Carboniferous Blattinopsidae: revision of Klebsiella and new genus and species from Avion (Insecta, Paoliida)

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Historical biology

Carboniferous Blattinopsidae: revision of *Klebsiella* and new genus and species from Avion (Insecta, Paoliida)

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ABSTRACT

The genus *Klebsiella* Meunier, 1908 from the latest Carboniferous of Commentry, is revised, confirming its attribution to the Blattinopsidae. The family name Klebsiellidae should have priority on its junior synonym Blattinopsidae, but the common usage over time could allow maintaining the later. The first Blattinopsidae from the Moscovian Konservat–lagerstätte of Avion is described as a new genus and species *Avionblattinopsis oudardi* gen. et n. sp. on the basis of a single forewing. It differs from the other genera of this family in the vein ScP distally fused to the vein RA. It increases our knowledge about this family, known between the Late Carboniferous and the Middle Permian. An emended family diagnosis is proposed.

Protoblattiniella minutissima Meunier, 1912, based on a mature nymph would better fit with the Paoliidae than with the Blattinopsidae.

KEYWORDS

Neoptera; Polyneoptera; wing venation; gen. et n. sp.; Moscovian; France.

Introduction

The small Paleozoic polyneopteran family Blattinopsidae currently contains 11 genera, but only four can be accurately considered as informative because six are based on very fragmentary fossils and one could be related to another group. Carpenter (1992) put the Blattinopsidae into the so–called 'Protorthoptera', Béthoux and Nel (2002) and Béthoux et al. (2009) supposed they were related to the Dictyoptera, but Béthoux and Jarzembowski (2010) considered that they were Archaeorthoptera sensu Béthoux and Nel (2002). More recently, Prokop et al. (2014a) included them in the Paoliida (as sister group of the Dictyoptera), on the basis of putative wing venation synapomorphies. These insects are mainly known and characterized by their wing venation, the body structures being either absent or poorly preserved. They are recorded between the Late Carboniferous and the early Middle Permian from Europe and North America. The Blattinopsidae were still unrecorded in the Konservat–lagerstätte of Avion, while this outcrop has already given an important diversity of insects, including Palaeodictyoptera, Diaphanopterodea, Odonatoptera, Archaeorthoptera, Caloneurodea, Paoliida, Dictyoptera, Plecoptera, Acercaria, and Holometabola (Nel et al. 2013, Prokop et al. 2013, 2014b, Coty et al. 2014; Schubnel et al. 2019a,b).

Material and methods

The imprint was prepared with a pneumatic hammer. It was observed under a Nikon SMZ1500 binocular microscope, photographed using a Nikon D800 and drawn using a camera lucida. The fossil insects were found in 'Terril N 7', a slag heap located in the Avion area comprising Moscovian–aged sediments derived from Liévin coal mines 3 and 4, specifically the Bolsovian or Westphalian C (311–308 Myrs) 'faisceaux de Ernestine', and the Asturian or Westphalian D (308–306 Ma) 'veines Arago, Dusouich, Marthe' informal beds (Bruno Vallois pers. comm.). Wing venation nomenclature follows Prokop et al. (2014a) and Schubnel et al. (2019c), especially concerning the presence of a postcubital veins in Pterygota. Abbreviations are as follows: arc arculus reinforced oblique crossvein between M and CuA; C costal vein; ScP subcostal posterior; RA radius anterior; RP radius posterior; M median vein; CuA cubitus anterior; CuP cubitus posterior; PCu postcubital vein; A anal vein(s).

Abbreviation for institution: MNHN Muséum National d'Histoire Naturelle de Paris, France.

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Systematic palaeontology

Order: Paoliida Handlirsch (1906)

Remark

The Paoliida currently comprise the three families Paoliidae Handlirsch, 1906, Anthracoptilidae Handlirsch, 1922, and Blattinopsidae Bolton, 1925.

