Plant–insect interactions from the Late Pennsylvanian of the Iberian Peninsula (León, northern Spain)

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ABSTRACT

We describe new evidences of plant–insect interactions from the Late Pennsylvanian of northern Iberian Peninsula (León, Spain). We document nine different Damage Types (DTs) among 216 fossil plant specimens. The interactions include four different Functional Feeding Groups (FFGs), including margin feeding (DT12 and DT13), hole feeding (DT09), galling (DT33, DT80, and DT116), and oviposition (DT67, DT100, and DT102) on Pteridophytes, Pteridospermatophytes, and Coniferophytes. Margin feeding and hole feeding were identified on different species of *Polymorphopteris* (*P. polymorpha*, *P.* cf. *pseudobucklandii*, and *P. integra*); galling on *Mixoneura wagneri*, *Pecopteris apicalis*, and *Oligocarpia gutbieri*; and oviposition on *Polymorphopteris integra, Cordaites* cf. *angulostriatus* and *Polymorphopteris* cf. *integra.* The oviposition scars represent the oldest record of oviposition from the Iberian Peninsula so far. In addition, it is the first evidence of plant–insect interactions on *Oligocarpia* and *Polymorphopteris* leaves in the area. These evidences reveal various ecological interactions between different groups of plants and insects in the Late Pennsylvanian forests of Spain, suggesting that these plants were a relevant source of food and lodge for a variety of arthropods (mainly insects). We also explore the possible culprits of these damages and the climatic implications.

1. Introduction

Although plant–insect interactions are known since the Silurian/Devonian (Trant and Gensel, 1985; Banks and Colthart, 1993; Edwards et al., 1995; Hueber, 2001; Labandeira, 2006, 2007), this type of ecological evidence does not begin to be relatively common until the Carboniferous, where the expansion of terrestrial ecosystems and the diversification of Functional Feeding Groups occur (Labandeira et al., 2014; Fernández and Chiesa, 2020; McCoy et al., 2021), from this period is also the first evidence of evolutive adaptations of plants against arthropod herbivorism, such as trichomes (Krings et al., 2003; McCoy et al., 2021). However, despite its apparent expansion during this period (Labandeira, 2006), little is still known about interactions between plants and insects in the Paleozoic (Feng et al., 2021). In the late Paleozoic, the Second Herbivore Expansion Phase (335–251 Ma) takes place (sensu Labandeira, 2006); during this phase, the major host-plant clades were Pteridophytes and Spermatophytes (Labandeira, 2006; McCoy et al., 2021) and the major arthropod herbivore clades were myriapods,

mites, palaeodictyopteroids, apterygotes, and protorthopteroids (Labandeira, 2006).

Studies of plant-arthropod interactions about Carboniferous are scarcer than those of other Mesozoic or Cenozoic periods (Schachat et al., 2022). Most of them are focused on isolated interactions (e.g., Van Amerom, 1966; Van Amerom and Boersma, 1971; Labandeira and Phillips, 1996; Béthoux et al., 2004; Jarzembowski, 2012; Laaß and Hoff, 2015; Correia et al., 2020). Nevertheless, very few studies have analyzed Carboniferous floras in larger plant assemblages (e.g., Castro, 1997; Cariglino and Gutiérrez, 2011; Fernández and Chiesa, 2020; Donovan and Lucas, 2021).

Carboniferous deposits in the Iberian Peninsula have been widely studied in the last decades, including the study of insects (Teixeira, 1948; Carpenter, 1963; Broutin, 1986; Álvarez-Ramis, 1989; Schneider, 1983; Iwaniw, 1985; Kukalová-Peck and Brauckmann, 1992; Brauckmann, 1993; Nel et al., 2009; Loureiro et al., 2010; Correia et al., 2013; Correia, 2016), other arthropods such as arachnids (Selden and Romano, 1983), and plants (e.g., Broutin, 1986; Wagner and Álvarez-Vázquez, 2010; Wagner and Castro, 2011; Correia et al., 2018, 2021a, 2021b; Knight and Álvarez-Vázquez, 2021). Despite this extensive knowledge about the Carboniferous plants and insects from

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Table 1

Record of plant–insect interactions from the Carboniferous of the Iberian Peninsula. Note that the age of the previous publications was updated according to Knight and Álvarez-Vázquez (2021).

FFG and host plants	Age	Location	Reference
External feeding on *Neuropteris* (*Mixoneura*, according to Lorenzo, 1980)	middle Gzhelian (Saberian)	Llombera, Ciñera-Matallana Coalfield (León, Spain)	Van Amerom (1966), Van Amerom and Boersma (1971)
Galling, external feeding and putative mining on *Mixoneura* spp., *Linopteris* sp., *Dicksonites*, *Pseudomaripteris* sp., and *Sphenopteris* sp.	middle Gzhelian (Saberian)	La Magdalena Coalfield (León, Spain)	Castro (1994, 1997)
Galling on *Annullaria*	Gzhelian	São Pedro da Cova (Portugal)	Correia et al. (2020)
Galling, margin feeding, hole feeding, oviposition on *Cordaites*, *Pecopteris*, *Polymorphopteris*, *Mixoneura*, *Oligocarpia*	middle-late Gzhelian (Saberian, Stephanian B)	Villablino/Carrasconte, El Bierzo, and La Magdalena coalfields(León, Spain)	This work

the Iberian Peninsula, little is known about the interactions between these two important groups.

Most of the studies of plant–insect interactions in the Iberian Peninsula are from the Cenozoic (e.g., Diéguez et al., 1996; Peñalver and Martínez-Delclòs, 1997; Peñalver et al., 2002; Montoya et al., 1996; Peñalver, 1997; Peñalver and Martínez-Delclòs, 1997; Peñalver and Martínez-Delclòs, 2004; Peñalver et al., 2016; Santos et al., 2017; Moreno-Domínguez et al., 2022). Nevertheless, few interactions have been reported from Mesozoic and Paleozoic deposits in Spain and Portugal. In the Mesozoic of the Iberian Peninsula, only interactions on angiosperm and gymnosperm leaves from the Aptian-Albian stand out in the Alcaine and Plou area (Estévez-Gallardo et al., 2018; Sender et al., under review; Santos et al., under review) and interactions in a flora dominated by Cyadales/Bennettitales established on a volcanic island during the Aalenian (Middle Jurassic), near the locality of Camarena de la Sierra (Santos et al., 2021). Paleozoic plant-arthropod interactions in the Iberian Peninsula are scarce (see Table 1): the evidences correspond to galling on *Annularia* from the Late Pennsylvanian (Douro Basin, Portugal) (Correia et al., 2020); evidence of external damage on *Mixoneura* from Late Pennsylvanian of Ciñera-Matallana Coalfield (León, Spain) (Van Amerom, 1966; Van Amerom and Boersma, 1971); and galling and external damage on *Mixoneura*, *Linopteris* and *Sphenopteris* in La Magdalena Coalfield (León, Spain) (Castro, 1994, 1997).

