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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*, from the Gzhelian of Southern France and Spain, respectively, are described and illustrated. 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 victoiriensis* 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 upper 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 lower and middle Permian strata of the Russian Federation. We proposed the first hypothesis to explain the diversification of the family and of its most speciose genera and to argue that 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 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 in blattinopsid genera is highly heterogeneous. Some genera encompass only one species (e.g., *Avionblattinopsis* Quispe et al., 2021 [1]) while others, such as *Blattinopsis* Giebel, 1867, or *Glaphyrophlebia* Handlirsch, 1906, have more than 20 documented species (https://paleobiodb.org (last access the 19 October 2022)). Of the two most speciose blattinopsid genera, *Blattinopsis* is the most diversified during the late Carboniferous, while the second most speciose blattinopsid genus, namely *Glaphyrophlebia*, is diversified later from the early to middle Permian, but is much rarer during the Carboniferous. This particular pattern of diversity is likely related to taphonomic biases because these insects are all of similar sizes and with similar wing shapes. It may indicate that these two genera occupied a similar ecological niche and one diversified when the other was less present (competition or diversity dependence). It may also reflect the effect of features related to global climate change (e.g., an increase of CO_2 concentration in the atmosphere, change in floral assemblages, glaciations) known to occur between the Carboniferous and the Permian (i.e., Carboniferous rainforest collapse) and could have affected the diversity dynamics of major insect clades as it does for vertebrates [9]. However, the poor delimitation 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, one of these species possibly not a *Glaphyrophlebia* (see below). Descriptions of well-preserved specimens are crucial to refining the limits of each genus and gathering information on morphological diagnostic characters. Based on the fossil record of the family and the genera *Blattinopsis* and *Glaphyrophlebia*, we propose that the diversification of the family was related to changes in climate and floral assemblages between the Carboniferous and 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 importance of the locality of Tante Victoire for future discoveries of fossil insects. We also describe the first specimen of Blattinopsidae from the Palaeozoic of Spain, increasing the distribution range of this family. This study is in line with recent descriptions of the few Carboniferous insects found both historically and recently in Spain [10,11].

2. Material and Methods

The holotype of the new species was found in 1996 during a preliminary field investigation in the ancient iron quarry of Tante Victoire, Var department (latitude 43.115573°, longitude 5.827614, altitude 94.05 m). The Spanish specimen was found by one of us (AHO) during Ph.D. research on the revision of the morphogenus *Pecopteris* on fossils collected 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 EOS 50D camera with an attached Canon 65 MPE camera lens and mounted on an automated stacking rail (StackShot); all these images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using the software 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 with an integrated digital camera, and with an Olympus Tough TG-5, respectively. The photograph of the wing fragment is a stacked image, unlike the plant remains images. The plate with these images was composed using Photoshop CS2 version 9.0.

The small ancient iron quarry of Tante Victoire (Playes Massif, Six-Fours-les-Plages town, Var department) is of Gzhelian age (late Stephanian), and the palaeoflora was composed of *Pecopteris*, *Calamites*, *Walchia*, and *Sigillaria* ('Notice de la Carte Géologique à 1/5000, BRGM, France' of Toulon). The holotype MNHN.F.A71360 is deposited in

the Palaeontological collection of the Muséum National d'Histoire Naturelle (MNHN.F), Paris, France.

The wing fragment of the Spanish specimen 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 (latitude 42°44′5′′ N, longitude 6°11′3′′ W, altitude 1.180 m). This mine belongs to the El Bierzo outcrop, Noceda Block, Tramo de Espina [12] and is of Gzhelian age based on the rich floral assemblage [13,14]. The specimen MGM-822H-1 is deposited 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. [15], especially concerning the presence of 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; and ScP, subcostal posterior.

Abbreviations for Museums: MNHN, Muséum national d'Histoire naturelle, Paris, France; and MGM, Museo Geominero (Instituto Geológico y Minero de España, CSIC), Madrid, Spain.

