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***Parabintoniella papierae* n. gen., n. sp., a new Triassic representative of the Bintoniellidae, a poorly known extinct family of Orthoptera (Insecta)**

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KEY WORDS

Fossil insect,
Middle Triassic,
Grès à Voltzia,
Vosges,
France,
Madygen,
Kyrgyzstan,
new genus,
new species.

ABSTRACT

A new species of stem-Orthoptera, *Parabintoniella papierae* n. gen., n. sp., is described from the Grès à Voltzia Formation (Middle Triassic) of the Vosges (France). This new species, represented by two forewings, can be confidently assigned to the Mesozoic family Bintoniellidae, but it differs from the known representatives by its unique combination of character states, including a simple MA and numerous branches of CuA+CuPa α . The size difference between the two forewings is probably due to sexual dimorphism. This discovery complements our knowledge of the disparity of the various stem-groups of Orthoptera which emerged during the Permian and became extinct during the Mesozoic.

RÉSUMÉ

Parabintoniella papierae n. gen., n. sp., un nouveau représentant triasique de Bintoniellidae, une famille d'orthoptères (Insecta) éteinte peu connue.

Une nouvelle espèce d'orthoptère souche, *Parabintoniella papierae* n. gen., n. sp., est décrite de la Formation du Grès à Voltzia (Trias Moyen) des Vosges (France). Cette nouvelle espèce, représentée par deux ailes antérieures, peut être assignée avec certitude aux Bintoniellidae, une famille mésozoïque, mais elle diffère des représentants connus par son unique combinaison d'états de caractères, incluant une MA simple et de nombreuses branches de CuA+CuPa α . La différence de taille entre les deux ailes est vraisemblablement due à un dimorphisme sexuel. Cette découverte complète notre connaissance de la disparité des divers groupes-souches d'orthoptères qui ont émergé au Permien et qui ont disparu au cours du Mésozoïque.

MOTS CLÉS

Insecte fossile,
Trias moyen,
grès à Voltzia,
Vosges,
France,
Madygen,
Kirghizistan,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Extant crickets, katydids and grasshoppers (Orthoptera) account for about 30000 species (Cigliano *et al.* 2021) and therefore represent the most diverse order among the polyneopteran insects. The crown-group is believed to have originated during the Late Devonian or the early Mississippian (Song *et al.* 2020), with the earliest unambiguous stem-group representatives known from Early to Middle Pennsylvanian localities (e.g. Gu *et al.* 2017; age according to Trümper *et al.* 2020), and the earliest unambiguous crown-group representatives from Permian ones (Béthoux *et al.* 2002; Béthoux 2020). Besides early relatives of the two extant suborders, namely the Ensifera (crickets and katydids) and the Caelifera (grasshoppers and locusts), the Orthoptera were also represented during the Permian and the Triassic by a tremendous diversity of stem-group taxa, including the spectacular titanopterids (Sharov 1968, 1971; Béthoux 2007). In contrast, there was a less impressive, rarer and yet distinctive lineage, the Bintoniellidae, which is known from a few Triassic and Jurassic localities (Carpenter 1992; Gorochov 1995a, b; and references therein). Herein we report the discovery from the Middle Triassic Grès à Voltzia formation (Upper Buntsandstein) of the Vosges (France) of two forewings which belong to a new genus and species of this family.

MATERIAL AND METHODS

FOSSIL MATERIAL

The studied material consists of two isolated forewings, both composed of a part and a counterpart, belonging to the collection Louis Grauvogel at the ‘Staatliches Museum für Naturkunde Stuttgart’, Stuttgart, Germany. One bears the inventory numbers 5589 and 5590 and comes from the locality Gottenhouse (Bas-Rhin, France), the other bears the inventory numbers 9122a, b and comes from the locality Bust (Bas-Rhin, France). The two specimens were collected by Louis Grauvogel from the Grès à Voltzia Formation, which belongs to the Upper Buntsandstein and is early Middle Triassic in age (Gall & Grauvogel-Stamm 2005).