In this work, we present the first data of galling, margin feeding, hole feeding, oviposition on *Cordaites*, *Pecopteris*, *Polymorphopteris,* and *Oligocarpia* from the Carboniferous of Spain. These new data represent the oldest oviposition case recorded to date in Spain and the first evidence of interactions in *Cordaites, Oligocarpia, Pecopteris,* and *Polymorphopteris* in the Iberian Peninsula. The objectives of this work are to (1) describe the new specimens and the evidences of plant–insect interactions from the Late Pennsylvanian of Spain, (2) compare the results with other plant–insect interactions of the same age, and (3) discuss the implications of these interactions.

2. Geological setting

The samples studied here were collected in different field trips during the last 5 years from different post-Asturian deposits from the Cantabrian area from the North of the Iberian Peninsula (see Fig. 1 to see the locations) corresponding to the 'Saberian' and Stephanian B sensu Saint-Étienne subfloors (Wagner and Álvarez-Vázquez, 2010). All of the fossil plants studied here are Gzhelian in age. The samples were obtained from three nearby coalfields: La Magdalena, El Bierzo, and Carrasconte, all in the space of 30 km.

La Magdalena is one of the most studied coalfields in the Cantabrian area and has been assigned to the *Alethopteris zeilleri* Megafloral Zone, "Saberian" substage (Wagner and Álvarez-Vázquez, 2010; Wagner and Castro, 2011). According to Knight and Álvarez-Vázquez (2021), based on radiometric data and biostratigraphy it is Gzhelian in age. Specimen MCNA 16973 comes from Irene mine in the La Magdalena Coalfield. This mine is located in the uppermost layers preserved in the coalfield. The sample was collected among the scattered remains that remained on the surface after the restoration of the mine, which

limited the obtaining of new materials for future investigations. In the layers where the specimen MCNA 16974 was collected, *Calamites* were found in living position, with remains of roots (*Pinnularia capillacea*), leaves (*Asterophyllites equisetiformis*) and fructifications (*Calamostachys germanica*), together with *Sphenophyllum oblongifolium, Cyperites bicarinatus, Nemejcopteris feminaeformis, Pecopteris apicalis, Pecopteris* cf. *ameromii, Linopteris neuropteroides* (with *Hexagonocarpus* seeds and possible rachis), *Pseudomariopteris cordato-ovata, Cordaites* sp. (some with possible insect ovipositions), *Poacordaites* sp. and freshwater bivalves. The existence of somewhat deteriorated leaves or small plant fragments would indicate moderate transport (e.g., *Cordaites* sp. or *Pecopteris* cf. *ameromii*). In contrast, other remains appear to have been autochthonous or parautochthonous (e.g., *Calamites, Linopteris neuropteroides*). The current data seem to indicate that the vegetation grew in a swampy area.

El Bierzo Coalfield is the largest of the post-Asturian coalfields in the Cantabrian area of the Iberian Peninsula. Fernández-García et al. (1984) made a stratigraphic and tectonic description of the coalfield, dividing it into five blocks without specifying their relative ages. These authors pointed out that the entire coalfield has a fairly homogeneous flora. Wagner and Álvarez-Vázquez (2010) confirmed that this coalfield is included in the Megafloral Zones *Alethopteris zeilleri* (in the lower part of the successions) and *Sphenophyllum angustifolium* (in the upper part), which correspond, in the Iberian Peninsula, to the Stephanian B sensu stricto and 'Saberian'. Based on Knight and Álvarez-Vázquez (2021) these substages would correspond to the Gzhelian. The specimens MCNA 16976 and MCNA 16978 were collected in the Casilda mine, in Tremor de Arriba (El Bierzo coalfield). MCNA 16977 sample comes from the Casilda mine, Bloque de Noceda (Useos section). The sample MCNA 16975 comes from Impensada mine, near the village of Valdesamario.

Some samples (MCNA 16979, MCNA 16980) were collected in the Carrasconte Coalfield (La Mora-Nueva Julia mine), in the locality of Cabrillanes (León). Wagner and Álvarez-Vázquez (2010) and, more recently, Knight et al. (2018) have proposed that this zone would correspond to the *Sphenophyllum angustifolium* Megafloral Zone (Stephanian B sensu stricto). Westward and in a small area to the North, the strata correspond to the *Alethopteris zeilleri* Zone but are outside the sampled area. This site is Gzhelian in age (Knight and Álvarez-Vázquez, 2021). This mine has recently been restored, so obtaining new materials of scientific interest has been severely limited.