Family: Blattinopsidae Bolton (1925)

Type genus. *Blattinopsis* Giebel, 1867

Other genera (after Fossilworks database). *Alienus* Handlirsch, 1906, *Balduriella* Meunier, 1925, *Glaphyrophlebia* Handlirsch, 1906, *Klebsiella* Meunier, 1908, *Microblattina* Scudder, 1896, *Protoblattiniella* Meunier, 1912, *Rhipidioptera* Brongniart, 1893, *Stephanopsis* Kukalová, 1958, *Westphaloblattinopsis* Béthoux and Jarzembowski, 2010.

Remarks

The genus *Protociccus*, listed in the Fossilworks database, was synonymized with *Glaphyrophlebia* by Hörnschemeyer and Stapf (2001).

We confirm below the attribution of the genus *Klebsiella* (type genus of the Klebsiellidae Handlirsch, 1919) to the same family as *Blattinopsis*. The name Klebsiellidae, as a valid and older family name, should have priority on the name Blattinopsidae Bolton, 1925. Nevertheless, we prefer to maintain the prevailing usage of names until the Commission of nomenclature will decide on this case.

Bolton (1925: 23) proposed the following diagnosis for the Blattinopsidae: 'Protoblattoidea with elongated, oval wings, folding backwards over the body. Radius (R & RA) strong and elevated basally, distally ending in feeble branches. Radial sector (RP) much branched. Median (M) arising from the radius or radial sector in two or more branches. Cubitus (Cu) two or three times branched. Anal area large, with few anal veins. Interstitial neuration a close reticulation, developing accessory veins along the distal inner and apical margins of the wing'. This diagnosis is not enough precise to characterize the family. Carpenter (1992: 103, fig. 59.10a) proposed another diagnosis: 'Fore wing with vein SC (ScP) terminating on costal margin well before apex; R (R & RA) usually sigmoidally curved, numerous oblique veinlets between R and costal margin beyond SC; RS (RP) with numerous branches; MA apparently absent; MP (M) often with one or more branches anastomosed with R or RS; CUA (CuA) anastomosed with basal portion of M, diverging away, and then fusing with CUA2; strong indentation at end

of CUP (CuP); anal veins straight; crossveins numerous, commonly forming meshwork of cells. Hind wing unknown.' This diagnosis is erroneous in an important point: Carpenter considered that 'CUA' (CuA) is basally fused with M and emerges from it to fuse with 'CUA2', but, as already noticed by Prokop et al. (2014a), CuA is the convex anterior branch of Cu and the so-called 'CUA' is a reinforced crossvein (arculus) between M and CuA. Thus we propose a new diagnosis for the Blattinopsidae, as follows: forewing with ScP ending into C or in RA; numerous crossveins between the main longitudinal veins; R (RA) sigmoidally curved; numerous posterior branches of RP, pectinate; a reinforced crossvein 'arculus' between M and CuA; a common stem Cu from which convex CuA and concave CuP separate distally; one concave anterior branch of CuA; broad area between CuA and CuP with numerous crossveins; area between CuP and PCu narrow; CuP and PCu basally curved and distally straight; area between PCu and first anal vein broad with a net of irregular cells; three anal veins.

The monotypic genus *Klebsiella* (*K. exstincta* Meunier, 1908), based on a specimen (MNHN.F.R51219) showing a forewing and the distal half of another (hind?) wing. It was very schematically drawn by Meunier (1908: fig. 2). Handlirsch (1919: 552, fig. 52) proposed the family Klebsiellidae for this genus, and re-drawned its wings. Handlirsch's diagnosis was rather precise, viz. 'Errichtet auf ein Fossil aus Commentry, welches in mancher Hinsicht etwas an die mit *Oedischia* verwandten Formen erinnert, aber in anderer Hinsicht wieder Charaktere der Protoblattoiden erkennen läßt. Die Flügel sind relativ breit mit verkürzter Subcosta, die namentlich im Vorderflügel ein breites Costalfeld begrenzt. Der Radius sendet eine Anzahl kurzer Ästchen zum Costalrand, sein Sector ist in normaler Weise reich verzweigt. Auch die beiden Äste der Medialis sind wiederholt gegabelt. Der Cubitus dagegen bildet nur drei bis vier Zweige. Das Analfeld war relativ groß und nach vorne fast geradlinig begrenzt, im Hinterflügel bildete es einen kleinen Fächer. Queradern schütter', translated as follows: 'Erected on a fossil from Commentry, which in some ways reminds us of the forms related to *Oedischia*, but in

