Article

Discovery of the First Blattinopsids of the Genus *Glaphyrophlebia* Handlirsch, 1906 (Paoliida: Blattinopsidae) in the Upper Carboniferous of Southern France and Spain and Hypothesis on the Diversification of the Family

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Simple Summary: Two new representatives of the blattinopsid genus *Glaphyrophlebia* are described and illustrated from the Gzhelian of Southern France and Spain. They suggest that the diversity of this genus began to increase during the latest Carboniferous, possibly in relation to the climatic changes occurring at that time.

Abstract: *Glaphyrophlebia victoriensis* sp. nov. (Paoliida: Blattinopsidae) is the third Gzhelian representative of the genus and is described based on a beautiful forewing from the Var department in Southern France. Together with the description of another forewing fragment of a *Glaphyrophlebia* sp. from the Province of León in NW Spain, they improve our knowledge of fossil insects from French and Spanish late Carboniferous deposits. The specimen of *Glaphyrophlebia* sp. is the first mention of the family in the Carboniferous of Spain and extends the geographical distribution of the genus. These descriptions suggest that the genus *Glaphyrophlebia* was speciose during the Upper Pennsylvanian, while otherwise, very diverse in the early and middle Permian strata of the Russian Federation. We proposed the first hypothesis to explain the diversification of family and of its most speciose genera, and argue their diversity dynamics were likely linked with the major environmental changes that followed the collapse of the Carboniferous rainforest notably the extension of arid biomes during the Permian period. The exquisite preservation and the fineness of the sediment from Tante Victoire, in which the new species was found, suggests that the locality is suitable for preserving other fossil insects and will require additional investigations.

Keywords; Insecta; Polyneoptera; Gzhelian; new insect locality; Pennsylvanian

1. Introduction

The small Palaeozoic polyneopteran family Blattinopsidae currently contains 12 genera, but only five of them can be accurately considered informative because six are based on very fragmentary fossils and one could be related to another group [1]. Prokop et al. [2] revised the systematic placement of the family and proposed to include it within the order Paoliida on the basis of putative wing venation synapomorphies (i.e., configuration of the cubital area). Recently, the family Blattinopsidae was the subject of several new descriptions and revisions, which have greatly increased its diversity, improved its temporal and geographical distribution, and refined the limits of its constitutive genera [1,3-8].

The number of species of each blattinopsid genus is highly heterogeneous with genera composed of only one species (e.g., *Avionblattinopsis* [1]), and others with more than 20 documented species such as *Blattinopsis* Giebel, 1867 or *Glaphyrophlebia* Handlirsch, 1906 (https://paleobiodb.org). Interestingly, *Blattinopsis* is the most diversified blattinopsid genus during the late Carboniferous while the other most speciose blattinopsid genus, namely *Glaphyrophlebia,* is diverse later during the early to middle Permian, but much rarer during the Carboniferous. This particular diversity pattern is maybe indicative of two genera occupying similar ecological niches and diversifying respectively when the other is less present (competition or diversity dependence). It may also reflect the effect of global changes (e.g., increase of CO_2 concentration in the atmosphere, change in floral assemblages) known to occur between the Carboniferous and the Permian (i.e., Carboniferous rainforest collapse) and thought to have affected the diversity dynamics of major insect clades. However, the poor delineation of several blattinopsid genera hampers our understanding of their diversification and extinction. This is notably the case of the genus *Glaphyrophlebia* known from two Moscovian and two Gzhelian species and a few specimens from North America and Western Europe, with one of these species likely not a *Glaphyrophlebia* (see below). Therefore, the description of well-preserved specimens is crucial to refining the limits of each genus while simultaneously bringing information on the value of morphological diagnostic characters. We used the fossil record of the family and of the genera *Blattinopsis* and *Glaphyrophlebia* to propose a hypothesis on the diversification of the family and its link with climate changes and changes in floral assemblages between the Carboniferous and the Permian periods.

During preliminary fieldwork in the Gzhelian quarry of Tante Victoire in the Var department (Southern France), we found a very well-preserved forewing that we confidently attribute to a new species of *Glaphyrophlebia*. This discovery highlights the potential of the locality of Tante Victoire, the latter being very promising for future discoveries of fossil insects. We also describe the first specimen of Blattinopsidae from the Palaeozoic of Spain, increasing the distribution of this family to this country; this study is in line with a very recent impulse to describe the few Carboniferous insects both historically and recently found in Spain [9, 10].

