterostigma lentoid, consisting of dense, tiny nodules, a vein-like boundary marking its bottom; Rs with five branches, Rs_1 with two branches, Rs_{1+2} slightly shorter than Rs_{3+4}; Rs_1 nearly as long as its branches; M with five branches, but only four preserved, M_2 single, M_4 preserves only one branch, but the broad space between the M_4 and CuA indicates that M_4 has two branches; M_{1+2}

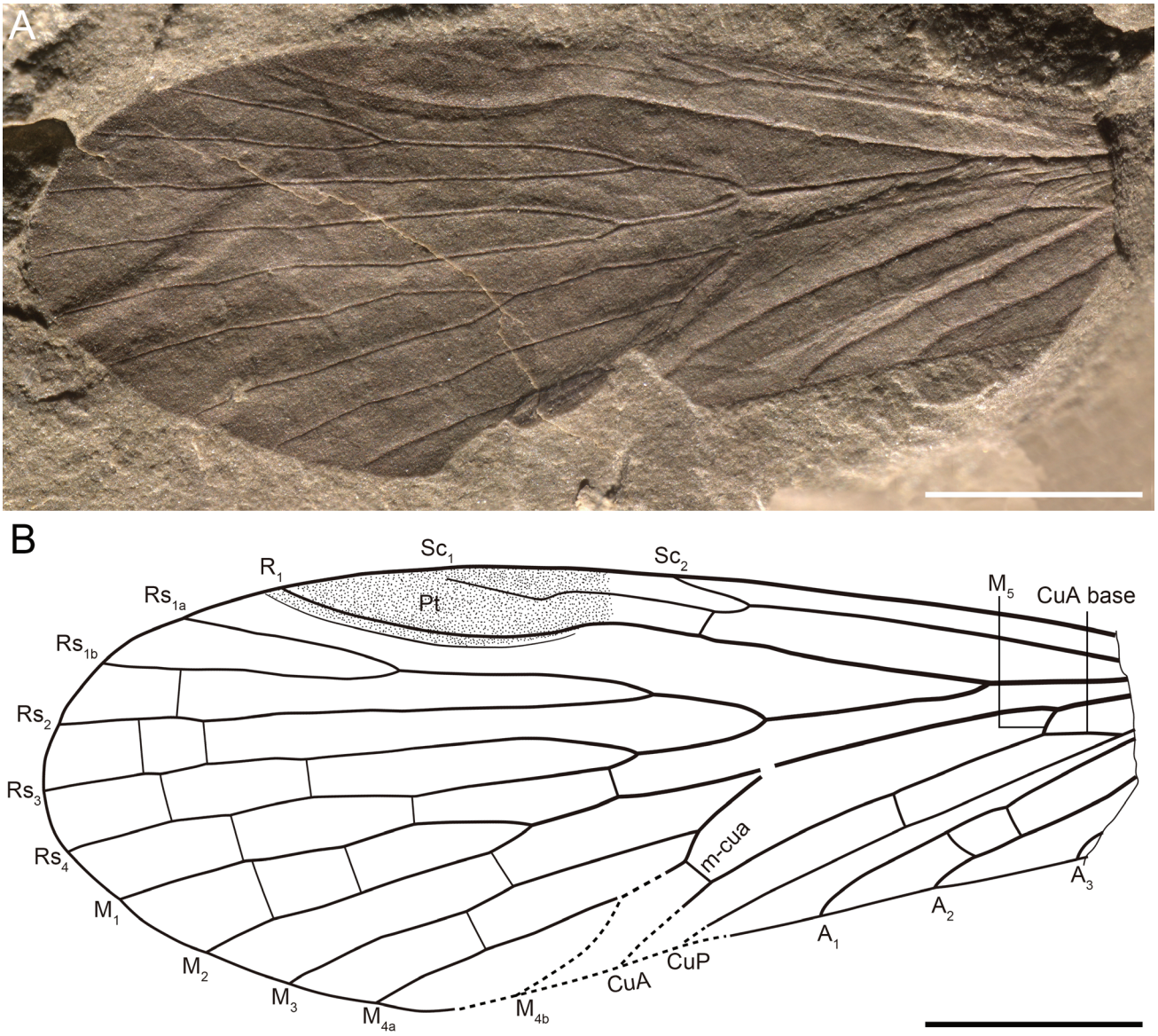

FIGURE 12. *Parachorista orienta* **sp. nov.**, holotype, NIGP209397. **A**, Photograph. **B**, Line drawing. Scale bars: 2 mm.

3× length of M_{3+4}, crossvein m-cua connected the sharply curved point of M_4 and CuA; CuA curved posteriorly, cubito-median Y-vein distinct, CuP straight and single, a crossvein connected the middle of CuA and CuP; three anal veins detected, two crossveins between A_1 and A_2; numerous faint crossveins between branches of Rs and M.

Remarks. Even though *Parachorista orienta* **sp. nov.** has a single M_2, which is an atypical character of parachoristid, the elongate and oblique Sc_2 together with the well-developed cubito-median Y-vein strongly supported its placement to Parachoristidae instead of "Orthophlebiidae".

***Parachorista* sp.**
(Fig. 13)

Material. NIGP209398, a well-preserved hindwing from the Middle-Upper Triassic Yanchang Formation at Hejiafang Village.

Description. Wing 12.5 mm long and 4.2 mm wide (L/W ratio 3.0); Sc single and shortened, terminating near level of Rs_{1+2} fork, a crossvein connecting Sc and R_1; R_1 forking into two small branches near apex; a sinuous crossvein connecting R_1 and Rs_1; Rs with five branches, Rs_{1+2} as long as Rs_{3+4}; M with four branches, M_{1+2} 4× length of M_{3+4}; M fork near the same level as M fork; crossvein m-cua connecting basal M_4 and CuA; CuA single, fused with M; CuP fused with the middle A_1; three anal veins present; numerous crossveins at branches of Rs and M, and between anal veins.

Remarks. This specimen is readily distinguished from the hindwing of *P. pulchra* **sp. nov.** by its smaller wing, R_1 fork being much closer to the wing margin, and Rs five-branched instead of six-branched; from the hindwing of *P. libaii* **sp. nov.** by its larger wing, and R_1 fork being much closer to the wing margin. However, an isolated hindwing is insufficient to erect a separate species, and it is herein regarded as an indeterminate species.