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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 and 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 and Jouault sp. nov.

Figures 1 and 2

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Etymology. Named after the type locality Tante Victoire.

Type 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.

Type locality, formation and age. Tante Victoire, Six-Fours-les-Plages, Var department, France, Gzhelian, Carboniferous.

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; and 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; RA with a posterior branch forked; fork of R located slightly distad r-m crossvein; base of RP at 5.0 mm from wing base, second fork of RP slightly distad M fork; first branch of RP simple; second branch of RP forked close to wing margin; third branch of RP forked, anterior branch forked extremely close to dichotomy with simple posterior branch; fourth branch of RP dichotomous; fifth branch of RP forked;

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 at least 11 zigzagged and rather weak posterior branches, first fork located proximal to M fork; CuP straight and simple; PCu simple and slightly sigmoidal; three main anal veins; numerous simple crossveins in radial and median areas; distinct longitudinal furrows between branches of RP and M, reaching edge of wing; and vein bow between RA and main stem of M only.

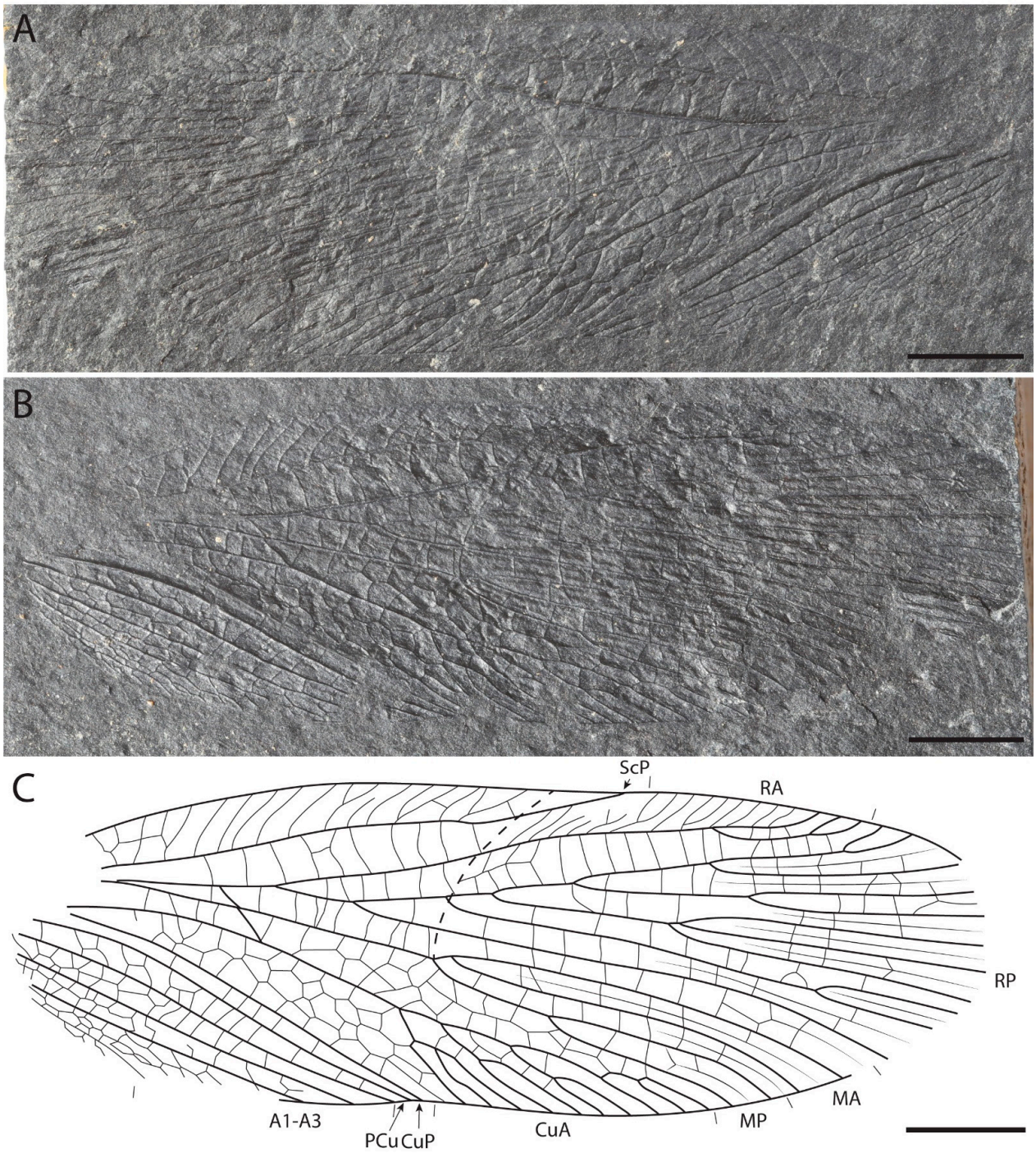

Figure 1. *Glaphyrophlebia victoiriensis* sp. nov., holotype MNHN.F.A71360, Gzhelian of Tante Victoire, France: (**A**) part; (**B**) counterpart; and (**C**) interpretative line drawing of counterpart with names of main veins labelled and vein bow indicated as a dotted line. Scale bars = 2 mm.

