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ARTICLE

New Middle Jurassic fossils shed light on the relationship of recent Panorpoidea (Insecta, Mecoptera)

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ABSTRACT
Examination of a diverse and abundant collection of Middle–Upper Jurassic scorpionflies from the Jiulongshan Formation of Daohugou village in Inner Mongolia, China, has enabled a further delimitation of the morphological variability of the polyphyletic family Orthophlebiidae. The family Protorthophlebiidae fam. nov. is herein erected on the basis of new characters present in new specimens of *Protorthophlebia* Tillyard, 1933 preserved with bodies. An emended diagnosis of the genus *Orthophlebia* is provided, adding morphological characters of the male abdomen and the head, and revising those of the wing venation. A new genus and species within the family Orthophlebiidae, *Juraphlebia eugeniae* gen. et sp. nov., and a new species of the genus *Orthophlebia* Westwood, 1845, *O. chinensis* sp. nov, are described. In the light of the new systematic concept and new taxonomic data relationships within the superfamily Panorpoidea and between the two modern families Panorpidae and Panorpodidae are discussed.
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Introduction

Mecoptera is a group of insects that were significantly more diverse in the past than today. At present, ca. 600 living species grouped in nine families are known. However, only two families, Panorpidae and Bittacidae, are currently diverse and abundant (Bicha 2010). At least 40 families of scorpionflies have been described from fossils (Mitchell 2018), but new fossil scorpionflies are still being described following new finds. Panorpidae, together with the relictual Panorpodidae, are the only living representatives of the superfamily Panorpoidea. According to Willmann (1989) and Archibald et al. (2013), the fossil Holcorpidae, Dinopanorpidae, Muchoridae, Austropanorpidae, Eorpidae, and the polyphyletic 'Orthophlebiidae' which are considered as stem group, belong to this superfamily, all of them forming a grade leading to the clade Panorpidae + Panorpodidae. The systematic position of the family Choristopanorpidae is unsolved. This family was considered as a possible sister taxon of Orthophlebiidae by Willmann (1989) but finally left as *incertae sedis* within Panorpomorpha. Within the family Orthophlebiidae, Handlirsch, 1906 used to include most of the taxa with a wing venation following the ground plan of the members of superfamily Panorpoidea (*sensu* Willmann 1987) but without a clear systematic position (e.g. Tillyard 1933; Handlirsch 1939; Willmann 1989). Soszyńska-Maj et al. (2017) discussed the systematic history of the Orthophlebiidae at length. The reconsideration of the ranges of Orthophlebiidae is necessary to form a basis for a phylogenetic analysis within the superfamily Panorpoidea. However, most taxa belonging to the former are in need of revision. Ongoing investigations of the family Orthophlebiidae started by excluding two Triassic species, i.e., *Orthophlebia gigantea* Tillyard, 1933 and *O. haradai* Ueda, 1991, which were transferred to the newly created family Worcestobiidae (Soszyńska-Maj et al. 2017). The following step was to clarify the systematic position of the family Austropanorpidae within the superfamily Panorpoidea, to which one species *O. martynovae* (Sukatsheva 1985) was transferred to genus *Austropanorpa*, known before only from Eocene Redbank Plains, Southeast Queensland in Australia (Riek 1967). It extended the age of Austropanorpidae back to the Early Jurassic (Krzemiński et al. 2017). After these taxonomic works, a total of 119 species belong to the family Orthophlebiidae. Subsequently, the new subfamily Gigaphlebiinae, within Orthophlebiidae, was erected, where large species of Jurassic scorpionflies with more developed medial and radial sector were assigned to (Soszyńska-Maj et al. 2018). These works merely aimed at starting the revision of the polyphyletic family Orthophlebiidae, of which the taxonomic boundaries ranges are still not established (Soszyńska-Maj et al. 2017). They also delimited the direction of the phylogenetic relationships study within the superfamily Panorpoidea, which reflects the evolutionary history of living Mecoptera.

A new abundant collection of well-preserved, often complete scorpionflies from the Daohugou locality in China, has proved paramount in understanding the early Middle Jurassic evolution of the Panorpoidea.

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Materials and methods

This paper is based on new specimens from the Jiulongshan Formation of Middle-Late Jurassic age at Daohugou village, Wuhua Township (previously Shantou Township), Ningcheng County, Inner Mongolia, China, where very a diverse and abundant Mecoptera fauna was found (Ren et al. 2009; Qiao et al. 2012; Wang et al. 2012; Lin et al. 2016; Li et al. 2017). Perfectly preserved and abundant fossils allow us to recognize the morphology of complete Jurassic scorpionflies from the investigated group. These specimens provide the opportunity to study the head morphology, wing venation variability, colour pattern of fore- and hindwings, leg, thorax and abdomen morphology, as well as often the structure of male and female genitalia and proportion between specific body parts. Holotypes, paratypes and additional materials of new species are housed in the collection of the College of Life Sciences, Capital Normal University (CNU) in Beijing. The revision of the type species of the genus *Protorthophlebia* was based on the holotype of *Protorthophlebia latipennis* Tillyard, 1933, NHM, I.10482 from the Lower Liass (Lower Jurassic), Binton, Warwickshire, England, housed in the collection of the Natural History Museum in London.

The specimens were studied with the use of a stereomicroscope under reflected light, wetting the alcohol. All photos were made by Agnieszka Soszyńska-Maj and Katarzyna Kopeć. Drawings were made from the photographs and digitally processed in Corel X7. The terminology of wing venation follows Tillyard, 1933 with slight modifications made by Soszyńska-Maj et al. (2017, 2018). Cladistic analysis was performed using the TNT v. 1.5 software (Goloboff and Catalano 2016). All data were compiled into Nexus files using Mesquite v. 3. 5 build 888 (Maddison and Maddison 2018).

Systematic palaeontology

Order **Mecoptera** Packard, 1886
Superfamily **Panorpoidea** Latreille, 1805
Family **Orthophlebiidae** Handlirsch, 1906
Subfamily **Orthophlebiinae** Handlirsch, 1906

Type genus

Orthophlebia Westwood, 1845

Genus ***Orthophlebia*** Westwood, 1845

Type species

Panorpa liassica Mantell, 1844 [= *Orthophlebia liassica* (Mantell, 1844)], from the Lias of England, for details see Soszyńska-Maj et al., 2017, p. 146, Figure 1.

Emended diagnosis

Subcosta in forewing reaches pterostigmal area, with two branches, in hindwing Sc simple and shorter; radial vein R_1 in fore and hindwings in pterostigmal area gently curved towards anterior wing margin, in hindwing forks around pterostigma; six or seven veins in radial sector; five veins in medial sector in forewing and four in hindwing; male abdomen longer than wings, segments VI–VIII longer than wider and tergites and sternites fused, VIII segment almost three times as long as wide; female abdomen longer than wings, gradually narrowing.

Remarks

Emending the diagnosis of genus *Orthophlebia* is possible on the basis of new abundant materials of Orthophlebiidae, which enabled us to find morphological characters in addition to those of wing venation.

Orthophlebia chinensis sp. nov. Soszyńska-Maj, Kopeć & Ren (Figures 1–3)

Diagnosis

Species is clearly differentiated from other congeners by a combination of following wing characters: six veins in the radial sector, Rs and Mb forks almost at the same level, Rs_{1+2} and Rs_{3+4} forks almost at the same level, dark irregular elongated spots spread evenly throughout wing, merging together around transparent spots.

Derivation of the name

Species name is dedicated to China where the specimens were found and abundant.

Material

Holotype CNU-MEC-NN-13548 forewing, perfectly preserved hindwing almost complete. Paratypes: CNU-MEC-NN-2018251 male, abdomen complete, wings, hind legs preserved; CNU-MEC-NN-13648 male, almost complete specimen without legs and antenna; CNU-MEC-NN-13508 female, specimen complete. Additional materials: CNU-MEC-NN-13508, CNU-MEC-NN -13549, CNU-MEC-NN-13569, CNU-MEC-NN-13573, CNU-MEC-NN-13603, CNU-MEC-NN-13651, CNU-MEC-NN -13697, CNU-MEC-NN-13817, CNU-MEC-NN-2018244, CNU-MEC-NN-2018245, all housed in the collection of CNU in Beijing.

Occurrence

Jiulongshan Formation of Middle-Late Jurassic age at Daohugou village, Wuhua Township (previously Shantou Township), Ningcheng County, Inner Mongolia, China.

Description

Wings (Figures 1(a) and 2) 12–14 mm long and ca. 4.2–4.7 mm wide, the same dark marking on both wings, fine colour pattern spread evenly throughout whole wings consisting of irregular spots merging together around transparent spots, cross-veins more abundant in distal part of wing; *Head.* Antennae ca. 6.3 mm long, scapus round and wide, pedicel as wide as long, flagellum with 37 elongated flagellomeres ca. twice as long as wide, basal flagellomeres slightly longer than distal ones (Figure 1(e)); *Legs.* All legs with two strong tibial spurs, ca. 0.8 mm. *Forewing* (Figures 1, and 2(a)). Subcosta two branched, Sc_1 reaching outer margin before the last forking of Rs_1, Sc_2 ends opposite forking of Rs_{1+2}; Rb forks beyond cross-vein m-cu(= M_5); R_1 slightly curved at distal part, ends beyond half of Rs_{1a}; Rs forks slightly before forking of Mb, Rs longer than Rs_{1+2}, as long as $Rs_{1a\text{-}c}$; Rs_{1+2} slightly longer than Rs_{3+4}; Rs_2, Rs_3, Rs_4

