



A puzzling Cretaceous psyllid-type forewing from the South of China

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Abstract

The new taxon *Fujianella paradoxa* **gen. et sp. nov.** is described and illustrated from the Early Cretaceous Bantou Formation, in Yong'an County, Fujian Province, southeastern China. It is placed in the insect suborder Sternorrhyncha (Hemiptera) but left unassigned to any family at present due to its controversial features. This fossil record represents the second psyllid-looking taxon reported from the Cretaceous of China, found mainly in the Jurassic. This discovery further showcases the similarities in entomofauna between the Middle Jurassic Yanliao biota in the North of China and the Early Cretaceous in the South of China.

Key words: fossil insect, Hemiptera, Psylliformes, Cretaceous, Aptian–Albian, Bantou Formation

Introduction

The Sternorrhyncha are a group of minuscule insects, encompassing around 19,000 described extant and extinct species. They are sucking-type pests feeding on phloem sap, some being notorious for causing major economic damages in the field of agriculture globally. Johnson *et al.* (2018) investigated the phylogenetic relationships between the orders Hemiptera, Thysanoptera, and Psocodea based on molecular analysis calibrated with fossils. They recovered the Sternorrhyncha as the sister taxon to all remaining hemipterans and inferred radiations within the suborder have begun in the late Carboniferous. On the other hand, the relationships between that different sternorrhynchan lineages remain a subject of investigation, particularly when fossils are considered (Drohojowska *et al.* 2020b).

Cretaceous taxa attributed to Psylloidea mainly belong to family Liadopsyllidae, widely reported, i.e., Lebanon, Mongolia, Myanmar, Russia, and the USA (Drohojowska *et al.* 2020a: table 1). These fossils are collected as both compressions and amber inclusions. Psylloidea discovered from China are very scarce and include only one valid record from the Cenozoic: *Cacopsylla trigona* Zhang, Luo, Yao & Ren, 2019 assigned to the Psyllidae from the Miocene. To date, there are no representatives of the family Liadopsyllidae from China.

Cretaceous taxa attributed to Protopsyllidoidea are also widely reported, i.e., China, England, Lebanon, Mongolia, Myanmar and USA (Handlirsch 1939; Shcherbakov, 1988; Grimaldi, 2003; Drohojowska *et al.* 2013, 2022; Hakim *et al.* 2019, 2021, 2022, 2023). These fossils are also collected as both compressions and amber inclusions, although mostly recorded from the latter. Described fossil taxa of the family Protopsyllidoidea are rather few from Chinese localities, with a total of three genera and six species collected from the Middle Jurassic Haifanggou and Yan'an formations in the North of China (Table 1). Other taxa assigned to the superfamily Protopsyllidoidea include the species *Parapropsyllidium shouchangense* Hakim & Huang, 2023 from the Cretaceous Shouchang Formation which was placed in the family Parapropsyllidoidea (Hakim *et al.* 2023) and the species *Triassopsyllidiida pectinata* Huang, Hakim, Fu & Nel, 2022 from the Triassic Yanchang Formation which was tentatively placed in the family Permopsyllidoidea (Huang *et al.* 2022). Xu *et al.* (2023) further mentioned undescribed records of Protopsyllidoidea from the Jurassic Yangshuzhuang Formation and Daohugou bed, illustrated in Xiu *et al.* (2003: fig. 16-1), Zhang (2003: fig. 46-2) and Huang (2016: fig. 5-57).

Herein, we describe *Fujianella paradoxa* **gen. et sp. nov.** from the Early Cretaceous Bantou Formation, as the second record of a psyllid-like sternorhynchan—aside from *Paraprotopsyllidium shouchangense*—reported from the Cretaceous in the Southeast of China.

TABLE 1. List of Jurassic protopsyllidiid taxa from China.

Species	Type locality
<i>Poljanka curticapillata</i> Lü, Luo & Yao, 2023	Daohugou, Inner Mongolia (Haifanggou Formation)
<i>Poljanka hirsuta</i> Yang, Yao & Ren, 2012	Daohugou, Inner Mongolia (Haifanggou Formation)
<i>Poljanka strigosa</i> Yang, Yao & Ren, 2013	Daohugou, Inner Mongolia (Haifanggou Formation)
<i>Sinopsocus oligovenus</i> Lin, 1976	Beipiao, West Liaoning Province (Haifanggou Formation)
<i>Sinopsocus yananensis</i> Xu, Hakim & Huang, 2023	near Peizhuang Village, Yan'an, Shaanxi Province (Yan'an Formation)
<i>Subaphidulum sinica</i> Xu, Hakim & Huang, 2023	near Peizhuang Village, Yan'an, Shaanxi Province (Yan'an Formation)