2. **Material and methods**

The holotype of the new species was found during an ancient preliminary field investigation in 1996 in the ancient quarry of iron of Tante Victoire, Var department. The Spanish specimen was found by one of us (AHO) during the preparation of a PhD focused on the revision of the morphogenus *Pecopteris* at the tip of a small coal mine near El Repoteo in Tremor de Arriba, Province of León. No additional preparation of the fossils was necessary for their study. The French specimen was photographed using a Canon 50D camera with an attached Canon 65 MPE camera lens and mounted on an automated stacking rail (StackShot), and all these images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures of the French specimen were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software. The Spanish wing specimen and plant remains (on the same slab´s surface) were photographed using a compound microscope Olympus BX53 equipped with an attached digital camera, and with an Olympus Tough TG-5, respectively. The wing fragment specimen is a stacked image, unlike the plant remains images. The plate with these images was composed using Photoshop CS2 version 9.0.

After the 'Notice de la Carte Géologique à 1/5000, BRGM, France' of Toulon, the small ancient iron quarry of Tante Victoire (Playes Massif, Six-Fours-les-Plages town, Var department) is of Gzhelian age (late Stephanian) according to studies of the palaeoflora notably composed of *Pecopteris*, *Calamites*, *Walchia*, and *Sigillaria*. The holotype is stored in the Palaeontological collection of the Muséum National d'Histoire Naturelle (MNHN.F), Paris, France.

The Spanish wing fragment was found on a sandstone slab at the tip of a small mine 2.4 km at the NW of Tremor de Arriba, Province of León. This mine belongs to the El Bierzo outcrop, Noceda Block, Tramo de Espina [11] and is of Gzhelian age based on the rich floral assemblage [12, 13]. The specimen is stored in the collection of the Museo Geominero (Instituto Geológico y Minero de España, CSIC), Madrid, Spain.

Wing venation nomenclature follows Prokop et al. [2] and Schubnel et al. [14], especially concerning the presence of a postcubital veins in Pterygota. Abbreviations are as follows: A anal vein(s); arc arculus reinforced oblique crossvein between M and CuA; C costal vein; CuA cubitus anterior; CuP cubitus posterior; M median vein; PCu postcubital vein;.RA radius anterior; RP radius posterior; ScP subcostal posterior.

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3. **Results**

Systematic Palaeontology

Order Paoliida Handlirsch, 1906

Family Blattinopsidae Bolton, 1925

Type genus. *Blattinopsis* Giebel, 1867

Other genera (after Paleobiology Database). *Avionblattinopsis* Quispe et al., 2021, *Glaphyrophlebia* Handlirsch, 1906, *Klebsiella* Meunier, 1908, and *Stephanopsis* Kukalová, 1958. The genera *Alienus* Handlirsch, 1906, *Balduriella* Meunier, 1925, *Microblattina* Scudder, 1896, *Protoblattiniella* Meunier, 1912, *Rhipidioptera* Brongniart, 1893, and *Westphaloblattinopsis* Béthoux & Jarzembowski, 2010 need to be revised according to Quispe et al. [1].

Genus *Glaphyrophlebia* Handlirsch, 1906

Type species. *Glaphyrophlebia pusilla* Handlirsch, 1906

Glaphyrophlebia victoiriensis Nel, Garrouste & Jouault sp. nov.

Figures 1–2

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Etymology. Named after the type locality Tante Victoire.

Material. Holotype MNHN.F.A71360 (part and counterpart of a nearly complete forewing, with extreme apex missing), stored at Muséum national d'Histoire naturelle, Paris, France.

Age and outcrop. Gzhelian of Tante Victoire, Var department, France.

Diagnosis. Forewing characters only. Wing large and elongate, ca. 18 mm long; costal area at base of RP slightly wider than subcostal area; ScP flexed S-line at its apex; vein bow between RA and main stem of M; RP with six main branches; M with four branches; anterior branch of M forked close to M fork; anterior branch of CuA zigzagged with numerous crossveins between anterior and posterior main branches; posterior branches of CuA zigzagged.

Description. No particular trace of coloration; wing ca. 18.0 mm long and ca. 5.7 mm wide; costal space with veinlets mainly simple; ScP ending on C well distad mid-wing; stem R weakly sigmoidal at base; base of RP at 5.0 mm from wing base, second fork of RP slightly distad M fork; convex arculus entering CuA well before its first fork; M with four branches, fork of anterior branch well-basad fork of second branch; CuA with a zigzagged anterior branch, and with 14 zigzagged and rather weak posterior branches, first fork located proximal to M fork; CuP straight and simple; PCu simple and slightly sigmoidal; three anal veins; numerous simple crossveins in radial and median areas; distinct longitudinal furrows between branches of RP and M, reaching edge of wing; vein bow between RA and main stem of M only.

Remarks. This fossil is undoubtedly a forewing because of the narrow anal area. It can be attributed to the order Paoliida *sensu* Prokop et al. [2] because of the following characters: concave ScP approximating RA in distal half of wing; strongly convex 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 family Paoliidae Handlirsch, 1906 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 family Anthracoptilidae Handlirsch, 1922 are excluded because they all have numerous anterior concave branches of CuA, while the new fossil has only one, as in the Blattinopsidae.