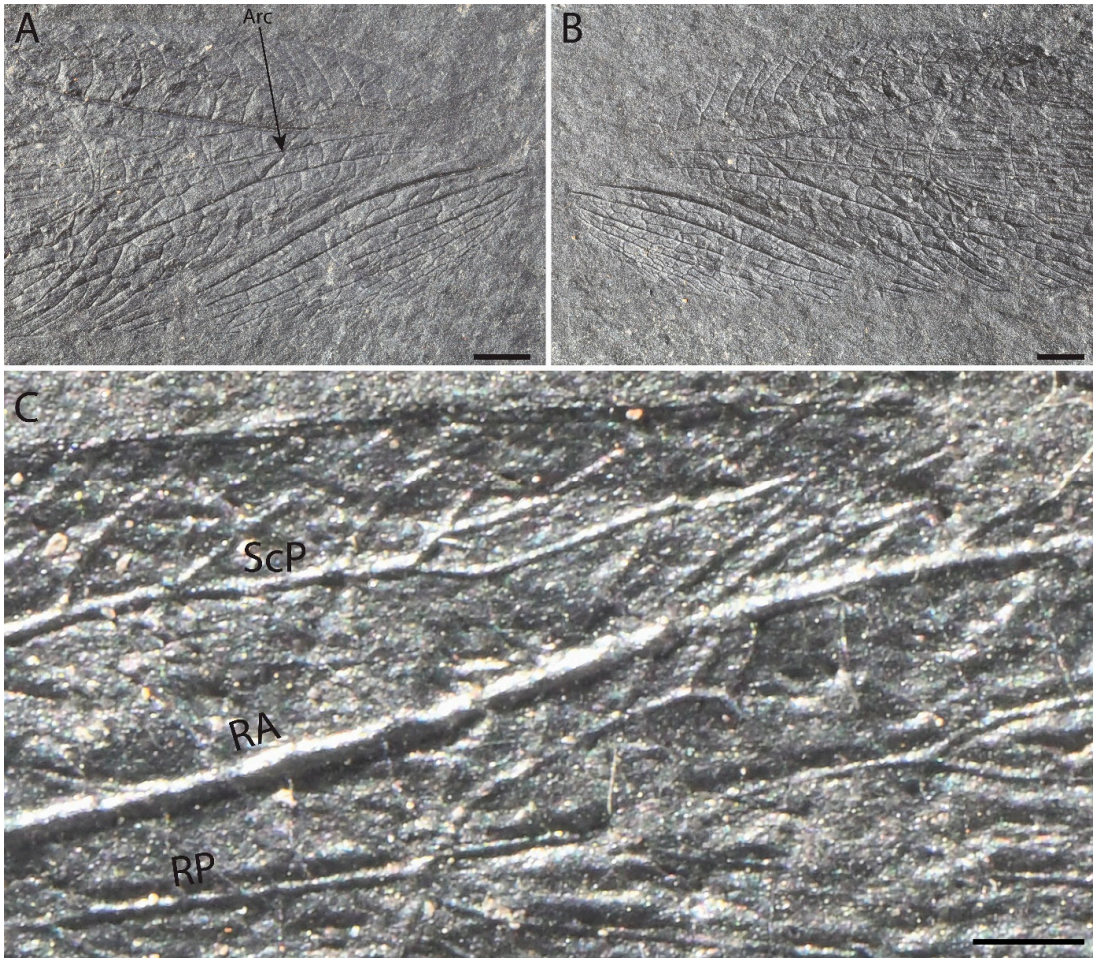

Figure 2. *Glaphyrophlebia victoiriensis* sp. nov., holotype MNHN.F.A71360, Gzhelian of Tante Victoire, France: (**A**) wing base, part; (**B**) wing base, counterpart; (**C**) region of apex of ScP with main veins labelled. Scale bars = 1 mm (**A**,**B**); 0.5 mm (**C**).

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 somewhat 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; and anal fan strongly reduced.

Affinities with the family Paoliidae Handlirsch, 1906, are excluded because the area between CuA and CuP is not very wide, just slightly wider than the 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 the area between ScP and C in *Avionblattinopsis*, while the two areas are of the same width in the new fossil [1]. Interestingly, the species

type of *Stephanopsis*, namely *Stephanopsis incerta* [16] (originally in the genus *Blattinopsis* Giebel, 1867), has an area between ScP and RA much narrower than that of *Avionblattinopsis*, excluding affinities of the new fossil with this genus [16].

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 also have rather numerous crossveins in the radial and median areas [7,8]. Therefore, the new species is attributed to the genus *Glaphyrophlebia*.

Differences from Other Species of Glaphyrophlebia

Following the key to the Permian *Glaphyrophlebia* sp. 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 and Stapf, 2001, *G. jeckenbachi* Hörnschemeyer and Stapf, 2001, and *G. rohwedderi* Hörnschemeyer and 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 [17]. 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 a comb-like posterior branch in the new fossil while the CuA is pectinate in *G. clava* and in *G. arnulfi* [18]. 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 [18].

