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Historical Biology

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ABSTRACT

The new archaeorthopteran family Roqueiidae is defined for the new genus and species *Roqueia alpine*, described from the Pennsylvanian (Kasimovian) of La Mure region (Isère, Alps, France). This new taxon is characterized by the set of characters: basal fusion of MA with R, its distal re-emergence from RP, and ending into vein MP. The Roqueiidae are tentatively assigned to the order Cnemidolestodea together with the family Cnemidolestidae.

KEYWORDS

Insecta; ?Cnemidolestodea; fam., gen. et sp. nov.; Kasimovian, French Alps.

Introduction

The superorder Archaeorthoptera Béthoux and Nel, 2002 (total group of the extinct and extant Orthoptera) reached a maximum of diversity during the late Paleozoic, with no less than four major orders (Cnemidolestodea, Caloneurodea, Titanoptera, crown Orthoptera) plus a series of families and genera representative of the stem group of the Panorthoptera. This diversity greatly decreased during the Triassic with only the Titanoptera and crown Orthoptera surviving and again after the extinction of the Titanoptera near the end of this period. An impressive series of recent discoveries of new Archaeorthoptera is going on, always confirming this general tendency of a highest diversity of the group during the late Carboniferous and the Permian (e.g., Schubnel et al. 2021).

Here we describe a new fossil Archaeorthoptera with a unique forewing venation from the Kasimovian of the French Alps. It is probably related to the order Cnemidolestodea sensu Béthoux (2005), but corresponds to a new family, genus, and species.

Material and methods

The fossil was found by one of us (H.D.) in the slag heap of the Villaret. It was examined under a Nikon SMZ1500 and photographed with an AmScope camera MU900. This outcrop corresponds to the Kasimovian (Baruellian, Stephanian A), with *Crenulopteris lamuriana* (Heer) as typical plant of the biozone (Wittry et al., 2014). We follow the wing venation terminology of Béthoux and Nel (2002), modified by Schubnel et al. (2020).

Wing vein terminology: A, anal vein; C, costa; CuA, cubitus anterior; CuP, cubitus posterior; CuPa, anterior branch of CuP; CuPb, posterior branch of CuP; MA, median anterior vein; MP, median posterior vein; PCu, postcubital vein; RA, radius anterior; RP, radius posterior; ScP, subcosta posterior.

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Systematic Palaeontology

Superorder Archaeorthoptera Béthoux and Nel, 2002

?Order Cnemidolestodea Handlirsch, 1937 (sensu Béthoux 2005)

Family Roqueiidae fam. nov.

urn:lsid:zoobank.org:act:C87D6416-9EB8-40CD-8A51-8BADF019AFB1

Type genus

Roqueia gen. nov.

Diagnosis

Wing characters only. In forewing, fusion of MA with R and distal re-emergence independently of MP+CuA (putative apomorphy, convergently present in the Cacurgidae); MA re-emerging from RP and ending into MP (putative autapomorphy); separation of MP from CuA basal of its fusion with CuPa; short stem of MP before its first posterior branch; ScP ending into C.

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Genus *Roqueia* gen. nov.

urn:lsid:zoobank.org:act:2A691E2A-8496-468F-BE84-193D42BEB7A8

Type species

Roqueia alpina sp. nov.

Etymology

Named after Patrick Roques, for his very efficient and kind help in the research on Carboniferous insects. Gender Feminine.

Diagnosis

As for the family, plus the following forewing characters: two posterior branches of MP basal of its distal fusion with MA; two posterior branches of MA+MP basal to its fusion with RP

Roqueia alpina sp. nov.

(Figs 1, 2)

urn:lsid:zoobank.org:act:546938FF-8C99-401B-A8AD-3AD8E98A37BC

Etymology

Named after the Alp mountains.

Holotype

Specimens Fa 0145 (imprint) and Fa 0145b (counterimprint) (fragments of legs, a nearly complete forewing, a less well-preserved forewing and a hind wing), stored at the Musée d'Histoire Naturelle of Grenoble, France.

Type locality

Slag heap of the Villaret, Susville, La Mure, Matheysine region, Isére, France

Stratigraphic occurrence

Kasimovian (Stephanian A), 'étage productif du houiller' of La Mure.

Diagnosis

As for the genus by monotypy.