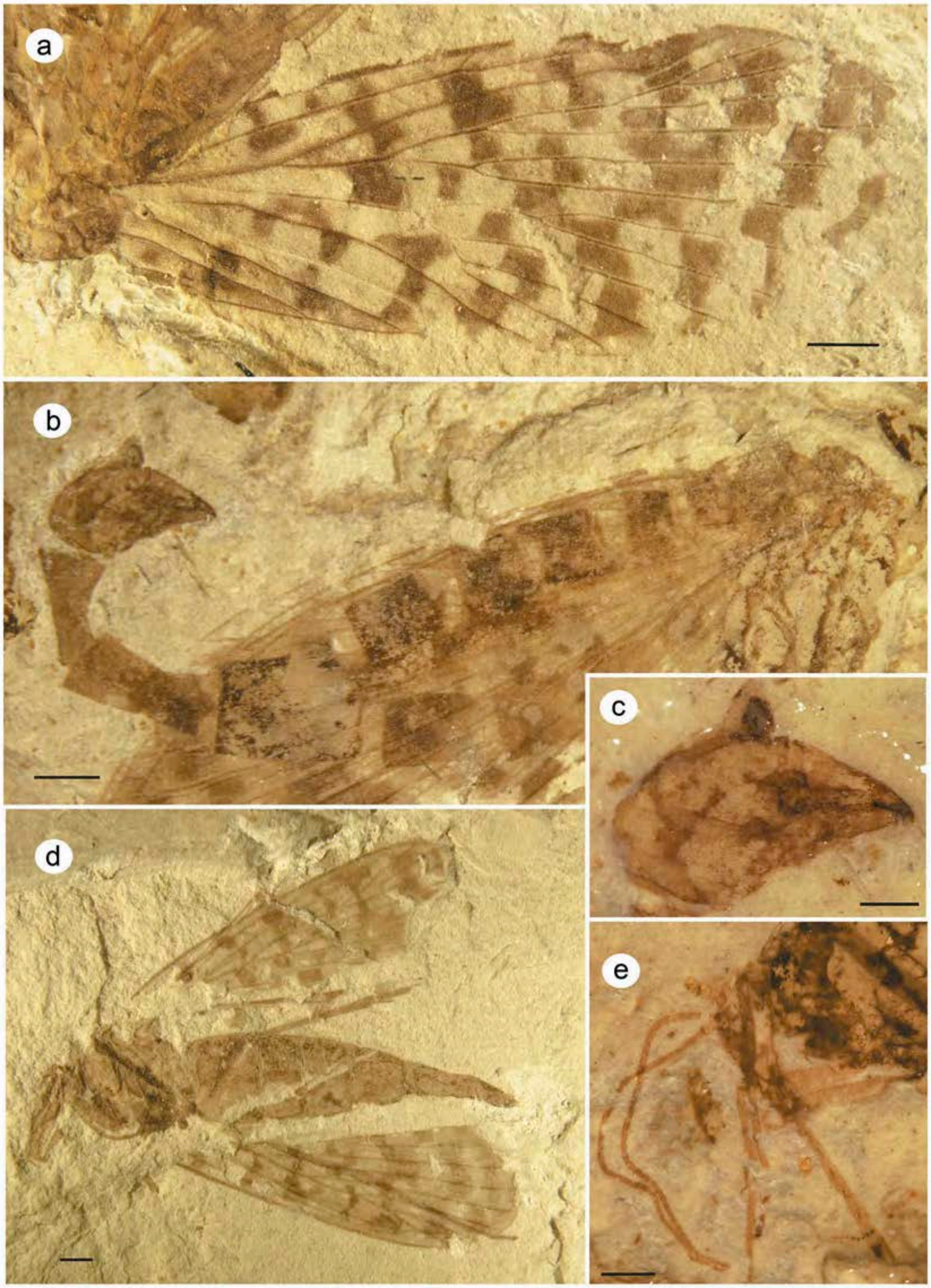

Figure 1. *Orthophlebia chinensis sp. nov.*; (a) Forewing of holotype CNU-MEC-NN-13548; (b). Habitus of male, paratype CNU-MEC-NN-2018251, C. Genital bulb, paratype CNU-MEC-NN-2018251, scale bar 0,5 mm; D. Habitus of female, paratype paratype CNU-MEC-NN-13772; E. Head with antennae CNU-MEC-NN-13697; photos C, E under alcohol, scale bar 1 mm.

single; M_{1+2} 3x as long as M_{3+4}; M_{3+4} slightly longer than M_{4ab}, m4-cu_1 beyond forking of M_4; Cu_1 curved, Cu_1 and Cu_2 have one stem; three anal veins. *Hindwing* (Figure 2(b)). Venation and colour marking similar to forewing except for shorter Sc which is single and reaches wing margin in one-third of $Rs1_{a-c}$; a medial sector with four branches reaching wing margin; Mb joins vein Cu_1 close to the basal part of the wing; one cross-vein between A_1 and Cu_2. *Male* (Figures 1(b,c)), and 3(a)). Abdomen longer than wings; basal abdominal segments twice as wide as long, abdomen clearly narrows and elongates beginning from VI segment, segments VI–VIII longer than wider, tergites and sternites of VI–VIII fused, VI segment slightly longer than wide, VII more than twice as long as wide, VIII almost three times as long as wide, wider at distal part. Genital bulb almost oval, gonostylus sharply ended, wide at base, the distal part of hypovalves distinctly widened; *Female* (Figures 1(d), and 3(b)).

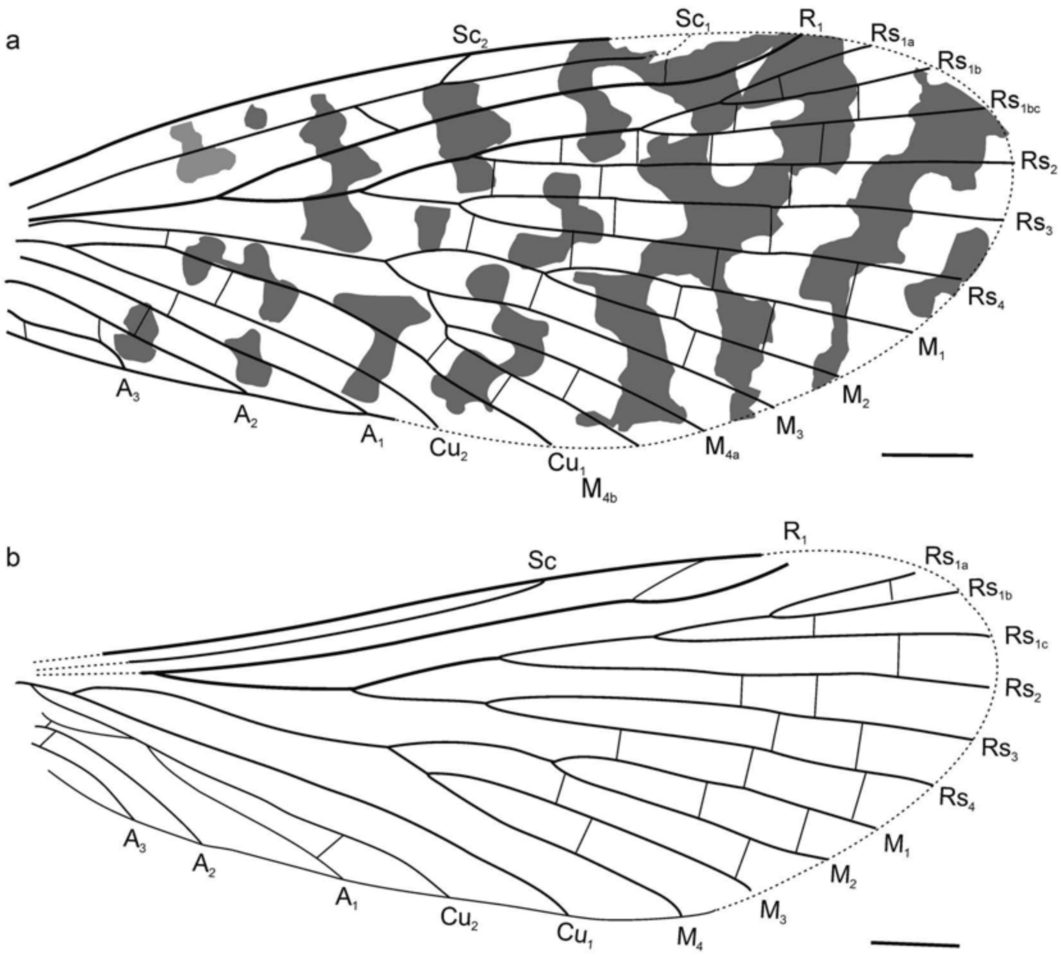

Figure 2. *Orthophlebia chinensis sp. nov.* holotype, CNU-MEC-NN-13548; (a) Forewing, (b) Hindwing without marking, scale bar 1 mm.

Abdomen longer than wings, gradually narrowing to distal part beginning from VI segment, basal abdominal segments wider than long, V segment almost as long as wide, VI–VIII segments significantly smaller almost as long as wide, IX segment elongated, termination of female abdomen not preserved.

Remarks

Hindwing most often preserved either fully lying under the forewing or the basal part lies on the body. Thus, the reconstruction of the hindwing in total is very hard and based on only one specimen. Among material, only two complete females were found but the termination of the female abdomen was too poorly preserved to be reconstructed. However, both abdomens were complete and certainly longer than the wings.

Genus ***Juraphlebia*** gen. nov. Soszyńska-Maj & Krzemiński (Figures 4–7)

Type species

Juraphlebia eugeniae sp. nov.

Diagnosis

Subcosta in forewing reaches pterostigmal area, with two branches, in hindwing Sc simple and shorter; radial vein R_1 in fore and hindwings very characteristic, at distal part in the pterostigmal area R_1 distinctly waved, thickened and convex; seven (exceptionally eight) veins in radial sector, five veins in medial sector in forewing, four medial veins in hindwing; male abdomen much shorter than wings, reaching ca. two-thirds length of wings, VI abdominal segment of male shorter than wide, VII segment as long as wide, only VIII segment narrow and twice as long as wider; female abdomen much shorter than wings, reaching 77% length of the wings at most, segments VI–X much shortened, altogether shorter than V segment.

Derivation of the name

Combination of Jura- for the Jurassic age of the fossil and the second part of the genus *Orthophlebia, plebia* originates from the Greek Phlebas (φλέβας) veins, to emphasize the close relationship to this genus. Gender feminine.

Juraphlebia eugeniae sp. nov. Soszyńska-Maj & Krzemiński (Figures 4–7)

Diagnosis

The same as for the genus by monotypy.

Derivation of the name

Name of the species is to honour the mother of the first author, Eugenia Soszyńska, whose help and support enable scientific work of the first author.