Genus *Sinoparachorista* Lian, Cai & Huang, 2023

Type and included species. *Sinoparachorista rara* Lian, Cai & Huang, 2023, *Sinoparachorista magna* **sp. nov.**

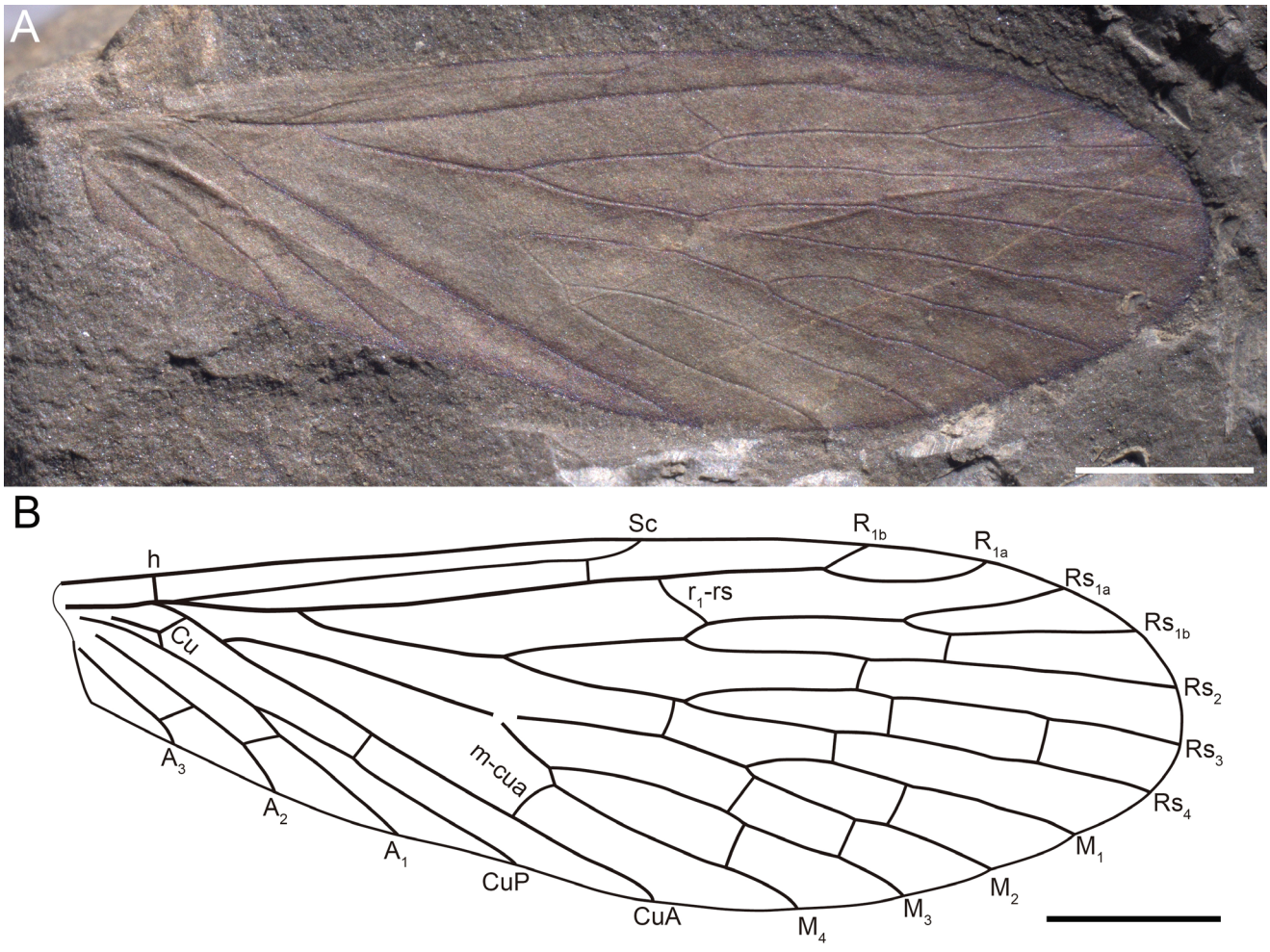

FIGURE 13. *Parachorista* **sp.**, NIGP209398. **A**, Photograph. **B**, Line drawing. Scale bars: 2 mm.

***Sinoparachorista magna* sp. nov.**
(Fig. 14)

Material. Holotype, NIGP209399a, b, part and counterpart, wing base missing.

Etymology. The species name is derived from the Latin word *magna*, referring to the large wing size.

Diagnosis. Forewing relatively large; pterostigma moderately elongate; Rs with seven branches; and Rs_{1+2} half the length of Rs_{3+4}.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. A relatively large forewing, 13.8 mm long (as preserved), 6.4 mm wide; Sc with two branches, Sc fork nearly at the same level as Rs fork, Sc_1 2.5× length of Sc_2, Sc_1 faint after entering pterostigma, an oblique crossvein connected basal part of Sc_1 and R_1; R_1 single, curved downwards after entering pterostigma, an oblique crossvein connected R_1 with apical Rs_1; pterostigma lentoid, coloured markings not distinct; Rs with seven branches, Rs_1 with four branches, Rs_{1+2} 0.6× length of Rs_{3+4}, Rs_1 2.2× length of Rs_{1+2}; M with seven branches, M_1, M_2, and M_4 forked into two branches, M_3 single, M_{1+2} 2.5× length of M_{3+4}, M_4 short and curved; M fork slightly distal to Rs fork, crossvein m-cua connected M_4 and

