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The snakefly family Mesoraphidiidae (Insecta: Raphidioptera) from the Lower Cretaceous Yixian Formation, China: systematic revision and phylogenetic implications

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Mesoraphidiidae is one of the major groups among the Mesozoic Raphidioptera, with 70 described species in 30 genera. However, many mesoraphidiid taxa need to be revised and the monophyly of this family is still questionable, lacking conclusive support from convincing autapomorphies. Here, we present a systematic revision of Mesoraphidiidae from the Lower Cretaceous Yixian Formation of north-eastern China. Nine genera and 12 species are described or re-described based on 27 fossil specimens, including four new genera and five new species, namely *Allocotoraphidia* gen. nov., *Yixianoraphidia* gen. nov., *Beipiaoraphidia martynovi* gen. et sp. nov., *Grammoraphidia ponomarenkoi* gen. et sp. nov., *Proraphidia jepsoni* sp. nov., *Proraphidia yixianensis* sp. nov. and *Styporaphidia willmanni* sp. nov. Two new combinations are proposed, *Yixianoraphidia anomala* (Ren, 1997) comb. nov. and *Allocotoraphidia myrioneura* (Ren, 1997) comb. nov. *Proraphidia* Martynova, 1947 and *Styporaphidia* Engel & Ren, 2008 are first recorded from the Lower Cretaceous of China. *Phiradia* Willmann, 1994 stat. rest. is restored as a valid genus. A preliminary phylogenetic analysis is performed to investigate the relationships among the genera of Mesoraphidiidae based on morphological data. The monophyly of the subfamily Alloraphidiinae and the tribe Nanoraphidiini, respectively, were supported in the present analysis; several genera with three forewing radial crossveins or with subradial crossveins (i.e. *Cretinocellia* Ponomarenko, 1988, *Allocotoraphidia* gen. nov., *Kezuoraphidia* Willmann, 1994 and *Xuraphidia* Hong, 1992) were assigned to earlier diverging groups in Mesoraphidiidae; however, the monophyly of Mesoraphidiinae was not recovered. The present study sheds light on the evolutionary history of Raphidioptera.

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Keywords: Raphidiomorpha; taxonomy; phylogenetic analysis; Mesozoic; fossil

Introduction

The holometabolan order Raphidioptera (snakeflies) represents one of the common components of the insect palaeofauna across the Jurassic–Cretaceous boundary, with rich fossil records (Engel 2002; Jepson & Jarzembowski 2008; Makarkin & Khramov 2015; Lyu *et al*. 2017). The most diverse group of the Mesozoic Raphidioptera is the extinct family Mesoraphidiidae, which contains approximately two-thirds of all known Mesozoic snakefly species (Engel 2002; Engel *et al.* 2018; Lyu *et al*. 2017). Mesoraphidiidae presently comprises two subfamilies, Alloraphidiinae and Mesoraphidiinae, including 30 genera and 70 species (Lü *et al*. 2015; Oswald 2020).

With respect to morphology, compared with Baissopteridae, the second-most species-rich Mesozoic snakefly family, Mesoraphidiidae possesses many fewer branches of the RP, MA and MP veins as well as fewer crossveins. Bechly & Wolf-Schwenninger (2011) proposed the triangular arrangement of three forewing discoidal cells as an autapomorphy of Mesoraphidiidae although this character state is missing in a few mesoraphidiid species (see Ponomarenko 1988; Liu *et al.* 2016). Actually, despite some previous phylogenetic studies on fossil Raphidioptera (Willmann 1994; Bechly & Wolf-Schwenninger 2011; Liu *et al*. 2014), the monophyly of Mesoraphidiidae has been often questioned as lacking conclusive support or convincing autapomorphies (Engel 2002; Liu *et al*. 2014; Makarkin & Archibald 2014) and still needs to be tested. This problem is correlated with the chaotic background to the taxonomy of Mesoraphidiidae, in which a number of genera and species are poorly defined with unreliable,

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or incorrectly illustrated, wing characters, and for which there is limited knowledge on the evolutionary polarity of their morphological characters (mostly wing characters).

The Yixian Formation of north-eastern China yielded abundant and exquisitely preserved insect fossils (Ren 1998; Gao *et al*. 2013, 2018; Wang *et al*. 2013; Yao *et al*. 2014; Ren *et al.* 2019). Hitherto, seven genera and 16 species of Mesoraphidiidae have been recorded from this deposit (Hong & Chang 1989; Hong 1992a, b; Ren 1994, 1997; Ren *et al*. 1995; Engel & Ren 2008; Lyu *et al.* 2018). However, most of these taxa were originally described based on a limited number of fossils, and the systematic positions of some genera and species are equivocal.

Here, we present a revision of Mesoraphidiidae from the Lower Cretaceous Yixian Formation of China based on 27 fossil specimens, including four new genera and five new species. These new fossils with well-preserved body and wings are valuable for reconsidering the identity and systematic positions of some genera of Mesoraphidiidae. A phylogenetic analysis was performed to recover the relationships among mesoraphidiid genera based on morphological characters. Accordingly, a revised generic classification of Mesoraphidiidae is proposed, with some taxonomic amendments. The present results provide new insights for understanding the phylogeny of Mesoraphidiidae and the early evolution of snakeflies.

Material and methods

Specimens examined

All fossil specimens herein examined are deposited in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University (CNU), Beijing. They are from the upper Barremian (126.1 ± 1.7 to 124.6 ± 0.1 Ma; Lower Cretaceous) Jianshangou Member (Bed) of the Yixian Formation (Wang & Zhou 2008; Walker *et al*. 2013; Lin *et al*. 2019) of the Huangbanjigou locality (41°36′44″ N, 120°49′48″ E) (Wang *et al*. 2015, fig. 1) in the Sihetun area, Beipiao City, Liaoning Province, China. Specimens were examined using a Zeiss Discovery V12 stereo microscope, and photographs were taken with a Nikon D800 digital camera, and drawings were made in Adobe Photoshop CC.

Terminology

Considering wing venation terminology, we accept the concept based on the hypothesis of Martynov (1928), in which M is interpreted to have a common stem but MA is fused with R or RP (e.g. Aspöck *et al*. 1991, figs 43, 44; Bechly & Wolf-Schwenninger 2011, fig. 16), and our terminology principally follows Aspöck *et al*. (1991) and Kukalová-Peck & Lawrence (2004). Breitkreuz *et al.* (2017) presented an alternative interpretation on the homology of wing venation in Neuropterida based on vein tracheation. The latter terminology differs from the former in homology interpretation and definition of MA, i.e. MA is not considered to be fused with R or RP at wing base. The venational terminology used for Raphidioptera in Makarkin & Archibald (2014) is in general similar to that of Breitkreuz *et al.* (2017). We follow the terms of crossveins in Makarkin & Archibald (2014) except for the r-m and irp crossveins. The 1r-m in Makarkin & Archibald (2014) is herein interpreted as MA in both fore- and hind wings, while the irp is herein named as rp-ma.

Abbreviations for longitudinal veins and spaces. A, anal; ***ac***, anal cell; **C**, costa; **Cu**, cubitus; **CuA**, cubitus anterior; **CuP**, cubitus posterior; ***dc***, discal cell; ***doi***, discoidal cell; **M**, media; **MA**, media anterior; **MP**, media posterior; ***m***, medial cell; **pt**, pterostigma; **R**, radius; **RA**, radius anterior; **RP**, radius posterior; ***r***, radial cell; ***sm***, submedial cell; ***sr***, subradial cell; **ScP**, subcosta posterior.

Phylogenetic analysis

The present phylogenetic analysis focused on recovering the intergeneric phylogeny within Mesoraphidiidae. In total, 31 genera of Mesoraphidiidae were included as the ingroup taxa except *Huaxiaraphidia* Hong, 1992a, *Jilinoraphidia* Hong & Chang, 1989, and *Sinoraphidia* Hong, 1982, which lack reliable morphological descriptions (Hong 1982, 1992a; Hong & Chang 1989). *Chrysoraphidia* Liu, Makarkin, Yang & Ren, 2013 (Chrysoraphidiidae), *Juroraphidia* Liu, Ren & Yang, 2014 (Juroraphidiidae) and *Baissoptera* Martynova, 1961 (Baissopteridae) were selected as the outgroup taxa. Chrysoraphidiidae represents the other suborder, i.e. Priscaenigmatomorpha, of Raphidioptera (Liu *et al.* 2013, 2014). Juroraphidiidae represents the transitional lineage between Priscaenigmatomorpha and Raphidiomorpha (Liu *et al.* 2014). Baissopteridae appears to be closely related to Mesoraphidiidae but as a relatively basal group in comparison with the latter family (Willmann 1994). Morphological characters and their coding for the ingroup and outgroup taxa were based mainly on our examination of the type species of some genera and reliable morphological descriptions of the type species of the remaining genera (Martynov

1925; Martynova 1947; Carpenter 1967; Ponomarenko 1988, 1993; Hong 1992b; Ren 1994, 1997; Ren *et al.* 1995; Grimaldi 2000; Engel 2002; Engel & Ren 2008; Pérez-de la Fuente *et al.* 2010, 2012; Bechly & Wolf-Schwenninger 2011; Jepson *et al.* 2011; Liu *et al.* 2016; Lyu *et al.* 2018). Characters of species that are not the type of the genus were not considered for the present analysis as such species might have incorrect generic placements. However, when coding some characters that are not preserved in the type species of certain genera, we used some definite congeneric species that are mostly similar to the type species of the genus and have better preservation for supplementary coding.

Morphological characters used in the phylogenetic analysis and the coding can be found in the Supplemental material. In total, 35 adult morphological characters were coded for three outgroup and 31 ingroup taxa. Twenty-three characters are coded as binary and 12 as multistate. Inapplicable and unavailable characters were respectively coded as '-' and '?'. The data matrix was produced in Mesquite v 3.04 (Maddison & Maddison 2015) (Supplemental material). The analysis was performed using parsimony methods in TNT v 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016) with a traditional search (random seed = 1100 replicates, tree-bisection-reconnection (TBR), 10 trees saved per replication). The Bremer support values/bootstrap values were calculated with the function implemented in TNT (TBR from existing trees, retain trees suboptimal by 100 steps). All characters were treated as unordered and with equal weight. Synapomorphies were mapped on the strict consensus tree, showing only unambiguous changes.

Systematic palaeontology

Order **Raphidioptera** Navás, 1916
Suborder **Raphidiomorpha** Engel, 2002
Family **Mesoraphidiidae** Martynov, 1925
Subfamily **Alloraphidiinae** Martynov, 1925
Genus ***Yixianoraphidia*** Lyu, Ren & Liu gen. nov.

Type species. *Alloraphidia anomala* Ren, 1997.

Diagnosis. Medium-sized snakeflies (body length 8.5–12.7 mm, forewing length 8.1–10.4 mm). Head ovoid, tapering caudad, with vertex obviously longer than eye diameter. Ocelli present. Pronotum elongate, nearly as long as head. In both fore- and hind wings, ScP long, terminating into costal margin at distal one-third; bicoloured pterostigma short, ~0.2 times wing length, with nearly constant width along its entire length; one RA veinlet within pterostigma; distal-most ra-rp crossvein (= 3ra-rp in Makarkin & Archibald 2014) posteriorly connecting to stem of RP; rp-ma crossvein (= irp in Makarkin & Archibald 2014) posteriorly connecting to stem of MA. Forewing: not distinctly narrowed, forewing length 3.0–3.5 times its maximum width; MA originating slightly distad from the initial branching point of MP; CuA distally fused with posterior branch of MP for a short distance; two radial cells (1*r* nearly as long as 2*r*), one discal cell, and three discoidal cells present. Hind wing: Costal space narrow, 1ra-rp posteriorly connecting to stem of RP + MA; three radial cells (3*r* longer than 1*r* and 2*r*), one discal cell, and one or two discoidal cells present.

Etymology. The generic name is a combination of the type locality of the type species of the genus, i.e. 'Yixian', and *raphidia*, a common genus-group name of Raphidioptera. Gender: feminine.

Remarks. The type species of this new genus, *Alloraphidia anomala* Ren, 1997, was suggested to be excluded from *Alloraphidia* by Makarkin & Khramov (2015), as the wings are relatively broad, the ScP is long, and the MP and CuA at least touch or are fused distally. Based on our examination of new fossils of *A. anomala*, we confirm the above characters, which indicate a different generic affinity of this species from *Alloraphidia*. In addition, *Yixianoraphidia* gen. nov. also differs from *Alloraphidia* by the distal-most ra-rp crossvein posteriorly connecting to stem of RP (in *Alloraphidia*, distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP) and the stem of forewing MA originating just slightly distad to the first branching point of MP (in *Alloraphidia*, stem of forewing MA originating obviously distad to the first branching point of MP).

Two characters, i.e. the forewing MA forked near wing margin (character [char.] 24:2) and the forewing CuA distally fused with MP for a short distance (char. 27:1), were assigned to be autapomorphies of this new genus, although both characters are also convergently derived in some other genera.

Yixianoraphidia anomala (Ren, 1997) comb. nov.
(Fig. 1)

1997 *Alloraphidia anomala* Ren: 181.

Diagnosis. Mostly as for the genus. Body dark-coloured, but head and prothorax slightly paler; head with frons very dark and with two longitudinal dark stripes on vertex. Pterostigma bicoloured, with basal portion pale brown and distal portion dark brown.

Figure 1. *Yixianoraphidia anomala* (Ren, 1997) comb. nov. **A,** habitus photo of CNU-RAP-LB-2017105, two males, lateral view; **B,** habitus photo of CNU-RAP-LB-2017118, female, dorsal view; **C,** habitus photo of CNU-RAP-LB-2017119, male, lateral view; **D,** habitus photo of CNU-RAP-LB-2017121, male, lateral view; **E,** drawing of wing venation, CNU-RAP-LB-2017119; **F,** drawing of wing venation, CNU-RAP-LB-2017121. Scale bar equals 1 mm.

Material examined. CNU-RAP-LB-2017105, two well-preserved males compressed laterally; CNU-RAP-LB-2017118 c/p, a well-preserved female compressed dorsoventrally, with wings partly preserved; CNU-RAP-LB-2017119, a well-preserved male compressed laterally; CNU-RAP-LB-2017120 c/p, a well-preserved specimen (sex unknown), without abdomen; CNU-RAP-LB-2017121, a well-preserved male specimen compressed laterally.