WING VENATION HOMOLOGIES AND TERMINOLOGY

Within the framework of the serial insect wing venation ground-plan (Lameere 1922, 1923), we follow topographic homology conjectures proposed by Béthoux & Nel (2001, 2002a) for total-Orthoptera (see Du *et al.* [2017] for references on alternative proposals and the related discussion). The adopted terminology and corresponding abbreviations are repeated below for convenience.

ABBREVIATIONS

AA	anterior Analis;
CuA	anterior Cubitus;
CuP	posterior Cubitus;
CuPa	anterior branch of CuP;
CuPa α	anterior branch of CuPa;
CuPa β	posterior branch of CuPa;

CuPb	posterior branch of CuP;
M	Media;
MA	anterior Media;
MP	posterior Media;
RA	anterior Radius;
RP	posterior Radius;
ScA	anterior Subcosta;
ScP	posterior Subcosta.

DATA ACQUISITION

Photographs were taken using a digital camera Canon EOS 5D Mark III coupled to a Canon MP-E 65 mm macro lens (all Canon, Tokyo, Japan) equipped with a polarizing filter. The embedding rock was used as reference for white balance. The resulting photographs were optimized using Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, United States).

Hand-made draft drawings were produced with the aid of a microscope equipped with a camera lucida (Zeiss SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10 \times /23 eye pieces, a Plan Apo S 1.0 \times FWD objective; all Zeiss, Jena, Germany). Drawings were finalized using Adobe Illustrator CS6 (Adobe Systems, San Jose, CA, United States) using both hand-made draft drawings and photographs.

SYSTEMATIC CONVENTIONS

Despite a moderate number of constituent species, the systematics of the Bintoniellidae fluctuated so far as to become confusing. The family was formally erected by Handlirsch in 1938 to include the Jurassic species *Bintoniella brodiei* Handlirsch, 1938. Then, Sharov (1968, 1971) added a further genus, including two species from the Triassic locality of Madygen, namely *Probintoniella triassica* Sharov, 1968 and *Probintoniella primaria* Sharov, 1968. According to this author the lack, in the forewing, of a distinct portion of CuPa α (his ‘CuA1’), commonly diverging from CuPa and fusing with CuA in Orthoptera (Béthoux & Nel 2002a), was the distinctive diagnostic character of the family. This led Béthoux (2012) to associate the corresponding character state on one hand, and the taxon on the other, under the proposal of cladotypic nomenclature, with the outcome that species lacking a basal free portion of CuPa α shall be assigned to the rankless, defined taxon *Bintoniellidae nom.* Handlirsch, 1938, *dis.* Sharov, 1968, *typ.* Béthoux, 2012.

In the interval and on the basis of material from the same origin as that studied by Sharov (1968, 1971), Gorochov (1987, 1989, 1994) erected a number of new genera to accommodate species very similar to those erected by Sharov (namely *Probintoniella triassica* Sharov, 1968 and *Oshiellana primaria* (Sharov, 1968)), of which the validity has been questioned (with the exception of *Eubintoniella ferganica* Gorochov, 1987; see Béthoux 2012). To avoid the issue of the delimitation of these genera and species it will suffice, in the following, to collectively refer to them as Oshiellinae Gorochov, 1987, in accordance with Gorochov (2005; and see Cigliano *et al.* 2021). It is noteworthy that *Oshiellana primaria* (Sharov, 1968), regarded by Gorochov (2005) as an Oshiellinae, displays a distinct basal free portion of CuPa α , which must then be regarded as a rare variant within the subfamily.

Furthermore, Gorochov (1989) transferred two other Madygen species erected by Sharov (1968), namely *Provitimia pectinata* Sharov, 1968 and *Proshiella ramivenosa* (Sharov, 1968), from the Vitimiidae to the Bintoniellidae. Gorochov (1989) created the new subfamily Proshielinae for them. It is noteworthy that the corresponding forewings display a distinct basal free portion of CuPa α . As a consequence, their assignment to the Bintoniellidae contradicted the delimitation of this taxon as proposed by Sharov (1968, 1971) as well as the subsequent definition proposed by Béthoux (2012). In other words, Gorochov (1989) expanded the delimitation of the Bintoniellidae in order to encompass the Proshielinae.