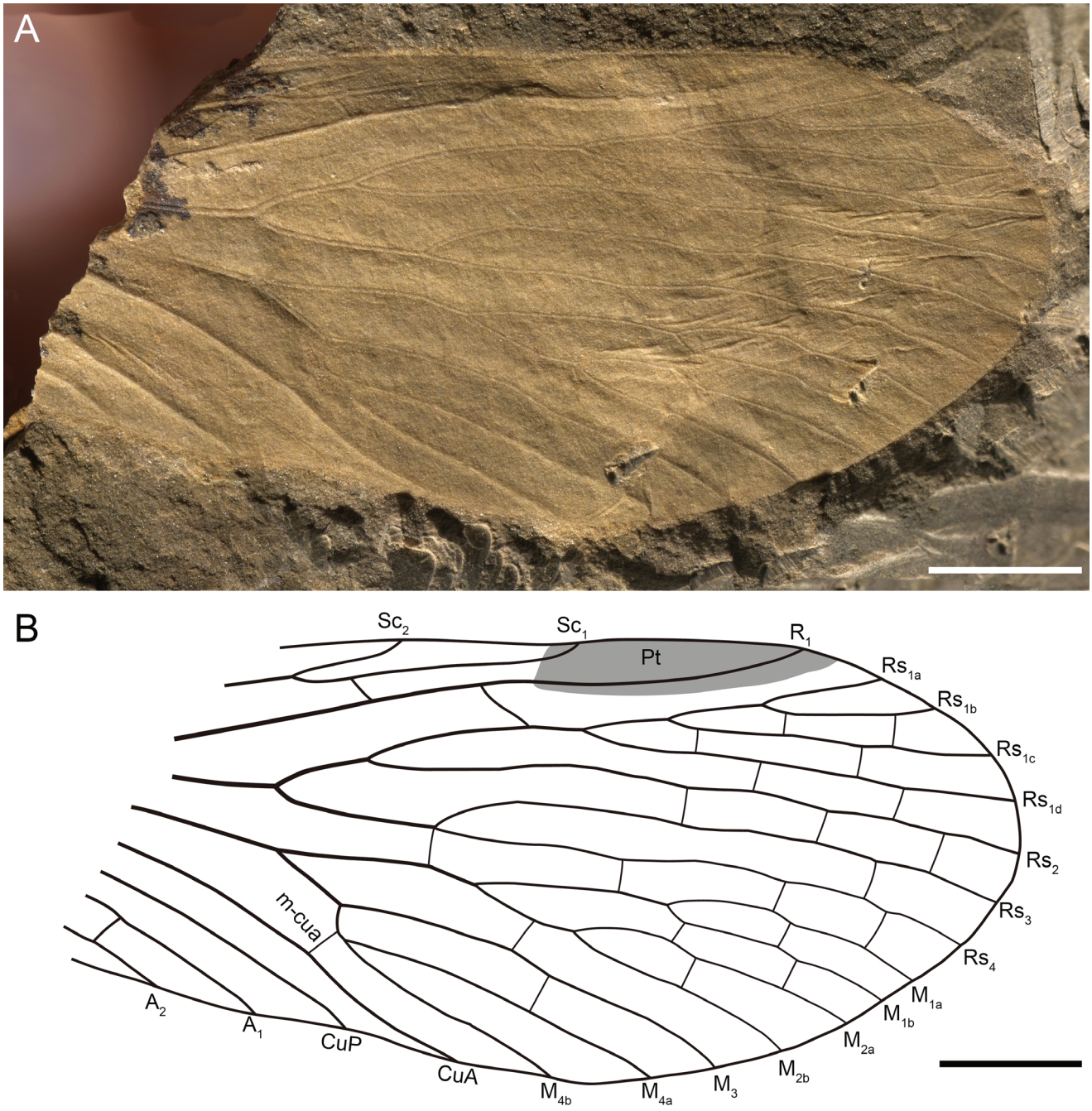

FIGURE 14. *Sinoparachorista magna* **sp. nov.**, holotype, NIGP209399a. **A**, Photograph. **B**, Line drawing. Scale bars: 2 mm.

CuA; CuA curved apically, CuP straight; two anal veins detected; numerous crossveins connected the branches of Rs and M.

Remarks. The new species, *Sinoparachorista magna* **sp. nov.**, differs from *S. rara* Lian, Cai & Huang, 2023 by the combination of the following characters: shorter pterostigma, longer Sc_2 (Sc_1/Sc_2 equal to 2.5 instead of 3.8), Sc fork at the same level as Rs fork instead of Sc fork distinctly proximal to Rs fork, Rs seven-branched instead of six-branched, and Rs_{1+2} 0.6× length of Rs_{3+4} instead of 1.5×.

Family Protorthophlebiidae Soszyńska-Maj, Krzemiński & Kopeć, 2019

Genus *Protorthophlebia* Tillyard, 1933

Type species. *Protorthophlebia latipennis* Tillyard, 1933.

***Protorthophlebia prajna* sp. nov.**
(Figs 15, 16)

Material. Holotype, NIGP209400, a complete forewing, wing 9.9 mm long, 3.3 mm wide (L/W = 3.0). Paratypes: NIGP209401a, b, part and counterpart, a complete forewing, 9.8 mm long, 3.2 mm wide (L/W = 3.1); NIGP209402, a complete forewing, 7.5 mm long, 2.6 mm wide (L/W = 2.9).

Etymology. The specific name is derived from a Sanskrit word "प्रज्ञा" ("*prajñā*", feminine), meaning "wisdom", a central concept in Buddhist philosophy.

Diagnosis. Forewing small, apically rounded; Sc single and short, terminating before pterostigma; basal M_{3+4} and crossvein m-cua unsclerotized.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. Based primarily on the holotype; forewing with broad and rounded apical part and thin basal part, wing margin concave at apex of CuP; Sc single, terminating at the level of Rs_{1+2} fork and before the pterostigma; costal area narrower than subcostal; a crossvein connecting apical Sc and R_1; pterostigma lentoid, slightly pigmented, lower margin demarcated by a vein-like boundary; Rs with five branches, Rs_{1+2} equal to or distinctly longer than Rs_{3+4} (Rs_{1+2} 1.2× length of Rs_{3+4} in holotype, 1.3× in NIGP209401, and Rs_{1+2} slightly shorter than Rs_{3+4} in NIGP209402); basal Rs_2 distinctly curved to the short crossvein rs_2-rs_3 (only in holotype); M with five branches, M_{1+2} 2.9× length of M_{3+4}, M_4 forking into two branches; basal M_4 sharply curved; basal M_4, crossvein m-cua, and basal M fork desclerotized; CuA single, slightly sinuate near apex, M_5 very short, crossvein-like, CuA base sharply curved; CuP single, straight; four anal veins, A_1 and A_2 single, A_3 with a small apical fork; numerous crossveins between veins of Rs, M, and cubito–anal veins.

Remarks. The new species, *Protorthophlebia prajna* **sp. nov.**, is placed in Protorthophlebiidae based on the pectinate Rs with only five branches (Soszyńska-Maj *et al*., 2019). The single-branched Sc, five-branched M, and poorly developed M_5 rule out its placement in Parachoristidae. The short Sc is unusual within "Orthophlebiidae", which commonly has the long Sc terminating inside the pterostigma. The new species differs from the holotype of the type species *Pr. latipennis* Tillyard, 1933 (see Soszyńska-Maj *et al*., 2019: fig. 8) by Sc being single instead of two-branched, terminating before, instead of inside, the pterostigma, crossvein m-cua connecting the stem M_4 instead of M_{4b}, and Rs fork distal to instead of proximal to, the M fork.

***Protorthophlebia ladinica* Hong, Chen & Liu, 2002**
(Fig. 17A–D)

Material. NIGP209403, hindwing, 10.0 mm long, 3.7 mm wide (L/W = 2.7); NIGP209404a, b, with part and counterpart, hindwing, 12.9 mm long (as preserved), 4.5 mm wide; NIGP209405, a fragment of hindwing.

Description (emended)**.** Sc short, terminating before pterostigma; a crossvein connecting Sc and R_1; R_1 apically forking into two branches; pterostigma consisting of small nodules, with a vein-like structure demarcating the bottom boundary; Rs with five branches, Rs_{1+2} shorter than Rs_{3+4}; M with four branches, M_{1+2} twice longer than M_{3+4}; crossvein m-cua connecting CuA with basal M_4; CuA straight, fused with M for a relatively long distance, and then fused with R near wing base; CuP single, fused with A_1 for a long distance; A_2 and A_3 short; crossveins well developed along the Rs and M branches.

Remarks. *Protorthophlebia ladinica* was established based on specimen TH99-1119 (Hong *et al*., 2002: figs 3, 4). The specimen was interpreted by Hong as a forewing; however, this interpretation is incorrect. The presence of a branched R_1 and a four-branched M unequivocally indicates that the specimen represents a hindwing.

***Protorthophlebia triassica* Hong, Chen & Liu, 2002**
(Fig. 17E–H)

Material. New material, NIGP209406, a hindwing missed basal part, 8.0 mm long (as preserved), 2.8 mm wide; and NIGP209407, a hindwing missed a small part of wing base, 5.4 mm long (as preserved), 2.1 mm wide.