Within the known Blattinopsidae except in *Avionblattinopsis*, ScP is ending on C as in the new fossil, precluding affinities with the latter genus. Additionally, the anterior branch of CuA is better defined in *Avionblattinopsis* than in the new fossil, and the area between ScP and R/RA is just half as wide as area between ScP and C in *Avionblattinopsis* while the two areas are of the same widths in the new fossil [1]. Interestingly, the type species of *Stephanopsis*, namely *Stephanopsis incerta* [15] (originally in the genus *Blattinopsis* Giebel, 1867) has an area between ScP and RA even much narrower than that of *Avionblattinopsis*, excluding affinities of the new fossil with this genus [15].

In the genus *Klebsiella*, ScP is strongly approximating RA before ending on C, and the crossveins in the radial and median areas are much less numerous than in the new fossil, which precludes affinities of the new specimen with this genus [1].

In the new fossil, and in the described species of the genus *Glaphyrophlebia*, there are distinct longitudinal furrows between branches of RP and M, reaching the edge of the wing, unlike in *Blattinopsis*. On the contrary, the new fossil would share with *Blattinopsis* the presence of numerous crossveins between branches of RP and M, unlike many *Glaphyrophlebia* [1, 3, 5], but some species currently attributed to the latter genus have also rather numerous crossveins in the radial and median areas [7, 8]. Therefore, the new species is attributed to the genus *Glaphyrophlebia*.

Following the key to the Permian *Glaphyrophlebia* spp. proposed by Aristov et al. [8], the character ‘M branching (besides terminal forks)’ excludes affinities with all these species except *G. anderhalterorum* Beckemeyer, 2013 (lower Permian of USA), *G. clava* Kukalová, 1965 (lower Permian of Czech Republic), *G. arnulfi* Hörnschemeyer & Stapf, 2001, *G. jeckenbachi* Hörnschemeyer & Stapf, 2001, and *G. rohwedderi* Hörnschemeyer & Stapf, 2001 (all three from lower Permian of Germany). The new fossil differs from *G. anderhalterorum* because there is no longitudinal vein emerging from R basad RP [16]. Affinities with the species *Glaphyrophlebia clava* and *G. arnulfi* are excluded because CuA is divided into an anterior branch with one-two terminal forks and comb-like posterior branch in the new fossil while the CuA is pectinate in *G. clava* and in *G. arnulfi* [17]. The new specimen further differs from *G. arnulfi* owing to its comparatively wide costal space (i.e., wider than subcostal space at the diverging point of RP) while the costal space of *G. arnulfi* is thinner than the subcostal space [17].

Glaphyrophlebia rohwedderi differs from the new fossil and *G. jeckenbachi* because of its ScP not flexed S-line at apex [17]. *G. rohwedderi* also differs from the new specimen owing to the strange branching pattern of the R i.e., with dichotomy (considered to be anterior branch of MP, [17]) and a second dichotomy creating RP. Similarly, the branching pattern of M (considered as the MP in [17]) in *G. rohwedderi* differs from that in the new specimen because it has posterior branch (MP as we interpreted it) forking close the wing margin (vs. well before in the new specimen).

The forewing length and width can be used as discriminatory characters between species when the range of these two measures greatly differs between two species. For example, the forewing length of *Glaphyrophlebia jeckenbachi* ranges between 10 and 14 mm for a width ranging between 4.1 to 4.8 mm, while in the new fossil, the wing is about 18 mm long (not entirely preserved) for a width of 5.7 mm [17]. Additionally, the anterior branch of CuA of *G. jeckenbachi* is better defined than in the new fossil in which it is more zigzagged with much more crossveins between the anterior and posterior main branches. The vein bow is between RA and CuA in *G. jeckenbachi* while it is located between RA and the main stem of M in the new fossil. Lastly, the new specimen has six main branches of RP while there are only five of them in *G. jeckenbachi*.

Glaphyrophlebia glinka Aristov, Rasnitsyn & Naugolnykh, 2022 (lower Permian of the Russian Federation) is based on the basal half of a forewing, ca. 10 mm long, which renders difficult a detailed comparison with the new fossil. Nevertheless, the new fossil differs from *G. glinka* in possessing a comparatively wide costal space (i.e., wider than subcostal space at the diverging point of RP), but also owing to its RP less pectinated (i.e., wider space between RP branches and apparently less of them) [8].

Glaphyrophlebia rossica (middle Permian of the Russian Federation) is based on the middle half of a forewing, with base and apex missing, ca. 7.5 – 8 mm long [18]. Nevertheless, the illustration of Martynov [18] suggests that the M is simple (a surprising configuration for this vein), and that the CuA is heavily branched and somewhat pectinate, which strongly differs from the forked M and the non-pectinate CuA of the new specimen.