Description

Forewing 35.4 mm long, 12.0 mm wide; area between C and ScP 1.5 mm wide; ScP straight, apically weakening and ending in C 23.8 mm from wing base; area between ScP and R as broad as that between C and ScP, with poorly preserved crossveins in basal part and elongate anterior branches of RA in distal part; area between C and RA broad with a series of complex branched veinlets in-between; base of RP 13.1 mm from wing base; RA weakly curved posteriorly; RP emitting a very strong posterior branch very close to its base, this branch ending into MP, interpreted as MA captured by R, fused with RP, and re-emerging distally to end into MP; main branch of RP long before its distal fusion with MA+MP; RP with three to four posterior branches; an elongate broadly triangular area limited by RP, MA and MP, apparently free of crossveins; MP+CuA basally fused with R, separating from it ca. 4.5 mm from wing base; stem of MP+CuA 4.1 mm long; MP weakly sigmoidal, very long before its fusion with MA, defining an elongate triangular area with R, RP+MA, and MA, this area with four faint crossveins; MP with two posterior branches basal to its fusion with MA; MA+MP with two posterior branches basal to its fusion with RP; basal free part of CuA very short, 1.4 mm long; an elongate CuPa ending into CuA; CuA+CuPa nearly straight, with two posterior branches; a broad area between CuA+CuPa, CuPa and CuPb; CuPb simple and nearly straight; PCu strongly arched and touching CuP in one point; two anal veins visible.

Hind wing poorly preserved, lying over second forewing, ca. 33.7 mm long, ca. 11.9 mm wide, without visible anal fan; no triangular elongate area between R and first anterior branch of MP+CuA+CuPa present.

Leg fragments poorly preserved, but tibia and femur elongate and relatively thin (Fig. 2B).

Discussion

This fossil is attributed to the Archaeorthoptera as it shares the main diagnostic characters of this superorder, namely the basal fusion of CuA with M (only its distal part MP+CuA being preserved) and subsequent connection of CuA with an anterior branch CuPa of CuP (Béthoux and Nel 2002: fig. 1). The elongate CuPa and the absence of an elongate vein between CuPa and CuPb exclude any affinities with the Panorthoptera. *Roqueia* gen. nov. has some similarities with the Oedischiidae that have also a triangular area between RP and M. But the presence of four posterior branches of MP also excludes affinities with this orthopteran group in which there is a single vein MP separating from the anterior branch MA that is itself parallel to R/RP and ending into RP. Also the Oedischiidae have an anal fan in the hind wing, unlike *Roqueia* gen. nov.

Roqueia gen. nov. shows important similarities with the archaeorthopteran genera *Omaliella* Béthoux and Nel, 2005 (*O. ramosa* Béthoux and Nel, 2005 and *O. polonica* Dvořák et al., 2019) and *Omalia* Van Beneden & Coemans, 1867 in the following characters: ScP not ending into RA, CuPa fused with CuA distal of the base of M, M shortly touching RP. But *Omaliella* and *Omalia* have branches MP and MA distally separating from a long stem M and no strong oblique vein in area between M and RP (Béthoux and Nel, 2005; Dvořák et al., 2019).

Furthermore, *Roqueia* gen. nov. has some characters very similar to those of the order Cnemidolestodea (sensu Béthoux, 2005, to include the Cnemidolestidae only), such as a specialized elongate triangular area between RP/MA and a long vein emerging from M+CuA, distally closed by the fusion of these veins; plus the vein MP emitting several parallel posterior branches. Notice that Aristov (2014) proposed a different definition of the Cnemidolestodea to include much more families in this order, but there is no clear synapomorphy supporting this order sensu Aristov (see Dvořák et al. 2021; Nel and Poschmann 2021).

Roqueia gen. nov. strongly differs from the Cnemidolestidae in the absence of a free MA separating from MP+CuA. The specialized triangular area in *Roqueia* gen. nov. is between