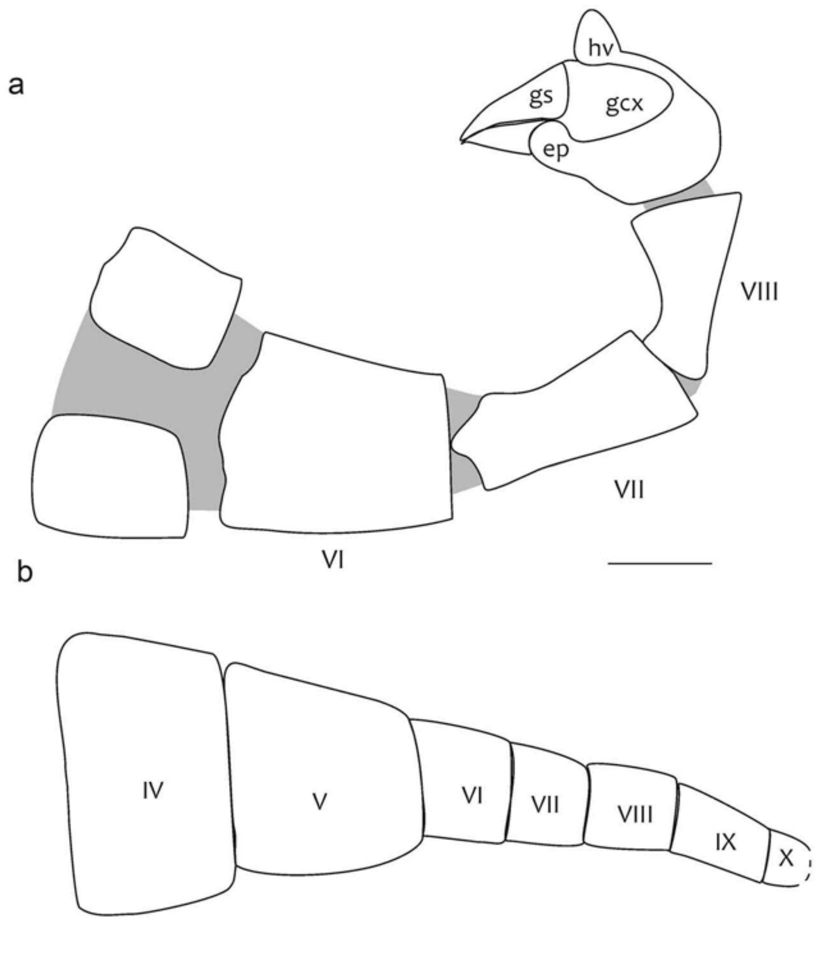

Figure 3. *Orthophlebia chinensis sp. nov*., (a). male abdomen of paratype, CNU-MEC-NN-2018251, gcx – gonocoxit, gs – gonostylus, hv – hypovalve; (b). female abdomen paratype CNU-MEC-NN-13772, scale bar 1 mm.

Materials

Holotype CNU-MEC-NN-2018200 P/CP, four wings preserved, part of the abdomen, sex unknown. Paratypes: CNU-MEC-NN-2018203 – male with complete thorax and abdomen, both right wings complete but overlapping, left wings partly preserved; CNU-MEC-NN-2018201 – forewing clearly preserved with venation very well visible, anal part of wing well preserved; CNU-MEC-NN-2018202 – female, all wings preserved and complete abdomen and female genitalia; CNU-MEC-NN-13733 – well preserved forewing and hindwing; Additional materials: CNU-MEC-NN-13500, CNU-MEC-NN-13529, CNU-MEC-NN-13533, CNU-MEC-NN-13577, CNU-MEC-NN-13605, CNU-MEC-NN-13613, CNU-MEC-NN-13622, CNU-MEC-NN-13623, CNU-MEC-NN-13629, CNU-MEC-NN-13641, CNU-MEC-NN-13643, CNU-MEC-NN-13645, CNU-MEC-NN-13681, CNU-MEC-NN-13721, CNU-MEC-NN-13746, CNU-MEC-NN-13751, CNU-MEC-NN-13765, CNU-MEC-NN-13778, CNU-MEC-NN-13809, CNU-MEC-NN-2018204, CNU-MEC-NN-2018205, CNU-MEC-NN-2,018,206, CNU-MEC-NN-2018207, CNU-MEC-NN-2018208, CNU-MEC-NN-2018209, CNU-MEC-NN-2018210, CNU-MEC-NN-2018211, CNU-MEC-NN-2018212, CNU-MEC-NN-2018213, CNU-MEC-NN-2018214, CNU-MEC-NN-2018215, CNU-MEC-NN-2018216; housed in the collection of CNU in Beijing.

Occurrence

Jiulongshan Formation of Middle-Late Jurassic age at Daohugou village, Wuhua Township (previously Shantou Township), Ningcheng County, Inner Mongolia, China.

Description

Head (Figures 5(b), and 7(a)) 3.8 mm, rostrum elongated, length 2.7x long of its maximal width; eyes oval; scapus short and wide at base, narrowing to distal part, pedicel small and oval; flagellum with short and narrow segments (flagellomeres), number of flagellomeres unknown, maxillary palps clearly visible, covered by short setae, two distal segments the same length. *Thorax* covered by long and strong setae. *Wings* (Figures 4, and 6) 16.6–17 mm length, 5.6–6.2 width, with characteristic colour markings almost the same in both wings, consist of three elements: at base one small spot between Rs and Mb, centrally irregular bend wider at base, situated between Rs_1 and Cu_1, distal part of the wing with numerous oval spots between longitudinal veins merging together; *Forewing* (Figures 4, and 6(a,b)). Sc long, forked into Sc_1 and Sc, reaching outer margin beyond the last forking of Rs_1, opposite end of Cu_1; R_1 ends opposite two-thirds of Rs_{1a}, distally in the pterostigmal area distinctly waved, thickened and convex dorsally; seven veins in radial sector reaching outer margin, Rb short, forks not far from cross-vein mb-cu_1, Rs forks slightly before forking of Mb, Rs longer than its two

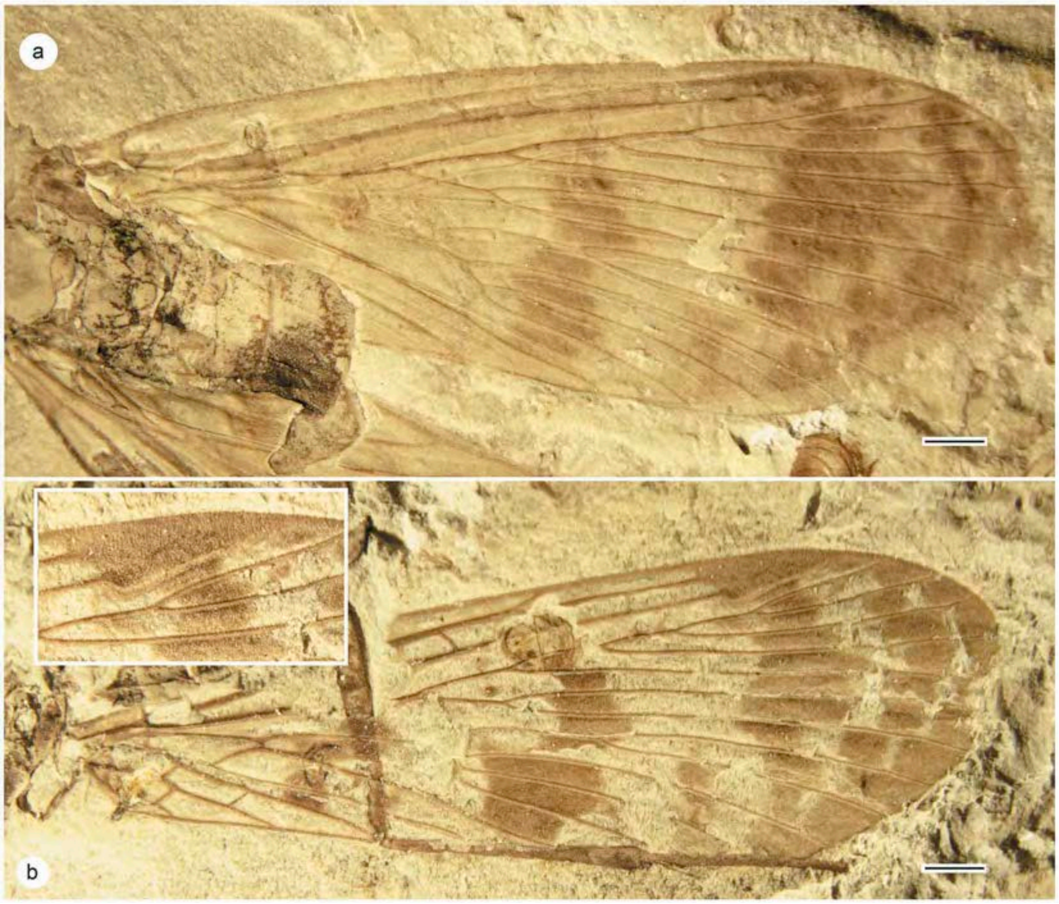

Figure 4. *Juraphlebia eugeniae* gen. et sp. nov.: (a) Hindwing, holotype CNU-MEC-NN-2018200, (b) Forewing, paratype, CNU-MEC-NN-2018201, scale bar 1 mm.

branches, Rs_{1+2} slightly longer than Rs_{3+4}, Rs_1 branched into four; R_2, Rs_3 and R_{s4} single; five medial veins; M_{1+2} less than 3x as long as M_{3+4}; M_1 more than twice as long as M_{1+2}; M_3 6x as long as M_{3+4}; M_{4a+b} half as long as M_{3+4}, cross-vein m4b-cu1 very short; vein Cu_1 and Cu_2 have one stem, one cross-vein between Cu_1 and Cu_2; three anal veins, five cross-veins in anal area. *Hindwing* (Figure 6(c)): hindwing shape looks more or less triangular, almost the same as forewing venation, with the exception of the following characters: Sc short, reaching outer margin opposite forking of Rs_1 and before end of Cu_1; R_1 ends opposite half of Rs_{1a}; Rs_{1+2} almost as long as Rs_{3+4}, Rs shorter than Rs_{1+2} and equal to Rs_1; four medial veins; M_1 twice as long as M_{1+2}; M_3 almost 4x as long as M_{3+4}; Mb joins Cu_1 before Rb forking; veins Cu_2 and A_1 fused, between Cu_1 and Cu_2 one cross-vein; number of anal veins unknown; Legs, covered with short setae, two long tibial spurs present, first segment of tarsus more than twice as long as second, two last tarsomeres of the same length; *Male* (Figures 5(a), and 7(b)). Abdomen with male terminalia combined together shorter than wings, VI segment of male abdomen shorter than wide, VII segment as long as wide, VIII segment narrow and three times as long as wide, genital bulb elongated, gonostyli short, wide at base and strongly narrowing to the end; *Female* (Figures 5(d), and 7(c)). Abdomen much shorter than wings, reaching 77% length of the wings at most, strongly narrowing in the central area to distal part, segments VI–X much shortened and narrow, all combined together shorter than V segment, cerci two-segmented;

Family *Protorthophlebiidae* fam. nov. Soszyńska-Maj, Krzemiński & Kopeć (Figures 8–12)

Type genus

Protorthophlebia Tillyard, 1933: 28–29.