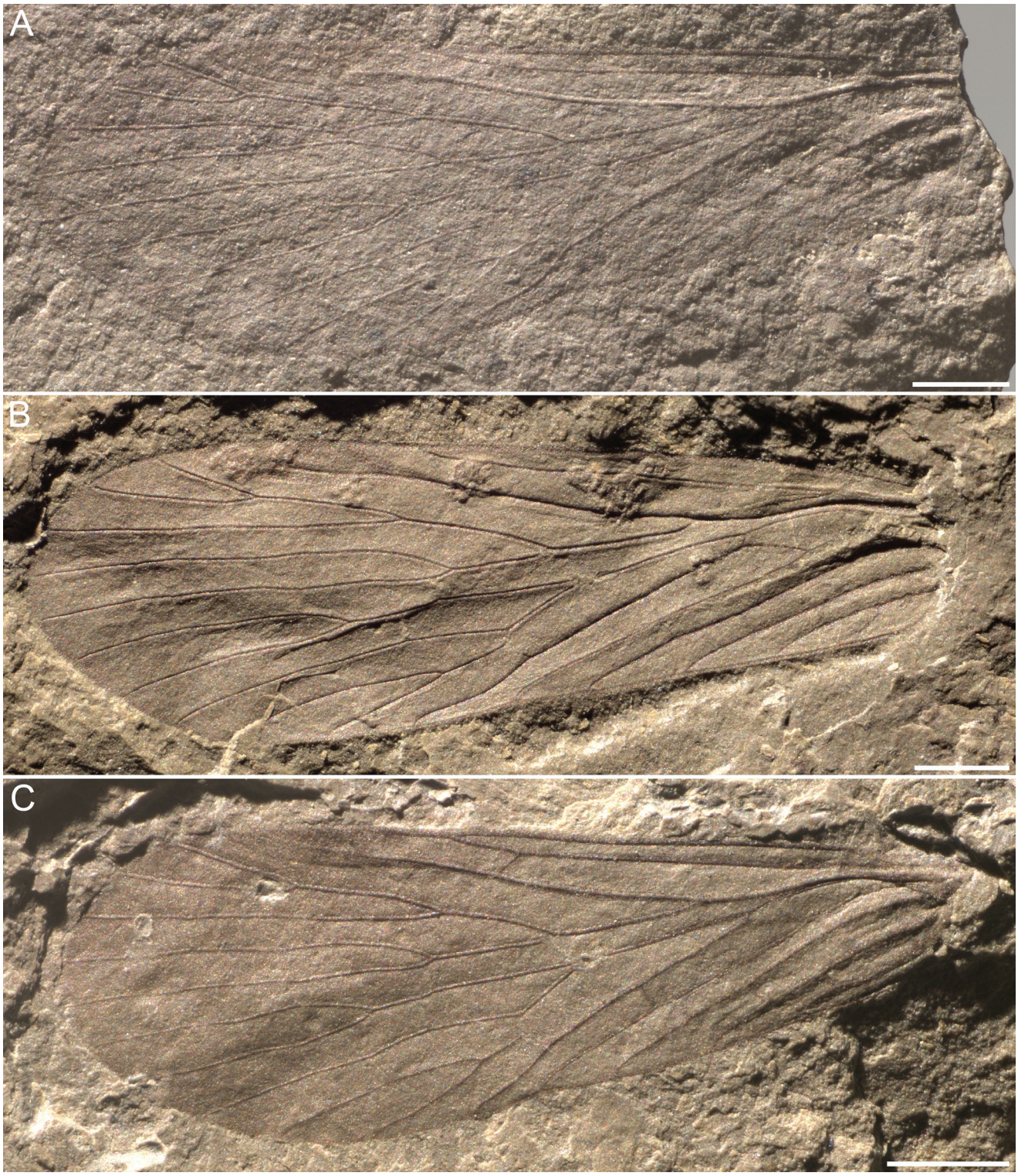

FIGURE 15. *Protorthophlebia prajna* **sp. nov. A**, Holotype, NIGP209400a. **B**, Paratype, NIGP209401. **C**, Paratype, NIGP209402. Scale bars: 1 mm.

Description (emended)**.** Hindwings with Sc short, terminating before Rs_{1+2} fork, costal area narrow; a crossvein connected apical Sc and R_1; pterostigma lentoid, pigmented; R_1 straight, slightly curved near apex; Rs with five branches, Rs_1 fork small, Rs_{1+2} *ca.* 1.5× length of Rs_{3+4}; M with four branches, M_{1+2} *ca*. twice as long as M_{3+4}; crossvein m-cua connecting M_{3+4} and CuA; CuA straight, fused with M for a long distance; apex of CuP and A_1 preserved; two crossveins connected Rs and M; one crossvein between M_{1+2} and M_{3+4}.

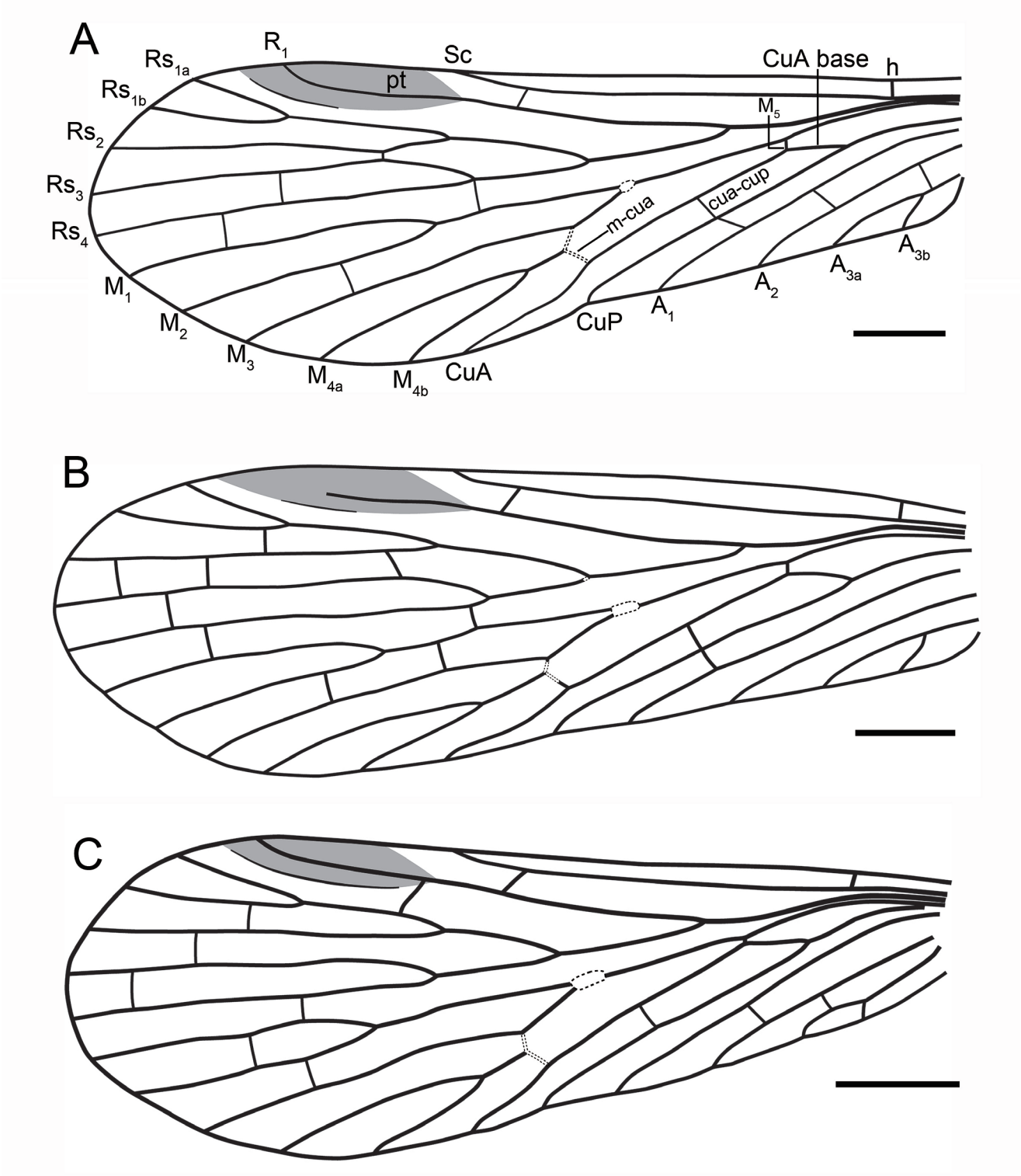

FIGURE 16. Line drawings of *Protorthophlebia prajna* **sp. nov. A**, Holotype, NIGP209400. **B**, Paratype, NIGP209401. **C**, Paratype, NIGP209402. Scale bars: 1 mm.