RA and MP, not between MA and the first anterior branch of MP+CuA+CuP; and MP is separating from CuA basal to fusion of CuA with CuPa. In this area of *Roqueia* gen. nov., there is a very strong oblique vein emerging from RP and ending into MP, which can only correspond to MA basally fused with R and re-emerging distally from RP, a character also present in few other Archaeorthoptera (e.g., Cacurgidae, see below). In the Cnemidolestidae, the vein MA is basally separating from MP+CuA and closely parallel to R/RP (Langiaux and Parriat 1974; Whalley 1979; Pinto and Pinto de Ornellas 1980; Béthoux and Nel 2005; Béthoux 2005; Martins-Neto et al. 2007; Gu et al. 2011, 2014; Aristov 2013, 2014; Dvořák et al. 2021; Nel and Poschmann 2021). The narrow area between MA and R/RP of the Cnemidolestidae is no longer present in *Roqueia* gen. nov. *Roqueia* gen. nov. could have some similarities with *Ivkinus* Aristov, 2014 (currently in the family Sylvabestiidae Aristov, 2000) in the presence of a triangular area between R/RP and M with several oblique crossveins in-between, but this last taxon is based on a rather poorly preserved fossil in which the vein CuPa is not preserved. Also Aristov (2014: fig. 13) considered that the vein M of *Ivkinus* is basally separated from CuA and distally forked into MA (ending into RP) and a free MP, which is a pattern completely different from that of *Roqueia* gen. nov.

A further, less important difference of *Roqueia* gen. nov. is the ScP ending in C, instead of RA in the genera of Cnemidolestidae (this character is subject to several homoplasies in the Archaeorthoptera).

The hind wings of the Cnemidolestidae are generally less well-known than their forewings. They are also less ‘complex’, without a well-defined triangular elongate area between MA and first anterior branch of MP+CuA+CuPa (Béthoux and Nel 2005). Their anal area are generally unknown, even in the well-preserved genus *Protodiamphipnoa* Brongniart, 1885.

The genera of the panorthopteran family Cacurgidae Handlirsch, 1911 share with *Roqueia* gen. nov. the two characters 'fusion of MA with R and its distal re-emergence independently of MP+CuA' and 'separation of MP from CuA basal of its fusion with CuPa' (Schubnel et al. 2019). They also share the characters 'ScP ending into C', 'presence of a posterior branch of MP basal of its distal fusion with MA', and 'presence of posterior branches of MA+MP basal to its fusion with RP'. The main differences between *Cacurgus* Handlirsch, 1911 and *Roqueia* gen. nov. are the presence of a first posterior branch CuPaβ of CuPa (characteristic of the Panorthoptera), and the re-emergence of MA directly from R in the former, while it re-emerges from RP in the latter. *Cacurgus* also differs from *Roqueia* gen. nov. in the very long stem of MP before its first posterior branch.

The character 'MA captured by R and distally re-emerging independently of MP+CuA' occurred at least two times in the superorder Archaeorthoptera. The very distal re-emergence of MA from RP instead of stem of R is a putative autapomorphy of *Roqueia* gen. nov. The general pattern of the presence of an elongate triangular area anteriorly and distally limited by R and RP and posteriorly by MP could be a putative synapomorphy of *Roqueia* gen. nov. with the Cnemidolestidae. Nevertheless, this hypothesis would need to be tested by a phylogenetic analysis of the whole Archaeorthoptera.

Conclusion

The present description of the new family Roqueiidae, for the genus *Roqueia* gen. nov., adds to the impressive diversity of the superorder Archaeorthoptera in the Late Carboniferous. Nevertheless, a phylogenetic analysis of the whole clade is more and more necessary to clarify the relationships between the different groups inside.

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References

Aristov DS. 2000. A new family of early Permian grylloblattids (Insecta: Grylloblattida) from the Ural Mountains. Far Eastern Entomologist **85**:1–4.

Aristov DS. 2013. New and little-known Eoblattida (Insecta) from the Paleozoic of Russia. Paleontological Journal 47:272–282. https://doi.org/10.1134/S0031030113030039

Aristov DS. 2014. Classification of the order Cnemidolestida (Insecta: Perlidea) with descriptions of new taxa. Far Eastern Entomologist 277:1–46.

Béthoux O, Nel A. 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. Zootaxa 96:1–88. https://doi.org/10.11646/zootaxa.96.1.1

Béthoux O. 2005. Cnemidolestodea (Insecta): an ancient order reinstated. Journal of Systematic Palaeontology 3:403–408. https://doi.org/10.1017/S147720190500163X

Béthoux O, Nel A. 2005. Some Palaeozoic ‘Protorthoptera' are 'ancestral' orthopteroids: major wing braces as clues to a new split among the 'Protorthoptera'. Journal of Systematic Palaeontology 2:1–25. https://doi.org/10.1017/S1477201904001488

Brongniart C. 1885. Les insectes fossiles des terrains primaires. Coup d’œil rapide sur la faune entomologique des terrains paléozoïques. Bulletin de la Société des Amis des Sciences Naturelles de Rouen (3) 21:50–68.