other ways reveals characters of the protoblattoids. The wings are relatively wide with a shortened subcostal (ScP), which, in particular, limits a wide costal area in the forewing. The radius (RA) sends a number of short branches to the costal margin, its sector (RP) is normally richly branched. The two branches of the media (M) are also forked repeatedly. The cubitus, on the other hand, only forms three to four branches. The anal area was relatively large and almost straight forward, it formed a small fan in the hind wing. Sparse crossveins'. This diagnosis is also not sufficient for an accurate determination of the family. Nevertheless, the family Klebsiellidae is valid because there were a diagnosis and designations of a type genus and species. Bolton (1925: 25) indicated: 'The genus *Klebsiella* Meunier (June 1908) was founded upon the distal two-thirds of what appear to be the fore and hind wings of one side. The radius terminates as in *Blattinopsis*, the radial sector is broken away over the area m which it should join the radius, and neither wing shows the relation of the median and radius. The general branching of the median, cubitus, and anal is similar to that of *Blattinopsis*, and there seems no satisfactory reason why the wings should be placed in a distinct genus'. Apparently Bolton (1925) ignored the work of Handlirsch (1919) that he did not cite. Carpenter (1992: 133) considered *Klebsiella* as a 'Prothoptera' of 'family uncertain'. Later, Hornschemeyer and Stapf (2001) attributed *Klebsiella* to the Blattinopsidae without further argument and no discussion on the family Klebsiellidae. In the internet site 'Fossilworks' (http://fossilworks.org/?a=taxonInfo&taxon_no=271212), the family Klebsiellidae is considered as an 'invalid subtaxon' of the Blattinopsidae, without precise reason.

Thus we need first to redescribe *Klebsiella*, in order to precise its affinities with *Blattinopsis*.

Klebsiella Meunier, 1908

Type species

Klebsiella exstincta Meunier, 1908

New diagnosis. Forewing characters only. ScP rather long, extending beyond mid wing level, strongly approximating RA before its apex into C; area between ScP and R not extremely narrow, nearly as wide as area between ScP and C; radial vein making a pronounced angle at base of RP, no reticulation in areas between main veins, especially in distal half of wing but only a few crossveins connecting branches of RP and M; area between RA and RP rather narrow; no distinct longitudinal furrows between branches of RP and M; area between CuA and CuP slightly broader than that between M and CuA; a concave distal anterior branch of CuA but no long posterior branches in area between CuA and CuP; postcubital–anal area not reticulated, with only four main veins.

Klebsiella exstincta Meunier, 1908

(Figures 1–2)

Type material

MNHN.F. R51219 (imprint and counterimprint of a forewing with a part of another (hind?) wing and fragments of body, possibly a very long and curved ovipositor, see arrow in Fig. 1).

Type locality

Commentry, Allier, France.

Stratigraphic occurrence

Gzehlian, Late Carboniferous.

174

175 *Description*

176 Forewing 32.6 mm long, 10.4 mm wide; with extreme bases of RP, M, Cu, PCu and anal vein
177 not well preserved; except for sinuate R–RA and ScP, longitudinal veins and branches straight
178 and evenly spaced, often parallel to a marked degree; vein ScP rather long, strongly
179 approximating RA, but ending on C at 24.3 mm from wing base; area between ScP and RA
180 rather broad, only slightly narrower than area between C and ScP; RA sinuate and terminating
181 29.8 mm from wing base, RP separating from RA at ca. 10.0 mm from wing base, RP with a
182 first fork 5.3 mm from its base, posterior branch forked twice, anterior branch forked again
183 distally, with posterior branch forked and anterior one forked again twice; M forked 4.3 mm
184 from its base, anterior branch with three branches; posterior branch forked two times; no
185 longitudinal furrows between branches of RP and MP; few simple crossveins in RP/M area; M
186 emerging from a common stem R+M; CuA with one concave anterior branch and no convex
187 posterior branches; area between CuA and M as wide as that between CuA and CuP; oblique
188 convex arculus not preserved (if present) in area between M and CuA; CuA and CuP separating
189 from a common stem well separated from M and PCu; CuP curved at base and straight and
190 strongly concave, while PCu strongly convex and curved; a short neutral vein between Cu and
191 PCu at wing base; in postcubital–anal area, nearly all crossveins all simple, four main veins, all
192 simple, except penultimate one with three branches; network of cells generally lacking except
193 in areas between M and CuA and below PCu.