Glaphyrophlebia pusilla (Moscovian, Mazon Creek, USA), type species of the genus, is not listed nor keyed in [8]. Handlirsch [19] indicated nothing on the vein bow. Its forewing is incomplete, but ca. 10 mm long. It also differs from the new fossil in its M with only two branches instead of four in the new fossil, and in its ScP not flexed S-line at its apex (vs. flexed in the new fossil).

Glaphyrophlebia pygmaea (Meunier, 1907) (Gzhelian of Commentry, France, recently attributed to this genus [17]) is not listed nor keyed in Aristov et al. [8] or in the other recent papers on Blattinopsidae [3-7]. It has the forewing venation characters proper to the genus *Glaphyrophlebia*, especially the presence of longitudinal furrows between branches of RP and M, reaching the edge of the wing. Its forewing is 12.2 mm long and 4.7 mm wide, thus quite shorter than that of the new fossil, and its vein bow is between RA and CuA. Lastly, its posterior branches of CuA are figured better organized, straight and well pectinate (Fig. 3), while they are zigzagged in the new fossil.

Glaphyrophlebia wettinensis [20] (Gzhelian of Germany, recently attributed to this genus [17]) is also not listed nor keyed in Aristov et al. [8]. It also has a vein bow between RA and CuA, no well-defined anterior branch of CuA, and a straight ScP, unlike the new fossil [17,20]. Additionally, the anterior branch of M is forked closed to the first dichotomy of M while simple or forked far distad the first dichotomy of M in *G. wettinensis* [17].

Glaphyrophlebia delicatula Bolton, 1934 (Moscovian, 314.6 Ma, South Wales, UK, recently attributed to this genus [17]) is also not listed nor keyed in Aristov et al. [8]. It is based on a very incomplete fragment of forewing. Bolton [21] did not indicated the presence of longitudinal furrows between branches of RP and M, and these are not visible in the photograph of the holotype. Therefore, the placement and attribution of the species to the genus *Glaphyrophlebia* is highly uncertain.

Based on the detailed comparison provided above, the new fossil represents a new species of the genus *Glaphyrophlebia*, and it is, therefore, the third one from the Carboniferous confidently placed in this genus.

Glaphyrophlebia sp.

Figure 4A

Material. Costo-apical portion of a forewing with the collection number MGM-822H-1 (previous collection number LE-24-101), stored at Museo Geominero (Instituto Geológico y Minero de España, CSIC), Madrid, Spain.

Age and outcrop. Gzhelian of El Bierzo, León Province, Spain.

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Description. Length of fragment ca. 8 mm; area between C and ScP ca. 0.6 mm wide in preserved part; ScP distally straight, ending into C; area between ScP and RA ca. 0.75 mm wide; area between RA and RP ca. 0.6 mm wide; RA with at least six weak apical branches; RP with six–seven weakly curved posterior branches, with distinct longitudinal furrows between them.

Remarks. This fossil also corresponds to a fragment of a forewing of *Glaphyrophlebia* because of the presence of distinct longitudinal furrows between branches of RP, ScP ending on C, area between ScP and RA slightly broader than area between ScP and C, and area between RA and RP very broad. The distal part of vein ScP nearly straight excludes affinities with *Glaphyrophlebia victoriensis* sp. nov., but could fit with *Glaphyrophlebia pygmaea*. Nevertheless, the incompleteness of this fossil prevents its attribution to a precise species. A complete floral assemblage was found on the same or on slabs close to the isolated wing (Fig. 4B-F).

4. **Macroevolutionary, Taphonomic, and Palaeoecological Comments**

The Blattinopsidae arose during the late Carboniferous and diversified during a period of drastic palaeoenvironmental changes i.e., the transition from Carboniferous wetlands to more and more arid forests and conditions during the Permian. In fact, the late Carboniferous is renowned for its ‘Coal Forests’ – widely distributed in Europe and North America around the equator – that developed under everwet conditions sometimes with a drier season [22]. Later, during the Pennsylvanian, a dramatic collapse of these rainforests began (commonly called the Carboniferous rainforest collapse, CRC), and led by the early Permian to their replacement in many regions by dryland vegetation as a more arid climate developed [23, 24]. We investigate a plausible link between these events and the diversification of the Blattinopsidae, a link that could be extended to other insect lineages.