Diagnosis

Small scorpionflies with round tips of the wings, subcosta in forewing reaches pterostigmal area, with two branches, in hindwing Sc simple and short; vein R_1 in fore and hindwings in pterostigmal area gently curved towards anterior wing margin; five veins in radial sector (Rs), five medial veins in forewing and four in hindwing; male and female abdomen ca. as long as wings, male abdomen wide, all abdominal segments wider than longer, abdominal segments gradually thicker, II segment more than three times as long as wider, V segment ca. twice wide as long, VI–VIII abdominal segments smaller and tergites and sternites fused, VIII segment only slightly wider than long; female abdomen longer than wings, gradually narrowing, cerci two segmented.

Genus *Protorthophlebia* Tillyard, 1933

Type species

Protorthophlebia latipennis Tillyard, 1933: p. 29–30, Figure 6.

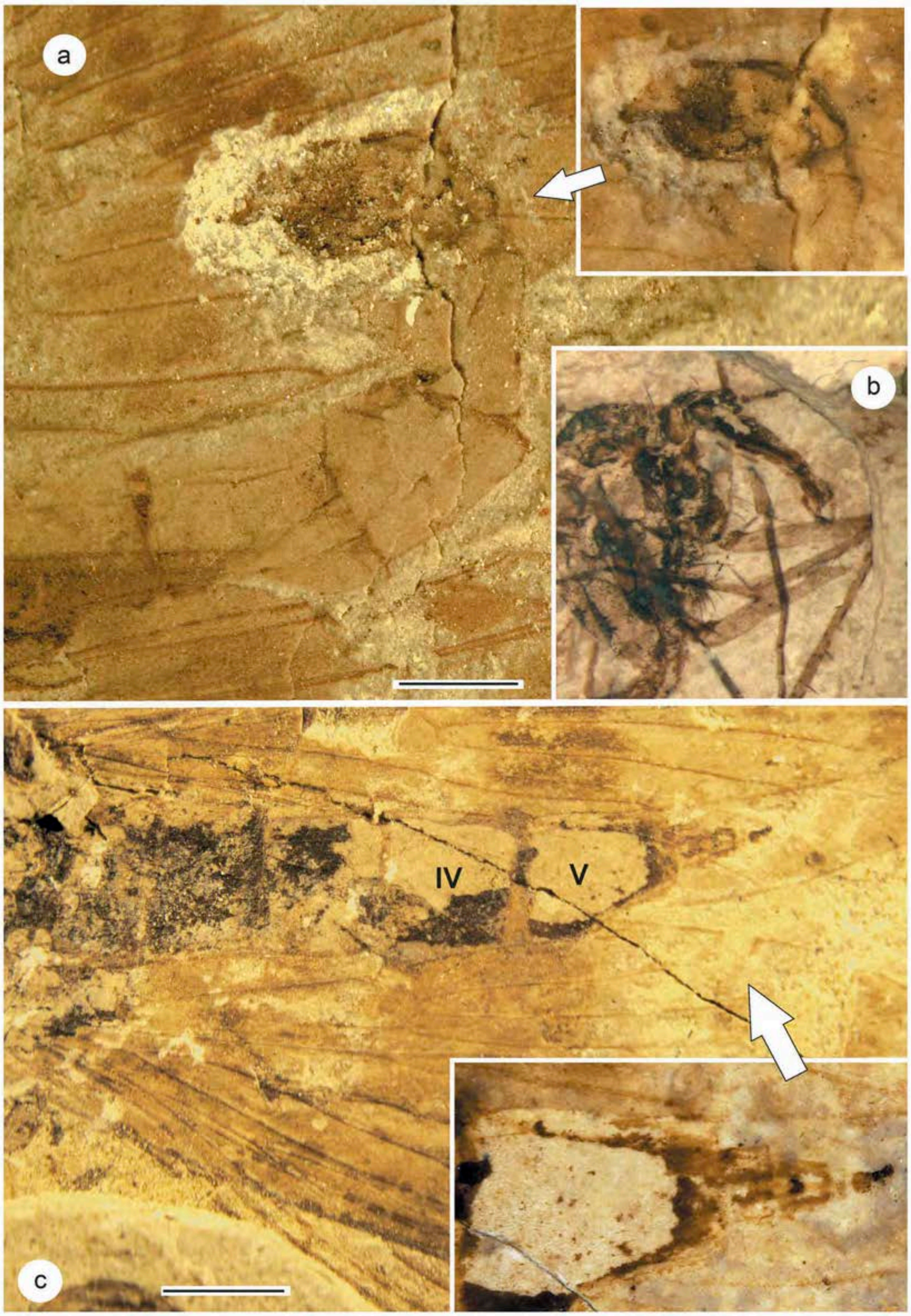

Figure 5. *Juraphlebia eugeniae* gen. et sp. nov.: (a) Male abdomen and genital bulb, paratype, CNU-MEC-NN-2018203, (b) Head, CNU-MEC-NN-2018209, (c) Female, paratype, CNU-MEC-NN-2018202; scale bar 1mm, magnificated genitalia.

Included species

P. ak-saji Martynova, 1948, *P. cuneata* Bode, 1953 (?), *P. curta* Hong, 2009, *P. egloni* Martynova, 1948, *P. hebes* Sukatsheva, 1985 (?), *P. lecta* Sukatsheva, 1985, *P. liadinica* Hong et al., 2002, *P. strigata* Zhang, 1996, *P. triassica* Hong et al., 2002, *P. yanqingensis* Hong et Xiao, 1997.

Diagnosis

The same as for the family by monotypy.

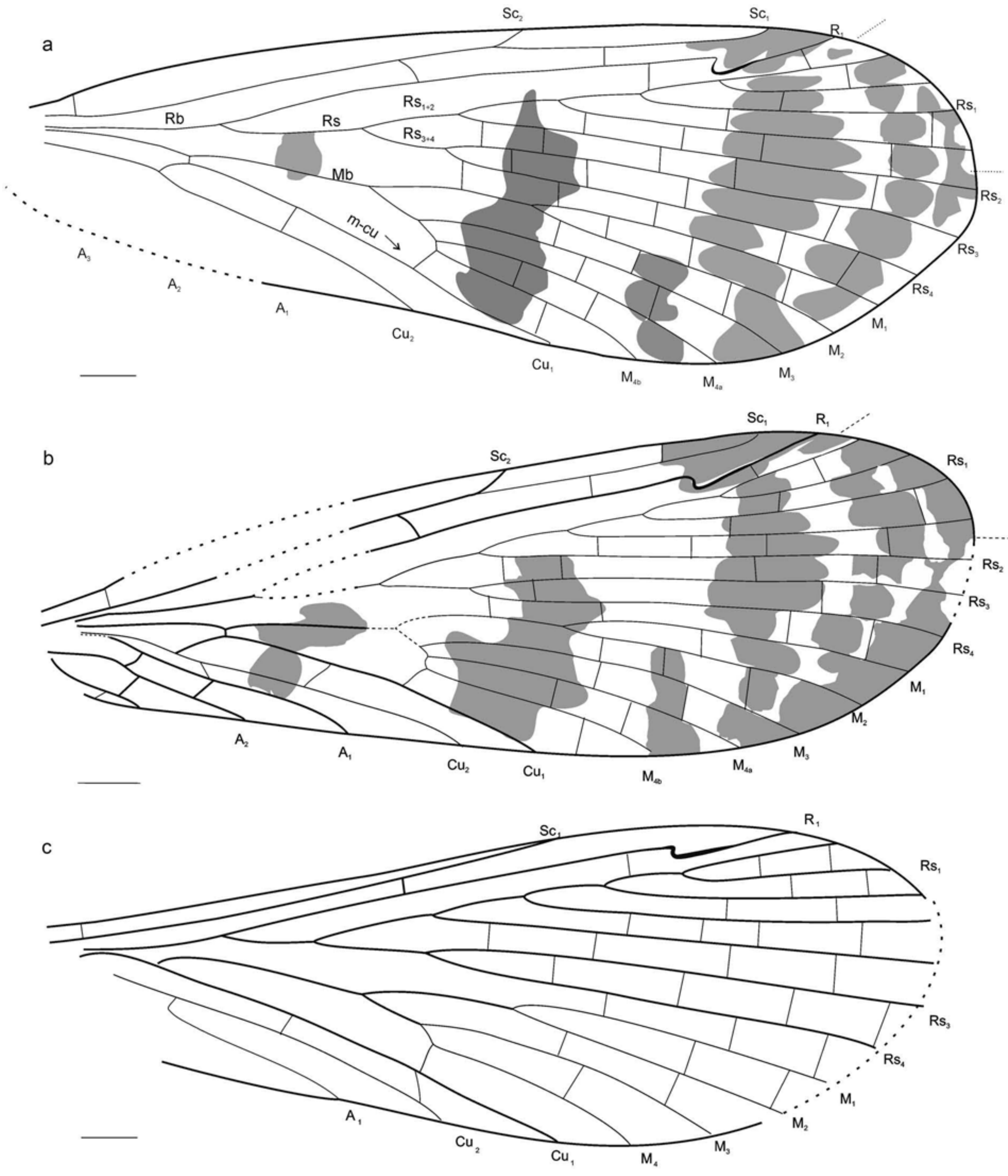

Figure 6. *Juraphlebia eugeniae* gen. et sp. nov., wings: (a) Forewing, holotype CNU-MEC-NN-2018200, (b) Forewing, paratype, CNU-MEC-NN-2018201, (c) Hindwing CNU-MEC-NN-2,018,200, scale bar 1 mm.

Protorthophlebia latipennis Tillyard, 1933 (Figure 8)

Material

Holotype No. 10,482 housed in NHM, London.

Occurrence

Species described from Upper Lias (Lower Jurassic), Binton, Warwickshire, Great Britain.