194

195 *Remark*

196 *Klebsiella* can be attributed to the order Paoliida sensu Prokop et al. (2014a) because of the
197 following characters: concave ScP approximating RA in distal half of wing; strongly convex
198 RA with weak, short but distinct anterior branches, unusually prominent steep elevation from

ScP to RA forming a characteristic wing profile; costal area between ScP and costal margin with series of simple, oblique veinlets; RP rather concave with numerous branches; M rather concave; convex CuA and concave CuP separating from a rather long basal stem Cu; CuA not in contact with the stem R+M; area between CuP and CuA broad compared to median and radial areas (autapomorphy), a general course of CuA making a double curve (autapomorphy); CuA has convex posterior branches, plus some weaker concave anterior branches; CuP simple, nearly straight; anal fan strongly reduced.

Affinities with the Paoliidae are excluded because the area between CuA and CuP is not very broad, just slightly broader than area between CuA and M in their basal parts. Affinities with the Anthracoptilidae are excluded because they all have numerous anterior concave branches of CuA, while *Klebsiella* has only one, as in the Blattinopsidae.

The character 'termination of ScP on RA vs. termination on C' is variable within the Paoliidae and the Anthracoptilidae (Prokop et al. 2014; Nel et al. 2015; Guan et al. 2016). Within the known Blattinopsidae, ScP is ending on C; but ScP strongly approximates RA in *Klebsiella*, unlike in the other taxa of the family. There are few other differences between *Klebsiella* and *Glaphyrophlebia* or *Blattinopsis*, the most visible ones being the less regular posterior pectination of RP, and the absence of long irregular veinlets in the area between CuA and CuP in *Klebsiella*. These differences are sufficient for a generic separation but not for a separation between two families Blattinopsidae and Klebsiellidae. Thus we reject the unformal identity of *Klebsiella* with *Blattinopsis* proposed by Bolton (1928), and we consider that Blattinopsidae and Klebsiellidae are the same families, with a problem of usage vs. potential junior synonymy between the two (see above).

Avionblattinopsis n. gen.

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Type species

Avionblattinopsis oudardi n. sp.

Diagnosis

Forewing characters only. ScP short, ending into RA (unique character among the Blattinopsidae); area between ScP and R not extremely narrow, just half as wide as area between ScP and C; radial vein making a pronounced angle at base of RP, no reticulation in areas between main veins, especially in distal half of wing but only a few crossveins connecting branches of RP and M; area between RA and RP broad; no distinct longitudinal furrows between branches of RP and M; area between CuA and CuP slightly narrower than that between M and CuA; a concave distal anterior branch of CuA; postcubital–anal area not reticulated, with only four main veins.

Etymology

Named after the outcrop of Avion and *Blattinopsis*.

Avionblattinopsis oudardi n. sp.

(Figure 3)

urn:lsid:zoobank.org:act:741B740E-593B-423E-82BC-A303C62F70D5

Etymology

Named after our friend and colleague Jacques Oudard, who greatly helps us to collect fossil insects in the site of Avion.

Type material

MNHN.F.A71321 (coll. Patrick Roques, imprint and partial counterimprint of a forewing, with extreme base and a portion of mid part missing).

Type locality

'Terril N 7' site, Avion, Pas–de–Calais, France.

Stratigraphic occurrence

Moscovian (Westphalian C/D, equivalent to the Bolsovian/Asturian European local stages).

Diagnosis

As for the genus.