The fossil remains (especially plants) from these Late Pennsylvanian deposits have been widely studied. These plant communities were located in a single foreland basin that drained the Variscan Mountains, situated to the North and West, into the nearby Paleothetys Ocean to the East (Wagner and Castro, 2011; Knight and Álvarez-Vázquez, 2021) under tropical or subtropical conditions(Tabor and Poulsen, 2008). However, other authors have suggested global aridification of the climate during the end of the Carboniferous period, although the areas around the Rheic Ocean (i.e., Spain) presented onshore winds that bring moisture from ocean to continent (Ziegler, 1990; Roscher and Schneider, 2006). Colmenero et al. (1996) and Bashforth et al. (2010) support the idea that most sedimentary deposits were fluvial. The paleosols that seem to have been dominant in the basins are azonal
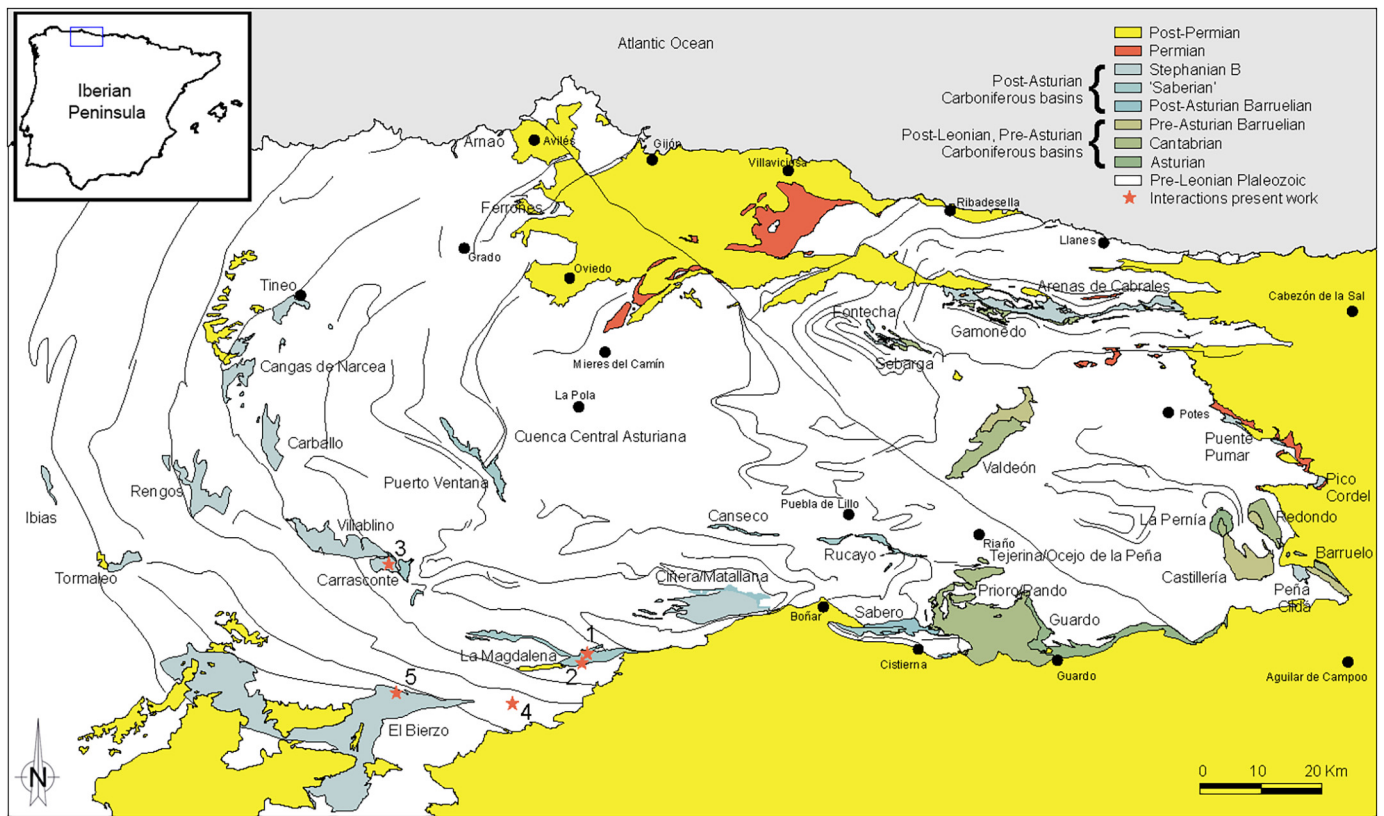
Fig. 1. Upper Moscovian (Asturian) to lower Permian deposits from the NW of the Iberian Peninsula and the points of origin of the plant–insect interactions (Based on data from Wagner and Álvarez-Vázquez, 2010; Knight and Álvarez-Vázquez, 2021). The numbers (1–5) indicate the studied deposits: (1) Garaño, (La Magdalena Coalfield); (2) Irene Mine (La Magdalena Coalfield); (3) La Mora-Nueva Julia Mine (Carrasconte/Villablino Coalfield); (4) Valdesamarino Mine (El Bierzo Coalfield); (5) Casilda Mine (El Bierzo Coalfield).

(alluvial very little evolved, colluvial in the areas closest to the mountains, with little humus, frequently altered by fluvial processes) or intrazonal, formed in more stable substrates (soils more or less hydromorphs). Bashforth et al. (2010) analyze the vegetation that could be found in different depositional facies of the La Magdalena coalfield. These authors detect evident ecological gradients in this coalfield. In general, the marginal wetlands (near the coalfield's edges) were dominated by pteridosperms. Instead, fern-dominated communities are linked to disturbance-prone braided channel belts and interfluvial wetlands near braided rivers. A mixture of pteridosperm and fern-dominated communities was established in interfluvial wetlands.

3. Material and methods

In this study, we have selected the plant-arthropod interactions in 216 specimens of plant leaves collected from Late Pennsylvanian deposits of northern Spain, including different genera of Pteridophyta, Pteridospermatophyta, and Coniferophyta. The fossil plants studied here consisting of impressions or carbonizations that preserve taxonomic details such as the veining allowing the identification.

The fossil remains were collected in different Gzhelian deposits in the Province of León (Castilla y León, NW Spain) (see Fig. 1). The fossil samples were processed using brushes, needles, glues, and air scribes. The photographs were taken using a Leica MC170-HD camera attached to a Leica M205-C stereomicroscope at the Laboratory of Paleobotany (Universidade de Vigo and Universidad del País Vasco).

We have used the classical literature of the study area to identify the taxa that constitute the plant substrate on which the interactions develop. The descriptions are strictly limited to characters that allow identification.

Identification of plant–insect interactions was based on the guide of Labandeira et al. (2007) and the posterior unpublished addenda, paying special attention to damage indicators (such as reaction rim or specific patterns). This identification is based on the attribution of the interaction to different damage types (DTs) denoted numerically into six Functional Feeding Groups (FFGs): hole feeding, margin feeding, surface feeding, skeletonization, piercing and sucking, and galling. In addition, we will also refer to oviposition as a type of Functional Feeding Group, although it is not strictly so.

4. Results

4.1. Palaeobotanical context

Class: Filicopsida Pichi-Sermolli 1958
Order: FILICALES
Family: SERMAYACEAE Eggert & Delevoryas 1967
Genus: **Oligocarpia** Göppert 1841
Oligocarpia gutbieri Göppert 1841 emend. Brousmiche 1983
Plate II.D and E
Material: MCNA 16973.
Location: Mina Irene, Canales (La Magdalena Coalfield).
Description: This specimen is a small 13 mm pinna fragment of *Oligocarpia gutbieri*. The features are typical of the species, with 4.3 × 3.3 mm pinnules (l / b ratio = 1.3: 1) with a flat, apparently very thin pinnules, generally ovate in shape, margin with rounded lobes and fused bases. The veins are prominent and well-marked, with the main nerve very decurrent and from which the secondary nerves are bifurcated or with 3 branches with bifurcation away from the primary nerve.