Remarks

The investigation of the holotype showed that the specimen was broken into two pieces and improperly glued together. The new drawing is an emended reconstruction of the holotype (Figure 8). Genus description by Tillard (1933) was based on one forewing *Protorthophlebia latipennis* Tillyard (Figure 8(a,b)). All species described further were included to this genus following its wing venation. Until now, the body morphology of the genus *Protorthophlebia* has not been recognized. Taxonomical investigations showed significant differences which distinguish

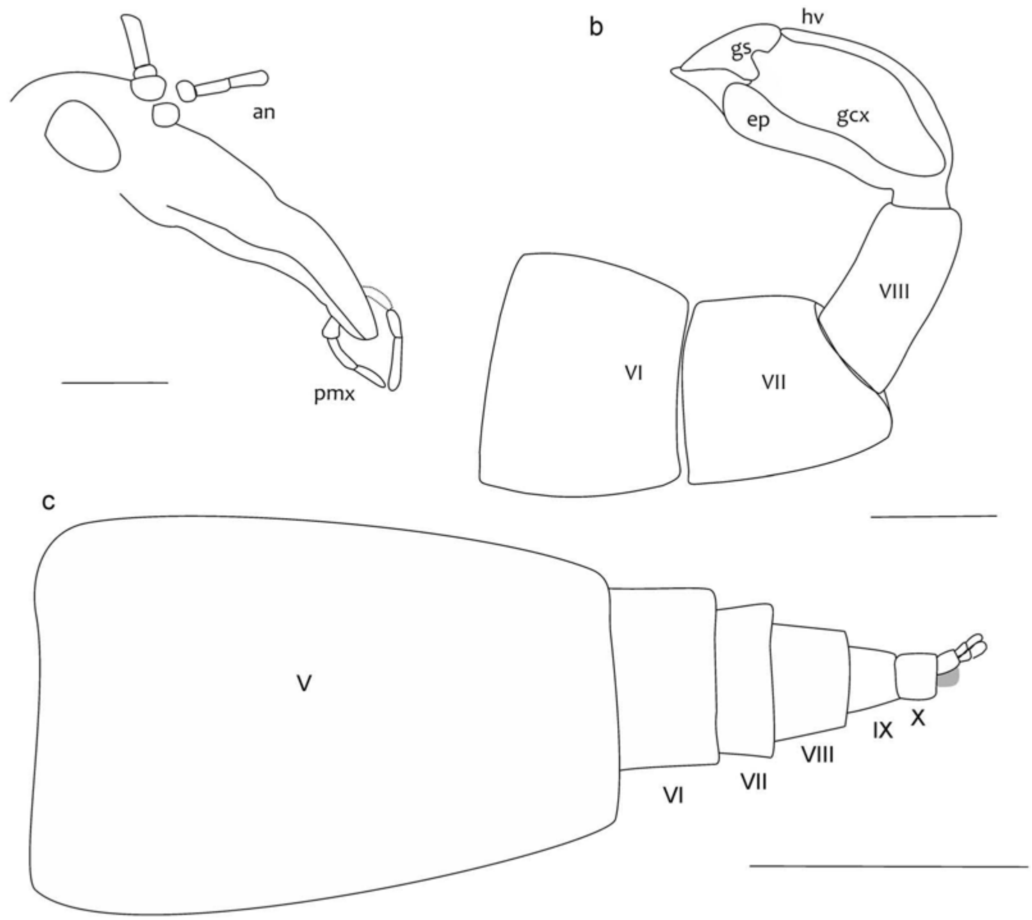

Figure 7. *Juraphlebia eugeniae* gen et sp. nov., wings: (a) Head, CNU-MEC-NN-2018209, (b) Male genital bulb, paratype, MEC (82), gcx – gonocoxite, gs – gonostylus, hv – hypovalve, (c) Female abdomen, paratype, MEC (89); scale bar - 1mm.

species of *Protorthophlebia* from the remaining taxa included in the family Orthophlebiidae. Thus, we decided to transfer the genus *Protorthophlebia* to the family Protorthophlebiidae fam. nov. The revision of some holotypes of genus *Protorthophlebia* and Orthophlebiidae is necessary to present the final list of the new family.

Protorthophlebia punctata sp. nov Soszyńska-Maj, Krzemiński & Kopeć (Figures 9–12)

Diagnosis

Species differs from remaining congeneric by combination of the following characters: numerous oval-shaped small regular dark spots on the membrane all situated between veins spread evenly throughout the whole wings, more transparent areas than dark, Rs forks slightly beyond Mb forks in forewing, Rs_{1+2} almost twice as long and Rs_{3+4}, basal part of M_{4b} in forewing and M_4 in hindwing strongly oblique and situated with cross-vein m-cu on one line.

Derivation of the name

Species name reflects the characteristic pattern marking of the wings.

Material

Holotype CNU-MEC-NN-13768, almost complete male, without part of the legs, Paratypes: CNU-MEC-NN-13601, almost complete male; CNU-MEC-NN-13708 male, CNU-MEC-NN-2018217, very well-preserved wings without body, sex unknown; CNU-MEC-NN-2018218 male, without most parts of the legs and antennae, CNU-MEC-NN-2018219; Additional materials: CNU-MEC-NN-13512, CNU-MEC-NN-13517, CNU-MEC-NN-13550, CNU-MEC-NN-13576, CNU-MEC-NN-13586, CNU-MEC-NN-13609, CNU-MEC-NN-13742, CNU-MEC-NN-13798, CNU-MEC-NN-13820, 24 specimens from CNU-MEC-NN-2018220 to CNU-MEC-NN-2018243, all specimens housed in the collection of CNU, Beijing.

Occurrence

Jiulongshan Formation of Middle-Late Jurassic age at Daohugou village, Wuhua Township (previously Shantou Township), Ningcheng County, Inner Mongolia, China.

Description

Body length 9.5–10.3 mm, abdomen shorter than wings; wings 9.3–10 mm length, 3.3 mm wide; *Head* (Figures 10 (d), and 12(b)) 1.85 mm long, rostrum 1.5x as long as its maximal width, eyes oval, small size, only three segments of maxillary palps visible; antennae: scapus short and wide,

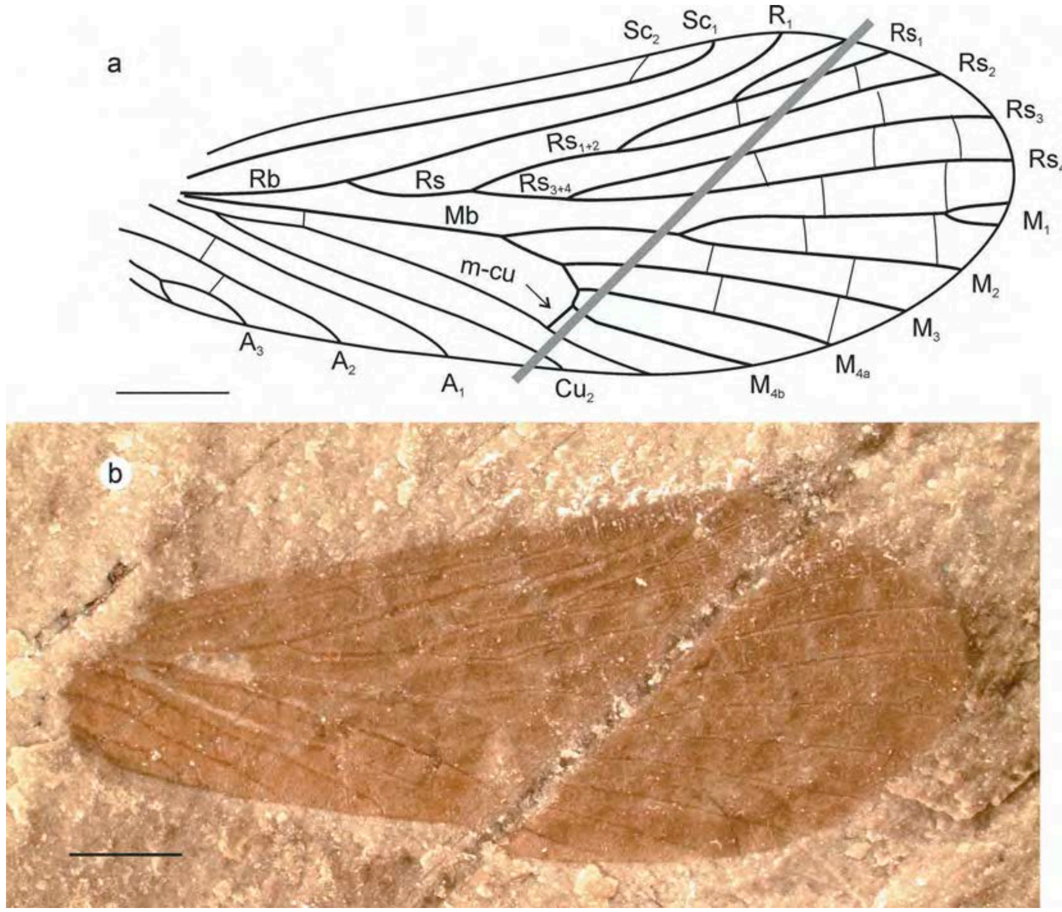

Figure 8. *Protorthophlebia latipennis* Tillyard, 1933, holotype NHM 10482; (a) Drawing of the forewing, reconstructed from broken pieces, (b) forewing; scale bar 1 mm.

pedicel small, oval, flagellum with short, narrow segments (flagellomeres); *Thorax*. Wings with a clearly visible pattern, consist of small, regular, oval spots, well preserved in most specimens, pattern vary probably within intraspecific diversity or connected with fossilization, the colour pattern of hindwings almost the same as in forewings but poorly visible. *Forewing* (Figures 9, 10(a,b), and 11(a)). Sc long, two-branched ends beyond the last forking of Rs_1, opposite one-third length of Rs_{1a}, Sc forks opposite two-thirds length of Rs_{1+2} and almost opposite forking Rs_{3+4}; R_1 long, ends opposite two-thirds Rs_{1a}; five radial veins reaching outer margin; Rb forks far beyond cross vein mb-cu_1; Rs forks slightly before forking of Mb; Rs_{1+2} almost twice as long as Rs_{3+4}; Rs about one-third shorter than Rs_{1+2}, as long as Rs_{1a+b} and Rs_{1a}, Rs_2 single, twice as long as Rs_{1+2}; Rs_3 and Rs4 single; five medial veins reaching outer margin, M_{1+2} almost 6x as long as M_{3+4}; M_1 two-thirds as long as M_{1+2}; M_3 more than 11x as long as M_{3+4}; M_{3+4} almost as long as $M_{4,}$ basal part of M_{4b} strongly oblique and situated with cross-vein m-cu on one rounded line; veins Cu_1 and Cu_2 joins not far from cross-vein mb-cu_1 (M_5), between Cu_1 and Cu_2 one cross vein; three anal veins, between A_1 and A_2 two cross-veins. *Hindwing* (Figures 10(b), and 11(b)). Sc long, ends opposite forking of Rs_{1+2}; between Sc and R_1 one cross-vein; Rs about 1/3 shorter than Rs_{1+2} and longer than Rs_1ab and as long as Rs_{1a}; Rs_2 single and 1.5x as long as R_{1+2}; Rs_3 2.5x as long as Rs_{3+4}; four medial veins; M_{1+2} 4x as long as M_{3+4}; M_1 1 and two-thirds as long as M_{1+2}; M_3 almost 8x as long as M_{3+4}, basal part of M_4 in hindwing strongly oblique before reaching cross-vein m--cu, m-cu oblique towards to basal part of the wing; Mb joining Cu_1 in most basal part of the wing; the stem of Cu_1 and Cu_2 is invisible; A_1 fused with Cu_2, one cross-vein between Cu_2 and A_1, A_2 and A_3 shorter than in forewing. *Legs*. with big, double tibial spurs. Abdomen wide in the central part and gradually narrow in distal part in males and females. *Male* (Figures 9(a), 10(a,c) and 12(c,d)). Abdomen with genital bulb curved forward thus shorter than length of forewing, all abdominal segments wider than long, abdominal segments gradually thicker, II segment more than 3x as long as wide, V segment ca. twice as wide as long, VI-VIII abdominal segments smaller and tergites and sternites fused, VIII segment only slightly wider than long; gonocoxites wide, gonostyli wide at base and strongly narrow, strong sclerotized at distal part. *Female* (Figures 10(b), and 11(a)). Subgenital plate pale, poorly sclerotized, pleural membrane of IX segment probably fused with the subgenital plate, cerci two-segmented.