Currently, the fossil record of the Blattinopsidae is heterogeneous from the Middle Pennsylvanian to the middle Guadalupian (Fig. 5A), with its highest diversity during the Gzhelian and Asselian i.e., around the Carboniferous/Permian boundary (C/P boundary) (https://paleobiodb.org). Another period of high diversity is the Kungurian, but it is difficult to assess the effect of one or a few variables (e.g., changes in floral assemblages, temperature, concentration of CO_2 in the atmosphere) on changes in the dynamics of the family (Fig. 5). From a pure correlation perspective, which does not necessarily imply causality, the highest level of diversification of Blattinopsidae and of the genus *Blattinopsis* is documented during a relatively cold period corresponding with the C/P boundary [25,26]. Oppositely, the genus *Glaphyrophlebia* is highly diversified during the Kungurian, a comparatively hot period [25,26]. This observation is not surprising as variations in warming and cooling periods are a probable driver of the diversification of some insect clades and are known to result in diversification changes over the evolutionary history of insects [27, 28].

The Blattinopsidae and the genus *Blattinopsis* are also highly diversified just after the CRC i.e., after the gradual rise of opportunistic ferns during the late Moscovian [29] followed during the earliest Kasimovian by the extinction of the dominant lycopsids and their replacement by tree fern-dominated ecosystems [30, 31]. As aforementioned, the period of diversification of the Blattinopsidae also corresponds with the beginning of the development of arid and warm temperate biome and with the diminution of wet tropical [32]. Therefore, we assume that the diversification of the Blattinopsidae is linked with the CRC (i.e., with changes in floral assemblages), the rise of new plant lineages and their diversification, and the expansion of arid biome after the C/P boundary. Similar correlations have already been demonstrated for other insect clades and are likely to occur for putative phytophagous lineages strongly linked with their host plants [33].

This hypothesis is also supported by the floral assemblages found in the Spanish outcrop of El Bierzo. In fact, the thin slab where the Spanish wing fragment and associated plant remains were found is a sandstone, containing fossils with a shallow relief (positive molds) preserving only testimonial portions of carbonaceous films. The plants in this assemblage are very diverse, containing many species represented: cf. *Asterophyllites equisetiformis* (Schlotheim, 1820) Brongniart, 1828, *Sphenophyllum oblongifolium* (Germar & Kaulfuss, 1831) Gutbier, 1843 (Fig. 4F), *Sphenophyllum* cf. *alatifolium* Renault, 1890, *Oligocarpia gutbieri* Göppert, 1841, *Oligocarpia leptophylla* (Bunbury, 1853) Grauvogel-Stamm & Doubinger, 1975 (Fig. 4D), *Sphenopteris* sp.-1, *Sphenopteris* sp. aff. *mathetii* (Fig. 4F), *Diplazites unitus* (Brongniart, 1836) Wagner & Martínez-García, 1998, *Pecopteris daubreei* Zeiller, 1888 (Fig. 4E), *Pecopteris* sp., *Dicranophyllum gallicum* Grand'Eury, 1877, cf. *Mixoneura* sp., cf. *Odontopteris* sp. (Fig. 4F) and *Dicksonites* sp. Although there are many species/morphotypes (14+wing) most of them are very broken remains, occasionally they are really tiny, in accordance with their deposition in the stream of a river. Only three species are large enough to be considered parautochthonous:

Oligocarpia gutbieri (Fig. 4B): this plant lived in variable habitats, from lowland places to hillside environments [34].

Dicranophyllum gallicum (Fig. 4C): this species developed on mesophytic or even xerophytic communities on basin-margin slopes [35-38].

Diplazites unitus (Fig. 4D,F): as *O. gutbierii*, occupied variable habitats, from lowland places as floodplains or swampy areas to hillside environments [34, 37].

The sample contains an essentially allochthonous flora, but in part parautochthonous plants that allow us to infer the palaeoenvironment where the *Glaphyrophlebia* could live. The sandstone was formed from the sediments deposited by a river far from the most basal parts of the basin and that ran through areas close to topographic reliefs that allowed the development of mesophytic or even xerophytic floras.

Similarly, the presence of *Walchia* in the French locality also supports mesophytic affinities of the flora, but additional studies have to be conducted to provide a full picture of the floral assemblage and taphonomy of Tante Victoire.

Despite the fact that the remains of the genus *Glaphyrophlebia* are mainly fossilized in water bodies or very humid local environments of preservation, on a regional scale it seems these insects developed or lived in mesophytic and/or xerophytic palaeoenvironments. The fossil record of the genus *Glaphyrophlebia*, which likely could have fed on spores (phytophagous) according to Aristov et al. [8], also fits with a long xerophytic period (Pennsylvanian–late Permian). The expansion of this genus in the Permian of Russia, which corresponds to a relatively arid and warm time period, might be correlated with an increase in the abundance of xerophytic vegetation (to which the *Glaphyrophlebia* are putatively adapted), but additional data and statistical testing will be required.