Material and methods

The type material was collected from the Lower Cretaceous Bantou Formation at a locality near the Jishan Village, Yong'an City, Fujian Province, SE China. The age of the Bantou Formation has been debated by different authors. There are three major opinions: 1) the Late Jurassic; 2) the Barremian of Early Cretaceous; 3) the Aptian to Albian of Early Cretaceous (Cao *et al.* 1990). The biostratigraphic correlation indicates the fossil assemblage of the Bantou Formation is clearly younger than those from the Shouchang Formation of Zhejiang Province (Cao *et al.*; Chen 1990). Isotopic dating reveals U-Pb zircon ages are 144 ± 2 Ma and 116 ± 2 Ma from lower parts of the Bantou Formation at Yong'an (with present fossil locality) and Chong'an basins respectively (Hu *et al.* 2011). An Aptian–Albian age of the Bantou Formation may be supported by integrated biostratigraphic and isotopic analyses whereas the zircons for 144 ± 2 Ma would be recycled. The age of the Bantou Formation is close to that of the Lushangfen–Xiazhuang Formation in West Beijing, Shahaifuxin Formation in West Liaoning, and Guantou Formation in Zhejiang.

The specimen was examined and photographed with a Zeiss AxioZoom V16 stereomicroscope. Photographs were stacked using Helicon Focus 6 software. The line drawing and photographs were processed into plates using Adobe Photoshop CC 2019 software. The holotype is deposited at the Nanjing Institute of Geology and Palaeontology (NIGPAS), Chinese Academy of Sciences, Nanjing, China.

We mainly follow herein the wing venation terminology of Nel *et al.* (2012), modified after Schubnel *et al.* (2020) for the presence of the PCu vein in the Neoptera and especially the Hemiptera. Wing venation abbreviations: R, radius; RA, radius anterior; RP, radius posterior; M, media; CuA, cubitus anterior; CuP, cubitus posterior; cua-cup, cubitus anterior-cubitus posterior; AP, areola postica; PCu, postcubital vein; A, anal vein.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843

Family *Incertae sedis*

Genus *Fujianella* **gen. nov.**

Type species. *Fujianella paradoxa* **sp. nov.**; by present designation.

Etymology. The generic epithet is named 'fujian' after Fujian Province from which the material was collected; gender feminine.

Diagnosis. Common stem of R+M+CuA fork at 1/5 of wing length; stem of R fork around 1/3 of wing length; long common stem M+CuA; cua-cup absent; stem of CuA short, equal to CuA₂ in length; CuP present; A present, likely joining PCu into a Y-shape.

Fujianella paradoxa sp. nov.

(Figs 1, 2)

Type material. Holotype, NIGP206134 (with part and counterpart), nearly complete forewing missing upper distal section.

Type locality and horizon. Near Jishan Village, Yong'an City, Fujian Province, SE China; Early Cretaceous (Aptian–Albian).

Etymology. The specific epithet is named after the term 'paradox', due to the combination of inconsistent forewing features from both Protopsyllioidea and Psylloidea; gender feminine.

Diagnosis. As for genus.

Description. Forewing elongate, about 5.90 mm long, reaching maximum width at 2/3 of wing length, about 2.31 mm wide at maximum width, ratio length/width = 2.55. Common stem R+M+CuA forking near wing base, at 1.19 mm from wing base (at 20% of total wing length). Common stem R short, about 0.95 mm long; fork RA and RP at 2.14 mm from wing base, before wing mid-length (around 36% of total wing length); RA forked slightly before wing mid-length, at 2.81 mm from wing base, fork at 45° angle; RA₁ very faint and straight, RA₂ curved. Common stem M+CuA long, 1.17 mm long, forked shortly after common stem R at 2.33 mm from wing base (around 40% of total wing length). Vein M forked at 3.71 mm from wing base; common stem M shorter than fork M₁+M₂; M₁ and M₂ weakly sinusoidal, slightly diverging distally. Vein CuA forked at 2.90 mm from wing base, at wing mid-length; common stem CuA slightly shorter (almost equal) to branch CuA₂ in length; CuA₁ curved, CuA₂ straight and slightly under half length of CuA₁, resulting in wide and short AP cell; crossvein cua-cup absent. Vein CuP thinner than other veins, straight. PCu close and parallel to CuP; A present, running alongside wing margin for most its length, possibly joining PCu distally.