Dvořák T, Pecharová M, Krzemiński W, Prokop J. 2019. New archaeorthopteran insects from the Carboniferous of Poland: insights into tangled taxonomy. Acta Palaeontologica Polonica 64:787–796. https://doi.org/10.4202/app.00614.2019

Dvořák T, Pecharová M, Leipner A, Nel A, Prokop J. 2021. New archaeorthopteran insects from the Pennsylvanian of Piesberg reveal unexpected mosaic of morphological traits and colouration pattern of the tegmina. Historical Biology, https://doi.org/10.1080/08912963.2020.1867127

Gu J-J, Béthoux O, Ren D. 2011. *Longzhua loculata* n. gen. n. sp., one of the most completely documented Pennsylvanian Archaeorthoptera (Insecta; Ningxia, China). Journal of Paleontology 85:303–314. https://doi.org/10.1666/10-085.1

Gu J-J, Béthoux O, Ren D. 2014. A new cnemidolestodean stem-orthopteran insect from the Late Carboniferous of China. Acta Palaeontologica Polonica 59:689–696. https://doi.org/10.4202/app.2011.0204

Handlirsch A. 1911. New Paleozoic insects from the vicinity of Mazon creek, Illinois. American Journal of Science 31:297–326 + 353–377. https://doi.org/10.2475/ajs.s4-31.185.353.

Handlirsch A. 1937. Neue Untersuchungen über die fossilen Insekten. Annalen des Naturhistorischen Museums in Wien 48:1–140. https://www.jstor.org/stable/41768379

Langiaux J, Parriat H. 1974. Faune entomologique du bassin de Blanzy-Montceau. La Physiophile 81:62–74.

Martins-Neto RG, Gallego OF, Brauckmann C, Cruz JL. 2007. A review of the South American Palaeozoic entomofauna. Part I: the Ischnoneuroidea and Cacurgoidea, with description of new taxa. African Invertebrates 48:87–101. https://hdl.handle.net/10520/EJC84588

Nel A, Poschmann MJ. 2021. A new representative of the 'orthopteroid' family Cnemidolestidae (Archaeorthoptera) from the Early Permian of Germany. Acta Palaeontologica Polonica 66:641–646. https://doi.org/10.4202/app.00879.2021

Pinto, I.D. and Pinto de Ornellas, L. 1980. Upper Carboniferous insects from Argentina. 2. Familia Narkemocacurgidae (Paraplecoptera). Boletin de la Academia Nacional de Ciencias de Cordoba 53:287–291.

Schubnel T, Desutter-Grandcolas L, Legendre F, Prokop J, Mazurier A, Garrouste R, Grandcolas P, Nel A. 2020. To be or not to be: postcubital vein in insects revealed by microtomography. Systematic Entomology 45:327–336. https://doi.org/10.1111/syen.12399

Schubnel T, Legendre F, Roques P, Garrouste P, Cornette R, Perreau M, Perreau N, Desutter-Grandcolas L, Nel A. 2021. Sound vs. light: wing-based communication in Carboniferous insects. Communications Biology 4 (794):1–11. https://doi.org/10.1038/s42003-021-02281-0

Schubnel T, Roberts D, Roques P, Garrouste R, Desutter-Grandcolas L, Nel A. 2019. Moscovian fossils shed light on the enigmatic polyneopteran families Cacurgidae and Eoblattidae (Insecta: 'Eoblattida', Archaeorthoptera). Journal of Systematic Palaeontology 18:499–511. https://doi.org/10.1080/14772019.2019.1627595

van Beneden P-J, Coemans E. 1867. Un insecte et un gastéropode pulmoné du terrain houiller. Bulletin de l'Académie Royale de Belgique (2) 23:384–401.