Remarks. *Protorthophlebia triassica* was established based on specimen TH99-1/CJ101, which preserves two isolated hindwings and a fragmentary forewing (Hong *et al*., 2002: fig. 2). However, one of the hindwings was misinterpreted by Hong as a forewing, an error similar to that made for *Protorthophlebia ladinica*.

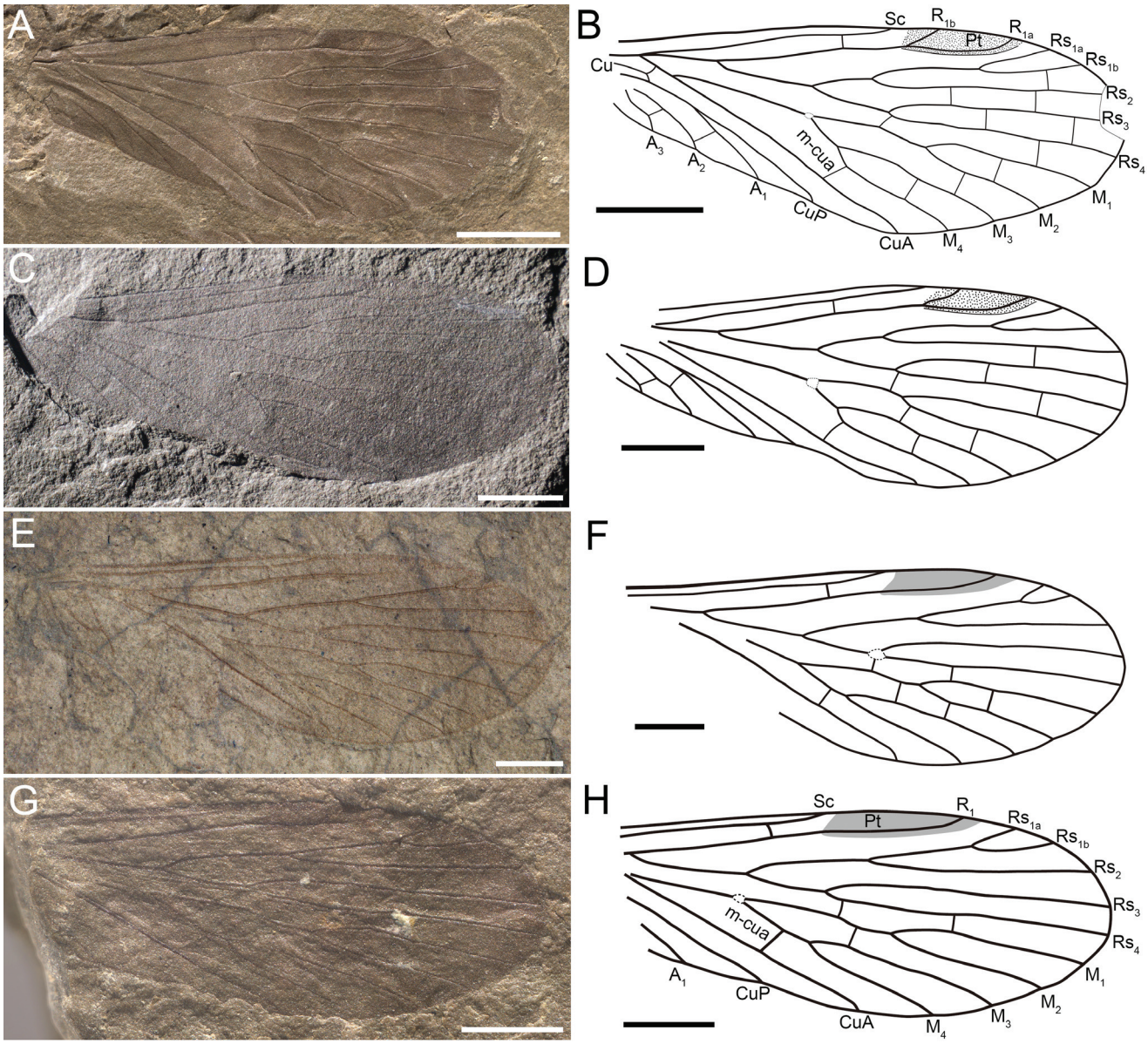

FIGURE 17. Line drawings of Protorthophlebiidae. **A**–**D**, *Protorthophlebia ladinica* Hong, Chen & Liu, 2002. **E**–**H**, *Protorthophlebia triassica* Hong, Chen & Liu, 2002. **A**, Photograph of NIGP209403. **B**, Line drawing of **A**. **C**, Photograph of NIGP209404. **D**, Line drawing of **C**. **E**, Photograph of NIGP209406. **F**, Line drawing of **E**. **G**, Photograph of NIGP209407. **H**, Line drawing of **G**. Scale bars: 2 mm in **A**–**D**, 1 mm in **E**–**H**.

Family Orthophlebiidae Handlirsch, 1906
Genus *Orthophlebia* Westwood, 1845

***Orthophlebia xiangyu* sp. nov.**
(Fig. 18)

Material. Holotype, NIGP209408, a nearly complete forewing lost wing base, and posterior wing distorted.

Etymology. The species name *xiangyu* is dedicated to Xiang Yu, the famous historical Chinese general, in honor of his legendary courage and strength.

Diagnosis. Forewing nearly fully covered with coloured markings, crossveins accompanied with hyaline bands; Sc single and long; Rs with six branches.

Type locality and horizon. Hejiafang Village, Tongchuan City, Shaanxi Province; the lower part of the Middle-Upper Triassic Yanchang Formation, Ladinian.