Phylogenetic analysis

Only four families from the superfamily Panorpoidea were included in the analysis just to check their preliminary mutual relationships: Orthophlebiidae, Protorthophlebiidae, Panorpidae and Panorpodidae. Records on other Panorpoidea make

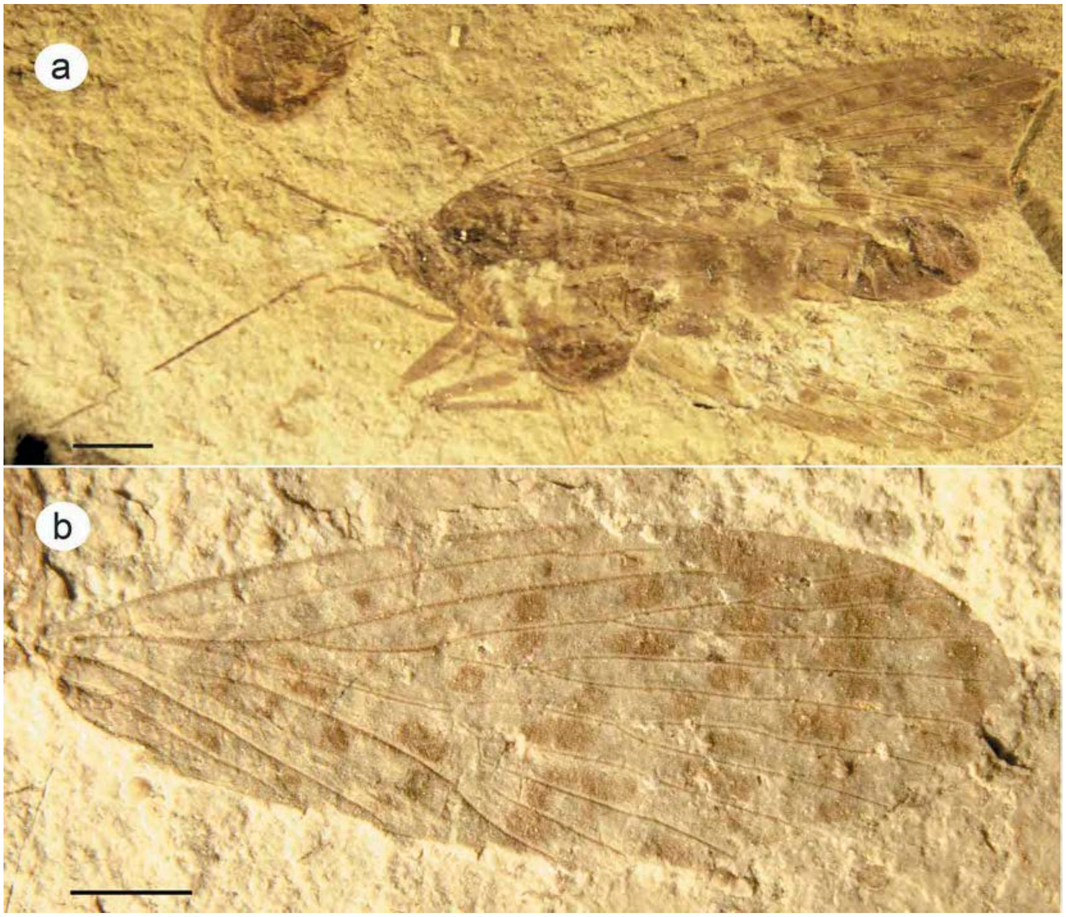

Figure 9. *Protorthophlebia punctata* sp. nov.; (a) Holotype CNU-MEC-NN-13768, habitus of male, (b) Forewing, paratype CNU-MEC-NN-2018217; 1 mm scale bar.

comparative morphological analysis impossible as their morphology is for now insufficiently described. However, new materials from Burmese amber as well as from the Jurassic collection from Daohugou and a re-study of some already described specimens provide a promising basis for further investigations and analysis. The extant families Panorpidae and Panorpodidae are known in detail as all morphological characters are available. However, for two fossil families Orthophlebiidae and Protorthophlebiidae fam. nov. only limited characters are available. Consequently, 11 multistate characters of the head, wing venation and male abdomen and genitalia were included, all treated as unordered and unweighted. For the outgroup we chose the Permian subfamily Permochoristidae as the oldest group with the body preserved (Novokshonov 1997). The data matrix (Table 1) was analysed using TNT v.1.5 (Goloboff and Catalano 2016) and characters used in the analysis are listed as follows:

(1) Branches of subcostal veins in forewing: (0) three and more branches, (1) 2–3 branches, (2) only two branches, (3) one branch.
(2) Rs_1: (0) only forked, (1) pectinated.
(3) Rs_4: (0) forked or simple, (1) always simple.
(4) Loss of one medial vein in hindwing: (0) yes, (1) no.
(5) M terminal branches in the forewing, M_2: (0) variable 5–6 branches, M_2 forked, (1) always 5, M_2 simple; (2) 5&6, M_2 simple, (3) always 4, M_2 simple.
(6) Rostrum: (0) absent, (1) present.
(7) Rostrum, if present: (0) elongated, (1) short.
(8) Last abdominal segments of male (VI to VIII): (0) wide and short, not narrowing distally, (1) shorter and narrower than preceding segments, (2) elongated and narrower than preceding segments.
(9) Genital bulb: (0) absent, (1) present.
(10) Tergites and sternites of last male abdominal segments: (0) not fused, (1) VII with a narrow trace of pleural membrane, only VIII segment is fused, (2) VI–VIII segments fused, only trace of the pleural membrane could be visible.
(11) Notal organ on abdomen: (0) absent, (1) could occur.

Discussion

The new samples from the Middle–Upper Jurassic Jiulongshan Formation in China have allowed us to detect multiple morphological characters crucial for defining a revised morphological and taxonomic range for the family Orthophlebiidae. A detailed study of the morphology of the male abdomen based on multiple specimens with their bodies preserved resulted in a clarification of the relationships between the genera within the family. The narrowing and elongation as well as fusion of tergites and sternites of pregenital abdominal segments are confirmed in three orthophlebiid genera. Within the genus *Orthophlebia* the elongation of

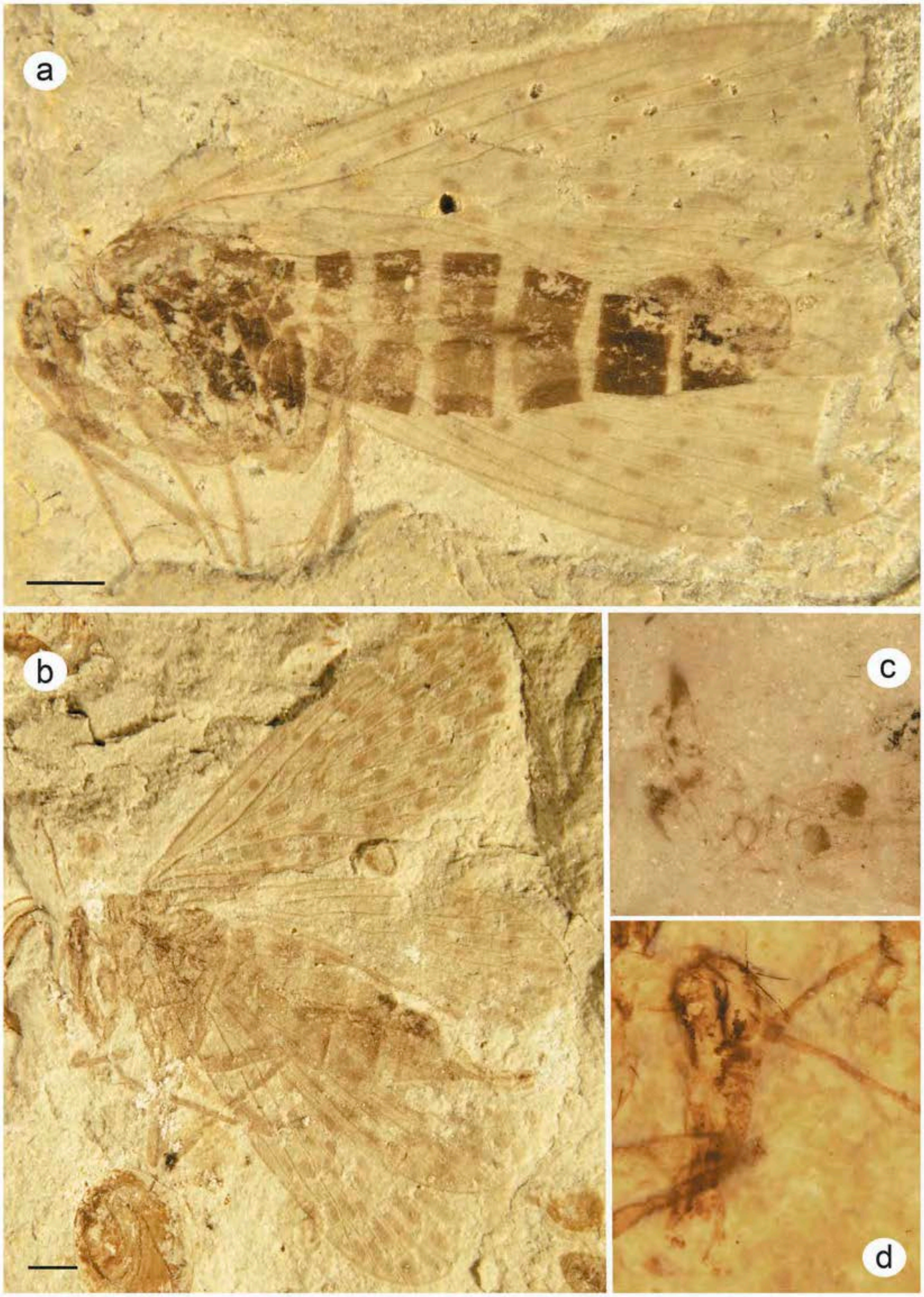

Figure 10. *Protorthophlebia punctata* sp. nov.; (a) Male abdomen, paratype CNU-MEC-NN- 13708, (b) Habitus of female CNU-MEC-NN-2018218, (c). Genital bulb, male CNU-MEC-NN- 13601, (d) Head with mouthparts CNU-MEC-NN-2018267, scale bar 1mm; photos C-D under alcohol.