Class: Marattiopsida Doweld 2001

Order: Marattiales Link 1833
Family: Psaroniaceae Unger in Endlicher 1842
Genus: **Pecopteris** Brongniart, 1828
Pecopteris apicalis Knight 1985 emend. Knight & Sardina 2016.
Plate II.B and C
Material: MCNA 16974.
Location: Garaño village (La Magdalena Coalfield).
Description: 27 mm last order pinna fragment of *Pecopteris apicalis*. This specimen presents typical features of this species, with oblong, vaulted pinnules, measuring 5.5 × 2.5 mm (ratio l / b = 2: 1). The main nerve is thick and non-decurrent. The secondary nerves are all bifurcated, with branches that separate at a wide angle from the main vein itself.

Genus: **Polymorphopteris** Wagner 1959
Polymorphopteris polymorpha (Brongniart 1834) Wagner 1959
Plate I.A and C

Material: MCNA 16976.
Location: Casilda mine, Tremor de Arriba (El Bierzo Coalfield).
Description: The specimen is quite small, has four last-order pinna fragments with very characteristic features of *P. polymorpha*. The pinnules are oblong, with an obtusely acute apex, with a contracted base, apparently thick, doubly vaulted, with the main nerve not decurrent, thick and sunken in the limb. The lateral nerves are dense, polymorphopteroid, quite straight in their final development and attaining the margin at an oblique angle.

Polymorphopteris integra (Andrae in Germar 1849) Wagner 1999
Plate I.B, III.A and C
Material: MCNA 16979.
Location: La Mora-Nueva Julia mine, Carrasconte (Carrasconte/Villablino Coalfield).
Description: Sample MCNA 16979 contains a magnificent specimen of *Polymorphopteris integra*. It is a terminal n-1 order pinna of 180 ×
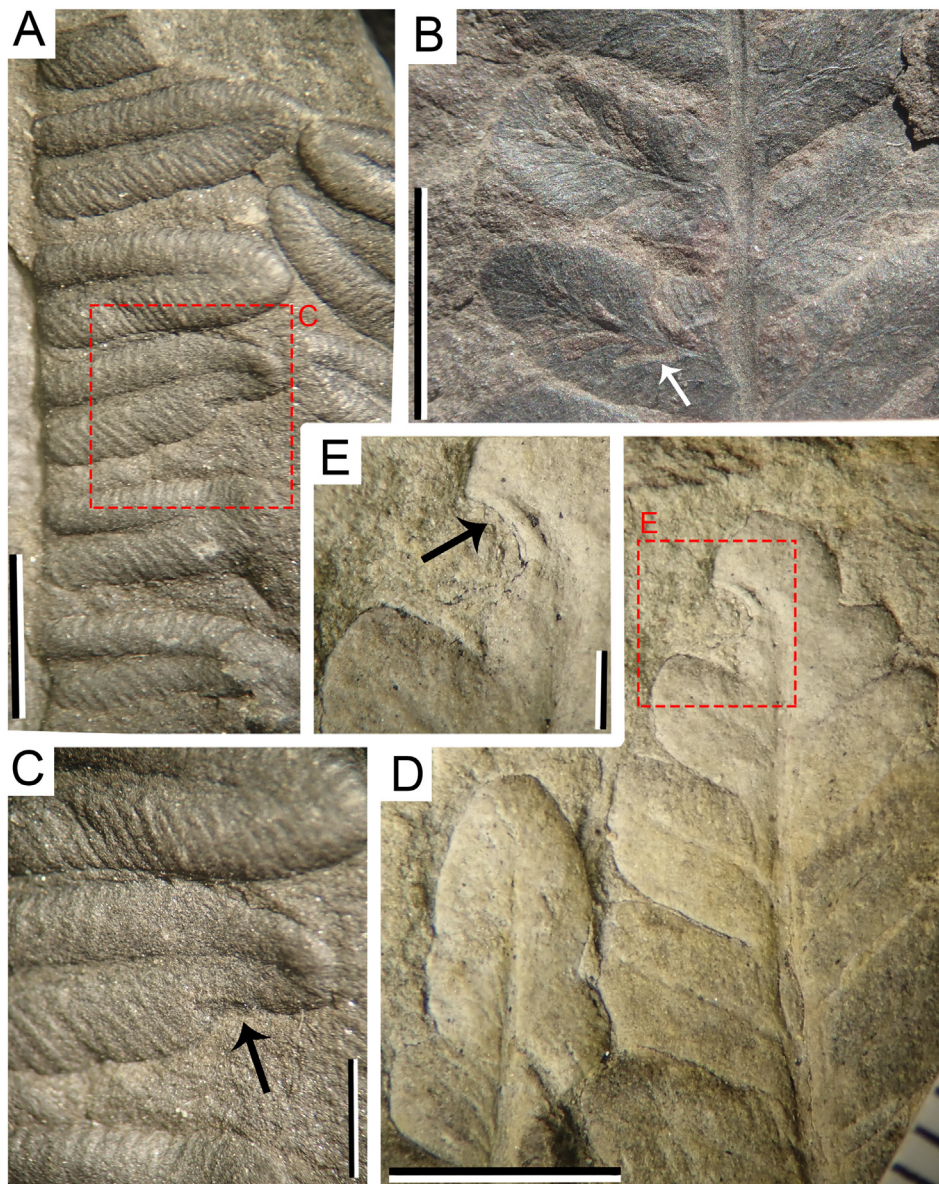

Plate I. A. Margin Feeding (DT12) on *Polymorphopteris polymorpha*, specimen MCNA 16976. Scale bar = 5 mm; Tremor de Arriba, El Bierzo; B. Hole Feeding (DT09) on *Polymorphopteris integra*, specimen MCNA 16979. Scale bar = 5 mm; Cabrillanes, Carrasconte; C. Detail of (A), Margin Feeding (DT12) on *Polymorphopteris polymorpha*, specimen MCNA 16976. Scale bar = 2 mm; Tremor de Arriba, El Bierzo; D. Margin Feeding (DT13) on *Polymorphopteris* cf. *pseudobucklandii*, specimen MCNA 16977. Scale bar = 5 mm; Tremor de Arriba, El Bierzo; E. Detail of (D), Margin Feeding (DT13) on *Polymorphopteris* cf. *pseudobucklandii*, specimen MCNA 16977. Scale bar = 1 mm; Tremor de Arriba, El Bierzo.