It is also important to mention that the reduced number of specimens and species of Blattinopsidae (compared with the Carboniferous or earliest Permian) found in Permian deposits may be directly linked with the fossilization that occurred mostly in palaeolakes. The latter are often surrounded by non-xerophytic vegetation and are, therefore, not favorable to the development of Blattinopsidae, which limits their potential for fossilization.

5. **Conclusions**

Glaphyrophlebia victoriensis sp. nov. is the third Gzhelian species of this genus. Together with the discovery of the first known fossil wing of *Glaphyrophlebia* from Spain, it serves to increase the diversity and distribution of blattinopsids documented from the Western European Carboniferous deposits and helps to document the wing venation variability found in the genus *Glaphyrophlebia*. The new species is direct evidence of the underestimated diversity of this genus during the late Carboniferous because the genus is otherwise very speciose in the early and middle Permian strata, especially in deposits of the Russian Federation.

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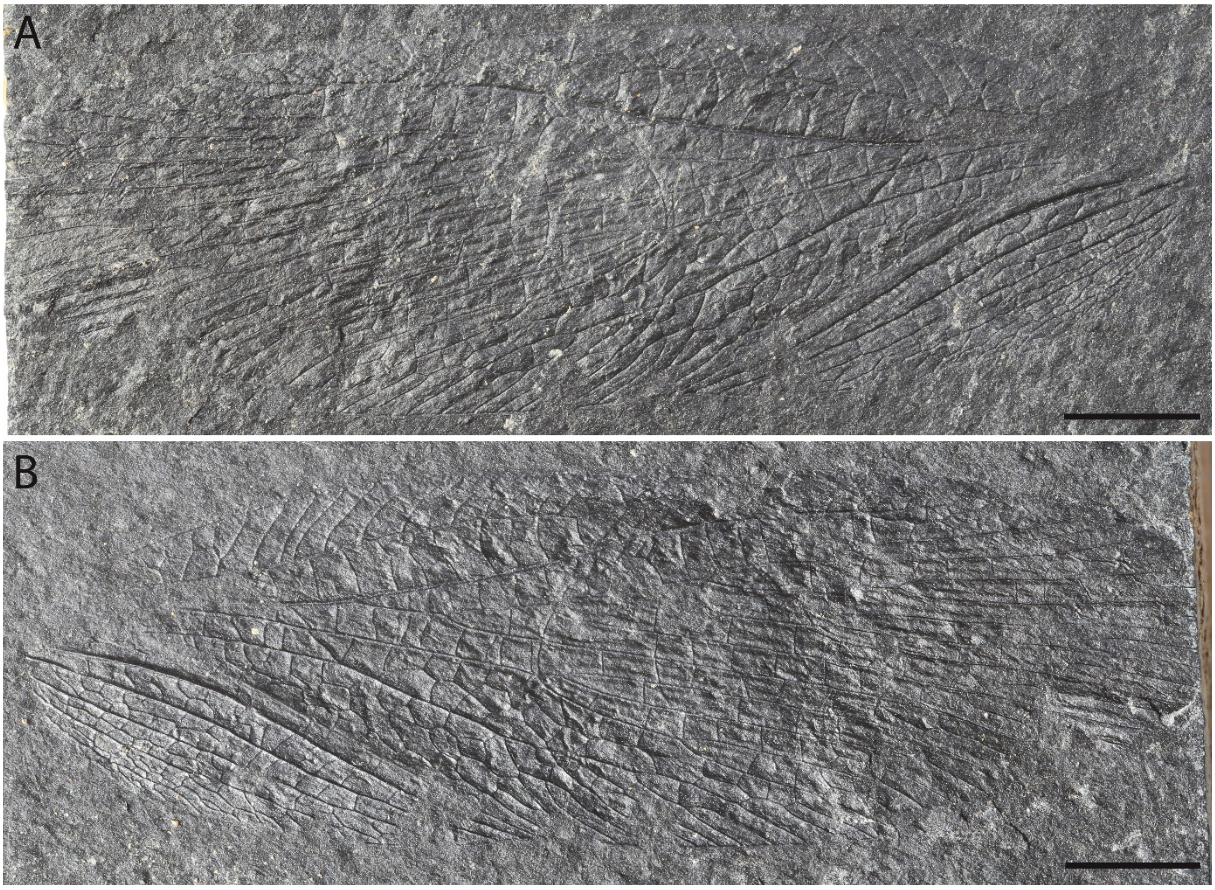

Figure 1. *Glaphyrophlebia victoriensis* sp. nov., holotype MNHN.F.A71360, Gzhelian of Tante Victoire, France. (**A**) Part. (**B**) Counterpart. Scale bars = 2 mm.