Description. Forewing relatively broad, 8.8 mm long (as preserved), 3.5 mm wide; wing nearly fully covered with coloured markings, with all crossveins enclosed within narrow hyaline bands, and two relatively big hyaline bands located at middle part of anterior wing; Sc single, parallel to costa, apically curved and terminating inside pterostigma; R_1 strongly curved at apical part; pterostigma with a vein-like structure demarcated its bottom boundary; Rs with six branches, Rs_{1+2} slightly longer than Rs_{3+4}, Rs_{1+2} longer than Rs_1, and Rs_1 longer than Rs_{1a+b}; base of Rs_{3+4} desclerotized; M with five

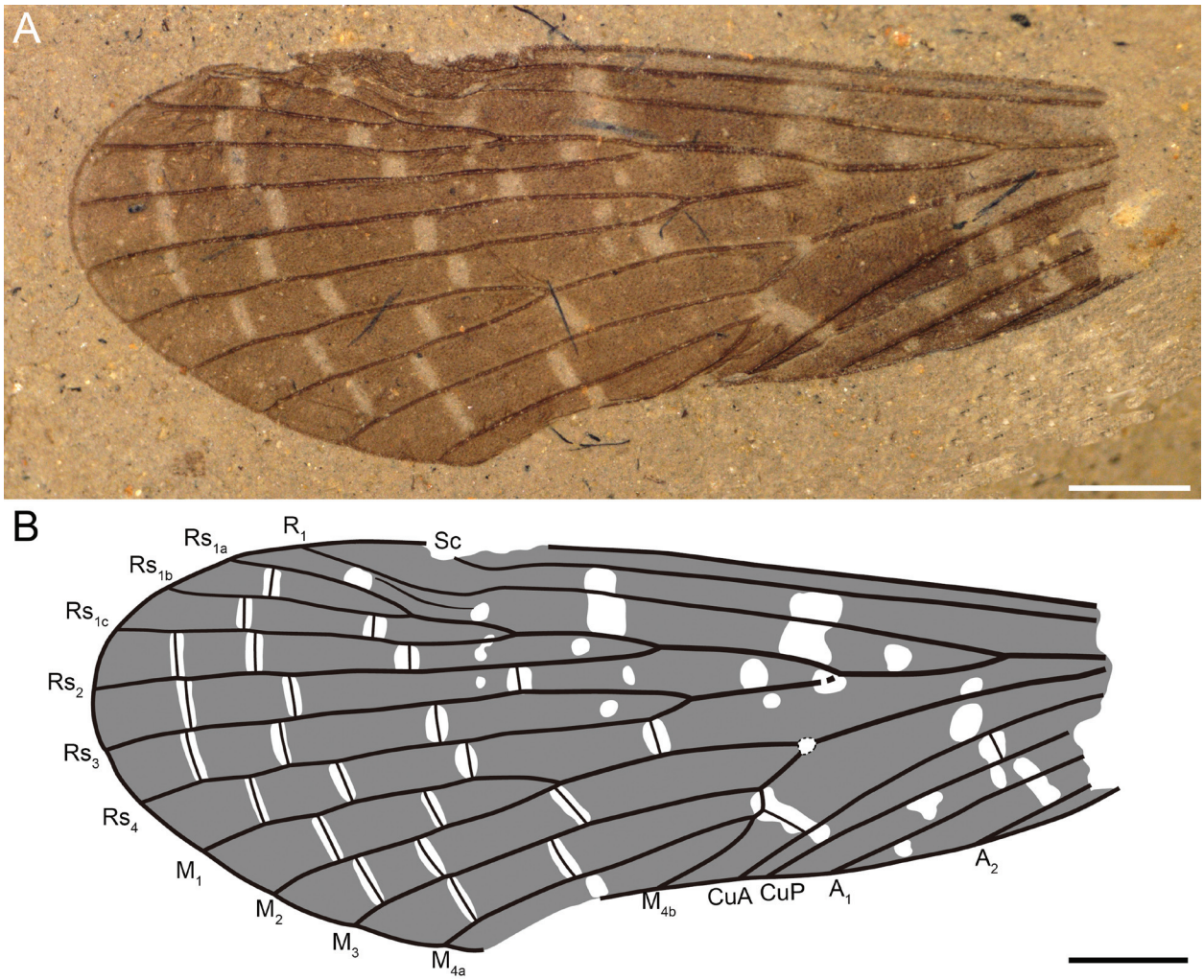

FIGURE 18. *Orthophlebia xiangyu* **sp. nov.**, holotype, NIGP209408a. **A**, Photograph. **B**, Line drawing. Scale bars: 1 mm.

branches, M_{1+2} 4.1× length of M_{3+4}, M_4 sharply curved at the connection of crossvein m-cua; a hyaline band along m-cua; Rs fork proximal to M fork; CuA and CuP single and straight, crossvein cua-cup present; two anal veins preserved; crossveins between branches of Rs and M somewhat arranged in line.

Remarks. *Orthophlebia xiangyu* **sp. nov.** can be confidently placed in the family Orthophlebiidae s. str. by the single-branched Sc, six-branched Rs, and five-branched M (Soszyńska-Maj *et al*., 2019). The species is readily distinguished by its unique pattern of dark coloration interrupted by narrow hyaline bands. Furthermore, the exceptionally long Sc (terminating close to R_1) and sharply curved stem M_4 separate it from all other known species of *Orthophlebia*.

Discussion

The relationship of "Orthophlebiidae" and Parachoristidae

The resemblance between Parachoristidae and "Orthophlebiidae" in both venation and body structures indicates a close relationship between the two families (Novokshonov, 1997). However, although many authors have considered "Orthophlebiidae" as a basal stem group of Panorpoidea, Parachoristidae has often been overlooked in this context (Archibald *et al*., 2013; Krzemiński *et al*., 2016). Those interpretations may have been influenced by Willmann, who considered the forked M_2 as a primitive and crucial character for determining the placement of taxa within Mecopteroidea (Willmann, 1989). Consequently, he regarded Parachoristidae as a highly basal group of Antliophora, unrelated to "Orthophlebiidae". Even though M_2 is forked in the majority of individuals of Parachoristidae, some parachoristids (*e.g*., *Neoparachorista* and *P. orienta* **sp. nov.**) possess a single M_2. This suggests that the condition of M_2, whether single or forked, cannot serve as a diagnostic character at the ordinal level, nor can it be used to exclude Parachoristidae from a close affinity with "Orthophlebiidae". On the other hand, with the continuous discovery of additional fossil specimens, the morphological similarity exhibited by these two mecopteran taxa is undeniable. Both Parachoristidae and "Orthophlebiidae" share pectinate Rs_1, which is a synapomorphy of Panorpoidea. Parachoristidae possess

a primitive M_2 fork and are considered to fill the wing venation gap between the Permian Permochoristidae and "Orthophlebiidae" (Hong, 2009a). It is worth noting that Novokshonov not only emphasized the close phylogenetic relationship between Parachoristidae and "Orthophlebiidae", but also formally placed Parachoristidae within Panorpoidea (Novokshonov, 2002). However, this concept was oddly neglected by subsequent authors. *Parachorista comica* Novokshonov, 1997 from the Middle-Upper Triassic Madygen Formation exhibits long filiform antennae, rostrate mouthparts, and long legs with pubescence arranged in a ring—characters shared with "Orthophlebiidae" (Novokshonov, 1997). It is also plausible that parachoristids possessed bulbous, upturned, scorpion-like genitalia similar to those of Panorpoidea. Considering these morphological similarities, Parachoristidae should replace "Orthophlebiidae" as the most basal clade within Panorpoidea.

The two families are generally easy to distinguish. Parachoristidae differ from "Orthophlebiidae" in venation by: (1) more expanded costal and subcostal areas; (2) Sc with a long and oblique Sc_2; (3) M usually has more than six branches (M_2 usually forked); and (4) cubito-median Y-vein well-developed (Novokshonov, 1997). All orthophlebiids lack a forked M_2, which serves as one of the most decisive characters distinguishing Parachoristidae from "Orthophlebiidae". Although some parachoristids have a single M_2, their assignment is supported by the presence of an elongate and oblique Sc_2, another decisive character unique to Parachoristidae. In rare cases, Sc_2 is reduced to a short crossvein-like anterior branch in Parachoristidae (*e.g.*, *P. sana* Novokshonov, 2001; *P. temperata* (Novokshonov, 2001) **comb. nov.**). The cubito-median Y-vein, similar to the characters discussed above, is retained by all parachoristids. "Orthophlebiidae" commonly share an undeveloped, crossvein-like M_5 and smooth CuA base, which is an apomorphy of advanced Panorpoidea. While a developed cubito-median Y-vein is retained in some orthophlebiids, such as the Middle Triassic *Choristopanorpa* and several Jurassic species (Novokshonov, 2001). The presence of a well-developed cubito-median Y-vein alone cannot be used to rule out assignment to "Orthophlebiidae".