Glaphyrophlebia rohwedderi differs from the new fossil and *G. jeckenbachi* because of its ScP not flexed S-line at apex [18]. *Glaphyrophlebia rohwedderi* also differs from the new specimen owing to the strange branching pattern of the R, i.e., with dichotomy (considered to be an anterior branch of MP in [18]) and a second dichotomy creating RP. Similarly, the branching pattern of M (considered as the MP in [18]) in *G. rohwedderi* differs from that in the new specimen because it has a posterior branch (MP as we interpreted it) forking close to 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 and 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 [18]. 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 and Naugolnykh, 2022) (lower Permian of the Russian Federation) is based on the basal half of a forewing, ca. 10 mm long, which renders a detailed comparison with the new fossil difficult. 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 the base and the apex missing, ca. 7.5–8 mm long [19]. Nevertheless, the illustration of Martynov [19] 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, IL, USA), the type species of the genus, is not listed nor keyed in [8]. Handlirsch [20] 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 [18]) 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 (Figure 3), while they are zigzagged in the new fossil.

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

Glaphyrophlebia wettinensis [20] (Gzhelian of Germany, recently attributed to this genus [18]) 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 [18,21]. Additionally, the anterior branch of M is forked close to the first dichotomy of M, while simple or forked far distad the first dichotomy of M in *G. wettinensis* [18].