three last abdominal segments (VI to VIII) is described in: *O. elenae* and *O. heidemariae*, both Willman & Novokshonov, 1998, *O. nervulosa* Qiao et al., 2012 and hereby in *O. chinensis* sp. nov. (Figures 1(b) and 3(a)). Also, large Jurassic scorpionflies from the genus *Gigaphlebia* had the same shape of the abdomen. However, scarce evidences of the fossils of this genus enabled to describe such morphology only in one species, *G. riccardii* (Petrulevicius & Ren, 2012) (Soszyńska-Maj et al. 2018). The third genus is the monotypic *Juraphlebia* gen. nov. (Figures 4–7). The elongation of only the 8th male abdominal segment of *J. eugeniae* (Figures 5(a) and 7(b)) is one of the unique characters of the genus described herein. Such elongation and narrowing of abdominal segments cause the characteristic scorpion-tail-like look of male scorpionflies` abdomen. Such a habitus is typical only for the extant family Panorpidae (Figure 13) and, especially, for fossil

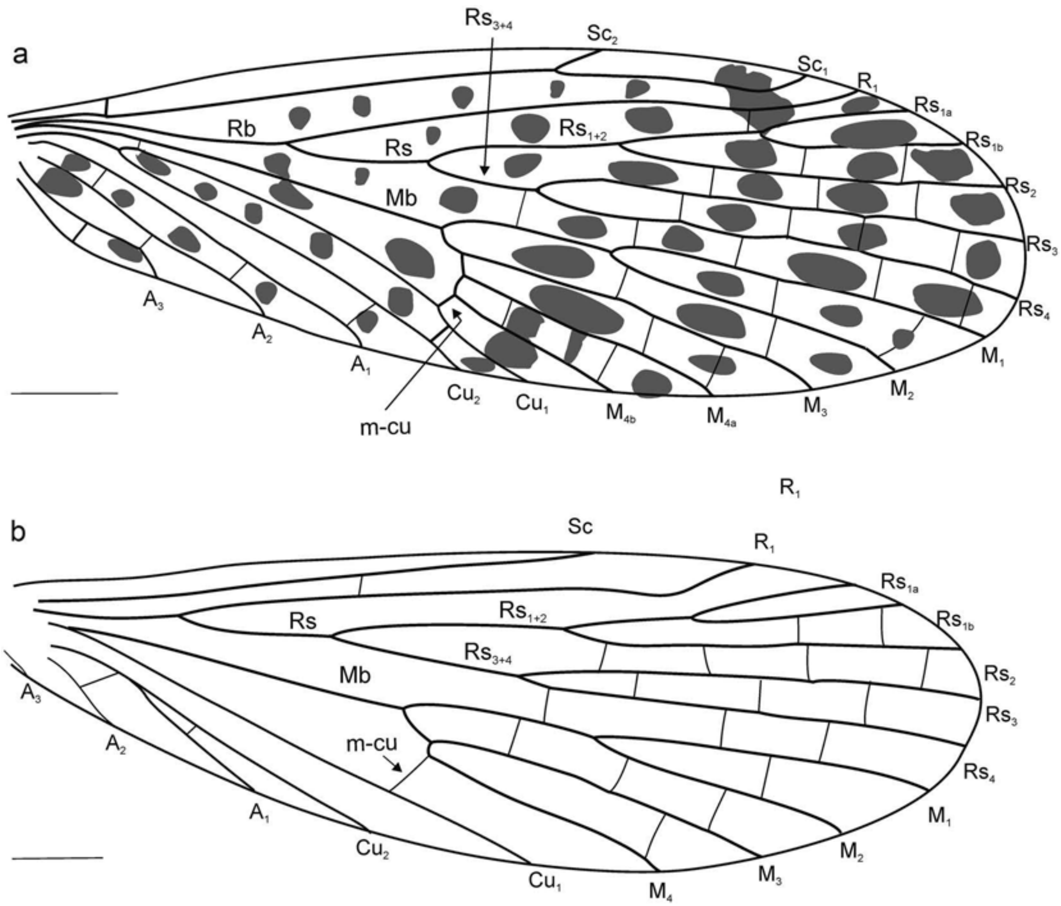

Figure 11. *Protorthophlebia punctata* sp. nov., (a) Forewing, Holotype CNU-MEC-NN-13768 (b) Hindwind paratype CNU-MEC-NN-2018219; 1 mm scale bar.

Holcorpidae (Wang et al. 2013). The differences in length of the pregenital segments between genera of Orthophlebiidae are comparable to those known within individual genera of recent Panorpidae (Hu et al. 2015), e.g. last three abdominal segments in *Leptopanorpa* are extremely prolongated (Lieftinck 1936), in the genus *Neopanorpa* they are less prolongated (Wang and Hua 2017), in *Panorpa* they are only 2–5 times as long as their width depending on the species (Issiki 1933), and in *Furcatopanorpa* only the VIII segment is slightly elongated (Ma and Hua 2011).

Our study indicated that the abdomen morphology is quite different in representatives of the genus *Protorthophlebia*, which was therefore determined based only on the wing venation and included so far into Orthophlebiidae. The male abdomen of *Protorthophlebia* is at most as long as the wings and shorter when curved forward, all the abdominal segments are wider than long, tergites and sternites of abdominal segments are connected by the pleural membrane, except VI-VIII segments where tergites and sternites are fused. Consequently, their abdomens do not have such distinct a scorpion-tail-like appearance (Figure 12(b,c)). The abdomen morphology and other characters such as a shortened rostrum and the wing venation allow us to classify genus *Protorthophlebia* in its own family. New diagnostic characters of the genus *Protorthophlebia* strikingly resemble those found in the recent genus *Panorpodes* from the family Panorpodidae (Figure 13). The habitus of the holotype of *Protorthophlebia punctata* sp. nov. (Figures 9 and 10(a)), with a genital bulb bent up and laying on VI–VIII abdominal tergites, bears a high resemblance to the habitus of extant *Panorpodes kuandianensis* Zhong et al., 2011 (Zhong et al. 2011, Figure 1). All known extant species from the family Panorpodidae (Tan & Hua 2008) as well as fossil *Panorpodes* spp. are characterized by such abdomen followed by the shortened rostrum. However, five veins in radial sector combined with five veins in the medial sector of the forewing, reduction of one medial vein in the hindwing, and lack of unique characters of Panorpodidae such as an angular R_1 at pterostigmal area exclude including the genus *Protorthophlebia* into the Panorpodidae.

Very scarce data on abdomen morphology are known in the oldest scorpionflies from the Permian. The abdomens of only few specimens of Permochoristidae were described from fossil compression by Novokshonov (1997), who concluded that the plesiomorphic condition of the abdomen of scorpionflies lacks specializations (Novokshonov 2002). This suggests that the unspecialized abdomen of Panorpodidae and Protorthophlebiidae fam. nov. is more primitive than that in other families discussed herein. However, the presence of the genital bulb makes it more apomorphic than in the Permochoristidae.

Recognition of the abdomen morphology of fossil species included so far to the family Orthophlebiidae, enables us to reconsider mutual relationships within living representatives