100 mm that presents the typical features of this species. Last order pinnae, up to 55 × 10 mm, have very gradual and fused terminals. The 5.5 × 3 mm mature pinnules (l / b ratio = 1.8: 1) are thin, oblong to slightly subfalcate, with very decurrent bases on the basiscopic side and contracted to highly contracted on the acroscopic side. Patent nerves, with a very decurrent main nerve, with basal secondary nerves that emerge from the base of the main nerve with the appearance of arising directly from the rachis. Secondary nerves with polymorphopteroid bifurcations. It is accompanied by some small fragments of *Lobatopteris corsinii* and *Cyperites bicarinatus*.

Polymorphopteris cf. *integra* (Andrae in Germar 1849) Wagner 1959.
Plate III.D
Material: MCNA 16980.
Location: La Mora-Nueva Julia mine, Carrasconte (Carrasconte/Villablino Coalfield).
Description: MCNA 16980 has a pinna fragment of order n-1, with features that are not totally typical in the species since the pinnules are somewhat flexed at their base, which has caused them to be arranged somewhat perpendicular to the rachis and hyde the pinnula bases. So, the decurrence of the basiscopic side and the contraction of the acroscopic area is not very pronounced. The rest of the traits are those of the species, with very gradual and fused pinna terminals. Mature pinnules of 7 × 3 mm (l / b ratio = 2.3: 1), oblong and fine. Well-marked venation, with a very decurrent main nerve with secondary polymorphopteroides nerves, the basal one appearing to arise directly from the rachis. This sample is also accompanied by some small fragments of *Lobatopteris corsinii* and *Cyperites bicarinatus.*

Polymorphopteris cf. *pseudobucklandii* (Andrä in Germar 1853) Wagner 1959.
Plate I.D and E
Material: MCNA 16977.
Location: Casilda mine, Tremor de Arriba (El Bierzo Coalfield).
Description: The sample contains a penultimate order pinna fragment with oblong pinnules, measuring 190 × 900 mm, lacking the terminal. The last order pinnae, 60 × 14 mm with gradual pinna terminals with ovate terminal pinnules, elongated from 4.5 × 3 to 7 × 4 mm. Mature oblong pinnules, somewhat vaulted, 7 × 3 mm, with slightly fused bases, sometimes with slightly decurrent basiscopic side and slightly contracted acroscopic side. Main nerve slightly sunken, slightly decurrent to decurrent. It is not appreciated if there are nerves that appear to come directly from the rachis because the secondary nerves have not been well preserved. Polymorphopterid veins.

Class: Pteridospermatopsida Emberger 1968
Order: Medullosales Corsin 1960
Family: Cyclopteridaceae Laveine ex Cleal & Shute 2003
Genus: **Mixoneura** Weiss 1869
Mixoneura wagneri Lorenzo 1980
Plate II.A
Material: MCNA 16975.
Location: Impensada mine, Valdesamario (El Bierzo Coalfield).
Description: This specimen consists of an incomplete pinnula about 30 × 15 mm, but possibly originally reached 40 × 15 mm. It has a fine, oval pinnula with a cordate base with basal lobes. The thin but well-marked veins with distant secondary nerves (about 15 nerves/cm) arise obliquely from the main vein and bifurcate several times, curving slightly reaching the margin at an oblique angle. The lowermost veins arise from the base of the main nerve in a radiated fashion.

This isolated and incomplete pinnule of *Mixoneura wagneri* presents the characteristic features of pinnules located in the lower part of the fronds of this species. *M. wagneri* is a species that is frequently found in the form of loose pinnules. They have a strong intraspecies variability, it was frequently confused with *Neuropteris praedentata* in the Cantabrian area (i.e., van Amerom, 1966).

Class: Cordaitopsida Rothmaler 1951
Order: Cordaitales Engler 1882
Family: Cordaitaceae Grand'Eury 1877
Genus: **Cordaites** Unger 1850 emend. Ledran 1966
Cordaites cf. *angulostriatus* Grand'Eury 1877 emend. Ledran 1966
Plate III.B
Material: MCNA 16978.
Location: Casilda mine, Tremor de Arriba (El Bierzo Coalfield).
Description: The sample consists of three *Cordaites* leaf fragments. The identification of species in this genus is based on epidermal features, but in these coalfields, the degree of metamorphism that the rocks have undergone prevents the conservation of the epidermis. Therefore, the determination of species can only be tentative. In the specimens present in this sample, the following characteristics can be seen. Thick limbs, with a maximum width of 53 mm in the available fragments, correspond to large leaves that would easily exceed 50 cm. of length. Parallel nerves with a density of 24–32 nerves/cm, with 3–6 longitudinal striae between the nerves, without transverse striae. This makes these specimens compatible with *C. angulostriatus*, but without epidermal analysis it is not possible to ensure this.

4.2. Plant–insect interactions

Nine different types of plant-arthropod interactions have been documented in nine different specimens among 216 fossil plant remains (see Table 2), each specimen has only one type of DT. The damages include evidence of four Functional Feeding Groups: margin feeding (DT12, DT13), hole feeding (DT09), galling (DT33, DT116, DT80), and oviposition (DT67, DT100, DT134), although oviposition, the laying of eggs into or on plant tissues is not a feeding group, it is treated informally as herbivory, and has a significant fossil record (e.g., Sarzetti et al., 2009; Gnaedinger et al., 2014). The evidence of damage has been found on leaves of different genera (see Table 2).

4.2.1. Margin feeding
Margin feeding on *Polymorphopteris polymorpha*
Plate I.A and C
Material: MCNA 16976.
Description: The damage is located in the margin of a pinnula of *P. polymorpha*, close to the apical area. The damage is relatively shallow (up to 0.4 mm deep) and arc-shaped, it is about 1.2 mm long, affecting the secondary nerves of the pinnula, but it does not reach the principal nerve. It presents a dark reaction rim between 0.1–0.2 mm wide. The description of this margin feeding is consistent with a DT12.

Margin feeding on *Polymorphopteris* cf. *pseudobucklandii*
Plate I.D and E
Material: MCNA 16977.
Description: This margin feeding affects the apical part of a pinnula located in the apical part of a pinna of *P.* cf. *pseudobucklandii*. The herbivory mark is about 1.4 mm long and has removed around ¾ of the total length of the pinna, including the complete apical area. The feeding trace affects not only the secondary veins but also the primary vein of the pinnula. A thin reaction rim is observed around the margin. This margin feeding matches with a DT13.