Description

Forewing 12.0 mm long, 3.5 mm wide; extreme wing base not well preserved, so that the extreme bases of Cu, PCu and anal vein cannot be recognized; except for sinuate R–RA and ScP, longitudinal veins and branches straight and evenly spaced, often parallel to a marked degree; vein ScP short, terminating on RA, at 5.0 mm from wing base (near mid wing); area between ScP and RA narrow, about half width of area between C and ScP; RA sinuate and terminating 9.0 mm from wing base, RP separating from RA at 2.0 mm from wing base, RP with a first fork 2.8 mm from its base, posterior branch simple, anterior branch forked again distally, with posterior branch forked and anterior one simple; M forked 5.0 mm from its base, anterior branch forked again very distally; posterior branch forked two times; no longitudinal furrows between branches of RP and MP; few simple crossveins in RP/M area; M emerging from a common stem R+M; CuA with one concave anterior branch and four convex posterior branches; area between CuA and M slightly narrower than that between CuA and CuP; an

oblique convex arculus in area between M and CuA; CuA and CuP separating from a common stem well separated from M and PCu; CuP curved at base and straight and strongly concave, while PCu strongly convex and curved; a short neutral vein between Cu and PCu at wing base; in postcubital–anal area, nearly all crossveins all simple, four main veins, all simple, except penultimate one with three branches; network of cells generally lacking except in areas between M and CuA and below PCu.

Remark

Avionblattinopsis gen. nov. can be attributed to the order Paoliida sensu Prokop et al. (2014a) because of the same list of characters indicated above. Affinities with the Paoliidae are excluded for the same reasons as above.

As already noticed, the character 'termination of ScP on RA vs. termination on C' is variable within the Paoliidae and the Anthracoptilidae (Prokop et al. 2014; Nel et al. 2015; Guan et al. 2016). Within the known Blattinopsidae, ScP is ending on C, unlike in *Avionblattinopsis* n. gen. But in *Klebsiella*, ScP is strongly approximating RA before ending on C, supporting the hypothesis that, also in Blattinopsidae, ScP terminates on RA or on C, depending on the taxa.

Avionblattinopsis n. gen. greatly resembles the forewing of the blattinopsid genus *Glaphyrophlebia* in the organization of the distal branches of RA, RP, M, CuA, and CuP (see Hörnschemeyer and Stapf 2001: fig. 8). More generally, it shares with the Blattinopsidae the presence of only one concave anterior branch of CuA. Many Blattinopsidae have a curved line in the middle of the forewing (vb. sensu Hörnschemeyer and Stapf, 2001). In *Avionblattinopsis* n. gen., we cannot decide if this structure is present or not because, if present, it would be exactly in the missing part of forewing.

After the diagnoses of the different genera proposed by Hörnschemeyer and Stapf (2001), *Avionblattinopsis* n. gen. differs from *Stephanopsis* and *Klebsiella* in the area between ScP and R not extremely narrow, just half as wide as area between ScP and C.

More precisely, the type species of *Stephanopsis*, *Stephanopsis incerta* (Laurentiaux, 1950) (originally in the genus *Blattinopsis*) has an area between ScP and RA relatively much narrower than in of *Avionblattinopsis* n. gen. (Laurentiaux 1950: pl. 1, fig. 1a,b). It differs from *Avionblattinopsis* n. gen. in the radial vein not making a pronounced angle at base of RP, the area between CuA and CuP much broader than that between M and CuA, and the presence of a reticulation in the areas between main veins. *Stephanopsis elegans* (Schlechtendal, in Handlirsch 1906) (originally in the genus *Blattinopsis*) is based on an incomplete forewing, with the area between C and ScP not preserved, thus it is not possible to estimate the relative widths of this area compared to that between ScP and R. Nevertheless, it has a straight R, as in the type species of *Stephanopsis*, and unlike *Avionblattinopsis* n. gen. Also its area between RA and RP is very narrow (Handlirsch 1906: pl. 16, fig. 8). *Stephanopsis mirandus* (Richardson, 1956) (originally in the genus *Glaphyrokoris* Richardson, 1956) has a proportion between the area between ScP and R and the area between C and ScP very close to that of *Avionblattinopsis* n. gen., but it differs from *Avionblattinopsis* n. gen. in the area between CuA and CuP as wide as that between M and CuA (Richardson, 1956: fig. 18).