Glaphyrophlebia delicatula (Bolton, 1934, Moscovian, 314.6 Ma, South Wales, UK, recently attributed to this genus [18]) is also not listed nor keyed in Aristov et al. [8]. It is based on a very incomplete fragment of forewing. Bolton [22] did not indicate 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

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 leptophylla* (left), MGM-822H-4, and *Diplazites unitus* (right), MGM-822H-5; (**E**) *Pecopteris daubreei*, MGM-822H-6; (**F**) *Diplazites unitus*: (1) *Sphenopteris* sp. aff. *mathetii*, (2), cf. *Odontopteris* sp., (3) *Sphenophyllum oblongifolium*, and (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**).

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.

Locality, formation and age. El Bierzo, León Province, Spain, Gzhelian, Carboniferous.

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; and 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 victoiriensis* sp. nov., but could fit with *Glaphyrophlebia pygmaea*. Nevertheless, the incompleteness of this fossil prevents its attribution to a precise species. A floral assemblage was found on the same slabs or on slabs close to the isolated wing (Figure 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 arid forests and conditions during the Permian. The late Carboniferous is renowned for its 'Coal Forests'—widely distributed in Europe and North America around the equator—developed under ever wet conditions, sometimes with a drier season [23]. A dramatic collapse of these rainforests began during the Pennsylvanian (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 [24,25]. 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 (Figure 5A), with its highest diversity during the Gzhelian and Asselian, i.e., around the Carboniferous/Permian boundary (C/P boundary) (https://paleobiodb.org (last access the 19 October 2022)). 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, and concentration of CO_2 in the atmosphere) on changes in the dynamics of the family (Figure 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 [26,27]. Conversely, the genus *Glaphyrophlebia* is highly diversified during the Kungurian, a comparatively hot period [26,27]. 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 [28,29].

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 [30], during the earliest Kasimovian by the extinction of the dominant lycopsids, and their replacement by tree fern-dominated ecosystems [31,32]. 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 [33]. 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 [34].