In the following we use the family name 'Bintoniellidae' as delimited by Sharov (1968, 1971) and defined by Béthoux (2012). In other words, we consider that it encompasses the subfamilies Bintoniellinae Handlirsch 1938 and the Oshielinae as delimited by Gorochov (2005), but that it excludes the Proshielinae.

SYSTEMATIC PALAEOLOGY

Order ORTHOPTERA Olivier, 1789
Family BINTONIELLIDAE Handlirsch, 1938

Genus *Parabintoniella* n. gen.

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TYPE SPECIES. — *Parabintoniella papirae* n. sp.; monotypic genus.

ETYMOLOGY. — After the name of a closely-related genus, namely *Bintoniella*, associated with the prefix 'para', i.e. 'beside' in Ancient Greek, indicative of the assumed close relationships between *Bintoniella* and the new genus.

DIAGNOSIS. — As for the type species.

Parabintoniella papirae n. gen., n. sp.
(Figs 1; 2)

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HOLOTYPE. — Specimen 5589/5590 (collection Louis Grauvogel at the 'Staatliches Museum für Naturkunde Stuttgart', Stuttgart, Germany) (Fig. 1A, B).

PARATYPE. — Specimen 9122a, b (collection Louis Grauvogel at the 'Staatliches Museum für Naturkunde Stuttgart', Stuttgart, Germany) (Figs 1C, D; 2).

DIAGNOSIS. — Forewing (and see Fig. 3): no distinct base of CuPa α diverging from CuPa (and fusing with CuA or M+CuA) (derived state shared with all Bintoniellidae as delimited herein); MA simple (derived state shared with *Bintoniella brodiei* and *Eubintoniella ferganica*); CuA+CuPa α with more than two branches (plesiomorphy shared with Proshielinae and Oshielinae); cross-veins forming loose, convex intercalaries between ScP branches (shared with Proshielinae, polarity unclear).

ETYMOLOGY. — The species epithet honours the late Francine Papier, who significantly contributed to the knowledge of the 'Grès à Voltzia' fossil insects.

TYPE LOCALITY AND STRATIGRAPHY. — The holotype specimen 5589/5590 was collected at Gottenhouse (Bas-Rhin, France) and the paratype specimen 9122a, b was collected at Bust (Bas-Rhin, France). Both specimens come from the 'Grès à Voltzia' (Upper Buntsandstein; early Middle Triassic; Gall & Grauvogel-Stamm 2005).

GENERAL DESCRIPTION

Forewing: length about 22.4–28.0 mm, width 6.4–8.0 mm; ScA conspicuous; in its median part, area between anterior wing margin and ScP broad, with cross-veins forming loose, convex intercalaries between ScP branches (concave); ScP reaching the anterior wing margin from two-thirds to three-quarters of wing length; RA/RP split slightly distal to wing mid-length; RA with anterior veinlets and cross-veins between them; RP without well-organized branching pattern, with five to eight terminal branches/veinlets covering the apex; M+CuA(+CuPa α) splitting into M and CuA+CuPa α at about the first third of wing length; free basal portion of M (between the M/CuA(+CuPa α) split and the MA/MP split) relatively long; both MA and MP simple (known in holotype only); CuA+CuPa α posteriorly pectinate, with four branches; no distinct base of CuPa α diverging from CuPa (and fusing with CuA or M+CuA; better visible in specimen 9122); CuPa β and CuPb simple; CuPb reaching posterior wing margin at wing mid-length; AA with at least four, simple veins; cross-veins reticulated (i.e. forming 2–3 cells between two main veins) between ScP veinlets, in the apical half, elsewhere mostly scalariform; along the posterior wing margin, areas between CuPb and AA branches with numerous, sigmoidal cross-veins; membrane uniformly hyaline.

SPECIMEN DESCRIPTIONS

Specimen 5589/5590 (Fig. 1A, B): adpression of an isolated, nearly complete left forewing, in both dorsal (5590) and ventral (5589) aspects, presumably of a female insect (see Remarks section); preserved length 26.6 mm (estimated complete length about 28.0 mm), width 8.0 mm (at its widest); RP with either eight terminal branches or seven with an intercalary vein between its most posterior branch and MA.