Subfamily **Mesoraphidiinae** Martynov, 1925
Genus ***Allocotoraphidia*** Lyu, Ren & Liu gen. nov.

Type species. *Phiradia myrioneura* Ren, 1997.

Diagnosis. Large-sized snakeflies (body length 20.1–22.3 mm, forewing length 15.5–18.1 mm). Head ovoid, with vertex obviously longer than eye diameter. Ocelli present. Pronotum subquadrate, slightly shorter than head. In both fore- and hind wings, ScP terminating into C at wing midpoint; pterostigma short, no RA veinlet within pterostigma; two crossveins present between RP branches; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; 1rp-ma crossvein posteriorly connecting to anterior branch of MA; a crossvein present between MA branches. Forewing: stem of MA originating from first branching point of MP; three radial cells (1*r* slightly longer than 2*r* and 3*r*), two subradial cells, two discal cells, one submedial cell, three medial cells, and three discoidal cells present. Hind wing: 1ra-rp crossvein posteriorly connecting to RP + MA; four radial cells, two subradial cells, two or three discal cells, one submedial cell, two medial cells, and three discoidal cells present.

Etymology. The generic name is a combination of the Greek adjective '*allocot-*', extraordinary, and *raphidia*, a common genus-group name of Raphidioptera. Gender: feminine.

Remarks. The type species of this new genus, *Phiradia myrioneura* Ren, 1997, was transferred to *Mesoraphidia* Martynov, 1925 by Engel (2002), along with the treatment of *Phiradia* as a junior synonym of *Mesoraphidia*. However, this species greatly differs from all *Mesoraphidia* species in the following characters: the presence of three forewing radial cells (two forewing radial cells present in *Mesoraphidia*); the presence of crossveins between RP branches and between MA branches in both fore- and hind wings (crossveins absent between RP branches and between MA branches in *Mesoraphidia*); and the presence of three hind wing *doi* (only one or two *doi* present in *Mesoraphidia*). Accordingly, *P. myrioneura* should not be placed in *Mesoraphidia*. Moreover, the type species of *Phiradia*, *Mesoraphidia pterostigmalis* Martynova, 1947, should not be placed in *Mesoraphidia* due to the possession of three hind wing *doi*. Therefore, *Phiradia* stat. rest. is herein restored as a valid genus of Mesoraphidiidae.

Furthermore, we consider that *M. myrioneura* should not be placed back into *Phiradia* because this species has several crossveins between the branches of RP and between the branches of MA, while this feature is absent in *P. pterostigmalis* (Martynova, 1947). Therefore, *M. myrioneura* represents a new genus, named herein as *Allocotoraphidia* gen. nov. Besides *Phiradia*, the new genus also appears to be closely related to *Cretinocellia* Ponomarenko, 1988 in having similar forewing crossvenation between branches of RP and branches of MA and presence of three hind wing *doi*, but it can be distinguished from the latter genus by the short pterostigma and the deeply forked forewing MA. In *Cretinocellia* the pterostigma is much longer and the forewing MA is deeply forked, being apparently proximad to the initial branching point of RP. However, no autapomorphy was recovered for this new genus in our phylogenetic analysis as the overall wing characters in this genus are relatively plesiomorphic.

Allocotoraphidia myrioneura (Ren, 1997) comb. nov.
(Fig. 2)

1997 *Phiradia myrioneura* Ren: 178.

Diagnosis. Mostly as for the genus. Body dark-coloured, but head much paler. Abdomen dorsally with a sub-triangular pale marking on terga 1–7 posteromedially.

Material examined. CNU-RAP-LB-2009003, a well-preserved male compressed dorsoventrally.

Genus ***Beipiaoraphidia*** Lyu, Ren & Liu gen. nov.

Type species. *Beipiaoraphidia martynovi* Lyu, Ren & Liu sp. nov.

Diagnosis. Medium-sized snakeflies (body length 11.4 mm, forewing length 10.8 mm). Head ovoid, tapering caudad, with vertex nearly as long as eye diameter. Ocelli present. Pronotum nearly equal in length to head. In both fore- and hind wings, pterostigma elongate, no RA veinlet present within pterostigma; distal-most ra-rp crossvein posteriorly connecting to stem of RP; rp-ma crossvein posteriorly connecting to stem of MA. Forewing: MA separating from MP obviously proximad to first branching point of MP; two radial cells (1*r* as long as 2*r*), one discal cell, and three discoidal cells present. Hind wing: 1ra-rp

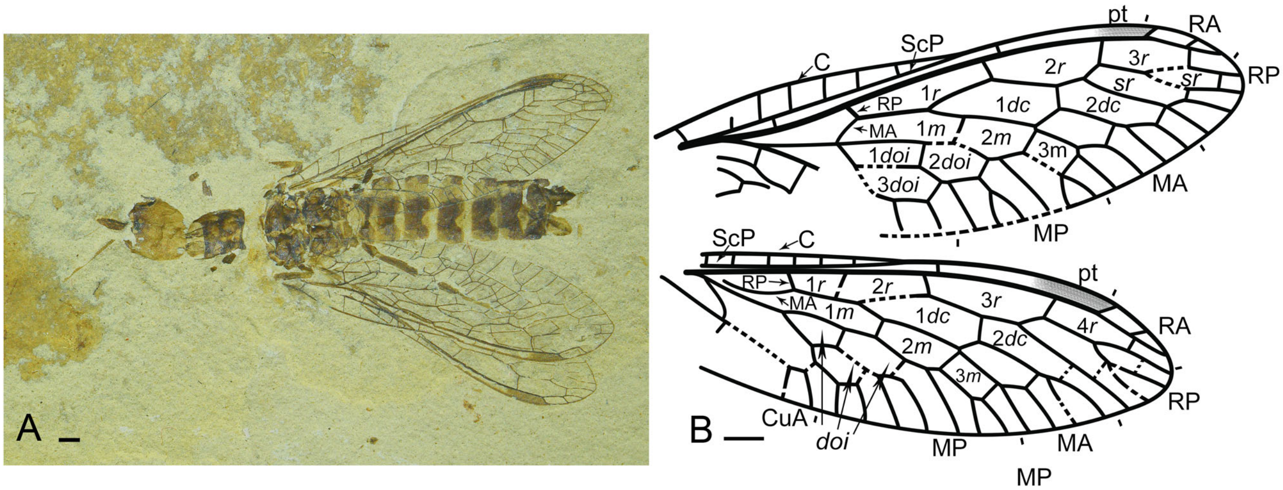

Figure 2. *Allocotoraphidia myrioneura* (Ren, 1997) comb. nov. **A,** habitus photo of CNU-RAP-LB-2009003, sex unknown, dorsal view; **B,** drawing of wing venation, CNU-RAP-LB-2009003. Scale bar equals 1 mm.

posteriorly connecting to stem of RP + MA; three radial cells, one discal cell, and one discoidal cell present.

Etymology. The generic name is a combination of '*Beipiao-*', type locality of the type species of the genus, and *raphidia*, a common genus-group name of Raphidioptera. Gender: feminine.

Remarks. The new genus resembles *Iberoraphidia* and the genera of Nanoraphidiini in having a similar forewing MA stem proximad to the initial branching point of MP. However, it differs from *Iberoraphidia* in lacking the medially interrupted forewing pterostigma (forewing pterostigma medially interrupted by an immaculate section in *Iberoraphidia*), and it differs from the genera of Nanoraphidiini by the presence of three forewing *doi* (only one or two forewing *doi* present in Nanoraphidiini).

Four characters were assigned to be autapomorphies of this new genus, i.e. the bifurcate forewing RA (char. 12:1), the absence of forewing RA veinlets within pterostigma (char. 14:1), the bifurcate forewing RP (char. 18:1), and the forewing MA stem proximad initial branching point of MP (char. 22:0). However, all of these characters can be found in some other genera, suggesting a convergent pattern of evolution.

Beipiaoraphidia martynovi Lyu, Ren & Liu sp. nov.
(Fig. 3)

Type material. Holotype: CNU-RAP-LB-2017073c/p, a well-preserved female specimen compressed dorsoventrally.

Locality and horizon. Yixian Formation (upper Barremian, Lower Cretaceous), Huangbanjigou locality (41°36′44″ N, 120°49′48″ E), Beipiao city, Liaoning Province, north-eastern China.

Diagnosis. Mostly as for the genus. Body dark except for pale head, which medially has a longitudinal stripe on vertex.

Etymology. The new species is dedicated to the Russian entomologist and palaeontologist Andreas V. Martynov for his contributions to the taxonomy of fossil snakeflies.

Description of holotype female. Body dark except pale head, 11.4 mm long excluding ovipositor. Head ovoid, 1.9 mm long, pale, medially with a longitudinal dark stripe on vertex; vertex as long as eye diameter and tapering caudad. Ocelli present. Antenna length ~3.7 mm, nearly as long as head plus prothorax, with *c.* 40 flagellomeres. Pronotum sub-quadrate, 1.9 mm long, nearly as long as head. Meso- plus metathorax 2.5 mm long. Legs slender.

Forewing: length 10.8 mm, width 3.6 mm; costal space distinctly broadened (~1.5 times width of pterostigma at widest point); six costal crossveins present; ScP terminating into costal margin slightly distad to midpoint of wing; 1sc-r present at proximal one-quarter; two RA veinlets present, with posterior branch continuous with RA stem; uniformly coloured pterostigma elongate (2.5 mm long), ~0.25 times forewing length, with nearly constant width along its entire length, closed by 2scp-r proximally, and distally closed by anterior veinlet of RA, RA veinlet absent within pterostigma; two radial crossveins present between RA and RP, 1*r*

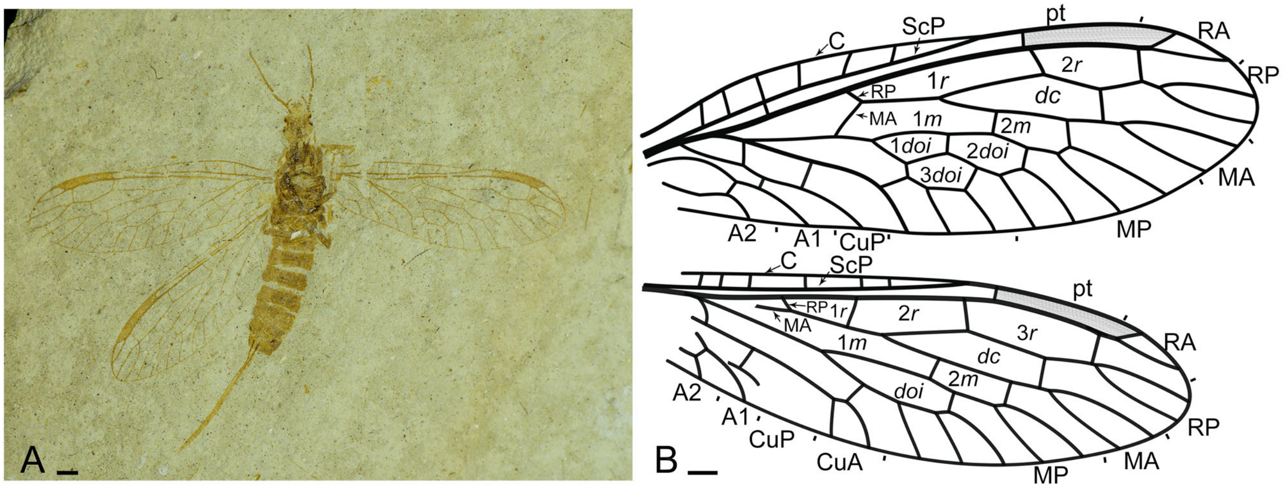

Figure 3. *Beipiaoraphidia martynovi* gen. et sp. nov. **A,** habitus photo of holotype CNU-RAP-LB-2017073, female, dorsal view; **B,** drawing of wing venation, holotype CNU-RAP-LB-2017073. Scale bar equals 1 mm.

nearly 1.5 times as long as 2*r*; distal-most ra-rp crossvein posteriorly connecting to stem of RP; RP bifurcated; 1rp-ma crossvein posteriorly connecting to stem of MA, forming a long discal cell; stem of MA much longer than stem of RP, originating from MP obviously proximad to initial branching point of MP, MA distally bifurcated, with branches nearly as long as that of RP; two crossveins present between MA and MP, forming a long 1*m* and a short 2*m*; MP deeply forked, with four terminal branches and three discoidal cells; CuA trifurcated, CuP simple; A1 simple.

Hind wing length 10.2 mm, width 3.4 mm; costal space distinctly narrower than that of forewing; six costal crossveins present; ScP terminating into costal margin slightly distad to midpoint of wing; two RA veinlets present, with posterior branch continuous with RA stem; uniformly coloured pterostigma elongate (2.7 mm long), ~0.25 times hind wing length, with nearly constant width along its entire length, closed by 2scp-r proximally, and distally closed by anterior veinlet of RA, RA veinlet absent within pterostigma; three radial crossveins present between RA and RP, 1*r* shortest, 2*r* shorter than 3*r*; 1ra-rp crossvein posteriorly connecting to stem of RP + MA; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; RP bifurcated; 1rp-ma crossvein posteriorly connecting to stem of MA, forming a long discal cell; MA stem incomplete, MA distally bifurcated, with branches nearly as long as that of RP; two crossveins present between MA and MP, a long 1*m* and a short 2*m*; MP deeply forked, with five terminal branches and a single discoidal cell; CuA bifurcate; CuP incomplete; A1 simple.

Abdomen 6.3 mm long, 2.0 mm wide in dorsal view; ovipositor 6.0 mm long.

Genus ***Caloraphidia*** Ren, 1997

Type species. *Caloraphidia glossophylla* Ren, 1997.