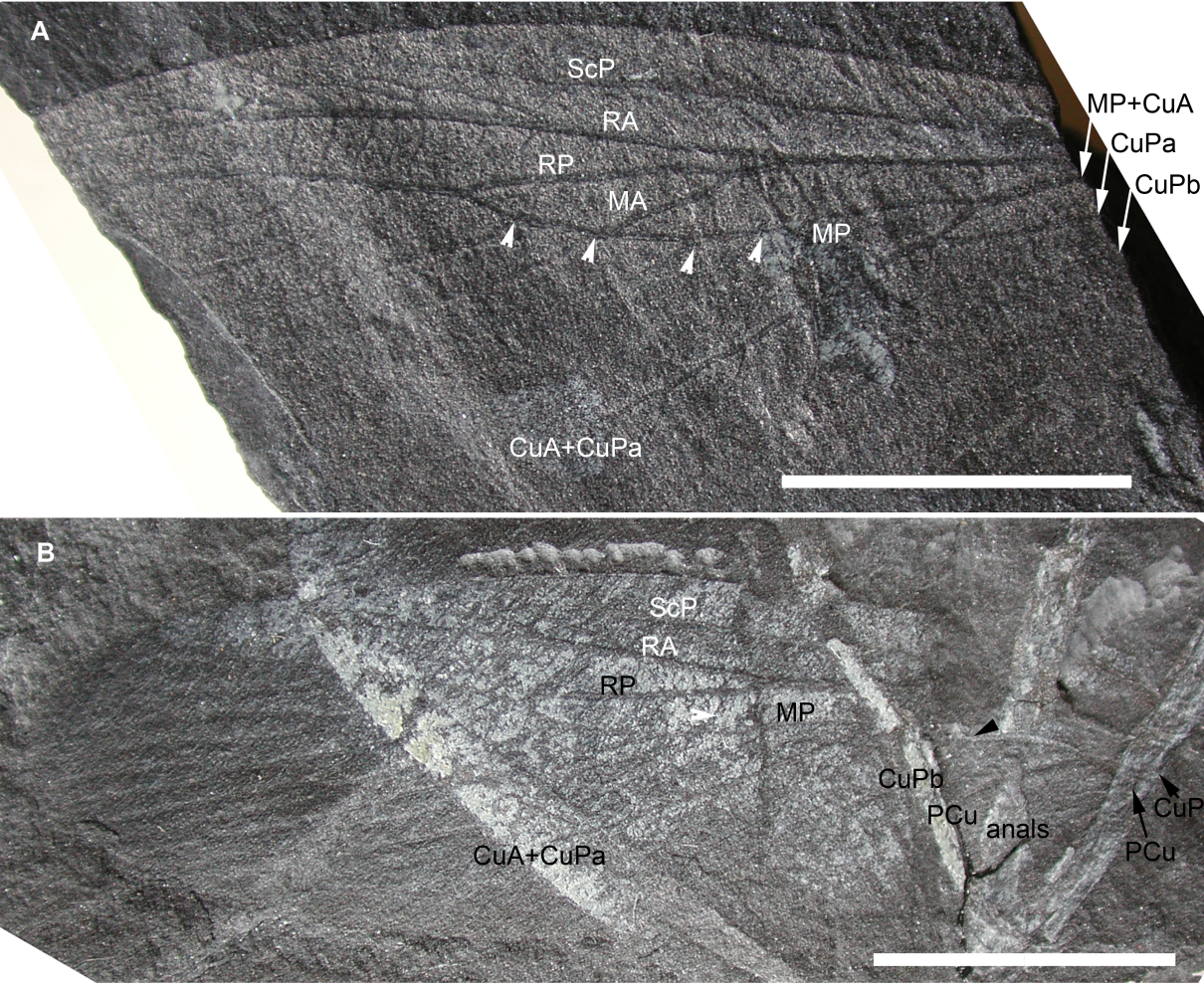
Wagner RH, Álvarez-Vázquez C. 2010. A redescription of the Stephanian species *Callipteridium virginianum* (Fontaine & White, 1880) comb. nov. and *Alethopteris leonensis* Wagner, 1964. Scripta Geologica Special Issue **7**:93–139.

Whalley PES. 1979. New species of Protorthoptera and Protodonata (Insecta) from the Upper Carboniferous of Britain, with a comment on the origin of wings. Bulletin of the British Museum of Natural History Geology 32:85–90. http://creativecommons.org/licenses/by-nc-sa/4.0/

Wittry J, Glasspool IJ, Béthoux O, Koll R, Cleal, CJ. 2014: A revision of the Pennsylvanian marattialean fern *Lobatopteris vestita* auct. and related species. Journal of Systematic Palaeontology 13:615–643. https://doi.org/10.1080/14772019.2014.936915

Figure 1. *Roqueia alpina* gen. et sp. nov. Nel & Duquesne, holotype. (A) Forewing Fa 0145b (counterimprint), white arrowheads bases of posterior branches of MP; (B) Second forewing Fa 0145 (imprint), black arrowhead base of CuPb, white arrowhead MA. Scale bars = 10 mm.