4.2.2. Hole feeding
Hole feeding on *Polymorphopteris integra*
Plate I.B
Material: MCNA 16979 b
Description: At least eight different hole feedings are observed in three pinnulas of this specimen of *P. integra*. The holes are elliptical to coma-shaped, between 1 and 1.4 mm long and about 0.3 mm wide, and start very close to the primary vein, spreading to the pinnules margin without consuming the secondary veins. This herbivory marks culprit(s) only affected the soft tissue between secondary and primary
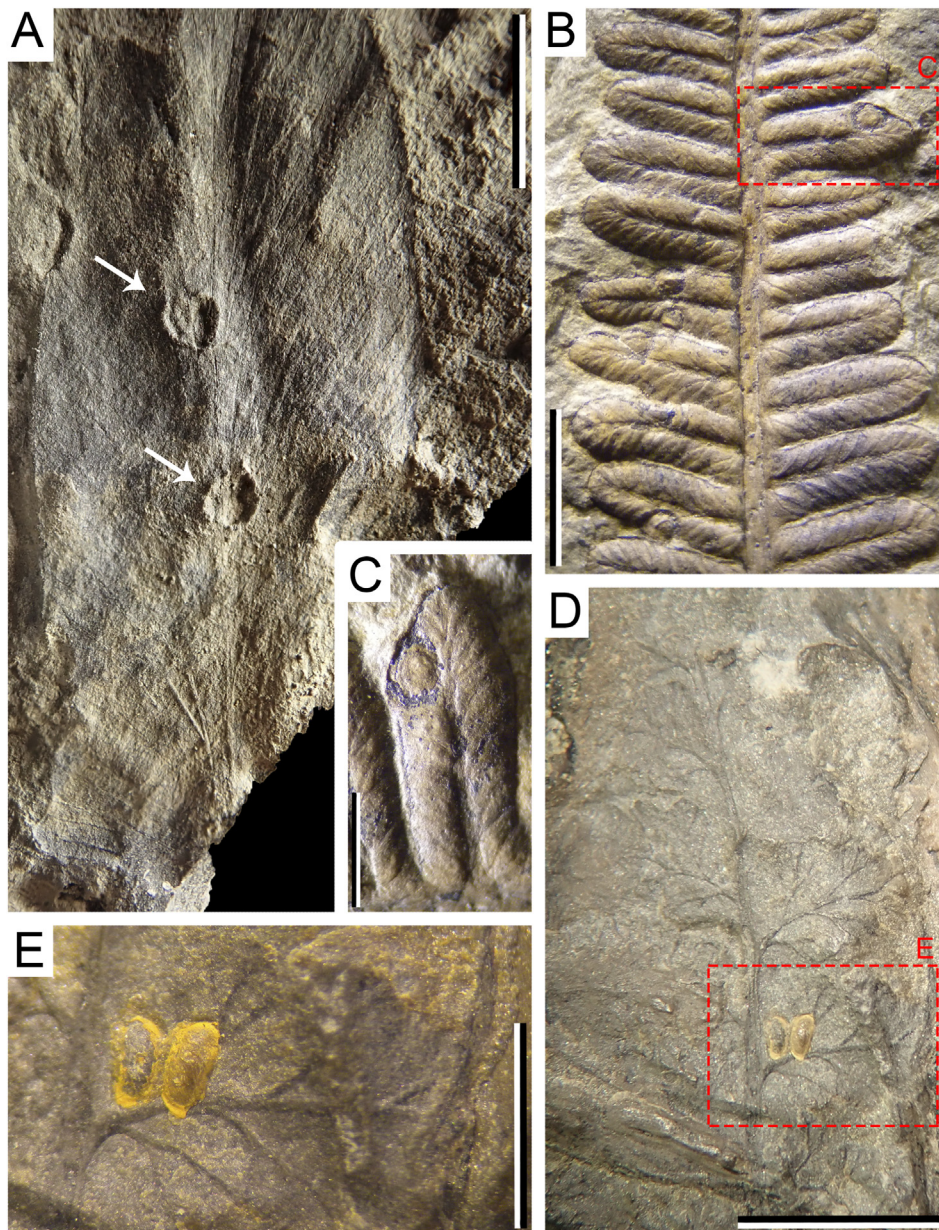
Plate II. A. Galling (DT33) on *Mixoneura wagneri*, specimen MCNA 16975. Scale bar = 5 mm; Valdesamario, El Bierzo; B. Gall structures (DT80) on pinnulas of *Pecopteris apicalis*, specimen MCNA 16974. Scale bar = 5 mm; Garaño, La Magdalena; C. Detail of (B), gall (DT80) on *P. apicalis*, specimen MCNA 16974. Scale bar = 2 mm; Garaño, La Magdalena; D. Galling (DT116) on *Oligocarpia gutbieri*, specimen MCNA 16973. Scale bar = 5 mm; Canales, La Magdalena; E. Detail of (D), Gall structures (DT116) on *O. gutbieri*, specimen MCNA 16973. Scale bar = 2 mm; Canales, La Magdalena.

veins. Thin dark reaction rims are observed around the holes, suggesting that the fern was alive during the attack. These hole feedings are consistent with the DT09.

4.2.3. Galling

Galling on *Mixoneura wagneri*
Plate II.A
Material: MCNA 16975.
Description: Two gall structures are observed in a leaf of *Mixoneura wagneri*. The galls consist of (semi)circular protrusions between 1.3 and 1.6 mm in diameter, and both structures present slight depressions around the protrusions between 0.1–0.3 mm wide. They are placed on the central vein or closely attached to it. These gall-like structures are consistent with the DT33.