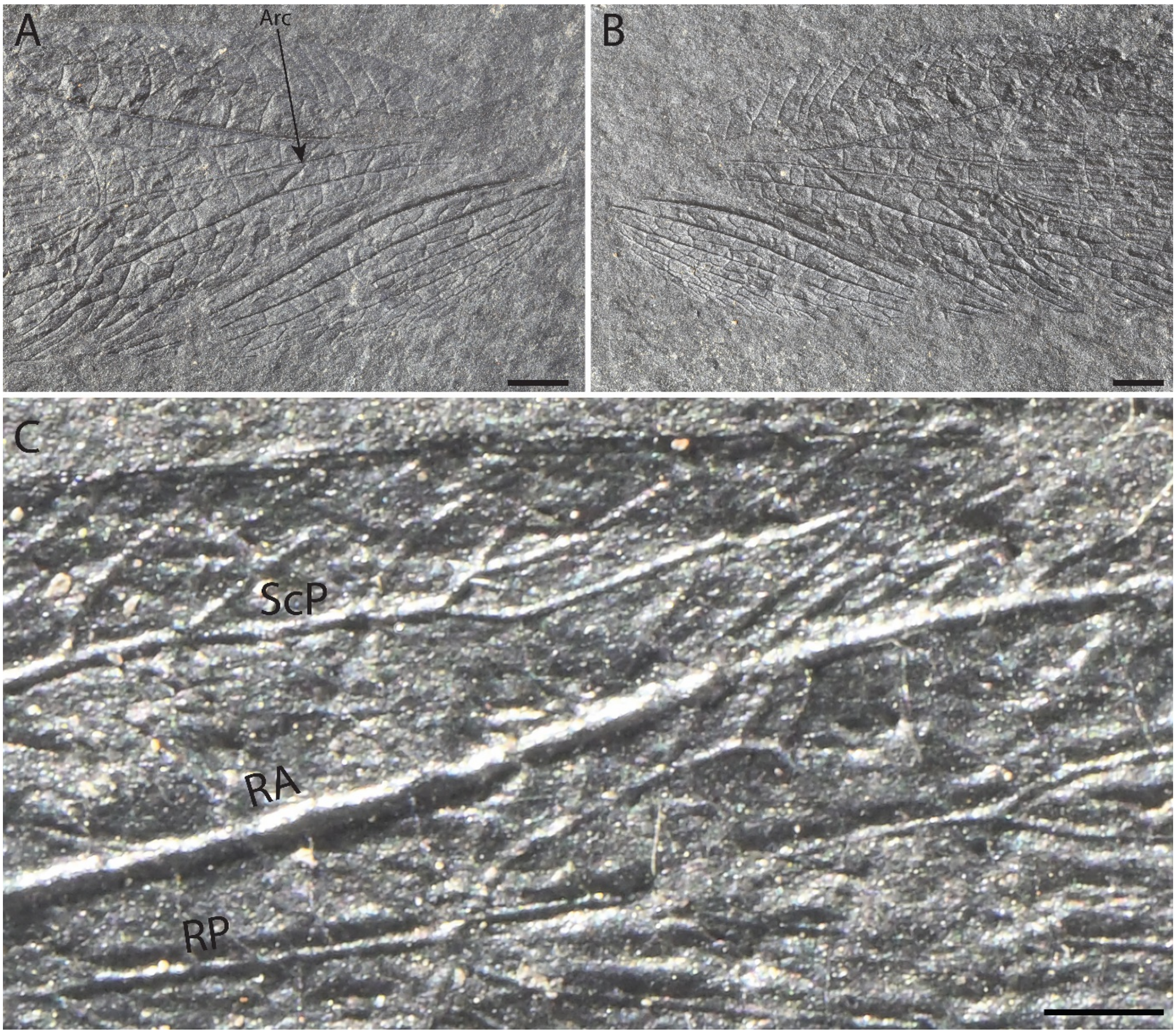

Figure 2. *Glaphyrophlebia victoriensis* sp. nov., holotype MNHN.F.A71360, Gzhelian of Tante Victoire, France. (**A**) Wing base, part. (**B**) Wing base, counterpart. (**C**) Region of apex of ScP. Scale bars = 1 mm (**A**,**B**), 0.5 mm (**C**).

Figure 3. *Glaphyrophlebia pygmaea* (Meunier, 1907), holotype MNHN.F.R51519, Gzhelian of Commentry, France. Photograph credits Gaëlle Doitteau, 2016. Scale bar = 5 mm.

Figure 4. Assemblage of wing fragment and plant remains in the same slab (MGM-822H), Gzhelian of El Bierzo, Spain. Photographs. (A) Wing fragment of *Glaphyrophlebia* sp., specimen MGM-822H-1. (B) *Oligocarpia gutbieri*, MGM-822H-2. (C) *Dicranophyllum gallicum*, MGM-822H-3. (D) *Oligocarpia*

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leptophylla (left), MGM-822H-4, and *Diplazites unitus* (right), MGM-822H-5. (E) *Pecopteris daubree*, MGM-822H-6, (F) *Diplazites unitus* (1), *Sphenopteris* sp. aff. *mathetii* (2), cf. *Odontopteris* sp. (3) and *Sphenophyllum oblongifolium* (4), specimens MGM-822H-7 to MGM-822H-10, respectively. All stacked images. Abbreviations: RA = radius anterior, RP = radius posterior; ScP = subcostal posterior. Scale bars = 1 mm (A), 1 cm (B–F).