Remarks. The distal section of A is weakly pronounced and very thin, but based on our observations, seems to join with PCu to form a long Y shape, a character very frequent in the Auchenorrhyncha but rarely encountered in the Sternorrhyncha.

Discussion

Fujianella paradoxa gen. et sp. nov. is preserved as a single forewing, with no other body characteristics available. Consequently, the attribution of this taxa to a family is very challenging and debatable. Amongst fossil sternorrhynchans, the presence of a common stem M+CuA instead of R+M is found only in representatives of the superfamilies Protopsyllidioidea and Psylloidea. In fact, the forewing venation observed in the new taxon matches at variable degrees with the general patterns found in these groups. The placement of the new species in one of these genera cannot be confidently supported nor refuted based on just the forewing, as some features are generally shared. Arguments can be proposed against any assignation. Consequently, we tentatively place the new species in a separate genus until more material is available to clarify and revise its taxonomic status.

The new taxon can be excluded from all Permian genera in Protopsyllidioidea, except for *Protopsyllidium*, by having vein M with two branches (instead of three or more). While it shares with *Protopsyllidium* the presence of a forked vein RA (first branch weak), the new taxon is distinguished from the genus by the longer common stem R+M+CuA, the branching of M+CuA after the branching of R, the much longer common stem M+CuA, and the shorter common stem CuA almost equal to CuA₂ (Becker-Migdisova 1985).

The new species is clearly distinguished from *Postopsyllidium* Grimaldi, 2003 and all the genera assigned to Paraprotosyllidiidae by the larger size, the broader wing shape and various characteristics in the wing venation pattern, e.g., the shape and length of the areola postica, RA curved (convex) and forked well before reaching margin, and M with two branches (one in some species of Paraprotosyllidiidae and three in *Postopsyllidium*). On the other hand, it is excluded from *Lodevopsyllidium* Boderau *et al.*, 2024 by the lack of a long ScP close to the costal margin, RP simple (vs. branched), and the presence of a forked RA.

The new species also differs from the Mesozoic protosyllidiids by the longer common stem R+M+CuA, and the clearly shorter common stem CuA. The presence of a forked vein RA, the late branching of R and the longer common stem M+CuA are variable depending on the species considered. Grimaldi (2003) mentions that strong setae are present in several Mesozoic species, likely in all Protopsyllidiidae (they are also present in *Postopsyllidium*