Specimen 9122a,b (Figs 1C, D; 2): adpression of an isolated left forewing, in both dorsal (9122a) and ventral (9122b) aspects, with most of the postero-distal area and area basal to the claval furrow (itself located along CuPb; i.e. the remigulum) missing, presumably of a male insect (see Remarks section); preserved length 20.6 mm (estimated complete length about 22.4 mm), width 6.4 mm.

REMARKS

From the difference in width of the two forewings at their widest, which is the single and most accurate comparable dimension between them, the size of the smallest one (Fig. 1C, D) is 80% that of the largest (Fig. 1A, B). This difference in size falls within the range of intra-specific variability and more particularly within that of sexual size dimorphism (SSD),

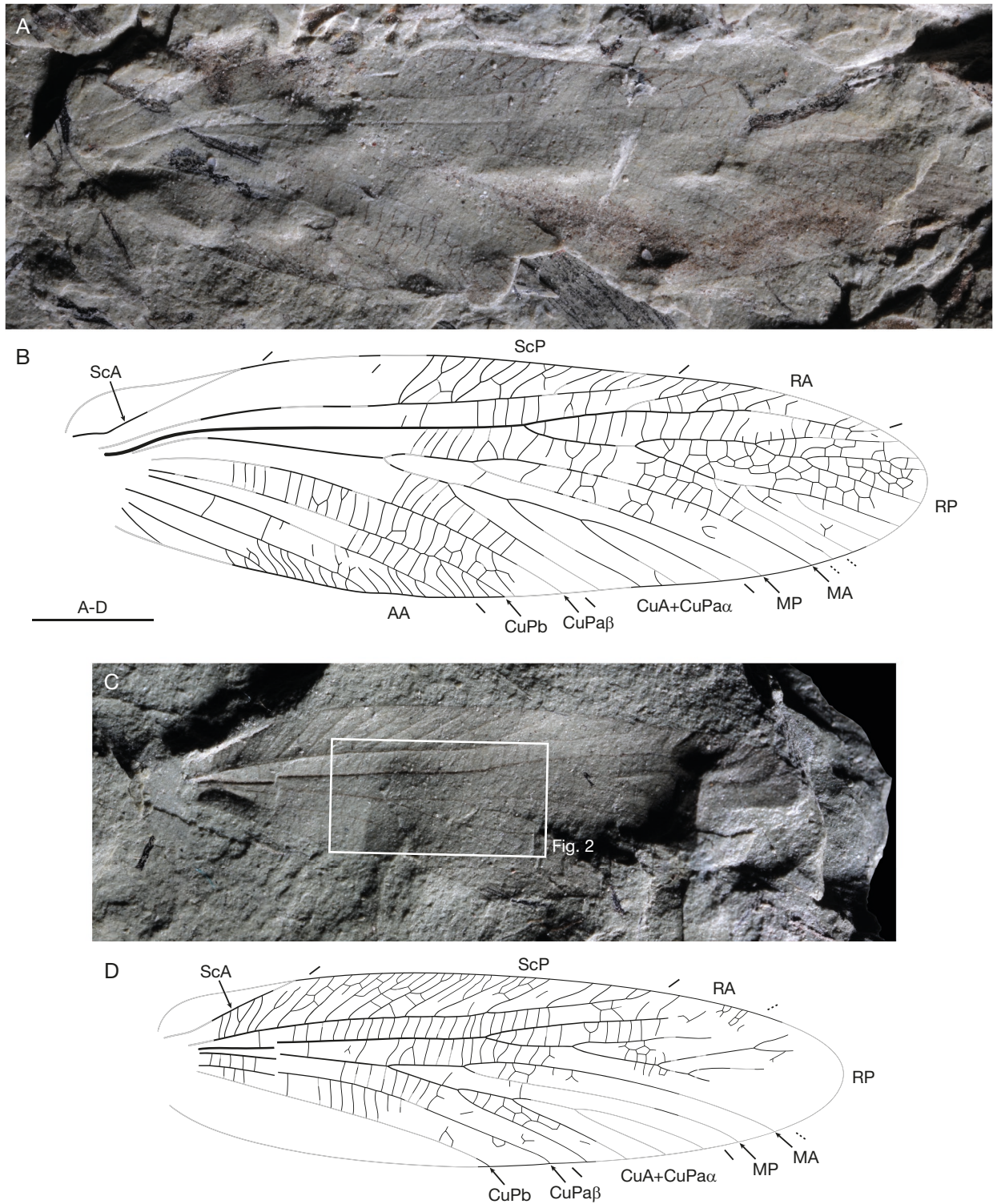


FIG. 1. — *Parabintoniella papierae* n. gen., n. sp.: **A, B**, holotype, specimen 5589/5590, left forewing (collection Louis Grauvogel at the ‘Staatliches Museum für Naturkunde Stuttgart’); **A**, photograph, ventral aspect (5589), light-mirrored; **B**, drawing of venation (reconstructed parts in grey); **C, D**, specimen 9122a, b, right forewing (collection Louis Grauvogel at the ‘Staatliches Museum für Naturkunde Stuttgart’); **C**, photograph, ventral aspect (9122b), light-mirrored (the white frame indicates the section enlarged in Fig. 2); **D**, drawing of venation (reconstructed parts in grey). Scale bar: 4 mm.

commonly female-biased in extant Orthoptera (Hochkirch & Gröning 2008). Moreover, such phenomenon is also known to occur in early stem-Orthoptera (Du *et al.* 2017) and has already been assumed for the related species *Bintoniella brodiei*,

with a similar ratio (Whalley 1982). As the other differences are minimal, it is doubtless that the two specimens belong to the same species, the specimen 5589/5590 presumably being a female, and the specimen 9122a, b a male.

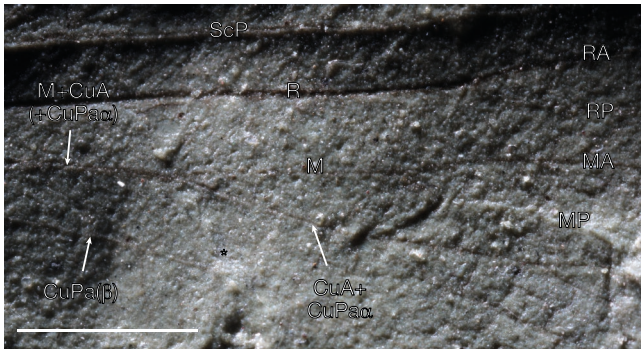