Diagnosis. Large-sized snakeflies (body length 19.4–23.1 mm, forewing length 19.0–21.5 mm). Head slender, elongate; length between eyes less than eye diameter; vertex slightly longer than eye diameter. Ocelli present. Prothorax sub-quadrate, nearly two-thirds of head length. In both fore- and hind wings, ScP terminating into costal margin slightly distad to midpoint of wing; uniformly coloured pterostigma elongate, ~0.25 times wing length, with nearly constant width along its entire length; an RA veinlet present at distal one-fifth of pterostigma; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; rp-ma crossvein posteriorly connecting to anterior branch of MA. Forewing: two radial cells (1*r* nearly as long as 2*r*), one discal cell, and three discoidal cells present. Hind wing: 1ra-rp posteriorly connecting to stem of RP + MA; three radial cells, one discal cell, and three discoidal cells present.

Remarks. The genus *Caloraphidia* was established by Ren (1997) but treated as a junior synonym of *Mesoraphidia* by Engel (2002). Bechly & Wolf-Schwenninger (2011) rejected the synonymy of *Caloraphidia* with *Mesoraphidia*, and tentatively transferred this genus to Ororaphidiinae, which, however, was synonymized with Mesoraphidiinae by Lyu *et al.* (2017). Given the distinctly narrowed head and the presence of three hind wing *doi*, *Caloraphidia* should stand as a different genus from *Mesoraphidia*.

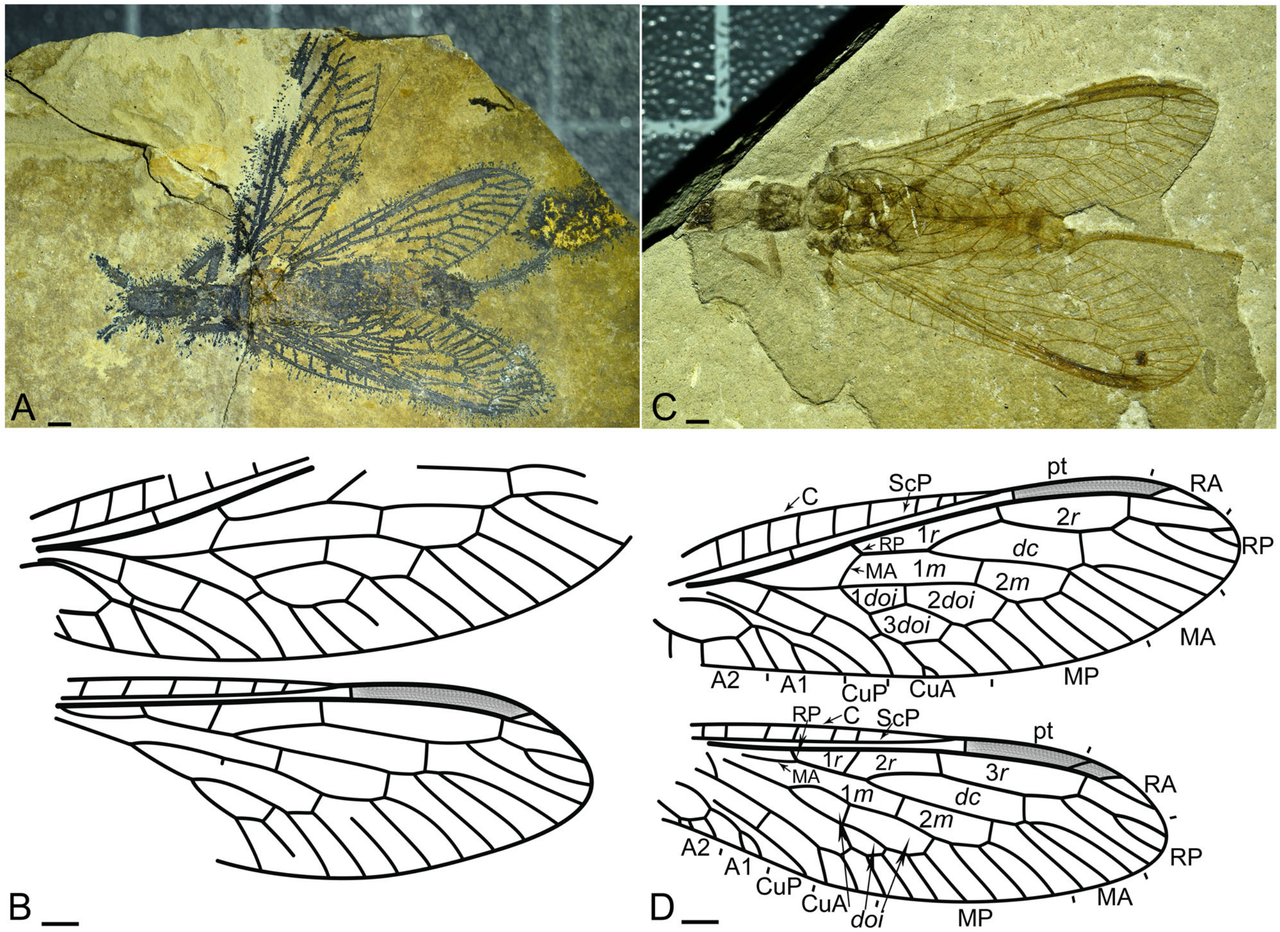

Figure 4. *Caloraphidia glossophylla* Ren, 1997 stat. rest. **A,** habitus photo of CNU-RAP-LB-2017129, female, dorsal view; **B,** drawing of wing venation of CNU-RAP-LB-2017129. **C,** habitus photo of CNU-RAP-LB-2009002, female, dorsal view; **D,** drawing of wing venation, CNU-RAP-LB-2009002. Scale bar equals stat rest 1 mm.

Caloraphidia glossophylla **Ren, 1997**
(Fig. 4)

1997 *Caloraphidia glossophylla* Ren: 183.

Diagnosis. Mostly as for the genus. Head with dark-coloured frons and pale-coloured vertex.

Material examined. CNU-RAP-LB-2017129c/p, a well-preserved female specimen compressed dorsoventrally; CNU-RAP-LB-201763, an incomplete specimen compressed dorsoventrally; CNU-RAP-LB-2009002, a well-preserved female specimen compressed dorsoventrally.

Genus ***Grammoraphidia*** Lyu, Ren & Liu gen. nov.

Type species. *Grammoraphidia ponomarenkoi* Lyu, Ren & Liu sp. nov.

Diagnosis. Large-sized snakeflies (body length 22.2 mm, forewing length 18.2 mm). Head ovoid, slightly wider caudad, with vertex slightly longer than eye diameter. Ocelli present. Pronotum slightly shorter than head. In both fore- and hind wings, pterostigma extremely short, no RA veinlet within pterostigma; distal-most ra-rp crossvein posteriorly connecting to fourth branch of RP; 1rp-ma crossvein posteriorly connecting to anterior branch of MA; a grade series of crossveins present in branching field of RP + MA. Forewing: two radial cells (2*r* at least as long as 1*r*), two subradial cells, two discal cells, and three discoidal cells present. Hind wing: 2scp-r crossvein present (probably present also in forewing but could not be confirmed due to preservation condition); three radial cells, two subradial cells, two discal cells present.

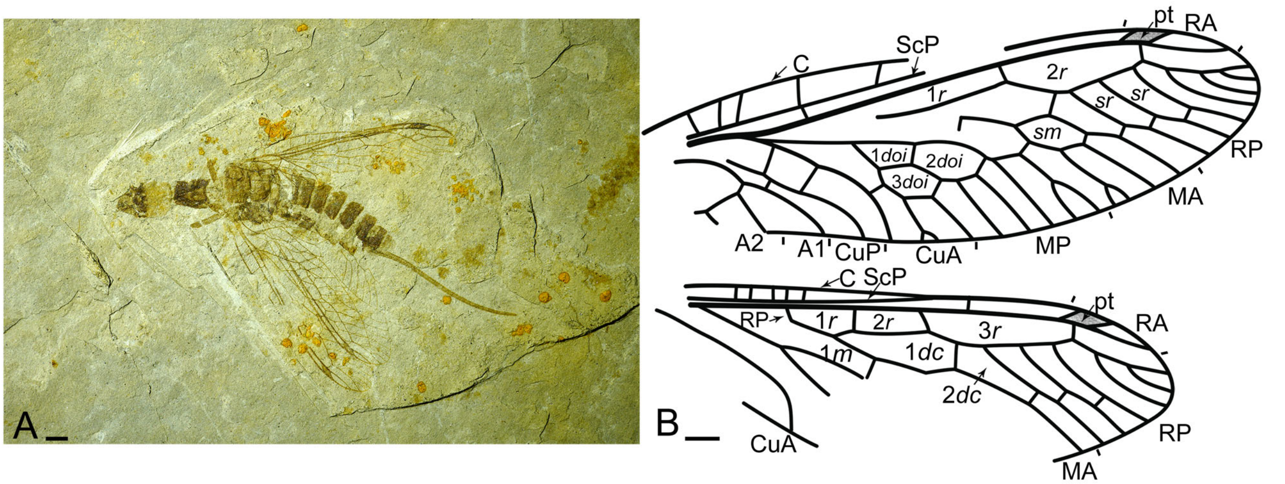

Figure 5. *Grammoraphidia ponomarenkoi* gen. et sp. nov. **A,** habitus photo of holotype CNU-RAP-LB-2017125, female, dorsal view; **B,** drawing of wing venation, holotype CNU-RAP-LB-2017125. Scale bar equals 1 mm.

Etymology. The generic name is a combination of the Greek adjective '*grammicus*' and *Raphidia*, a common genus-group name of Raphidioptera, in reference to the profusely and pectinately branched RP. Gender: feminine.

Remarks. The new genus resembles *Cretinocellia* and *Allocotoraphidia* gen. nov. in having similar crossvenation between branches of RP and MA, but it can be distinguished from the latter two genera by the extremely short pterostigma (the pterostigma are elongate in the latter two genera) and the profusely branched forewing RP with seven branches (the forewing RP has 3–4 branches in the latter two genera) (Fig. 4; Ren 1997, fig. 5). The new genus shares the extremely short pterostigma with *Proraphidia*, but it can be distinguished from the latter genus by the profusely branched RP and the presence of crossveins between branches of RP and MA (RP has 2–3 branches and no crossveins between branches of RP and MA in *Proraphidia*).

Grammoraphidia ponomarenkoi Lyu, Ren & Liu sp. nov. (Fig. 5)

Type material. Holotype: CNU-RAP-LB-2017125, a well-preserved almost complete female compressed dorsoventrally.

Diagnosis. Mostly as for the genus. Head ovoid, with dark frons and pale vertex. Pronotum dark. Pterostigma uniformly coloured.

Etymology. The new species is dedicated to the Russian palaeoentomologist Dr Alexandr G. Ponomarenko for his contribution to the taxonomy of fossil snakeflies.

Description of holotype female. Body 22.2 mm long. Head ovoid, 4.9 mm long, with dark frons and pale vertex, and with vertex nearly twice as long as eye diameter and slightly wider caudad. Ocelli present. Pronotum sub-trapezoidal, 2.6 mm long, nearly two-thirds of head length, entirely dark. Meso- plus metathorax 4.5 mm long. Only profemora observed, slender and dark.

Forewing: 18.2 mm long, 5.6 mm wide. Costal space with five crossveins preserved; ScP incomplete; RA distally trifurcated, with posterior branch continuous with RA stem; uniformly coloured pterostigma short, 1.5 mm long, present conspicuously distad termination of ScP, proximally and distally both closed by a veinlet of RA, no RA veinlet present within pterostigma; two crossveins present between RA and RP, forming two radial cells; distal-most ra-rp crossvein posteriorly connecting to fourth branch of RP; RP with seven pectinate simple branches; two crossveins present between posterior three RP branches; two rp-ma crossveins present, 1rp-ma crossvein posteriorly connecting to anterior branch of MA, forming two discal cells; MA with three branches, posterior-most branch marginally forked; one crossvein present between MA branches; crossveins in branching field of RP + MA allied into a short gradate series; two crossveins present between MA and MP, forming two medial cells; MP deeply forked, with five terminal branches and three discoidal cells; CuA trifurcated, CuP simple; A1 simple, A2 bifurcated.

Hind wing: 15.8 mm long. Costal space with at least five crossveins; ScP terminating into costal margin near wing midpoint; a scp-ra crossvein present distad termination of ScP; RA distally trifurcated, with posterior branch continuous with RA stem; uniformly coloured pterostigma short, 1.5 mm long, conspicuously distad termination of ScP present, proximally and distally both closed by a veinlet of RA, no RA veinlet present within pterostigma; three crossveins present between RA and RP, 3*r* as long as 1*r*+2*r*; distal-most ra-rp crossvein posteriorly connecting to fourth branch of RP; RP with six pectinate simple branches; two crossveins present between posterior three RP branches; two rp-ma crossveins present, 1rp-ma crossvein posteriorly connecting to anterior branch of MA, forming two discal cells; remaining part of wing largely not preserved.

Abdomen 9.9 mm long, dark except terminal segment pale. Ovipositor elongate, 13.3 mm long.

Genus ***Mesoraphidia*** Martynov, 1925

Type species. *Mesoraphidia grandis* Martynov, 1925.

Diagnosis. Medium-sized snakeflies (forewing length 7.2–18.0 mm). Head ovoid, tapering posteriad. Ocelli present. Pronotum sub-quadrate, slightly shorter than head. In both fore- and hind wings, ScP terminating at costal margin at or slightly distad to midpoint of wing; pterostigma elongate, ~0.25–0.33 times wing length, an RA veinlet usually present within pterostigma; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP. Forewing: MA stem connecting MP at initial branching point of MP; two radial cells, one discal cell, and three discoidal cells present. Hind wing: three radial cells, one discal cell, and one or two discoidal cells present.