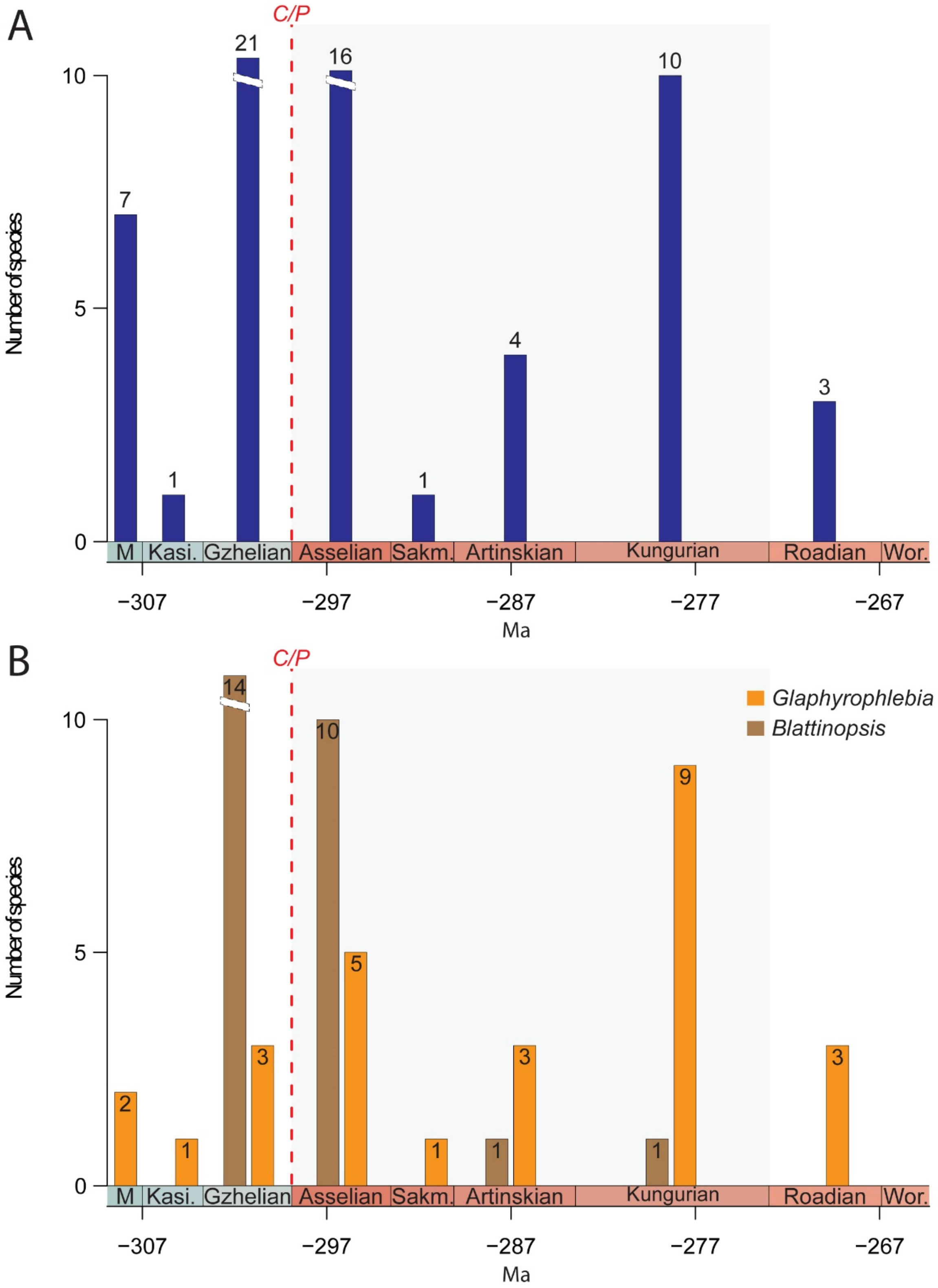

Figure 5. Diversity of major blattinopsid clades through time. (A) Number of species by stage. (B) Number of species of *Glaphyrophlebia* and *Blattinopsis* by stage. Data from https://paleobiodb.org. Abbreviations: C/P = Carboniferous/Permian boundary, Kasi. = Kasimovian, M = Moscovian, Sakm. = Sakmarian, Wor. = Wordian.