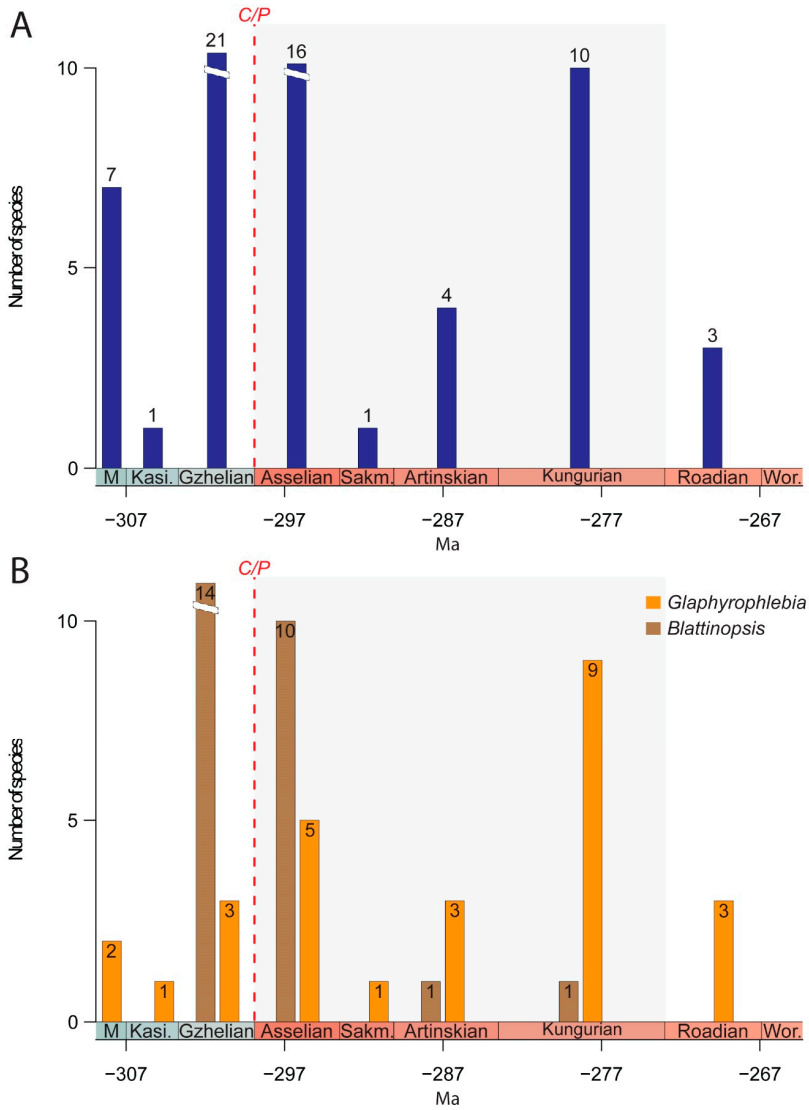

Figure 5. Diversity of major blattinopsid clades through time: (**A**) number of blattinopsid species by stage; and (**B**) number of species of *Glaphyrophlebia* and *Blattinopsis* by stage. Data from https://paleobiodb.org (last access the 19 October 2022). Abbreviations: C/P = Carboniferous/Permian boundary, Kasi. = Kasimovian, M = Moscovian, Sakm. = Sakmarian, Wor. = Wordian.

At the outcrop of El Bierzo, the thin slab where the 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 (see Table 1: list of plants from El Bierzo): cf. *Asterophyllites equisetiformis* (Schlotheim, 1820 and Brongniart, 1828), *Sphenophyllum oblongifolium* (Germar and Kaulfuss, 1831 and Gutbier, 1843) (Figure 4F), *Sphenophyllum* cf. *alatifolium* (Renault, 1890), *Oligocarpia gutbieri* (Göppert, 1841), *Oligocarpia leptophylla* (Bunbury, 1853 and Grauvogel-Stamm and Doubinger, 1975) (Figure 4D), *Sphenopteris* sp.-1, *Sphenopteris* sp. aff. *mathetii* (Figure 4F), *Diplazites unitus* (Brongniart, 1836 and Wagner and Martínez-García, 1998), *Pecopteris daubreei* (Zeiller, 1888) (Figure 4E), *Pecopteris* sp., *Dicranophyllum gallicum* (Grand'Eury, 1877), cf. *Mixoneura* sp., cf. *Odontopteris* sp. (Figure 4F) and *Dicksonites* sp. Although there are many plant species/morphotypes (14 + wing) most of them were broken remains, occasionally really tiny, in accordance with their deposition in the stream of a river. Only three plant fossil species are large enough to be considered parautochthonous:

Table 1. List of plants from El Bierzo outcrop.