Avionblattinopsis n. gen. differs from *Klebsiella* in the very narrow area between ScP and RA and the pattern of the branches of RP and M.

In *Glaphyrophlebia*, there are, between all branches of RP and M, distinct longitudinal furrows, starting at the vein–bow or slightly proximad of it and reaching the edge of the wing, unlike in *Avionblattinopsis* n. gen. and *Blattinopsis*. But *Avionblattinopsis* n. gen. and *Glaphyrophlebia* have no reticulation in the distal half of the wing, and only a few crossveins connecting the branches of RP and M, unlike *Blattinopsis*.

Westphaloblattinopsis was originally interpreted as an Archaeorthoptera, with a concave anterior branch of CuP ending into CuA, unlike all the other Blattinopsidae. This taxon needs to be revised. Nevertheless, it differs from *Avionblattinopsis* n. gen. in a ScP ending into C, a very narrow area between RA and RP, no concave distal anterior branch of CuA and an anal area strongly reticulated (Béthoux and Jarzembowski 2010: Fig. 1).

Alienus (*A. lebachensis* (Goldenberg, 1877)) is based on the mid part of a fore (?) wing, without any diagnostic character (Handlirsch 1906: pl. 37, fig. 29).

Balduriella (*B. latissima* Meunier, 1925) is based on the distal two–third of a wing. It differs from *Avionblattinopsis* n. gen. in an anteriorly pectinate anterior branch of RP, and a very long ScP, ending well distal the base of RP. The others structures are hardly discernable on the original photograph of Meunier (1925: fig. 1).

Microblattina (*M. perdita* Scudder, 1895) is based on an incomplete distal third of a wing, showing no special character that would support and attribution to the Blattinopsidae (Scudder 1895: pl. 3, fig. 5).

Protoblattiniella (*P. minutissima* Meunier, 1912) is based on a mature nymph of a Polyneoptera (MNHN.F.R51518), blattoid–like, with wing pad rather well–developed (Fig. 4). It has a very broad area between CuA and CuP, plus anterior branches of CuA, supporting an attribution to the clade Paoliida. But it has only three branches of RP, unlike the Blattinopsidae (Meunier 1912, 1921). It would better fit with the Paoliidae sensu Prokop et al. (2014a).

Rhipidioptera (*R. elegans* Brongniart, 1893) is based on an incomplete hindwing (MNHN.F.R51226) (Fig. 5). It differs from *Avionblattinopsis* n. gen. in the very broad reticulated area between CuA and CuP, and much more branches of RP.

Conclusion

The revision of *Klebsiella* shows that this genus can be attributed to the Blattinopsidae, in a genus different from the others. *Avionblattinopsis* gen. nov. does not fit with any other blattinopsid genera, with the most important difference being the distal fusion of ScP with RA. Of course this character alone could be considered as potentially variable among the Dictyoptera (viz. the roachoid *Miroblattites costalis* (Laurentiaux–Vieira and Laurentiaux 1987) that has ScP ending into RA in its left wing and in C in its right wing), but it seems to be more stable among the Paoliida. *Avionblattinopsis oudardi* gen. et n. sp. is not only the first record of the Blattinopsidae from the outcrop of Avion but it increases our knowledge on the biodiversity of this family during the earliest late Carboniferous.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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445 **Figure 1**. *Klebsiella exstincta* Meunier, 1908, holotype: MNHN.F. R51219. Photograph of
446 imprint. Scale bar 10 mm.

447 **Figure 2**. *Klebsiella exstincta* Meunier, 1908, holotype: MNHN.F. R51219. Photograph of
448 counterimprint. Scale bar 10 mm.

449 **Figure 3**. *Avionblattinopsis oudardi* n. gen. et n. sp., holotype: MNHN.F.A71321. Forewing.
450 A, photograph; B, reconstruction. Scale bars 1.0 mm.