The Triassic "Orthophlebiidae"

"Orthophlebiidae" was a superdiverse and dominant lineage of Panorpoidea during the Jurassic (Zhang, 1996; Lian *et al*., 2021a; Zhang *et al*., 2021), which replaced the Triassic-dominant Parachoristidae. The venational pattern of "Orthophlebiidae" is distinguished by a pectinate Rs_{1+2}, and M typically five-branched (M_4 bifurcated) in the forewings and M four-branched in the hindwings. Giganphlebiinae, the large-sized orthophlebiids, have the forewings have a six-branched M (M_4 with three branches), whereas the hindwings have a five-branched M (M_4 bifurcated) (Qiao *et al*., 2012; Soszyńska-Maj *et al*., 2018; Lian *et al*., 2021a). Members of Giganphlebiinae also exhibit an increased number of Rs branches (up to 8–9), implying that expansion of wing size was accompanied by greater venational reinforcement for structural support.

Despite their remarkable diversification during the Jurassic, Triassic representatives of "Orthophlebiidae" remain limited. A list of the known Triassic "Orthophlebiidae" is provided (Table 1), showing that most of "Orthophlebiidae" were reported from China. The Late Triassic species share the typical venational characters of the Jurassic Period and can be regarded as unequivocal "Orthophlebiidae," whereas the Middle Triassic forms warrant closer scrutiny, as several aberrant Parachoristidae are difficult to distinguish from "Orthophlebiidae". The Middle Triassic species previously reported from the Tongchuan entomofauna were based mainly on isolated hindwings, and many illustrations and descriptions are problematic (Hong *et al*.,

TABLE 1. Global list of Triassic Orthophlebiidae s. str. and Protorthophlebiidae.

Species	Country	Age	References
Orthophlebia exculpta	China	Late Triassic	Zhang, 1996
Orthophlebia prajna **sp. nov.**	China	Middle Triassic	this paper
Protorthophlebia macula	China	Late Triassic	Lin, 1992
Protorthophlebia strigata	China	Late Triassic	Zhang, 1996
Protorthophlebia ladinica	China	Middle Triassic	Hong *et al*., 2002; this paper
Protorthophlebia triassica	China	Middle Triassic	Hong *et al*., 2002; this paper
Protorthophlebia curta	China	Middle Triassic	Hong, 2009b
Protorthophlebia ridibunda **comb. nov.**	Kyrgyzstan	Middle–Late Triassic	Novokshonov, 2001; this paper
Protorthophlebia xiangyu **sp. nov.**	China	Middle Triassic	this paper
Choristopanorpa opinata	Kyrgyzstan	Middle–Late Triassic	Novokshonov, 2001
Choristopanorpa bifasciata	Australia	Middle Triassic	Riek, 1950; Willmann, 1989

2002; Hong, 2009b). New materials provide the first unequivocal orthophlebiid forewings from the Triassic, permitting revision of the previously reported species. The forewings of *Protorthophlebia prajna* **sp. nov.** and *Orthophlebia xiangyu* **sp. nov.** possess a single Sc, a five-branched M, and a weakly developed cubito-median Y-vein, with M_5 short and crossvein-like, and can therefore be confidently placed within "Orthophlebiidae". These findings not only demonstrate that "Orthophlebiidae" had already diverged by the Middle–Late Triassic, but also call for re-evaluation of certain species previously attributed to Parachoristidae, which appear more closely allied to "Orthophlebiidae".

Choristopanorpa was originally placed within the family Orthophlebiidae, which is accepted by some subsequent authors (*e.g.*, Jell & Duncan, 1986; Krzemiński *et al*., 2015). Willmann (1989), however, established the family *Choristopanorpidae* to accommodate the genus, based mainly on the presence of the cubito-median Y-vein. While Novokshonov (2001) transferred *Choristopanorpa* to Parachoristidae and added several species from the Middle-Upper Triassic Madygen Formation to the genus. The type species, *Choristopanorpa bifasciata* Riek, 1950 from the Middle Triassic at Brookvale, New South Wales, Australia, bears forewings with a short and crossvein-like anterior subcostal branch (Sc_2), and a five-branched media—characters typical of "Orthophlebiidae" rather than Parachoristidae. Even though it possesses a well-developed cubito-median Y-vein, this character, as discussed above, cannot serve as a reliable diagnostic character at the familial level. Moreover, the absence of the crossvein r_1-rs, which is distinctly developed in Parachoristidae, further supports its exclusion from that family. Accordingly, *Choristopanorpa* is herein treated as a genus of Protorthophlebiidae based on the five-branched Rs.

Choristopanorpa drinnani Jell & Duncan, 1986 (see also Krzemiński *et al*., 2015) from the Lower Cretaceous Koonwarra fossil bed clearly does not conform to the defining characters of Parachoristidae. Its elongate forewing with a single-branched Sc, an undeveloped cubito-median Y-vein, and a five-branched M in both fore- and hindwings indicate that it belongs neither to *Choristopanorpa* nor to Orthophlebiidae s. str. (Willmann & Novokshonov, 1998).

Among the Madygen species that Novokshonov (2001) assigned to *Choristopanorpa*, their generic positions warrant re-evaluation. *Choristopanorpa temperata*, with a six-branched media (M_2 forked) and a well-developed cubito-median Y-vein, should be transferred to *Parachorista*. *Choristopanorpa opinata*, characterized by a five-branched M and a single-branched Sc, and a well-developed cubito-median Y-vein, is best retained within *Choristopanorpa* under Protorthophlebiidae. *Choristopanorpa ridibunda* Novokshonov, 2001 exhibits a short Sc_1, a crossvein-like Sc_2, and an undeveloped cubito-median Y-vein, consistent with "Orthophlebiidae"; the five-branched Rs supports its placement in Protorthophlebiidae.

The species *Panorpaenigma aemulum* Novokshonov, 2001 was previously considered as a possible earliest "Orthophlebiidae" (Novokshonov, 2001; Shcherbakov, 2008). It shares a narrow costal area, a crossvein-like Sc_2, a five-branched M, seven-branched Rs, and the undeveloped cubito-median Y-vein with a smooth CuA base (not sharply bent) at the junction with M_5, which can be confidently placed into Orthophlebiidae.

Palaeodiversity and systematic revision of Parachoristidae

In this study, eight new species of Parachoristidae are reported from the Tongchuan entomofauna, greatly expanding the known palaeodiversity of the family worldwide. Following a detailed revision of previously described taxa, Parachoristidae currently comprises 30 species in nine genera, assigned to two subfamilies (Tab. 2). Regionally, China hosts five genera and 12 species in one subfamily (Lian *et al*., 2023a); Kyrgyzstan, three genera and nine species in two subfamilies (Novokshonov, 1997, 2001); Australia, four genera and seven species in two subfamilies (Tillyard, 1926; Riek, 1950, 1955); and Argentina, two genera and two species in one subfamily (Lara *et al*., 2015; Lara & Bashkuev, 2020).