Remarks. *Mesoraphidia*, as the type genus of Mesoraphidiidae, is the most poorly defined genus, which probably includes some heterogeneous species. Up to now, a number of taxonomic changes regarding *Mesoraphidia* have been proposed in previous studies. Engel (2002) proposed several junior synonyms (i.e. *Phiradia* Willmann, 1994, *Yanoraphidia* Ren *et al*., 1995, *Mioraphidia* Ren, 1997, *Xynoraphidia* Ren, 1997 and *Caloraphidia* Ren, 1997) with *Mesoraphidia.* Bechly & Wolf-Schwenninger (2011) transferred some *Mesoraphidia* species, i.e. *M. luzzii* Grimaldi, 2000, *M. durlstonenesis* Jepson, Coram & Jarzembowski, 2009, *M. gaoi* (Ren *et al*., 1995), *M. heteroneura* Ren, 1997, *M. mitchelli* Jepson, Coram & Jarzembowski, 2009, *M. parvula* Martynov, 1925 and *M. purbeckensis* Jepson, Coram & Jarzembowski, 2009 to the genus *Grimaldiraphidia* Bechly & Wolf-Schwenninger, 2011, which belongs to the minute snakefly tribe Nanoraphidiini. Pérez-de la Fuente *et al*. (2010, 2012) restored the combinations *Yanoraphidia gaoi* Ren, 1995, *Mesoraphidia durlstonensis* Jepson, Coram & Jarzembowski, 2009 and *Mesoraphidia heteroneura*. Lyu *et al*. (2018) described a new genus, *Stenoraphidia*, and placed *Mesoraphidia obliquivenatica* (Ren, 1994) in this genus due to its the possession of an extremely elongate head.

Here, we redefine *Mesoraphidia* by the aforementioned diagnostic characters, which are present in *M. grandis* (the type species of *Mesoraphidia*). Among the Chinese *Mesoraphidia* species from the Yixian Formation, *M. amoena* Ren, 1997, *M. heteroneura* Ren, 1997, and *M. longistigmosa* (Ren, 1994) can be surely assigned to *Mesoraphidia*. However, *M. myrioneura* (Ren, 1997) and *M. glossophylla* (Ren, 1997) respectively belong to *Alloctoraphidia* gen. nov. and *Caloraphidia* (see above). Besides, the generic placements of *M. furcivenata* Ren in Ren *et al*., 1995, *M. polyphlebia* (Ren, 1994), *M. shangyuanensis* (Ren, 1994) and *M. sinica* Ren, 1997 are currently uncertain (see Discussion). Considering the *Mesoraphidia* species from other deposits, *M. hilli* Jepson, Ansorge & Jarzembowski, 2011 from the Wealden (Lower Cretaceous) of the UK and *M. phantasma* Engel, Lim & Baek, 2006 from the Upper Cretaceous of Korea (Jinju Formation) should not belong to *Mesoraphidia* (see Discussion).

Mesoraphidia amoena Ren, 1997
(Fig. 6)

1997 *Mesoraphidia amoena* Ren: 181.

Diagnosis. Medium-sized snakeflies (body length 9.1–10.0 mm, forewing length 9.0–10.6 mm). Head ovoid, pale. Ocelli present. Antenna slightly longer than head plus prothorax. Pronotum dark. Profemur with proximal two-thirds dark but distal one-third pale, protibia entirely pale. In both fore- and hind wings, ScP terminating into C at wing midpoint, uniformly coloured pterostigma elongate, ~0.25 times wing length, with width gradually increasing distad, RA veinlet absent within pterostigma; RP with one bifurcated anterior and one simple posterior branch; MA with one simple anterior and one simple or bifurcated posterior branch, branches of MA proximally parallel to each other. Forewing: two radial cells (1*r* slightly longer than 2*r*), one discal cell and three discoidal cells present. Hind wing: three radial cells, one discal cell, and one or two discoidal cells present.

Material examined. CNU-RAP-LB-2017077c/p, a specimen compressed dorsoventrally but with abdomen

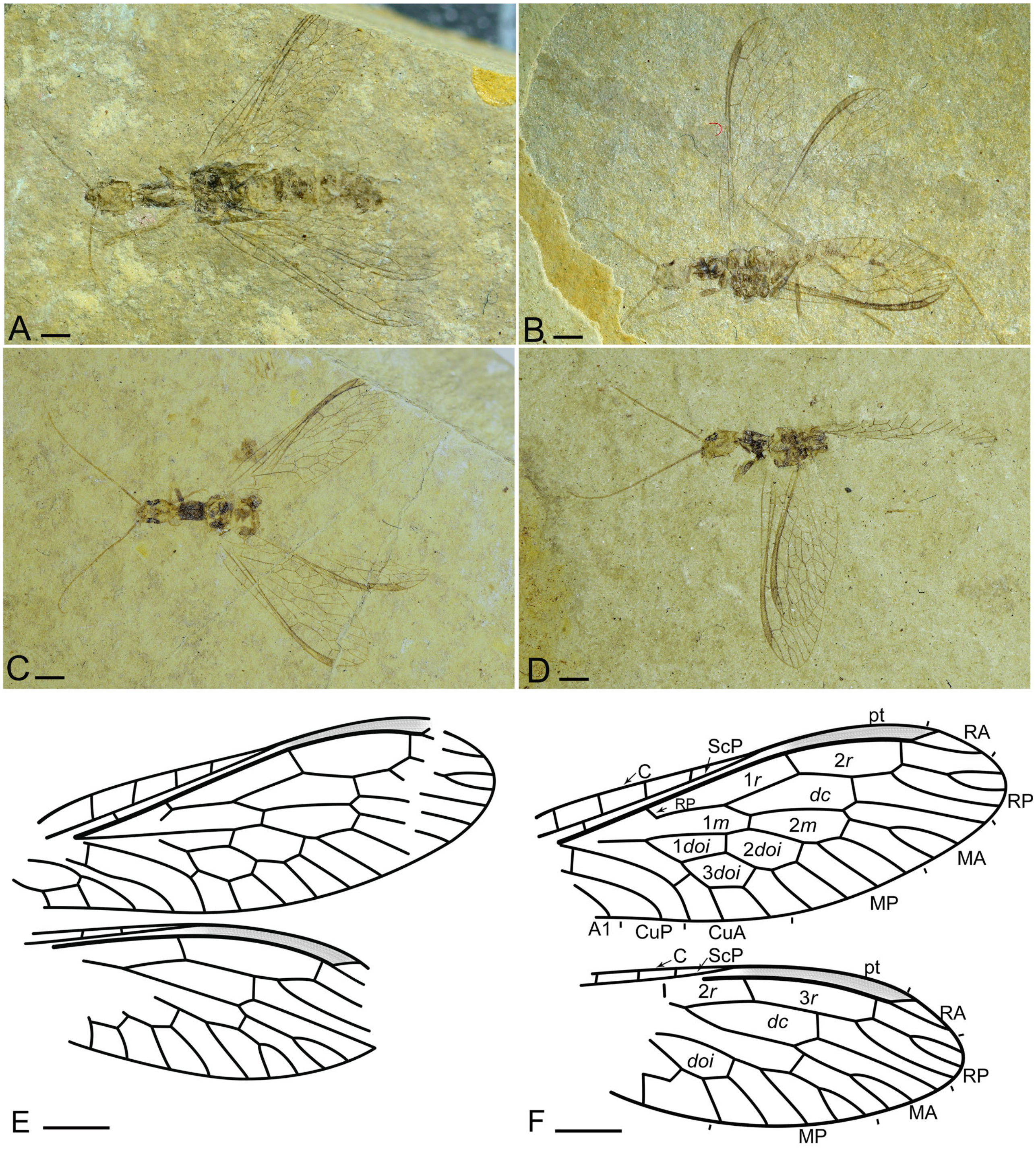

Figure 6. *Mesoraphidia amoena* Ren, 1997. **A,** habitus photo of CNU-RAP-LB-2017075, male, dorsal view; **B,** habitus photo of CNU-RAP-LB-20170110, sex unknown, dorsal view; **C,** habitus photo of CNU-RAP-LB-2017077, sex unknown, dorsal view; **D,** habitus photo of CNU-RAP-LB-2017080, sex unknown, lateral view; **E,** drawing of wing venation, CNU-RAP-LB-2017077; **F,** drawing of wing venation, CNU-RAP-LB-2017080. Scale bar equals 1 mm.

not preserved; CNU-RAP-LB-2017080c/p, a specimen compressed laterally but with abdomen not preserved; CNU-RAP-LB-2017090c/p, a well-preserved female specimen compressed laterally; CNU-RAP-LB-2017091c/p, a well-preserved female specimen compressed laterally.

Remarks. This species superficially resembles *M. heteroneura* in having a similar pale head and dark prothorax, while it differs from *M. heteroneura* by the configuration of MA (MA branches proximally parallel to each other in *M. amoena* but divergent in *M. heteroneura*). Regarding wing venation, *M. amoena* appears to be closely related to *M. sinica*, but differs from the latter by lack of the forewing 3ra-rp (forewing 3ra-rp present in *M. sinica*). However, the forewing 3ra-rp is absent in all species of *Mesoraphidia* except *M. sinica*. This crossvein might be artificial in the holotype of *M. sinica*. If so, there is a possibility that *M. amoena* and *M. sinica* are synonyms. However, we can only verify this hypothesis following examination of the holotype and additional material of *M. sinica*.

Mesoraphidia heteroneura Ren, 1997 (Fig. 7)

1997 *Mesoraphidia heteroneura* Ren: 179.

Diagnosis. Medium-sized snakeflies (body length 10.0–11.8 mm, forewing length 9.0–10.0 mm). Head ovoid, pale. Ocelli present. Antenna nearly as long as head plus pronotum. Prothorax dark. Profemur with proximal two-thirds dark but distal one-third pale, protibia entirely pale. In both fore- and hind wings, ScP terminating into C at wing midpoint, uniformly coloured pterostigma elongate, ~0.25 times wing length, with width slightly increasing distad, RA veinlet present at distal one-quarter of pterostigma; RP with one bifurcated anterior and one simple posterior branch; MA with one bifurcated anterior and one simple posterior branch, branches of MA proximally divergent. Forewing: two radial cells (1*r* nearly 1.5 times as long as 2*r*), one discal cell and three discoidal cells present. Hind wing: three radial cells, one discal cell and one discoidal cell present.

Material examined. CNU-RAP-LB-2017076, a well-preserved female specimen compressed laterally; CNU-RAP-LB-2017115, a well-preserved female specimen compressed dorsoventrally; CNU-RAP-LB-2017116, an incomplete female specimen compressed dorsoventrally, with head unpreserved; CNU-RAP-LB-2017127, an incomplete specimen compressed with only meso- and metathorax, legs and wings.

Mesoraphidia longistigmosa (Ren, 1994) (Fig. 8)

1994 *Alloraphidia longistigmosa* Ren: 133.

Diagnosis. Medium-sized snakeflies (body length 14.1 mm, forewing length 14.1–15.6 mm). Head ovoid, with dark frons and pale vertex. Ocelli present. Antenna nearly as long as head plus pronotum. Pronotum nearly twice as long as wide, entirely dark. Legs entirely dark. In both fore- and hind wings, ScP terminating into C at wing midpoint, uniformly coloured pterostigma elongate, ~0.33 times wing length, with width gradually increasing distad, an RA veinlet present at distal one-fifth of pterostigma; RP with four to five pectinate branches; MA with two branches, anterior branch simple or bifurcated, posterior branch bifurcated. Forewing: two radial cells (1*r* slightly longer than 2*r*), one discal cell and three discoidal cells present. Hind wing: three radial cells, one discal cell and one discoidal cell present.

Material examined. CNU-RAP-LB-2017072c/p, a well-preserved almost complete male compressed laterally.

Genus ***Proraphidia*** Martynova, 1947

Type species. *Proraphidia turkestanica* Martynova, 1947.

Diagnosis. Medium-sized snakeflies (body length 13.4–14.6 mm, forewing length 10.6–14.6 mm). Head ovoid, with vertex nearly as long as eye diameter and feebly tapering caudad. Pronotum slightly shorter than head. In both fore- and hind wings, ScP terminating into C at or slightly distad wing midpoint; uniformly coloured pterostigma short, proximally and distally both closed by a veinlet of RA, no RA veinlet present within pterostigma; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; rp-ma crossvein posteriorly connecting to anterior branch of MA. Forewing: two radial cells (1*r* slightly longer than 2*r*), one discal cell, two medial cells and three discoidal cells present. Hind wing: three radial cells, one discal cell, two medial cells and one or two discoidal cells present.

Remarks. This report provides the first record of this genus from the Lower Cretaceous of China. The other three species in this genus, *Proraphidia turkestanica* Martynova, 1947, *Proraphidia hopkinsi* Jepson & Jarzembowski, 2008 and *Proraphidia gomezi* Jepson & Jarzembowski, 2008, are from the Upper Jurassic of Kazakhstan and the Lower Cretaceous of England and Spain, respectively, and all of these species were described based on fossils with only fragmentary wings. *Proraphidia* is, in general, similar to *Mesoraphidia* in the shape of the head and wing venation. The short pterostigma is the only character known so far for distinguishing *Proraphidia* from *Mesoraphidia*.