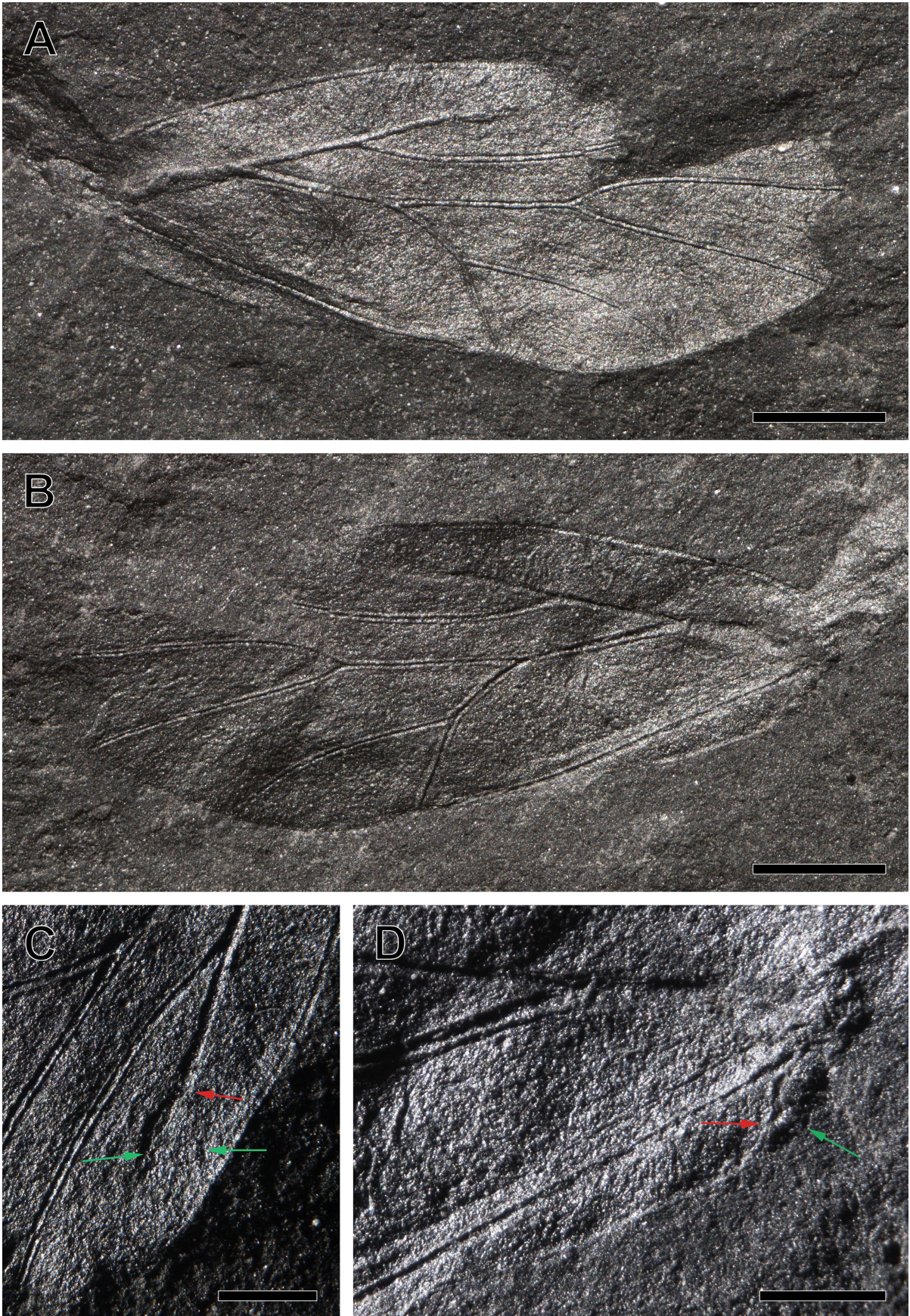


FIGURE 1. A, B, Forewing of *Fujianella paradoxa* gen. et sp. nov. (NIGP206134, part and counterpart). C, Fork of RA (red arrow pointed at fork; green arrows pointed at branches). D, PCu and anal veins (red arrow pointed at A; green arrow pointed at margin at wing base). Scale bars: 1 mm for A, B; 0.5 mm for C, D.