Galling on *Pecopteris apicalis*
Plate II.B and C
Material: MCNA 16974 b.
Description: Six gall-like structures partially carbonized are observed in five different pinnulas of *Pecopteris apicalis* (see Plate II). The galls are usually placed close to the pinnula margin and do not seem to affect the primary veins; they are circular shaped with a diameter ranging from 0.8 mm to 1 mm. These circular structures present a central protrusion surrounded by a depressed and dark halo between 0.1 and 0.3 mm wide (see Plate II.C). Generally, these galls are isolated, but in one pinnula, there are two galls that seem to produce a deformation in the affected pinnula. These gall-like structures are in tune with the description of DT80. Nevertheless, they seem to affect the secondary veins in the studied specimens.
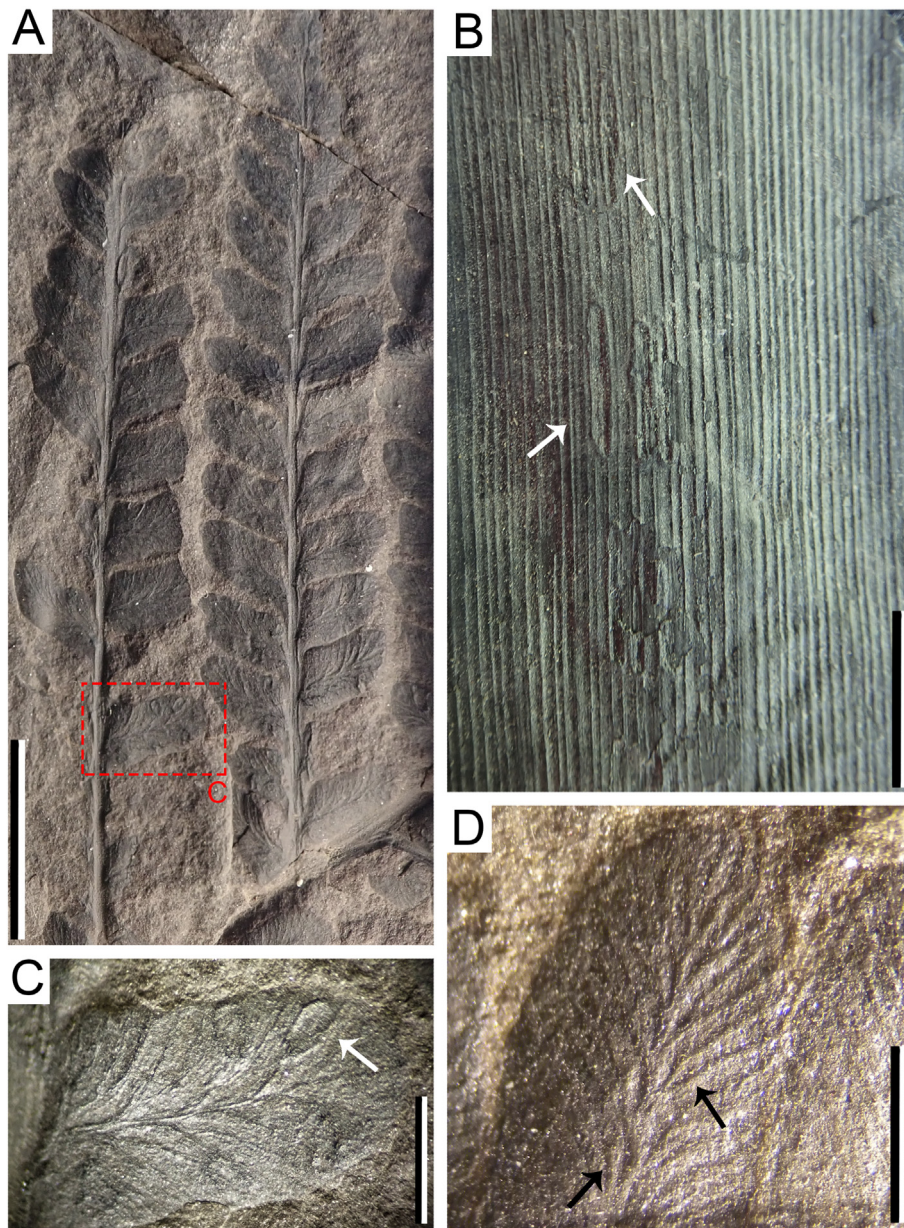
Plate III. A. Putative oviposition scars (DT102) on *Polymorphopteris integra*, specimen MCNA 16979. Scale bar = 1 cm; Cabrillanes, Carrasconte; B. Oviposition scars (DT100) on *Cordaites* cf. *angulostriatus*, specimen MCNA 16978. Scale bar = 5 mm; Tremor de Arriba, El Bierzo; C. Detail of (A), putative oviposition scars (DT102) on a pinnula of *P. integra*, specimen MCNA 16979 a. Scale bar = 2 mm; Cabrillanes, Carrasconte; D. Oviposition marks (DT67) in a pinnula of *Polymorphopteris* cf. *integra*, specimen MCNA 16980. Scale bar = 2 mm; Cabrillanes, Carrasconte.

Table 2
Summary of the studied interactions indicating the Damage Type, Functional Feeding Group, host plant, and specimen.

Functional feeding goup	Damage type	Host plants	Specimen
Margin feeding	DT12	*Polymorphopteris polymorpha* (Pteridophyta)	LE-13–44
	DT13	*Polymorphopteris* cf. *pseudobucklandii* (Pteridophyta)	LE-13–240
Hole feeding	DT09 (10 hole feeding marks)	*Polymorphopteris integra* (Pteridophyta)	LE-29–87(a)
Galling	DT33 (2 galls)	*Mixoneura wagneri* (Pteridospermatophyta)	LE-12–19
	DT80 (7 galls)	*Pecopteris apicalis* (Pteridophyta)	LE-8–17b
	DT116 (2 galls)	*Oligocarpia gutbieri* (Pteridophyta)	LE-5–28
Oviposition	DT102 (about 26 oviposition scars)	*Polymorphopteris integra* (Pteridophyta)	LE-29–87(b)
	DT100 (about 10 oviposition scars)	*Cordaites* cf. *angulostriatus* (Coniferophyta)	LE-13–331
	DT67 (about 9 oviposition scars)	*Polymorphopteris* cf. *integra* (Pteridophyta)	LE-29–232

Galling on *Oligocarpia gutbieri*
Plate II.D and E
Material: MCNA 16973.
Description: Two comma-shaped to columnar structures are present in a pinnula *Oligocarpia gutbieri*. The two structures are placed contiguously, ranging from 0.9 to 1.1 mm long and 0.5 mm wide, and cause a protrusion in the pinnula. The gall-like structures are deeply attached to the plant tissue and close to the primary veins basis. Both are enveloped by a thin yellow amber to yellow colored sediment (see Plate II.E), very different from the rest of the fossil. This yellow to amber sediment seems to cover the galls surface and could be the outer wall of the structure. These structures are consistent with the DT116, but are slightly different in shape.