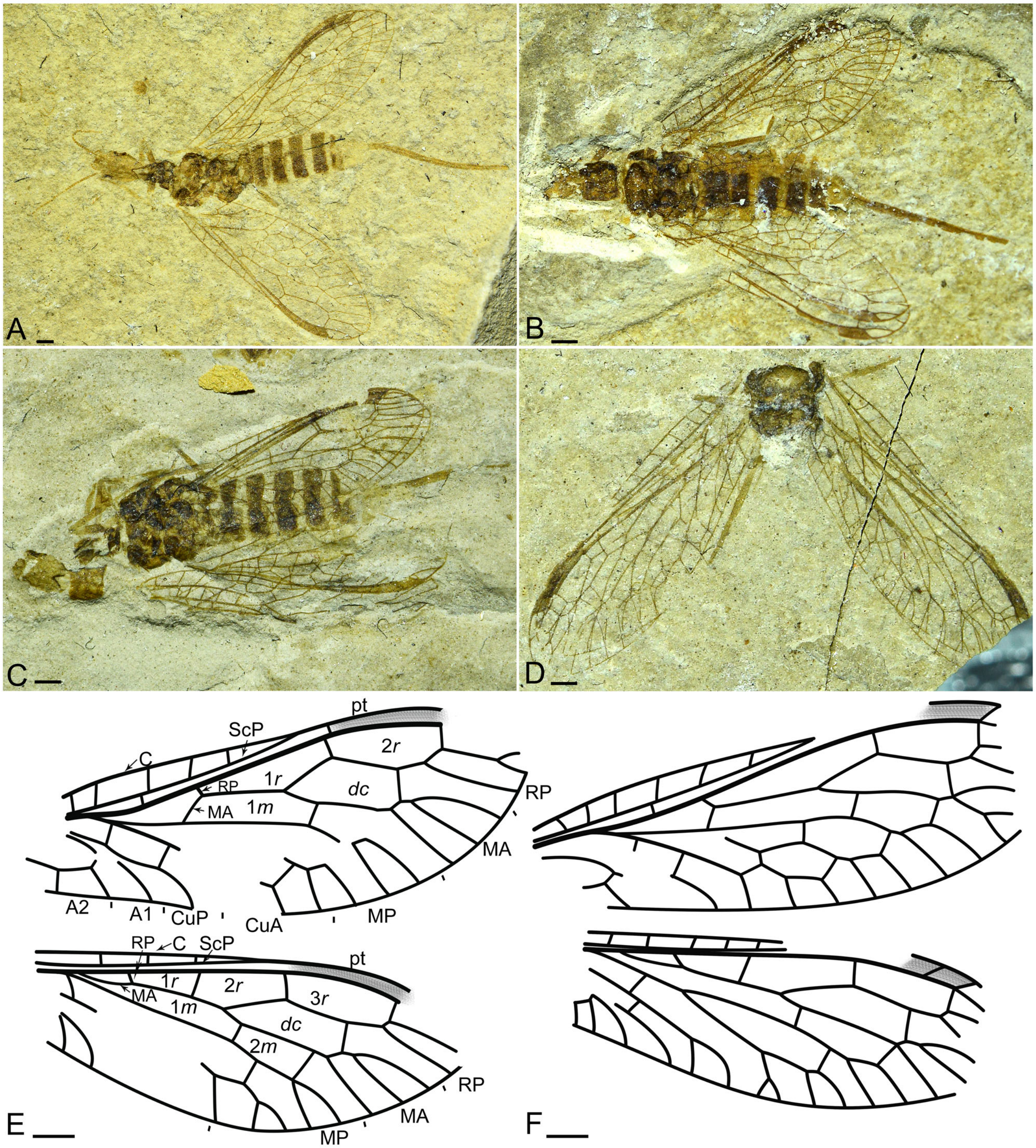

Figure 7. *Mesoraphidia heteroneura* Ren, 1997. **A,** habitus photo of CNU-RAP-LB-2017115, female, dorsal view; **B,** habitus photo of CNU-RAP-LB-2017116, female, dorsal view; **C,** habitus photo of CNU-RAP-LB-2017076, female, lateral view; **D,** habitus photo of CNU-RAP-LB-2017117, sex unknown; **E,** drawing of wing venation CNU-RAP-LB-2017116; **F,** drawing of wing venation CNU-RAP-LB-2017117. Scale bar equals 1 mm.

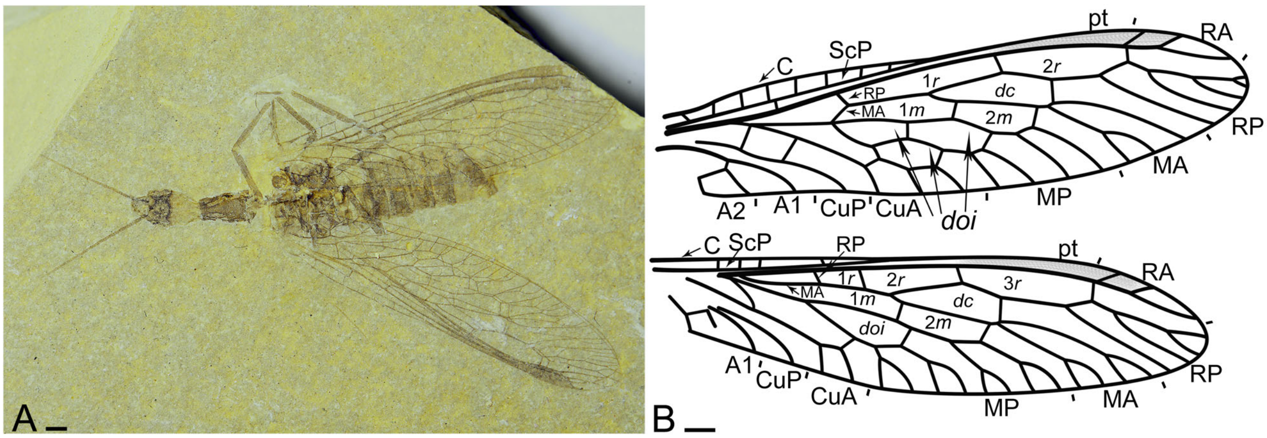

Figure 8. *Mesoraphidia longistigmosa* (Ren, 1994). **A,** habitus photo of holotype CNU-RAP-LB-2017072, female, dorsal view; **B,** drawing of wing venation, holotype CNU-RAP-LB-2017072. Scale bar equals 1 mm.

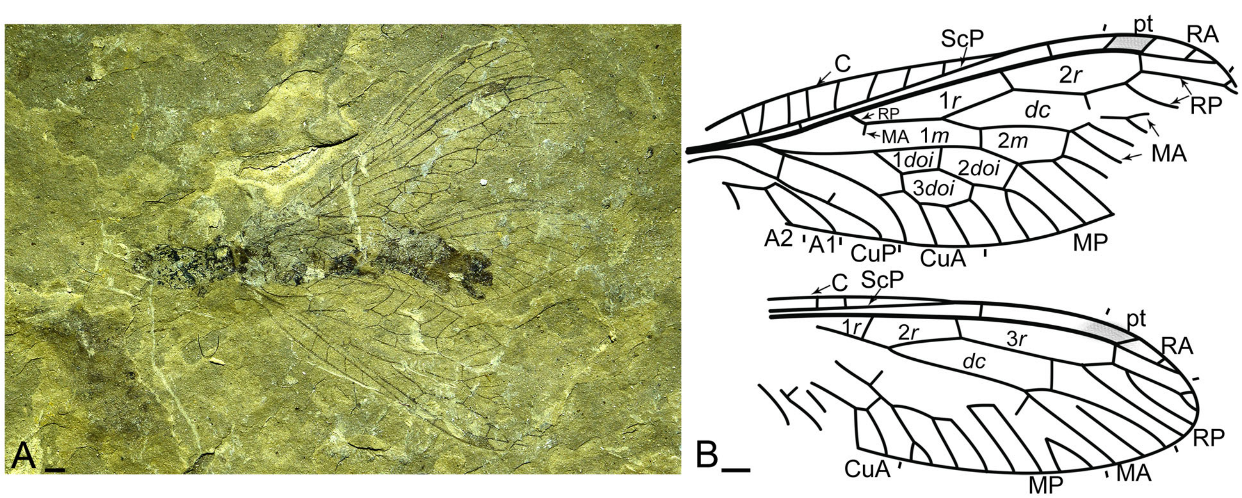

Figure 9. *Proraphidia jepsoni* sp. nov. **A,** habitus photo of holotype CNU-RAP-LB-2017102, female, dorsal view; **B,** drawing of wing venation, holotype CNU-RAP-LB-2017102. Scale bar equals 1 mm.

Proraphidia jepsoni Lyu, Ren & Liu sp. nov.
(Fig. 9)

Type material. Holotype: CNU-RAP-LB-2017102, a male specimen compressed laterally.

Diagnosis. Mostly same as for the genus. Head and pronotum entirely dark. MA with at least three long branches in both fore- and hind wings; hind wing 3*r* elongated and not distinctly widened distad.

Etymology. The new species is dedicated to the British palaeoentomologist Dr James E. Jepson for his contribution to the taxonomy of fossil Raphidioptera.

Description of holotype male. Body entirely dark, 14.6 mm long. Head ovoid, 2.9 mm long, with vertex slightly longer than eye diameter and feebly tapering caudad. Ocelli absent or not preserved. Pronotum sub-quadrate, 1.2 mm long.

Forewing: 14.6 mm long, 4.3 mm wide at widest point; costal space distinctly broadened (at widest point ~1.5 times width of pterostigma); eight costal crossveins present; ScP terminating into costal margin slightly distad to midpoint of wing; 1scp-r present at proximal one-quarter; 2scp-r present, distinctly distad termination of ScP; RA with four short branches distally, with posterior branch continuous with RA stem; uniformly coloured pterostigma short (1.5 mm long), proximally and distally both closed by an RA veinlet,

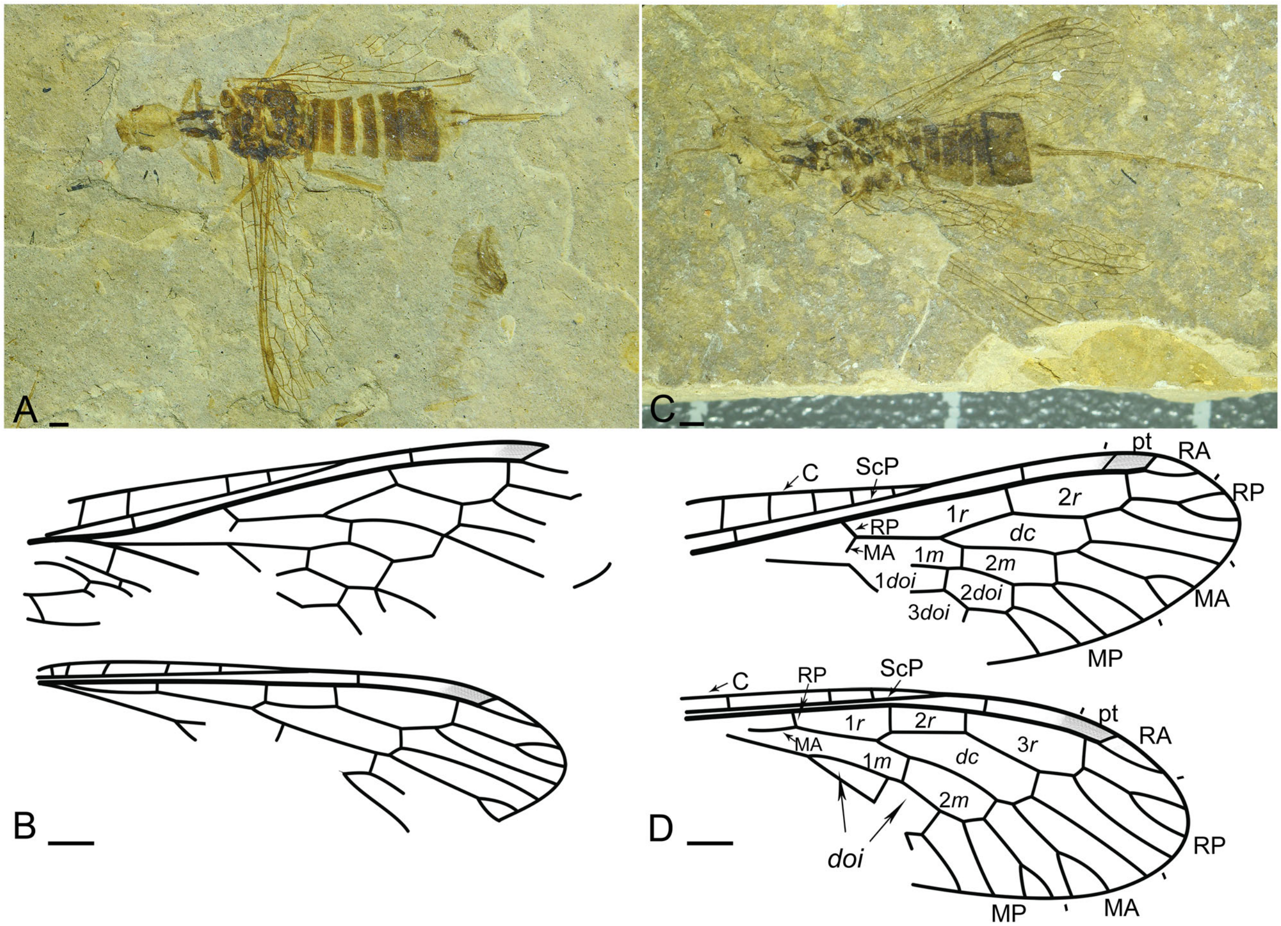

Figure 10. *Proraphidia yixianensis* sp. nov. **A,** habitus photo of holotype CNU-RAP-LB-2017114, female, dorsal view; **B,** drawing of wing venation, holotype CNU-RAP-LB-2017114; **C,** habitus photo, paratype CNU-RAP-LB-2017113, female, dorsal view; **D,** drawing of wing venation of paratype CNU-RAP-LB-2017113. Scale bar equals 1 mm.

no RA veinlet present within pterostigma; two crossveins present between RA and RP, 1*r* nearly as long as 2*r*; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; RP bifurcated, with anterior branch marginally forked; 1rp-ma crossvein posteriorly connecting to anterior branch of MA, forming a long discal cell; MA stem originating slightly proximad to initial branching point of MP, MA with at least four pectinate branches; two crossveins present between MA and MP, forming a long 1*m* and a short 2*m*; MP deeply forked, with three discoidal cells; CuA with four pectinate branches distally, CuP simple; A1 simple, A2 forked.

Hind wing 12.8 mm long, 3.8 mm wide at widest point; two costal crossveins preserved; ScP terminating into costal margin close to midpoint of wing; 2scp-r close to termination of ScP; RA distally with three short branches, posterior branch continuous with RA stem; uniformly coloured pterostigma short (1.5 mm long), distally closed by an RA veinlet, no RA veinlet present within pterostigma; two crossveins present between RA and RP, 2*r* shorter than 3*r*, which is elongated but not widened distad; 1ra-rp crossvein posteriorly connecting to stem of RP + MA; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; RP with three pectinate branches and third branch marginally forked; 1rp-ma crossvein posteriorly connecting to anterior branch of MA, forming a long discal cell; MA with three long branches; MP with eight terminal branches; CuA bifurcate.

Remarks. This new species differs from all other *Proraphidia* species by the RA terminally forked distad pterostigma in both fore- and hind wings. In the other *Proraphidia* species, the RA is terminally simple distad pterostigma. In addition, *P. jepsoni* sp. nov. differs from the contemporary species *P. yixianensis* sp. nov. by the entirely dark head, the MA with three or four long branches in both fore- and hind wings, and the hind wing

3r elongated but not widened distad. In *P. yixianensis* sp. nov., the head is entirely pale, the MA has two main branches, with the posterior branch marginally forked, and the hind wing 3r is distinctly widened distad.