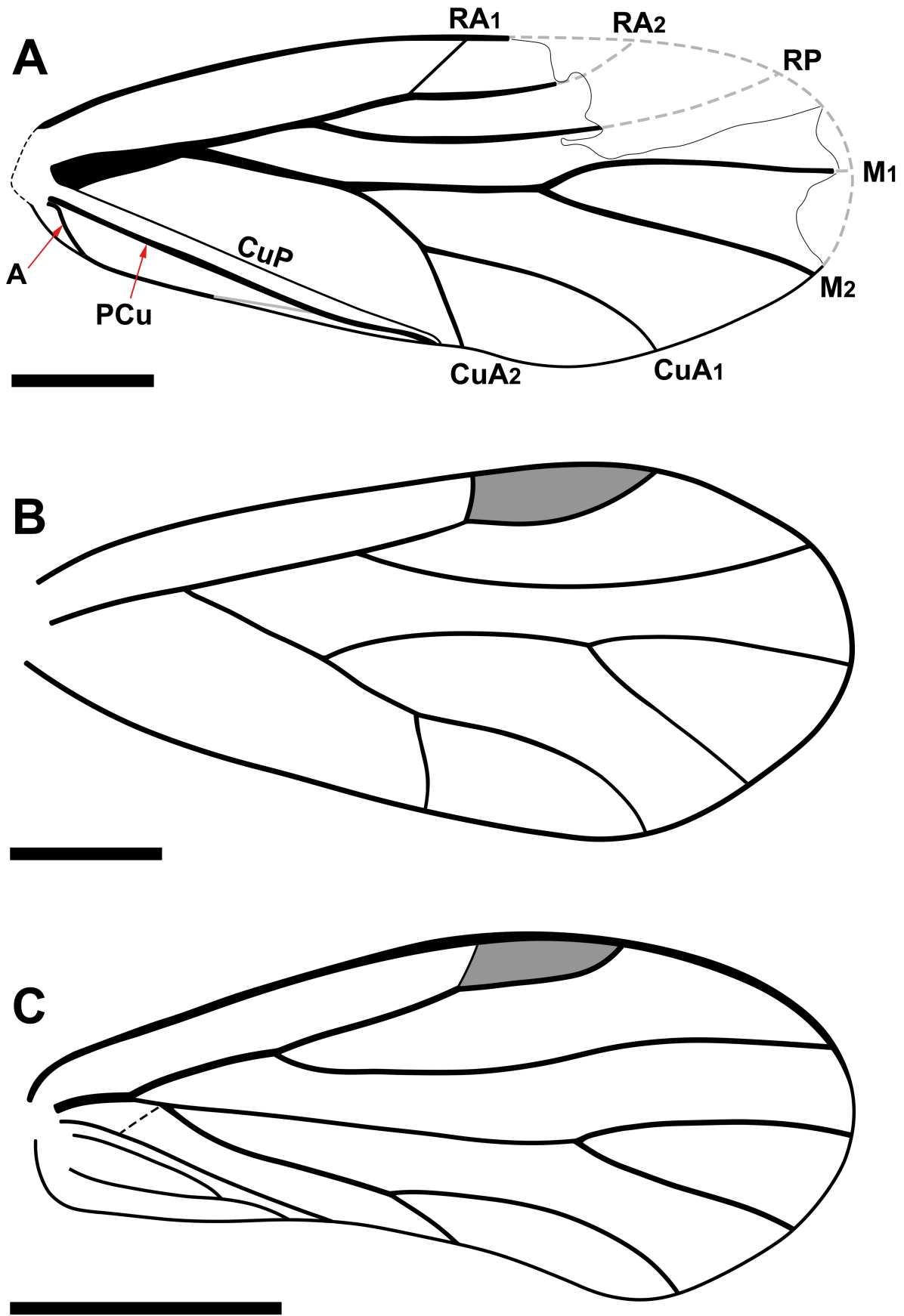


FIGURE 2. Forewing line drawings: **A**, *Fujianella paradoxa* gen. et sp. nov. **B**, *Gracilinervia mastigimatoides* Becker-Migdisova, 1985 (modified after Becker-Migdisova, 1985 and Shcherbakov, 2020). **C**, *Protopsyllidium sinuatum* Davis, 1942 (modified after Becker-Migdisova, 1985; setae on veins are not illustrated). Scale bars = 1 mm.

and species of Paraprotopsyllidiidae). Unlike these Mesozoic records, the new species shows no clear signs of setae or seta insertion points on the veins and wing margin; however, as only one specimen is available, we cannot fully discard the possibility of an artifact related to preservation.

The new taxon displays shared features with some genera of Liadopsyllidae (Becker-Migdisova 1985; Drohojowska *et al.* 2020a; Shcherbakov 2020): the long common stem R+M+CuA with the branching of common stems R and M+CuA taking place around the basal 1/5 of the wing length (usually shorter in Protopsyllidoidea—although Permian species *Permopsyllidium mitchelli* Tillyard, 1926 has a similarly longer common stem); the long common stem M+CuA; the shorter common stem CuA (usually very long in Protopsyllidoidea—although few taxa have it short, e.g., *Postopsyllidium* Grimaldi, 2003 and *Psocopsyllidium* Davis, 1942); the shape of the areola postica. The wing venation observed in the new species quite resembles the drawing of *Gracilinervia mastigimatoides* Becker-Migdisova, 1985 (Becker-Migdisova 1985: p 78, fig. 59), a species discovered from the Jurassic of Kazakhstan. However, *Fujianella paradoxa* **gen. et sp. nov.** has the anal vein present, and while the status of the anal region is unknown in *Gracilinervia mastigimatoides*, vein A is normally absent in the Liadopsyllidae (including the species described from amber where wing venation is more clearly preserved). Moreover, the clear presence of a fork RA as illustrated by Becker-Migdisova (1985) is unclear and cannot be confirmed in the photographs of *Gracilinervia mastigimatoides* by Becker-Migdisova (1985: plate XVI, fig. 2) and Shcherbakov (2020: p 133, fig. 29); Shcherbakov (2020) described the latter species as having a dark and distinct pterostigma. On the other hand, the rock in which *Fujianella paradoxa* **gen. et sp. nov.** is preserved does not conserve coloration; thus, it is not possible to tell at the moment if the new specimen displays any darkening coloration around the pterostigmal area. Other minor specific differences to *Gracilinervia mastigimatoides* include the bifurcation of R occurring before the bifurcation of M+CuA, the straight common stem M and CuA₂ (instead of curved), and variations to the wing shape, including the length to width ratio which around 2.55 in the new taxon (2:1 in *Gracilinervia mastigimatoides*). The length to width ratios are between 2.3–3.1:1 in most Jurassic and Cretaceous Protopsyllidoidea (except in Paraprotopsyllidiidae, the ratio is over 4); nonetheless, the Mesozoic liadopsyllid *Amecephala* Drohojowska, Szwedo, Müller & Burckhardt, 2020 has a higher ratio of 3:1.

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