FIG. 2. — *Parabintoniella papierae* n. gen., n. sp., specimen 9122b (collection Louis Grauvogel at the 'Staatliches Museum für Naturkunde Stuttgart'), photograph of detail of medio-cubital area (location as shown with a white frame in Fig. 1C); the sign * indicates the area where the free basal portion of CuPa α , present in the Orthoptera groundplan but absent in the Bintoniellidae, could be expected to occur. Scale bar: 2 mm.

With the aid of the systematic conventions posited above, the relationships between the species to which the new specimens belong can be discussed (Fig. 3). The occurrence of the character state 'in forewing, no distinct base of CuPa α diverging from CuPa (and fusing with CuA or M+CuA)' (to be understood as 'beyond the wing base') qualifies an assignment to the Bintoniellidae. In other words, affinities with the Proshiellinae can be excluded. This condition is best observed in the specimen 9122 (Fig. 2).

In contrast to all the Proshiellinae and the Oshiellinae, in which MA commonly has 3–4 branches in the forewing, the species to which the new specimens belong displays a simple MA. This feature, which is shared with *Bintoniella brodiei* (see Whalley 1982; Béthoux 2012) and *Eubintoniella ferganica* (see the original description), is definitely derived and represents the diagnostic trait of a yet unnamed taxon. Furthermore, in contrast to *Bintoniella brodiei* and *Eubintoniella ferganica*, in which CuA+CuPa α has two branches (rare exceptions are known in *Bintoniella brodiei*, see Béthoux 2012), the species to which the new specimens belong displays a CuA+CuPa α with four branches. This trait must be regarded as a plesiomorphy, as Proshiellinae and Oshiellinae commonly possess a 4- to 5-branched CuA+CuPa α . It follows that the species to which the new specimens belong is the sister-group of *Bintoniella brodiei* and *Eubintoniella ferganica* (Fig. 3A).