Proraphidia yixianensis Lyu, Ren & Liu sp. nov. (Fig. 10)

Type material. Holotype: CNU-RAP-LB-2017113, a well-preserved almost complete female compressed dorsoventrally. Paratype: CNU-RAP-LB-2017114, a well-preserved almost complete female compressed dorsoventrally.

Diagnosis. Mostly same as for the genus. Head entirely pale; pronotum entirely dark. MA with two long branches in both fore- and hind wings, and posterior branch of MA marginally forked; hind wing 3r nearly twice as long as 2r, distinctly widened distad.

Etymology. The new species is named after the Yixian formation, from where the type specimens come.

Description. Body 13.4 mm long. Head ovoid, entirely pale, 2.7 mm long. Ocelli absent or not preserved. Prothorax slightly shorter but much narrower than head, 1.6 mm long, entirely dark. Meso- and metathorax combined 3.0 mm long, entirely dark.

Forewing: 10.6 mm long, 3.9 mm wide at widest point. Costal space with five crossveins preserved; ScP terminating into costal margin at or slightly distad to wing midpoint; 1scp-r present at proximal 1/4; 2scp-r present, distinctly distad termination of ScP; RA distally with three short branches, posterior branch continuous with RA stem; uniformly coloured pterostigma short (1.1 mm long), proximally and distally both closed by an RA veinlet, no RA veinlet present within pterostigma; two radial crossveins present between RA and RP, 1r ~1.5 times as long as 2r; 2ra-rp crossvein posteriorly connecting to anterior RP branch; RP with three branches; 1rp-ma crossvein posteriorly connecting to anterior branch of MA, forming a long discal cell; MA with two long branches, and posterior branch marginally forked; two crossveins present between MA and MP, forming two medial cells; MP deeply forked, with three discoidal cells.

Hind wing: 9.3 mm long and 3.2 mm wide at widest point. Costal space with three crossveins preserved; ScP terminating into costal margin near wing midpoint; 2scp-r present slightly distad to termination of ScP; RA distally with at least two short branches, posterior branch continuous with RA stem; uniformly coloured pterostigma short (1.1 mm long), proximally diffused, distally closed by an RA veinlet, no RA veinlet present within pterostigma; three crossveins present between RA and RP, 3r nearly twice as long as 2r, distinctly widened distad; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; RP with three pectinate branches; 1rp-ma crossvein posteriorly connecting to anterior branch of MA, forming a long discal cell; MA with anterior branch simple and posterior branches marginally forked; two crossveins present between MA and MP, forming a long and a short medial cells; MP deeply forked, with at least five branches and two discoidal cells.

Abdomen 5.9 mm long, mostly dark, but terminally pale. Ovipositor 9.0 mm long.

Description of paratype female. Body characters and wing venation almost identical to that in holotype. Additional description: body 14.4 mm long. Head 2.6 mm long. Prothorax 1.9 mm long. Meso- and metathorax combined 3.4 mm long. Legs slender, entirely pale. Forewing: 12.3 mm long; A2 bifurcate. Hind wing: 10.5 mm long, MA with stem originating from R. Abdomen 6.2 mm long.

Remarks. The new species resembles *P. gomezi* in the presence of two hind wing discoidal cells, but it can be distinguished from the latter species by the RA and MA with marginally forked branches. In *P. gomezi* all branches of RA and MA are simple.

Genus ***Siboptera*** Ponomarenko, 1993

Type species. *Siboptera eurydictyon* Ponomarenko, 1993.

Diagnosis. Large-sized snakeflies (body length 14.4–18.4 mm, forewing length 13.2–20.2 mm). Head ovoid, slightly tapering caudad. Ocelli present. Antenna nearly as long as head plus pronotum. Prothorax subquadrate, slightly shorter than head. In both fore- and hind wings, ScP terminating into C at wing midpoint; uniformly coloured pterostigma elongate, ~0.2 times wing length, with width gradually increasing distad, one RA veinlet present at distal one-third of pterostigma; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; rp-ma crossvein posteriorly connecting to anterior branch of MA. Forewing: costal space relatively broad; RP + MA separating from R near midpoint of wing; stem of MA absent; two radial cells (1r slightly shorter than 2r), one discal cell, one medial cell and three discoidal cells present. Hind wing: three radial cells, one discal cell, one medial cell and one discoidal cell present.

Remarks. *Siboptera* is one of the most distinguishable snakeflies based on the absence of the stem of forewing MA, which forms an extremely long cell (Fig. 11; Ponomarenko 1993, fig. 12; Ren 1994, fig. 2). There are

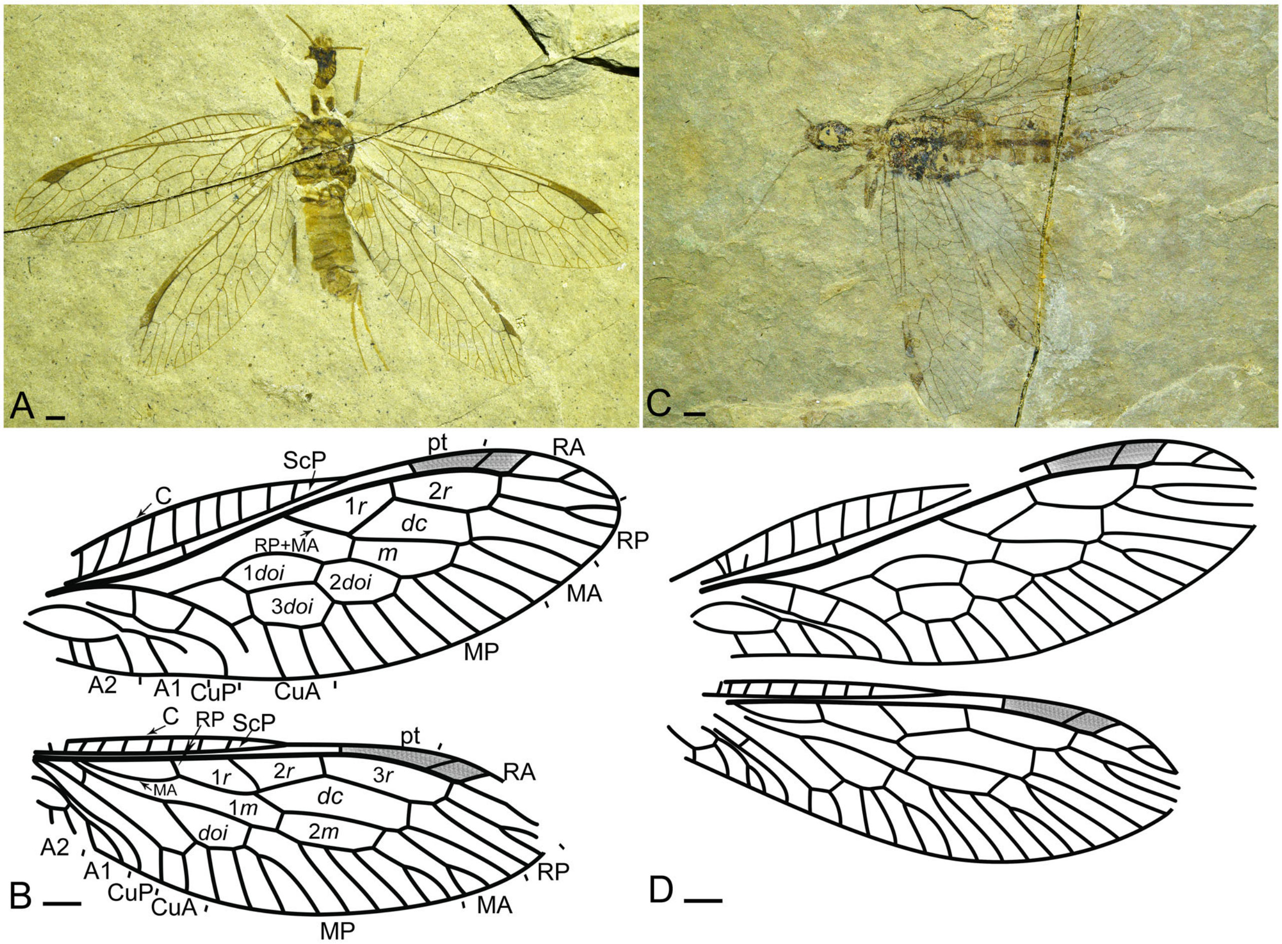

Figure 11. *Siboptera fornicata* (Ren, 1994). **A,** habitus photo of LB95108, female, dorsal view; **B,** drawing of wing venation LB95108; **C,** habitus photo of CNU-RAP-LB-2017031, female, dorsal view; **D,** drawing of wing venation, CNU-RAP-LB-2017031p. Scale bar equals 1 mm.

only two species of this genus, from the Lower Cretaceous of Russia (Baisa) and China (Beipiao), respectively.

Siboptera fornicata (Ren, 1994)
(Fig. 11)

1994 *Liaoraphidia fornicata* Ren: 133.

Diagnosis. Mostly same as for the genus. Additionally, head dark on frons and slightly paler on clypeus and vertex. Pronotum with anterior one-third pale and posterior two-thirds dark. In both fore- and hind wings, RA bifurcated distad to pterostigma. Forewing: costal space with 10 crossveins; MP and CuA with 9–10 branches running to wing margin.

Material examined. CNU-RAP-LB-2017031c/p, a well-preserved female compressed dorsoventrally; CNU-RAP-LB-2017127c/p, a well-preserved female compressed dorsoventrally; LB95108, a well-preserved female compressed dorsoventrally.

Remarks. This species differs from *S. eurydictyon* by the RA bifurcated distad to pterostigma, the forewing costal space with 10 crossveins, and the forewing MP and CuA with 9–10 branches running to wing margin. In the latter species, the RA is simple distad to pterostigma, the forewing costal space has six or seven crossveins, and the forewing MP and CuA together have six branches running to wing margin.

Genus ***Styporaphidia*** Engel & Ren, 2008

Type species. *Styporaphidia magia* Engel & Ren, 2008.

Diagnosis. Medium-sized snakeflies (body length 12.7–13.0 mm, forewing length 14.0–14.1 mm). Head ovoid, with vertex nearly as long as eye diameter and

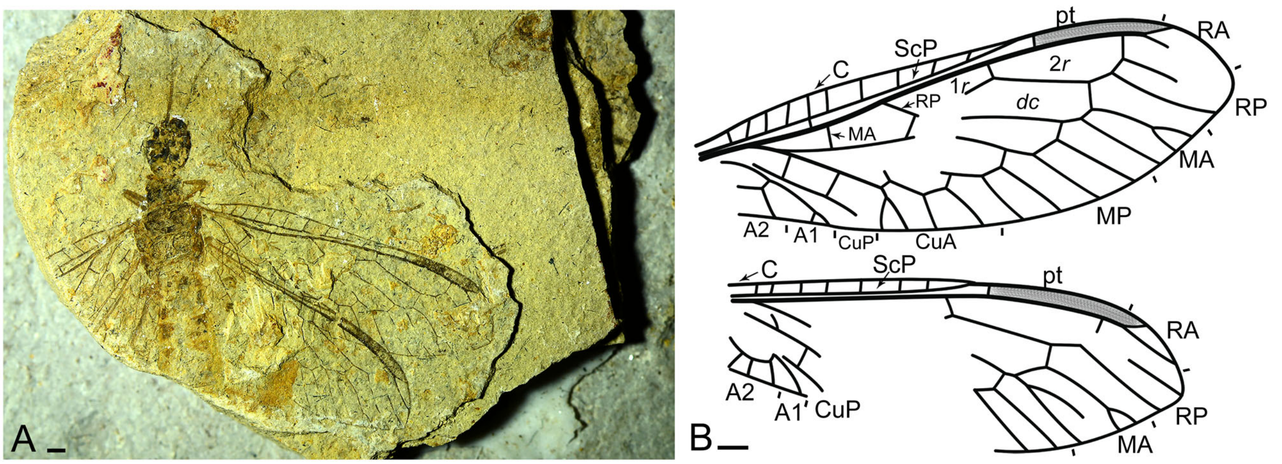

Figure 12. *Styporaphidia willmanni* sp. nov. **A,** habitus photo of CNU-RAP-LB-2017107, female, dorsal view; **B,** drawing of wing venation, CNU-RAP-LB-2017107. Scale bar equals 1 mm.

tapering caudad. Prothorax quadrate, nearly half length of head. In both fore- and hind wings, ScP terminating into C at distal one-third of wing; pterostigma elongate, ~0.25 times wing length, proximally diffused or closed by 2scp-r, two RA veinlet usually present within pterostigma; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; 1rp-ma crossvein posteriorly connecting to anterior branch of MA. Forewing: MA originating obviously proximad to initial branching point of MP and coalescent with stem of R for a short distance; 1ma-mp crossvein present between stem of RP + MA and anterior branch of MP; two or three radial cells, one discal cell, one medial cell and three discoidal cells present. Hind wing: three radial cells, one discal cell, one medial cell and three discoidal cells present.

Remarks. *Styporaphidia* was first discovered in the Middle Jurassic of China (Inner Mongolia), with the description of the type species *S. magia* Engel & Ren, 2008. Pérez-de la Fuente *et al*. (2012) described a new species from Lower Cretaceous Spanish amber and tentatively placed it in *Styporaphidia*, as *S. hispanica* Pérez-de la Fuente *et al*., 2012, although this species is known only from the distal part of a hind wing and male genitalia. Whether the important diagnostic character, i.e. the forewing MA stem connecting R and MP stem, is present in *S. hispanica* is unknown. The first record of *Styporaphidia* from the Lower Cretaceous of China is based on the following new species, which has the characteristic forewing MA.

Styporaphidia willmanni Lyu, Ren & Liu sp. nov. (Fig. 12)

Type material. Holotype: CNU-RAP-LB-2017107, a partially preserved specimen compressed dorsoventrally.

Diagnosis. Forewing: costal space with 10 crossveins present; anterior branch of MA marginally forked. Hind wing: anterior branch of MA marginally forked, posterior branch of MA deeply bifurcated.