451 **Figure 4**. *Protoblattiniella minutissima* Meunier, 1912, holotype: MNHN.F.R51518. General
452 habitus. A, dry; B, under alcohol. Scale bars 5.0 mm.

453 **Figure 5**. *Rhipidioptera elegans* Brongniart, 1893, holotype: MNHN.F.R51226. General
454 habitus. A, dry; B, under alcohol. Scale bars 5.0 mm.


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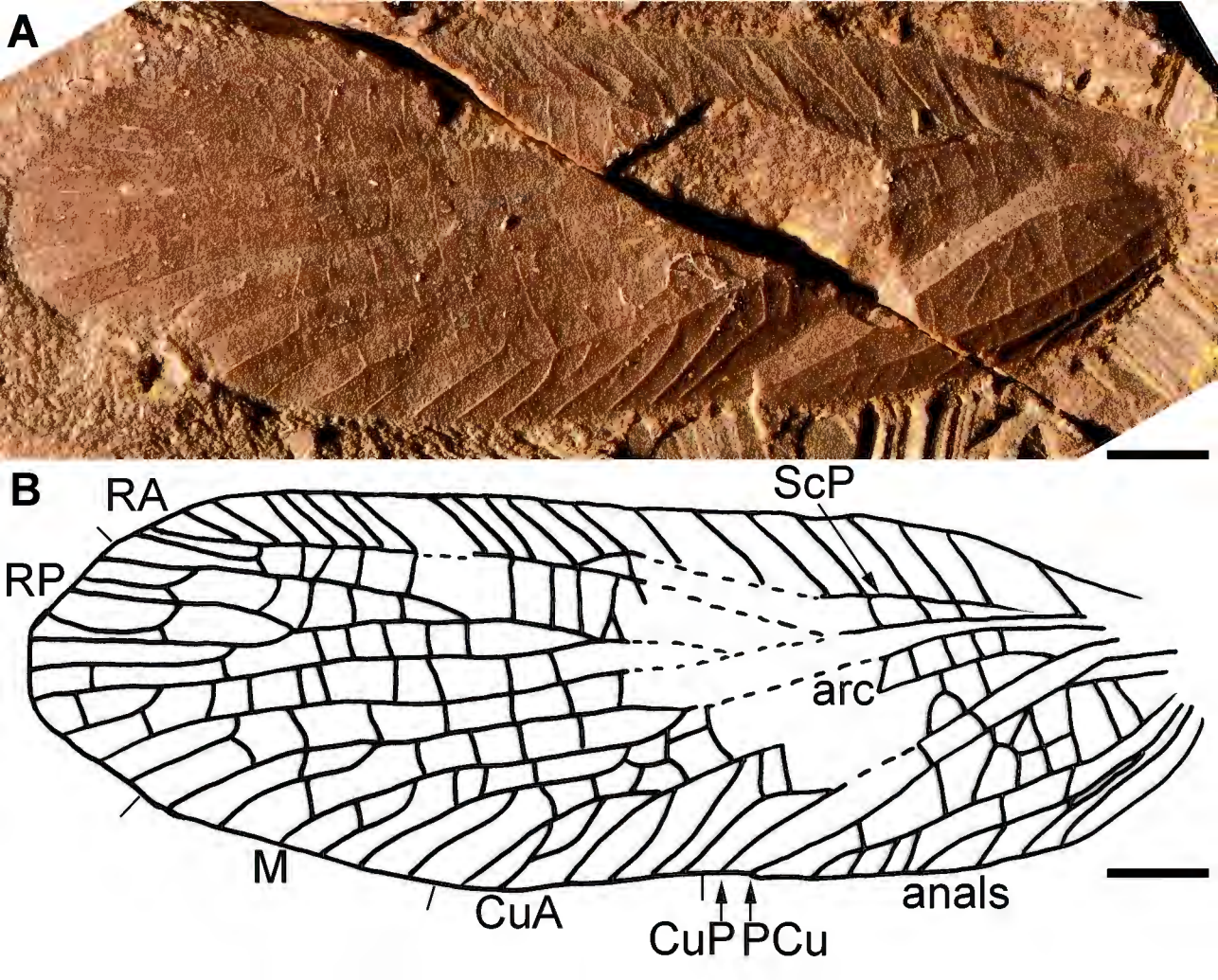
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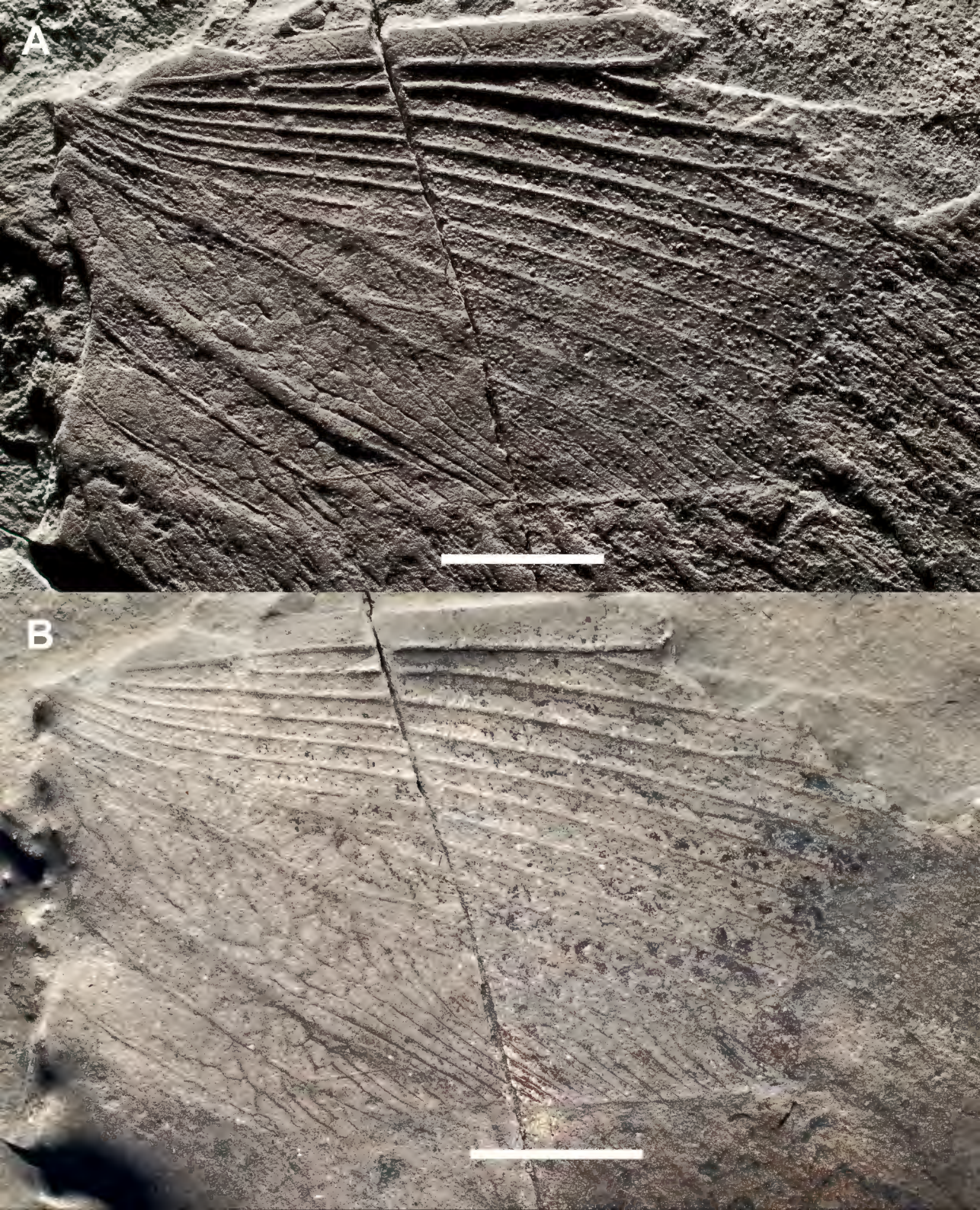
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