Unlike Bintoniellidae, in which no cross-veins occur between ScP branches, the species to which the new specimens belong displays cross-veins forming loose, convex intercalaries between ScP branches. This state occurring in Proshiellinae, it can then be regarded as a plesiomorphy within Bintoniellidae. Accordingly, the species to which the new specimens belong would be the sister-group of all other Bintoniellidae (namely, Oshiellinae, *Bintoniella brodiei* and *Eubintoniella ferganica*; Fig. 3B). Considering (i) that this scenario implies that the number of branches of MA would have been subjected to homoplastic evolution, and, on the other hand, (ii) that the occurrence of cross-veins between ScP veinlets, and their lack thereof, can both occur within

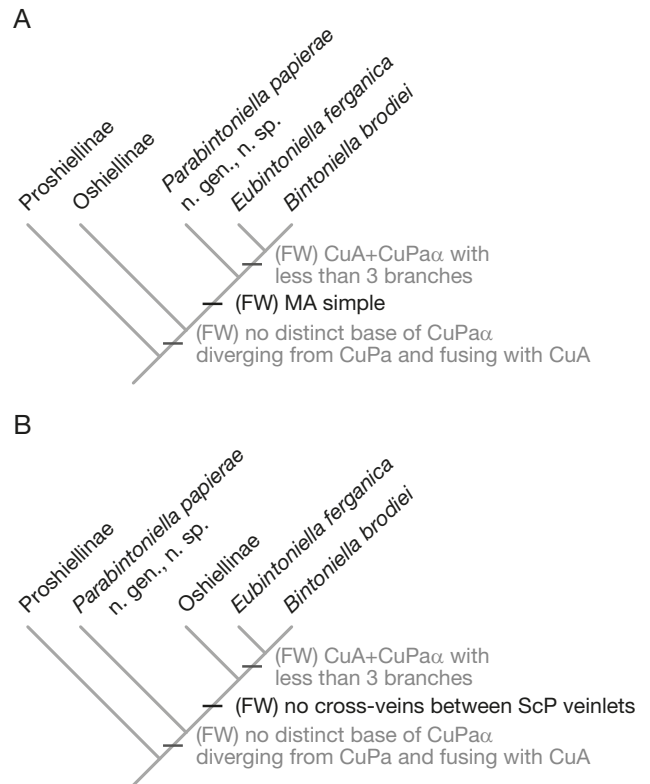


FIG. 3. — Summary of the assumed phylogenetic relationships of the taxa and species considered in this contribution (character states invariant under different hypotheses in dark grey): **A**, favoured hypothesis, assuming that *Parabintoniella papierae* n. gen., n. sp. is the sister-group of *Eubintoniella ferganica* Gorochov, 1987 and *Bintoniella brodiei* Handlirsch, 1939, owing to the occurrence of a simple MA in the forewing of these species; **B**, alternative hypothesis, assuming that *Parabintoniella papierae* n. gen., n. sp. is the sister-group of Oshiellinae, *Eubintoniella ferganica* and *Bintoniella brodiei*, owing to the occurrence of cross-veins between ScP veinlets in the forewing of *Parabintoniella papierae* n. gen., n. sp.

a single genus (such as in the Permian stem-Orthoptera genus *Tcholmanvissia* Zalesky, 1929; see Béthoux & Nel 2002b), we consider this hypothesis less likely.

CONCLUSION

Parabintoniella papierae n. gen., n. sp. is a new representative of the Bintoniellidae, a yet poorly documented family of Mesozoic Orthoptera. It complements our knowledge of the disparity of the various taxa composing the stem-group of Orthoptera which emerged during the Permian and became extinct during the Mesozoic.

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