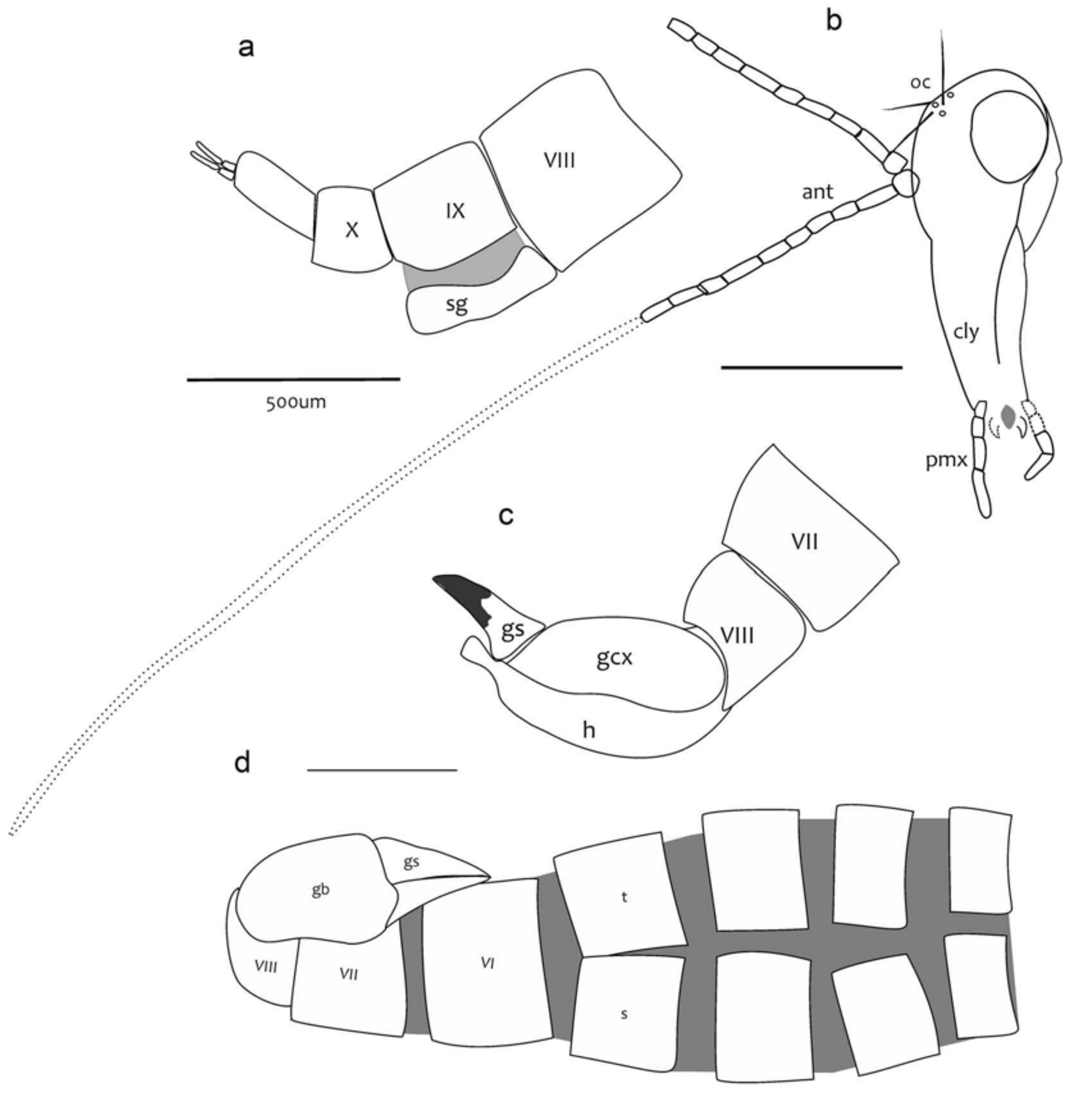

Figure 12. *Protorthophlebia punctata* sp. nov.; (a) Termination of female abdomen, paratype CNU-MEC-NN-2018218, (b) Head with mouthparts CNU-MEC-NN -2018267, ant – antennae, cly – clypeus, oc – ocelli, pmx – palpus maxillaris, (c) Genital bulb, male CNU-MEC-NN- 13601; (d) Male abdomen, paratype CNU-MEC-NN-13708, gcx – gonocoxite, gs – gonostylus, hv – hypovalve, t- ternite, s – sternite; scale bar – 1 mm.

Table 1. Data matrix.

	1	2	3	4	5	6	7	8	9	10	11
Orthophlebiidae	1	1	1	0	2	1	1	2	1	2	1
Protorthophlebiidae	2	1	1	0	1	1	0	1	1	2	0
Panorpidae	3	1	1	1	3	1	1	2	1	2	1
Panorpodidae	3	1	1	1	3	1	0	1	1	1	0
Permochoristidae	0	0	0	0	0	0	-	0	0	0	0

of superfamily Panorpoidea. Our taxonomic investigations prove that in fact the two living and seemingly closely related families Panorpidae and Panorpodidae do not represent the sister taxa, as Mickoleit (1978), Willman (1989) and others suggested, but they had derived from different evolutionary lines. The two former authors (op. cit.) considered a phylogeny of only living Mecoptera, while Willmann (1989) based his phylogeny on fossil and modern scorpionflies, although fossil data was at that time restricted to wing venation characters. According to Willmann's (op. cit.) phylogenetic tree, Panorpidae and Panorpodidae had a common ancestor during the Upper Jurassic. This view was followed by Grimaldi & Engel (2005) with some inexplicable modifications. However, two molecular studies on Mecoptera (Whiting 2002; Pollmann et al. 2008) raised doubts on Panorpidae and Panorpodidae being sister taxa. Whiting (2002) highlighted that the clade consisted of those two families that were 'never well supported in any of the gene partitions'. Similarly, Pollmann et al. (2008) concluded that their results did not confirm Willmann's hypothesis.

Our investigation allowed to describe the differences between Orthophlebiidae and Protorthophlebiidae fam. nov. Not only the abdomen morphology suggests that Panorpodidae are closer to the Protorthophlebiidae than to Orthophlebiidae. The concept is also supported by other characters: the shorter rostrum, and venation which includes five radial veins with a tendency to further reduction to four in the recent genus *Brachypanorpa* (Willmann 1989). On the other hand, the Panorpidae and Orthophlebidae, except a prolonged abdomen, share also an elongated rostrum, five veins in the radial sector with a tendency to increasing to six and seven in recent genera *Neopanorpa* and *Leptopanorpa*.

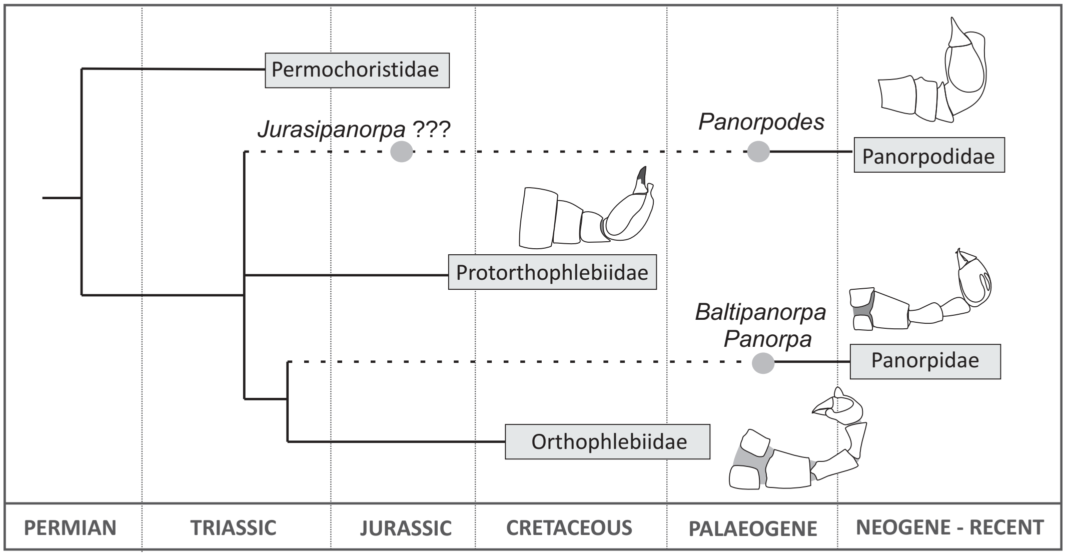

Figure 13. Diagram of the preliminary phylogenetic relationship between Orthophlebiidae, Protorthophlebiidae, Panorpidae and Panorpodidae (Ci = 0.944, Ri = 0.75).

Also, the notal organ on 3rd and 4th abdominal segments occurs in many extant, and even fossil Panorpidae (e.g. Krzemiński and Soszyńska-Maj 2012, Zhong and Hua 2013), was also found in *Orthophlebia* from Karatau (Willmann and Novokschonov 1998). This conclusion is supported by a very preliminary phylogenetic tree based on characters of the four families discussed above (Figure 13). Panorpidae and Orthophlebiidae form one clade on that tree, while Panorpodidae and Protorthophlebiidae are situated outside, closer to the Permochoristidae probably due to the more plesiomorphic abdomen morphology, what was pointed by Novokshonov (2002) and discussed in previous paragraphs.

The oldest representatives of Orthophlebiidae after excluding genus *Protorthophlebia* and transferring *W. haradai* (Ueda 1991) to Worcestobiidae (Soszyńska-Maj et al. 2018) are *Orthophlebia liassica* (Mantell 1844) from Rhaetian (Upper Triassic) of the United Kingdom, dated ca. 204 Ma (Cohen et al. 2013). The oldest representatives of Protorthophlebiidae are known from the Middle Triassic of China, i.e., *Protorthophlebia curta* Hong, 2009, *P. ladinica* Hong et al., 2002 and *P. triassica* Hong et al., 2002. Whereas, fossil members of the family Panorpidae are known from the Palaeogene, corresponding to an inclusion in Eocene Baltic amber (Carpenter 1954, Krzemiński and Soszyńska-Maj 2012) and compression fossils from the Oligocene of Florissant in Colorado, Rott/Siebengebirge in Germany and Isle of Wight in Great Britain (Willmann 1978). The oldest alleged panorpid scorpionflies were described from the Middle Jurassic (Ding et al. 2014). However, preliminary revision of the holotype of *Jurassipanorpa impunctata* Ding, Shih & Ren, 2014, as well as additional new materials, shows that the species is not a member of the Panorpidae (Soszyńska-Maj et al. in prep.). The oldest known members of the family Panorpodidae were described in the genus *Panorpodes* only from the Eocene Baltic amber (Hagen 1856; Carpenter 1954; Soszyńska-Maj and Krzemiński 2013, 2015). The recent molecular phylogeny of Panorpidae (Miao et al. 2018) indicated Lower Cretaceous (approximately 122.5 Ma) origin of Panorpidae and Palaeogene as a begging of the diversification of these scorpionflies.

Archibald (2013) suggested that the Orthophlebiidae formed an early grade of the superfamily Panorpoidea, being replaced in the Eocene by six families, two of which survived until today. However, the last five years have provided numerous new fossil finds. One species from the Eocene of Australia, *Austropanorpa australis* Riek, 1952 was classified within the family Austropanorpidae. Revision of the holotypes of the Orthophlebiidae resulted in extending the age of the Austropanorpidae back to the Early Jurassic (Krzemiński et al. 2017) and changing the taxonomic status of *Austropanorpa martynovae* (Sukatsheva 1985). Wang et al. (2013) and Li et al. (2017) described Holcorpidae from the Middle Jurassic, previously known only in the Palaeogene (Carpenter 1931; Archibald 2010), and access to the new collection of Chinese Mecoptera anticipate further descriptions within this family. New materials from Daohugou, as well as from Cretaceous amber, indicate also a greater diversity within Panorpoidea, what is now an object of ongoing investigations. However, the unchanging fact is that the only surviving lineages of the Panorpoidea are two extant families: the diverse Panorpidae and the relictual Panorpodidae.

Our studies on new fossil materials from the Jurassic of China support doubts raised by molecular studies (Whiting 2002; Pollmann et al. 2008) and suggest that Panorpidae and Panorpodidae belong to separate, much older phylogenetic lineages, and lacked a direct common ancestor (Figure 13). The fact that there is no fossil evidence of Panorpodidae before the Eocene, as well as some plesiomorphies which are absent in other Mecoptera, lead to the conclusion that their origin and phylogenetic relationships need further investigation. As this and our previous papers indicate, the family Orthophlebiidae is very important to the understanding phylogeny and taxonomy of Panorpoidea, but it needs also further study, first of all, the reconsideration of all other established genera and subgenera. A planned revision of remaining holotypes followed by new completely preserved specimens will help to clarify the phylogeny of this group of scorpionflies.

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Disclosure statement

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