Etymology. The new species is dedicated to Dr Rainer Willmann for his contribution to the phylogeny of fossil Raphidioptera.

Description of holotype. Preserved part of body 12.7 mm long. Head and thorax entirely dark. Head ovoid, 2.7 mm long, with vertex nearly as long as eye diameter and tapering caudad. Antenna length ~4.3 mm; flagellum with ~30 flagellomeres. Prothorax sub-quadrate, 1.4 mm long, nearly half length of head. Meso- and metathorax combined 2.8 mm long. Forelegs slender, with preserved part (partial femur and tibia) dark.

Forewing: 14.1 mm long, 4.5 mm wide at widest point; costal space narrow, costal space ~1.5 times width of pterostigma at widest point; 10 costal crossveins present; ScP terminating into costal margin at two-thirds of wing; RA distally bifurcated, with posterior branch continuous with RA stem; uniformly coloured pterostigma elongate (3.7 mm long), ~0.25 times forewing length, with nearly constant width along its entire length, proximally closed by 2scp-r, and distally ended at anterior branch of RA, no RA veinlets discernible within pterostigma; two radial crossveins present between RA and RP, 1*r* nearly slightly shorter than 2*r*; distal-most ra-rp crossvein posteriorly connecting to anterior branch of RP; RP with two long branches; 1rp-ma crossvein posteriorly connecting to anterior branch of MA; MA with stem originating proximad to initial branching point of MP and coalescent with stem of R for a short distance; two branches of MA present, nearly as long as those of RP, with posterior branch marginally forked; MP deeply forked, with five branches running to wing margin; three discoidal cells probably present; CuA trifurcated, CuP simple; A1 marginally forked.

Hind wing 11.9 mm long, 4.1 mm wide at widest point; costal space with seven crossveins; ScP terminating into costal margin slightly distad midpoint of wing; RA distally bifurcated, with posterior branch continuous with RA stem; uniformly coloured pterostigma elongate (3.7 mm long), ~0.33 times hind wing length, with nearly constant width along its entire length, proximally closed by 2scp-r, and distally ended at anterior branch of RA, no RA veinlets discernible within pterostigma; distal-most ra-rp posteriorly connecting to anterior branch of RP; RP deeply bifurcated; 1rp-ma crossvein posteriorly connecting to anterior branch of MA; MA with two long branches, anterior branch marginally forked, posterior branch deeply bifurcated. A1 simple, A2 with three pectinate short branches.

Abdomen with distal part not preserved, preserved part 5.5 mm long.

Remarks. The new species differs from *S. magia* by the forewing costal space with 10 crossveins and the MA with three or four branches running to wing margin. In *S. magia*, there are six costal crossveins in the forewing and the MA has only two branches running to wing margin. This new species is placed in *Styporaphidia* primarily based on the position of the forewing MA stem that is unique in Mesoraphidiidae. However, the presence of two RA veinlets (as in the type species of the genus) could not be found in *S. willmanni* sp. nov. This absence might be due to preservational issues as the RA veinlet within the snakefly pterostigma is often weak and unlikely to preserve well in compression fossils.

Key to genera of Mesoraphidiidae

This key includes 31 valid genera of Mesoraphidiidae except *Huaxiaraphidia*, *Jilinoraphidia* and *Sinoraphidia*, which have to be considered as doubtful genera here because of their poorly described characters and untraceable primary types. An illustrated key to the genera of Mesoraphidiidae can be found in the Supplemental material.

1. Three forewing discal cells present .... *Cretinocellia* Ponomarenko
–One or two forewing discal cells present 2

2. Pterostigma short (less than one-seventh to one-fifth of wing length), with RA veinlet within pterostigma 3
–Pterostigma elongated (more than one-quarter of wing length), otherwise, 2scp-r crossvein distinctly proximad to base of pterostigma, and RA veinlet absent within pterostigma 6

3. Two hind wing radial cells present .... *Pararaphidia* Willmann
–Three hind wing radial cells present 4

4. Forewing MA separating from M at or slightly distad to initial branching point of MP 5
–Forewing MA separating from M obviously distad to initial branching point of MP....... *Alloraphidia* Carpenter

5. 2scp-r crossvein closing pterostigma proximally .... *Yixianoraphidia* gen. nov.
–2scp-r crossvein distinctly proximad to base of pterostigma.......................... *Archeraphidia* Ponomarenko

6. Forewing length mostly >7.0 mm; pro- and mesotibiae slender 7
–Forewing length usually <6.0 mm; pro- and mesotibiae swollen 23

7. Crossveins present between RP branches as well as between MA branches in both fore- and hind wings 8
–No crossvein between RP branches as well as between MA branches in both fore- and hind wings 9

8. Forewing with seven RP branches and two radial cells .... *Grammoraphidia* gen. nov.
–Forewing with three RP branches and three radial cells .... *Allocotoraphidia* gen. nov.

9. Pterostigma divided into two parts in forewing .... *Iberoraphidia* Jepson, Ansorge & Jarzembowski
–Pterostigma not divided into two parts in forewing ... 10

10. Pterostigma short, less than one-ninth of wing length... *Proraphidia* Martynova
–Pterostigma long, more than one-quarter of wing length 11

11. Two RA veinlets present within pterostigma; stem of forewing MA connecting R and stem of MP....................................... *Styporaphidia* Engel & Ren
–Only one or no RA veinlet present within pterostigma; stem of forewing MA connecting RP or absent 12

12. Three crossveins present between RA and RP in forewing, forming three radial cells 13
–Two crossveins present between RA and RP in forewing, forming two radial cells 14

13. Forewing MA separating from M near initial branching point of MP; two discal cells and three medial cells present in forewing................... *Kezuoraphidia* Willmann

–Forewing MA separating from M obviously distad to initial branching point of MP; a single discal cell and two medial cells present in forewing .... *Xuraphidia* Hong

14. Forewing RA simple .... *Yanoraphidia* Ren
–Forewing RA distally at least bifurcated.................... 15

1RA veinlet within pterostigma sinuate..... *Necroraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel
–RA veinlet within pterostigma straight if present 16

16.Hind wing MA originating from M....... *Baisoraphidia* Ponomarenko
–Hind wing MA originating from R 17

17. Occiput extremely elongate, nearly half length of head .... *Stenoraphidia* Lyu, Ren & Liu
–Occiput very short and inconspicuous........................ 18

18. Forewing RP + MA separating from R at midpoint of wing; stem of forewing MA absent .... *Siboptera* Ponomarenko
–Forewing RP + MA separating from R at proximal one-third of wing; stem of forewing MA present 19

19. Hind wing with three discoidal cells 20
–Hind wing with one or two discoidal cells 21

20. Head slightly narrower than prothorax; forewing ScP terminating at costal margin distad to midpoint of wing .... *Caloraphidia* Ren stat. rest.
–Head much wider than prothorax; forewing ScP terminating at costal margin slightly proximad to midpoint of wing .... *Phiradia* Willmann stat. rest.

21. Forewing MA separating from M obviously proximad to initial branching point of MP .....*Beipiaoraphidia* gen. nov.
–Forewing MA separating from M near initial branching point of MP .... *Ororaphidia* Engel & Ren or *Mesoraphidia* Martynov

22. Diameter of compound eye shorter than or equal to length of vertex; antenna with a low number of flagellomeres ($\leq$30) 24
–Diameter of compound eye longer than length of vertex; antenna with a high number of flagellomeres ($\geq$38) 27

23. Metatibia without a process at its midpoint......... 25
–Metatibia with a process at its midpoint. .... *Cantabroraphidia* Pérez-de la Fuente, Nel, Peñalver & Delclòs

24. Forewing with one or two discoidal cells 26
–Forewing with three discoidal cells .... *Grimaldiraphidia* Bechly & Wolf-Schwenninger

25. Ocelli present between posterior half of compound eyes .... *Nanoraphidia* Engel
–Ocelli present between anterior half of compound eyes.. *Amarantoraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel

26. All tibiae swollen 28
–Pro- and mesotibiae swollen, but metatibiae slender.. 30

27. Antenna moderately elongate, with ~40 flagellomeres 29
–Antenna extremely elongate, with >100 flagellomeres............. *Dolichoraphidia* Liu, Lu & Zhang

28. Ocelli present; bilobed extensions of tarsomere 3 with distal digitiform processes.................*Alavaraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel
–Ocelli absent; bilobed extensions of tarsomere 3 without distal digitiform processes. *Rhynchoraphidia* Liu, Lu & Zhang

29. Pterostigma proximally diffused, with an incorporated RA veinlet .... *Burmoraphidia* Liu, Lu & Zhang
–Pterostigma proximally closed by 2scp-r crossvein, incorporated RA veinlet absent... *Lebanoraphidia* Bechly & Wolf-Schwenninger

Phylogenetic analysis

The phylogenetic analysis using TNT yielded 70 most parsimonious trees (MPTs) (length = 90 steps, consistency index = 0.53, retention index = 0.76). The strict consensus tree of all MPTs is shown in Figure 13. All genera of Mesoraphidiidae were found to form a monophylum supported by the following synapomorphies: the forewing MP with stem sub-equal to or longer than length of 1*doi* (char. 26:1) and the presence of two forewing *doi* (char. 29:2). Within Mesoraphidiidae, *Cretinocellia*, *Allocotoraphidia* gen. nov., *Kezuoraphidia* and *Xuraphidia* were identified as early diverging genera. *Cretinocellia* was recovered to be the sister group of all remaining mesoraphidiid genera, and the latter monophyletic group was supported by the long pterostigma (char. 13:2). In the latter monophyletic group, all genera except *Allocotoraphidia* gen. nov. formed a monophylum based on the absence of forewing subradial cells (char. 20:1). The mesoraphidiid genera except the above four basal genera formed a monophyletic group supported by the presence of RA veinlets within forewing pterostigma (char. 14:0) and two forewing radial cells (char. 19:2). The intergeneric relationships within this group were poorly resolved. *Grammoraphidia* gen. nov. and *Proraphidia* were clustered with genera in Alloraphidiinae (i.e. *Alloraphidia*, *Archeraphidia*, *Pararaphidia* and *Yixianoraphidia* gen. nov.) and the monophyly of this clade is supported by

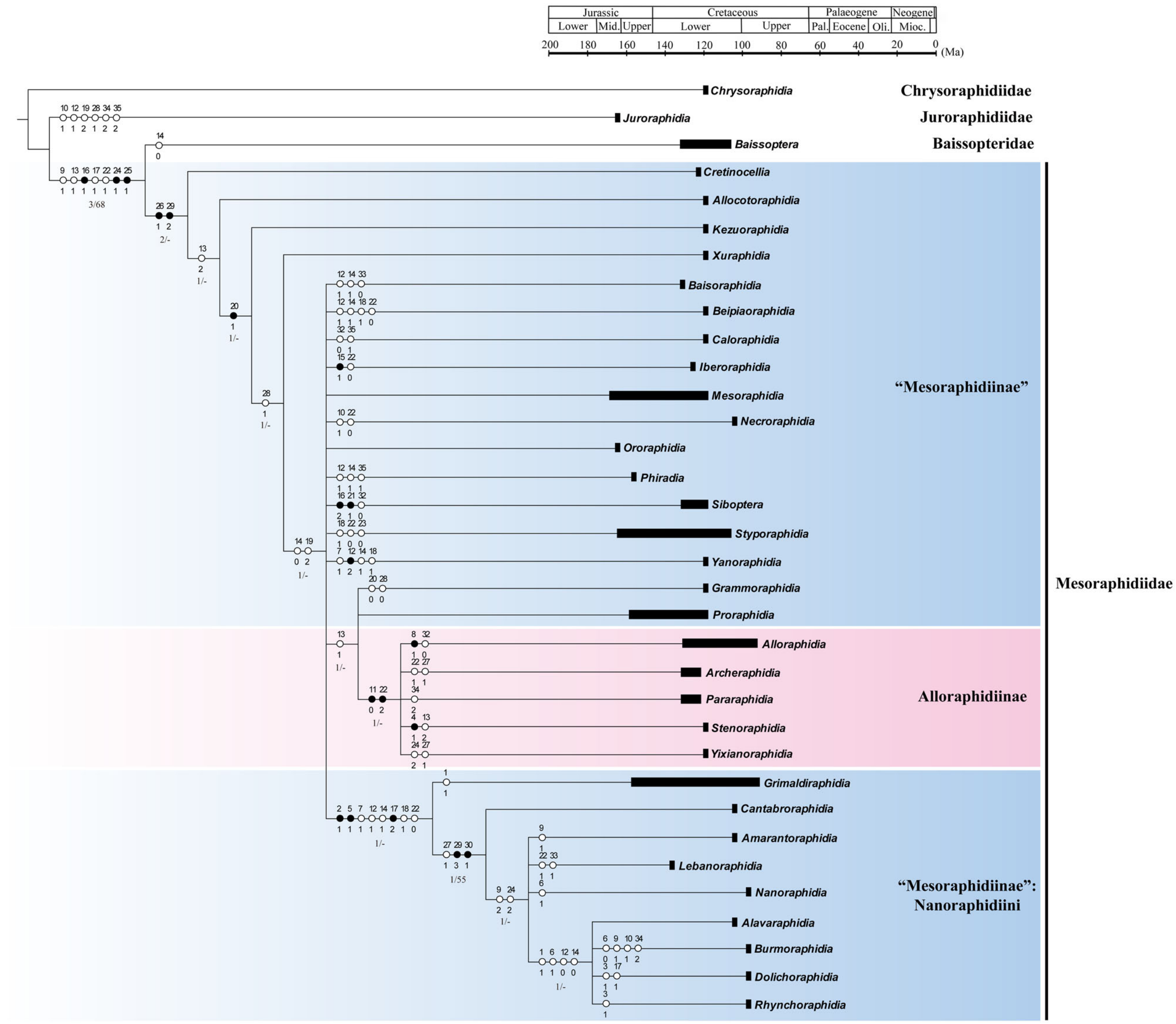

Figure 13. Phylogeny of Mesoraphidiidae. Topology represents the strict consensus tree of the 70 most parsimonious trees recovered from TNT. Unambiguous morphological character states are shown on the tree with a black circle as the homologous state and a white circle as the homoplasious state. Bremer support values/bootstrap values are shown at relevant nodes. Black bar indicates the geological range of the fossil genus.

the relatively short forewing pterostigma (char. 13:1). *Stenoraphidia* was recovered within Alloraphidiinae, whose monophyly was supported by a forewing with 2scp-r approximating RA1 (char. 11:0) and the stem of forewing MA diverged from M distinctly distad from the initial branching point of MP (char. 22:2). The monophyly of the tribe Nanoraphidiini was also recovered with a number of synapomorphic characters, i.e. the compound eye longer than one-third of the head length (char. 2:1), the pro- and mesotibiae swollen (char. 5:1), the forewing length shorter than 6 mm (char. 7:1), the forewing RA bifurcated (char. 12:1), the absence of RA veinlets in pterostigma (char. 14:1), the forewing RP initially branched at the very distal portion of wing (char. 17:2), the forewing RP bifurcated (char. 18:1), and the stem of forewing MA diverged from M proximad to the initial branching point of MP (char. 22:0).