The genus *Parachorista* was originally established under Permochoristidae (= Mesochoristidae) based on three species—*P. pincombeae*, *P. warnerensis*, and *P. splendida*—from the Upper Permian of Belmont and Warner's Bay, Australia (Tillyard, 1926). The nominal species *P. bairdae*, erected on an extremely incomplete wing, is herein considered invalid.

Permian parachoristids are currently known only from Australia, suggesting a Gondwanan origin for the family. Parachoristidae attained its greatest diversity during the Middle Triassic, declined in the Late Triassic, and went extinct at the end-Triassic mass extinction (Tillyard, 1926; Riek, 1955; Novokshonov, 1997, 2001; Hong, 2009a; Lara & Bashkuev, 2020). The most representative Middle–Late Triassic records occur in the Tongchuan entomofauna of China and the Madygen entomofauna of Kyrgyzstan, where parachoristids were among the dominant Mecoptera (Novokshonov, 2001). The Late Triassic representatives are from the Upper Triassic Potrerillos Formation of Argentina (Lara & Bashkuev, 2020) and Blackstone Formation of Australia (Riek, 1955). Additional records (lacking formal descriptions) have been reported from the Upper Triassic Protopivka Formation (Ukraine), the Momonoki Formation (Japan), and the Tologoy Formation (Kazakhstan), though these have not been formally described (Novokshonov, 2002).

TABLE 2. Global list of Parachoristidae.

Subfamily	Species	Age	Country	References
Parachoristinae	*Parachorista pincombeae*	Late Permian	Australia	Tillyard, 1926; Willmann, 1989
	Parachorista warnerensis	Late Permian	Australia	Tillyard, 1926; Willmann, 1989
	Parachorista splendida	Late Permian	Australia	Novokshonov, 1997; Willmann, 1989
	Parachorista asiatica	Middle–Late Triassic	Kyrgyzstan	Novokshonov, 1997
	Parachorista multivena	Middle–Late Triassic	Kyrgyzstan	Novokshonov, 1997
	Parachorista comica	Middle–Late Triassic	Kyrgyzstan	Novokshonov, 2001
	Parachorista arguta	Middle–Late Triassic	Kyrgyzstan	Novokshonov, 2001
	Parachorista religiosa	Middle–Late Triassic	Kyrgyzstan	Novokshonov, 2001
	Parachorista immota	Middle–Late Triassic	Kyrgyzstan	Novokshonov, 2001
	Parachorista sana	Middle–Late Triassic	Kyrgyzstan	Novokshonov, 2001
	Parachorista pulchra **sp. nov.**	Middle Triassic	China	this paper
	Parachorista libaii **sp. nov.**	Middle Triassic	China	this paper
	Parachorista ruga **sp. nov.**	Middle Triassic	China	this paper
	Parachorista triassica **sp. nov.**	Middle Triassic	China	this paper
	Parachorista elegantula **sp. nov.**	Middle Triassic	China	this paper
	Parachorista hongi **sp. nov.**	Middle Triassic	China	this paper
	Parachorista orienta **sp. nov.**	Middle Triassic	China	this paper
	Sinoparachorista rara	Middle Triassic	China	Lian *et al*., 2023a
	Sinoparachorista magna **sp. nov.**	Middle Triassic	China	this paper
	Virgulaparachorista elegans	Middle Triassic	China	Lian *et al*., 2023a
	Virgulaparachorista tongchuanensis	Middle Triassic	China	Lian *et al*., 2023a
	Triasoparachorista huaxiaensis	Middle Triassic	China	Hong, 2009a
	Kirgizichorista larvata	Middle Triassic	Kyrgyzstan	Novokshonov, 2001
Neoparachoristinae	*Neoparachorista perkinsi*	Late Triassic	Australia	Riek, 1955
	Neoparachorista splendida	Late Triassic	Australia	Riek, 1955
	Neoparachorista semiovena	Late Triassic	Australia	Riek, 1955
	Neoparachorista kirgizica **comb. nov.**	Middle–Late Triassic	Kyrgyzstan	Novokshonov, 1997; this paper
	Triassochorista nana	Late Triassic	Australia	Riek, 1955; Willmann, 1989
	Argentinopanorpa miguezi	Late Triassic	Argentina	Lara *et al*., 2015; Lara & Bashkuev, 2020
	Potrerillopanorpa macloughlini	Late Triassic	Argentina	Lara & Bashkuev, 2020

Within Mecoptera, the forking pattern of M branches is generally stable at the family level. Most Permian mecopterans retain the plesiomorphy of a six-branched M (M_2 and M_4 bifurcated), a feature also preserved in *Parachorista*. However, the degree and position of M forking vary among parachoristids. For instance, *Sinoparachorista* and *Potrerillopanorpa* exhibit forks in M_1, M_2, and M_4; *Virgulaparachorista* in M_2, M_3, and M_4; *Argentinopanorpa* in all four main M branches; *P. warnerensis* in M_2 and M_3 only; M_2 with three branches in *Parachorista multivena*, M_4 with three branches in NIGP209383 of *Parachorista libaii* **sp nov.** The Rs system is also variable, with Rs_2–Rs_4 occasionally forked, as in *P. multivena*, *Argentinopanorpa miguezi*, and *Potrerillopanorpa macloughlini*. When using these characters as diagnostic characters, particular caution is required. For example, although the fork of M_3 in *Virgulaparachorista* is relatively small, both species

within the genus share the characters, which can therefore serve as a diagnostic character at the generic level (Lian *et al*., 2023a).

Willmann (1989) treated *P. warnerensis* as a junior synonym of *P. pincombeae*, yet the two species clearly differ in the branching of R_1 and M, and should be maintained as separate species. *Parachorista* (?) *uralensis* Martynov, 1940, from the uppermost Lower Permian Chekarda of Russia—once regarded as the oldest Parachoristidae—was later transferred to *Kamopanorpa* (Trichoptera: Microptysmatidae) by Novokshonov (1992). *Parachorista opposita* Martynov, 1933, from the Middle Permian Iva-Gora Beds, was based on a hindwing with a single R_1, inconsistent with the forked R_1 of parachoristids, and is therefore excluded from the family.

Neoparachorista clarkae Jell & Duncan, 1986, described from the Lower Cretaceous Koonwarra fossil bed of Australia, was based on a specimen preserved with overlapping wings and body structures. However, the venation was insufficiently described, the species is excluded from Parachoristidae and is provisionally regarded as *incertae sedis* within Mecoptera pending further evidence.

Willmann (1989) established *Triassochorista* based on *Neoparachorista nana* Tillyard, 1955, arguing that *Triassochorista* differs from *Neoparachorista* in having smaller wing (*ca*. 12 mm *vs*. >20 mm), short Sc_2, and a five-branched M (M_4 forked). *Triassochorista kirgizica* Novokshonov, 1997, from the Madygen Formation, possesses a relatively long Sc that forks basally from the apex of Sc_1, and a six-branched M, characters more consistent with the genotype of *Neoparachorista*. Accordingly, the new combination *Neoparachorista kirgizica* (Novokshonov, 1997) **comb. nov.** is proposed.

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