Figure 2. *Roqueia alpina* gen. et sp. nov. Nel & Duquesne, holotype. (A) Fa 0145b (counterimprint); (B) Fa 0145 (imprint), F.W. forewing, H.W. hind wing. Scale bars = 10 mm.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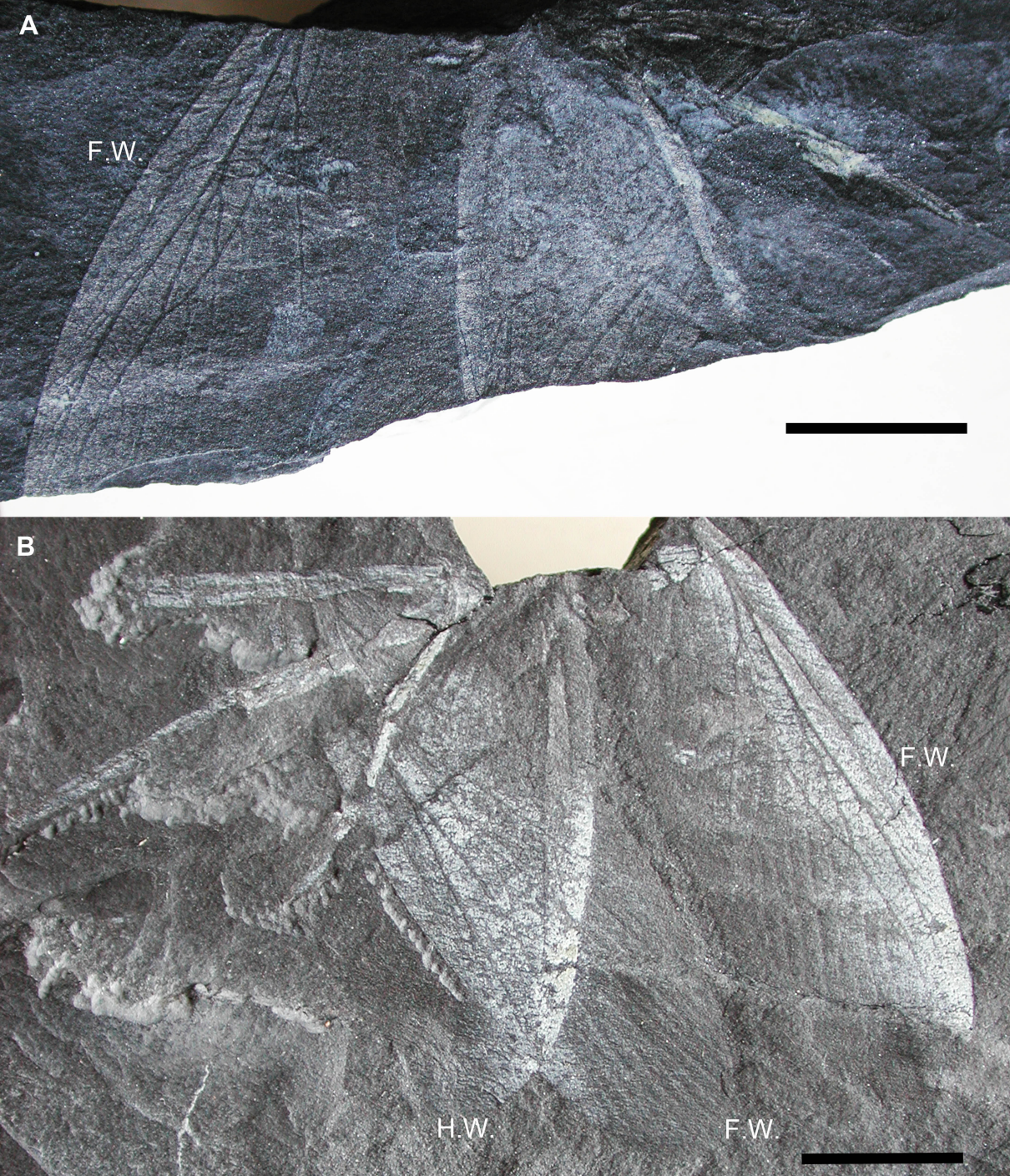
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