Allochthonous Flora
Order: Equisetales Trevisan, 1876
• Family: Calamostachyaceae Meyen, 1987
○ *Asterophyllites*? Brongniart, 1928
Order: Bowmanitales Meyen, 1978
• Family: Bowmanitaceae Meyen, 1978
○ *Sphenophyllum* cf. *alatifolium* Renault, 1890
○ *Sphenophyllum oblongifolium* (Germar and Kaulfuss, 1831) Gutbier, 1843 (Figure 4F)
Order: Filicales
• Family: Sermayaceae Eggert and Delevoryas, 1967
○ *Oligocarpia leptophylla* (Bunbury, 1853) Grauvogel-Stamm and Doubinger, 1975 (Figure 4D)
Order: Marattiales Link, 1833
• Family: Psaroniaceae Unger in Endlicher 1842
○ *Pecopteris daubreei* Zeiller, 1888 (Figure 4E)
○ *Pecopteris* sp. Brongniart, 1828
Order: Medullosales Corsin, 1960
• Family: Cyclopteridaceae Laveine ex Cleal and Shute 2003
○ cf. *Mixoneura* sp. Weiss, 1869
○ cf. *Odontopteris* sp. Brongniart, 1822 (Figure 4F)
Order: Callistophytales Rothwell, 1981
• Family: Callistophytaceae Stidd and Hall, 1970
○ *Dicksonites* sp. Sterzel, 1881
Order: *incertae sedis* (Filicophyta)
• Family: *incertae sedis*
○ *Sphenopteris* sp. aff. *mathetii* Zeiller, 1888 (Figure 4F)
○ *Sphenopteris* sp. Brongniart, 1822
Parautochthonous flora
Order: Filicales
• Family: Sermayaceae Eggert and Delevoryas, 1967
○ *Oligocarpia gutbieri* Göppert, 1841 (Figure 4B):
Order: Marattiales Link, 1833
• Family: Psaroniaceae Unger in Endlicher 1842
○ *Diplazites unitus* (Brongniart, 1836) Wagner and Martínez-García, 1998 (Figure 4D,F):
Order: Dicranophyllales Němejc, 1959
• Family: Dicranophyllaceae Němejc, 1959
○ *Dicranophyllum gallicum* Grand'Eury, 1877 (Figure 4C):

Oligocarpia gutbieri (Figure 4B): this plant lived in variable habitats, from lowland places to hillside environments [35].

Dicranophyllum gallicum (Figure 4C): this species developed on mesophytic or even xerophytic communities on basin-margin slopes [36–39].

Diplazites unitus (Figure 4D,F): as *O. gutbierii*, occupied variable habitats, from lowland places such as floodplains or swampy areas to hillside environments [35,38].

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 genus *Glaphyrophlebia* likely could have fed on spores (phytophagous) according to Aristov et al. [8], even if very little is known about their mouthparts, as Rasnitsyn [39] only indicated that they had 'clypeus not much convex, mouthparts chewing'. Therefore, very limited conclusions can be inferred about the biology of these insects. Its fossil record 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.

Remark. Rasnitsyn [40] put the Blattinopsidae in their own order, 'Blattinopsidea' (name later amended to Blattinosida), into a large clade that would comprise the 'Blattinopseida, Caloneurida, the holometabolous, paraneopteran ('psoco-rhynchotan') and palaeodictyopteran clades', defined on the basis of 'their pterothoracic sterna are characteristically invaginated along the midventral line called discrimen (see Figure 69 in the Ref. [40]), with the furcal arms mounting a common base elevated inside the thorax.' However, these characters are unknown in the Blattinopsidae and this set of taxa does not constitute a clade, as demonstrated by more recent analyses, after which the Palaeodictyoptera are palaeopteran insects.

5. Conclusions

Glaphyrophlebia victoiriensis sp. nov. is the third Gzhelian species of this genus. Together with the discovery of the first fossil wing of *Glaphyrophlebia* from Spain, they increase the diversity and distribution of blattinopsids from the Western European Carboniferous deposits and help to document the wing venation variability found in the genus *Glaphyrophlebia*. The diversity of this genus is high in early and middle Permian strata, especially in the deposits of the Russian Federation. The new species described here suggests that its diversity in the late Carboniferous is underestimated.

Our study proposes a new hypothesis on the diversification dynamics of insects during the Carboniferous period using the Blattinopsidae, and more specifically the *Glaphyrophlebia* and *Blattinopsis*, as study groups. We mainly discuss the hypothetic impact of the Carboniferous rainforest collapse on these groups, but it is also important to mention that other factors may have shaped the diversity dynamics of insects during the late Carboniferous. In fact, it has been demonstrated that the diversification and the extinction process are often found to correlate with multiple variables [34,41], and it is likely that aside from the CRC,

other factors such as glaciations or the proportion of mountain area have also played a key role in the radiation or decline of some lineages.

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