Discussion

The systematic revision of the mesoraphidiids from the Yixian Formation presented here and our phylogenetic analysis of the mesoraphidiid genera provide new evidence to clarify the classification and phylogeny of Mesoraphidiidae. By comprehensive comparison of external morphological characters, a number of characters are found to be useful in distinguishing mesoraphidiid genera, including the shape of head, the configuration of the pterostigma (e.g. length, number of incorporated RA veinlets, presence/absence and position of 2scp-r closing pterostigma, *etc*.), the position of the forewing MA stem, the number of radial, discal and discoidal cells in both fore- and hind wings, the presence/absence of subradial crossveins, and the presence/absence of distal fusion between the forewing MP and CuA (see more discussion in the character list provided for the phylogenetic analysis; Supplementary material) (Willmann 1994; Liu *et al.* 2009, 2014, 2018; Bechly & Wolf-Schwenninger 2011).

Our result corroborates the monophyly of Alloraphidiinae, as previously proposed by Bechly & Wolf-Schwenninger (2011). Autapomorphies of this subfamily comprise the forewing with 2scp-r approximating RA1 and the stem of forewing MA diverging from MP distinctly distad to the initial branching point of MP. However, the apparent triadic branching of R, M and CuA in the forewing proposed as a synapomorphy for Alloraphidiinae by Bechly & Wolf-Schwenninger (2011) was not recovered to support the monophyly of this subfamily as this character state is present in many mesoraphidiid genera outside Alloraphidiinae. The relationships among the genera within Alloraphidiinae were not resolved in the present analysis. Nevertheless, the separation of *A. anomala* from *Alloraphidia* is justified and consistent with the hypothesis in Makarkin & Khramov (2015) based on the broad wings, the longer ScP, and the distal fusion between forewing MP and CuA in *Yixianoraphidia* gen. nov.

Our results also support the monophyly of Nanoraphidiini, which was originally established by Bechly & Wolf-Schwenninger (2011). Most autapomorphies of this tribe proposed by Bechly & Wolf-Schwenninger (2011), except the long pterostigma, were also found herein to support the monophyly of this tribe, although some of them are interpreted in an alternative way. The long pterostigma is certainly not an autapomorphy of this tribe as this character state is widely present in various lineages of Mesoraphidiidae. However, the sister group of Nanoraphidiini is still unknown, and the placement of this tribe in Mesoraphidiinae (monophyly of this subfamily was not recovered herein) was not recovered in our analysis. Within Nanoraphidiini, *Grimaldiraphidia* was assigned to be the sister group of the clade comprising the remaining genera of this tribe. Compared with the other genera of Nanoraphidiini, *Grimaldiraphidia* possesses more plesiomorphic characters, especially the presence of three forewing discoidal cells that are arranged triangularly. It could be possible to further investigate the relationships among these genera in the future because these genera are known as amber specimens, in which more characters other than wing characters (e.g. genital characters) could be preserved and will be helpful for the phylogenetic analysis.

The other mesoraphidiid genera beyond the above two monophyletic groups have poorly resolved phylogenetic relationships. This is due to the limit of phylogenetically informative characters among these genera. Nevertheless, we corroborated the mesoraphidiid affinity of *Cretinocellia*, which was transferred from Baissopteridae into Mesoraphidiidae based on the typical triangular arrangement of three forewing discoidal cells by Bechly & Wolf-Schwenninger (2011). The presence of a long stem of the forewing M also supports the placement of *Cretinocellia* in Mesoraphidiidae. So far, this genus represents the basal-most lineage of Mesoraphidiidae. Additionally, by having three forewing radial cells or subradial cells, *Allocotoraphidia* gen. nov., *Kezuoraphidia* and *Xuraphidia* also have relatively basal positions in Mesoraphidiidae. However, despite the presence of forewing subradial cells, *Grammoraphidia* gen. nov., together with *Proraphidia*, were recovered to be closely related to Alloraphidiinae. Accordingly, Mesoraphidiinae turns out to be paraphyletic.

Based on the present revision, there are 13 genera and 21 species of Mesoraphidiidae from the Lower Cretaceous Yixian Formation. Among them, there are only three species of two genera that belong to the subfamily Alloraphidiinae, and there are no species of Nanoraphidiini. So far, 10 genera and 14 species have been confirmed to be valid by the present work and Lyu *et al*. (2018). However, the identity of the following genera and species are still unclear: *Kezuoraphidia*, *Xuraphidia*, *Yanoraphidia*, *Mesoraphidia furcivenata* Ren, 1995, *M. polyphlebia* (Ren, 1994), *M. shangyuanensis* (Ren, 1994) and *M. sinica*. In *Kezuoraphidia* and *Xuraphidia*, the presence of a ra-rp crossvein near the branching point between forewing RP and MA is very peculiar and only known in these two genera (see Hong 1992b, figs 3, 4; Willmann 1994, fig. 5). After checking the photograph of the holotype of *K. kezuoensis* presented by Hong (1992b, pls 1–4), we could not find this crossvein. Besides, in this photograph, we also could not find the additional crossveins between forewing RP and MA and between MA and MP (considered a diagnostic feature of *Kezuoraphidia* by Willmann [1994]). *Yanoraphidia* is characterized by the simple forewing RA (see Ren *et al*. 1995, fig. 3-59), which, however, is probably due to poor preservation of the distal part of RA, because in all the other species of Raphidioptera the forewing RA is at least bifurcated. Irrespective of this feature, the other wing venational characters as well as the small size (forewing length 5.0 mm) indicate a close relationship between *Yanoraphidia* and *Grimaldiraphidia*, as proposed in Bechly & Wolf-Schwenninger (2011). *Mesoraphidia furcivenata* has four crossveins between the main branches of the forewing MP (see Ren *et al*. 1995, fig. 3-58), but this feature is very strange and has never been found in Mesoraphidiidae. It cannot be excluded that this feature is attributed to incorrect drawing so re-examination of the primary type is required for confirmation. *Mesoraphidia polyphlebia* resembles *M. longistigmosa* but differs from the latter species in having an RP with five branches in both fore- and hind wings, and by the hind wing 1ra-rp posteriorly connecting to RP but not the stem of RP + MA. In the original description of *M. longistigmosa* (Ren 1994), the forewing and hind wing RP both have four branches. But, in the additional fossil of this species examined herein, there is a short marginal branch of the fourth forewing RP branch (see Fig. 8). Thus, the presence of only one more RP branch is not a reliable character for distinguishing species. The presence of a hind wing 1ra-rp posteriorly connecting to the RP in *M. polyphlebia* is also doubtful as the hind wing 1ra-rp is always posteriorly connected with the stem of RP + MA in all other mesoraphidiids. Therefore, it is possible that *M. polyphlebia* is a synonym of *M. longistigmosa*. The identity of *M. shangyuanensis* was previously discussed in Lyu *et al*. (2018), assuming the placement of this species in *Stenoraphidia*. *Mesoraphidia sinica* has three forewing ra-rp crossveins (see Ren 1997, fig. 7), while in the other *Mesoraphidia* species there are only two ra-rp crossveins in the forewing. If this species truly has this feature, it should be moved out of *Mesoraphidia*. Otherwise, it may be a synonym of *M. amoena* as these two species are almost identical in size and wing venation irrespective of the presence/absence of forewing 3ra-rp.

Besides the above-mentioned doubtful mesoraphidiid genera and species from the Lower Cretaceous Yixian Formation, the identities of *Huaxiaraphidia*, *Jilinoraphidia* and *Sinoraphidia* from the Lower Cretaceous of northern China are also unclear. Unfortunately, as the original illustrations of these three genera have many incorrectly drawn veins (see Hong 1982, 1992a; Hong & Chang 1989), we refrain from giving any assessment of their affinities until such time we can check the primary types. Nevertheless, it is clear that all of the new genera described herein greatly differ from these three problematic genera.

Based on our proposed morphological criteria to distinguish the mesoraphidiid genera (see Systematic palaeontology, above), we suggest taxonomic changes concerning several Cretaceous species of *Alloraphidia* and *Mesoraphidia* from other countries of Asia and Europe. However, any formal taxonomic treatments have to be made after the re-examination of the primary types and additional conspecific fossils of these species. First, we agree with Makarkin & Khramov (2015) that *Alloraphidia petrosa* Ponomarenko, 1988 from the Lower Cretaceous of Mongolia and *Alloraphidia asiatica* Ponomarenko, 1993 from the Lower Cretaceous of Russia do not belong to *Alloraphidia*. The former species has only two forewing discoidal cells and long distal fusion between forewing MP and CuA, while the latter species has broad wings, long ScP, and short distal fusion between the forewing MP and CuA. None of these characters are in the generic diagnosis of *Alloraphidia*. These species may represent two different genera of Alloraphidiinae.

Mesoraphidia hilli Jepson, Ansorge & Jarzembowski, 2011 from the Lower Cretaceous of England, which is known from only two pieces of hind wing, appears to be quite different from the type species as well as many other species of *Mesoraphidia* due to its short pterostigma. Notably, the distal-most subcostal crossvein is closer to the RA veinlet within the pterostigma in *M. hilli* (distantly separate from the pterostigmal RA veinlet in the typical *Mesoraphidia* species), while this feature is shared with Alloraphidiinae. Thus, *M. hilli* should be moved out of *Mesoraphidia* and may be placed in Alloraphidiinae. *Mesoraphidia phantasma* Engel, Lim & Baek, 2006 from the Lower Cretaceous of Korea has four radial crossveins in the forewing and a very short stem of M (see Engel *et al*. 2006, fig. 5). Both characters are absent in all other species of Mesoraphidiidae but are widely present in Baissopteridae (see Lyu *et al*. 2017). Therefore, it is highly likely that *M. phantasma* actually belongs to Baissopteridae.

Finally, returning to the question of whether Mesoraphidiidae is a monophyletic group, our results suggest that all genera presently placed in Mesoraphidiidae belong to the same monophylum. However, the present sampling does not include any species of Metaraphidiidae or the two extant families, i.e. Inocelliidae and Raphidiidae. *Metaraphidia*, as the type and only genus of Metaraphidiidae, with two species respectively from the Lower Jurassic of England and Germany, was originally placed in Mesoraphidiidae (Whalley 1985), but transferred to Metaraphidiidae by Bechly & Wolf-Schwenninger (2011). Bechly & Wolf-

Schwenninger (2011) considered the absence of crossveins between forewing CuA and CuP an autapomorphy of Metaraphidiidae and that this family was close to Inocelliidae and Raphidiidae due to possession of a stem of the hind wing MA that is proximally fused with MP. However, the former character is very doubtful, and Makarkin & Archibald (2014) mentioned that it may be due to poor preservation. The latter character is actually a plesiomorphic condition and also present in some genera of Mesoraphidiidae (see Liu *et al*. 2016). Liu *et al*. (2014) recovered a sister-group relationship between Mesoraphidiidae and Metaraphidiidae although the sampling in that phylogenetic analysis is very limited.

Inocelliidae and Raphidiidae were claimed to be more closely related to different taxa of Mesoraphidiidae than to each other due to some shared wing characters (Ren & Hong 1994; Makarkin & Archibald 2014). If so, phylogenetically, Inocelliidae and Raphidiidae should be nested within Mesoraphidiidae. Recent divergence time estimates based on genomic data (Wang *et al*. 2017; Winterton *et al*. 2018) dated the divergence between Inocelliidae and Raphidiidae back to the Mesozoic, which is rather earlier than the oldest fossil records of these two families (both from the Eocene) (Makarkin & Archibald 2014; Makarkin *et al*. 2019). Thus, the hypothesis proposed in Makarkin & Archibald (2014) is reasonable and consistent with the molecular evidence as the common ancestors of Inocelliidae and Raphidiidae might have diverged respectively from Mesozoic snakefly lineages. However, to critically test the above hypotheses based on phylogenetic analysis, more comprehensive sampling, including all above relevant taxa as well as more genera of Baissopteridae, is needed. Moreover, additional characters, especially genital characters, have to be included in future analysis as the presently available wing characters are insufficient to effectively resolve their phylogenetic relationships. Although the genital characters are rarely visible in compression fossils of snakeflies, it is promising to explore more genital characters of extinct Mesozoic snakeflies from amber specimens (see exemplar in Liu *et al*. 2016).

Conclusions

The present description and re-description of 12 species in nine genera of Mesoraphidiidae from the Lower Cretaceous Yixian Formation of north-eastern China enriches our knowledge of this extinct snakefly family. More importantly, this work comprehensively summarizes the morphological characters that are useful for distinguishing mesoraphidiid genera and that are informative for phylogenetic analysis. Accordingly, we performed the first phylogenetic analysis based on a comprehensive sampling of known mesoraphidiid genera and discussed the identity and systematic position of a number of mesoraphidiid taxa. Our results indicate that wing characters are not sufficient to resolve the intergeneric relationships of Mesoraphidiidae, although they are useful for distinguishing genera. Before further phylogenetic study of Mesoraphidiidae is conducted, future works should focus on two aspects: (1) revisions of described mesoraphidiid taxa based on re-examination of the primary types; and (2) systematic and morphological study of Cretaceous amber snakeflies.

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Supplementary material

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