4.2.4. Oviposition
Oviposition on *Polymorphopteris integra*.
Plate III.A and C.
Material: MCNA 16979 a
Description: Between 1 and 6 oviposition scars are arranged in the margin of several pinnulas of *Polymorphopteris integra*. They consist of ovoidal marks generally arranged in semicircular clusters around the margin of some pinnulas. The scars are ranging from 0.8 to 1.1 mm long and about 0.4–0.5 mm wide and present distinguish black reaction rims around the ovoidal structures. These structures do not affect the primary vein, and most of them seem to be oriented in the same direction of diverging veins, in addition, the oviposition was probably placed in the abaxial surface. The marks are unlikely to be sori since their number, position, and shape are irregular. These oviposition scars seem to fit in the description of DT102.

Oviposition on *Cordaites* cf. *angulostriatus*
Plate III.B
Material: MCNA 16978.
Description: Several ovoidal to ellipsoidal foliar scars are placed between *Cordaites* cf. *angulostriatus* specimen veins. These oviposition marks are arranged in linear clusters oriented parallel to the veins. They are between 1.5 and 4.2 mm long and range from 0.3 and 0.5 mm wide. These scars occupy the space between two parallel veins and show a thin black reaction rim that delimits the interaction. In addition, the edge of the scars is slightly bulging. These interactions are in tune with DT100.

Oviposition on *Polymorphopteris* cf. *integra*
Plate III.D
Material: MCNA 16980.
Description: Seven discrete oviposition scars are arranged in a pinnula of *Pecopteris* cf. *integra*. The oviposition scars are ovoidal in shape and small in size, ranging from 0.3 to 0.5 mm long and from 0.2 to 0.3 wide. They are subparallel orientated, forming clusters around the main vein of the pinnula and close to the bases of the secondary veins. The reaction rim is not observed, maybe because the interaction was produced when the fern was dead or probably because the reaction rim was not preserved due to taphonomic processes. These marks do not seem to be sorus since sporangia would need to be linked to the vascular system, and the position in the pinnula does not fit with these reproductive structures. These oviposition scars are consistent with the description of DT67.

5. Discussion

We have found few plant–insect interactions on *Polymorphopteris polymorpha*, *Mixoneura wagneri*, *Pecopteris apicalis*, *Oligocarpia gutbieri*, *Polymorphopteris integra*, *Cordaites* cf. *angulostriatus*, and *Polymorphopteris* cf. *pseudobucklandii*. The most affected botanical groups were the Pteridophytes (*Polymorphopteris*, *Oligocarpia*, and *Pecopteris*). In this group of plants we found seven of the nine identified Damage Types of four

different FFGs. Interactions on Coniferophytes (Oviposition in *Cordaites*) and Pteridospermatophytes (galling in *Mixoneura*) were less frequent and diverse (in number of DTs). Evidence of external damage was only found in ferns, but not in Gymnosperms.

As far as we know, the interactions on *Polymorphopteris*, *Pecopteris*, and *Oligocarpia* are the first report of arthropod damage in these genera, at least, for the Iberian Peninsula (check Table 1). It is also the first evidence of interactions on *Cordaites* from the Iberian Peninsula. Previous studies such as Correia et al. (2020) and Van Amerom and Boersma (1971) were focused on single occurrences, galling on *Anullaria* from the Gzhelian of Portugal, and external damage on *Neuropteris* (*Mixoneura* sensu Lorenzo, 1980) from the Gzhelian of León (Spain) respectively. However, the study of Castro (1994, 1997) involves more plant genera (*Mixoneura* spp. *Linopteris* sp., *Dicksonites*, *Pseudomaripteris* sp., and *Sphenopteris* sp.) showing evidence of galling, external feeding, and putative mining, as well as fungal damage. Nevertheless, Castro (1994, 1997) is before Labandeira et al. (2007) guide, therefore, this author does not determine the interactions in "Damage Types". The plants and the interactions are different from our assemblage. Only the general margin and hole feeding are common with the new assemblage; probably DT12 and DT09 are also present in Castro (1994, 1997, see pl. I, fig. 1–4), but on different taxa.

The evidence of different Functional Feeding Groups, including external damage (margin feeding and hole feeding), oviposition scars, and galls on different plants from the Carboniferous plant communities in northern Spain, suggest a mature forest with diverse ecological relations between plants and insects. While margin and hole feeding are general types of external foliage feeding, gall-inducing arthropods are one of the most specialized herbivores since galls are adaptations that allow some arthropod taxa to feed on high-quality vegetal tissues and protect themselves from natural enemies and abiotic factors (Price et al., 1986; Fernandes et al., 1994; Gonçalves-Alvim and Fernandes, 2001; Schachat and Labandeira, 2015; Cariglino et al., 2021). So, the presence of different Damage Types of galling would indicate different specialized gall-inducing species in the studied ecosystem. On the other side, external damage such as margin and hole feeding could be caused by various orders of arthropods, but culprits of causing these Functional Feeding Groups would need a robust mandibular system to penetrate the coriaceous tissue and nerves of *Polymorphopteris polymorpha*, *P. pseudobucklandii*, and *P. integra*. Considering the insect diversity recorded in Carboniferous deposits from the Iberian Peninsula, these herbivory patterns could be consistent with (pan)orthopteroid insects, probably of small size due to the millimetric dimensions of the external damage found in this flora.

In the studied deposits have been found different insect remains: an unnamed fossil of Palaeodictyoptera (Camprecios, 2013), an Archaeorthoptera fossil identified as *Omalia anae* (Brauckmann et al., 2001) and several specimens of Dictyoptera, including *Xenoblatta* sp., and *Compsoblatta ovata* (*Phyloblatta munobilis*?) (Álvarez-Ramis et al., 1986; Brauckmann, 1993). In addition, several new specimens of insects have been found in the studied sites recently, including species of Paoliida, Palaeodictyoptera, Megasocoptera, and Dictyoptera (Santos et al., under review). Based on the knowledge about the mouth anatomy of these orders, Archaeorthoptera would be the more consistent candidates for the external damage interactions on *Polymorphopteris* spp., still, other arthropods cannot be ruled out. The link between margin feeding and surface feeding with Archaeorthoptera has been proposed in other Gzhelian floras (e.g., Labandeira et al., 2007; Xu et al., 2018). The oviposition scars are difficult to assign to some concrete order since all the studied orders/superorders found in the area (e.g., Palaeodictyoptera, Archaeorthoptera, Paoliida, and Megasocoptera) could be theoretically culprits of the oviposition scars, even dictyopteran insects could be responsible for these interactions since it is well documented that during Carboniferous this group also have ovipositors (Hörnig et al., 2018). However, in the case of the oviposition in *Cordaites*, the size of oviposition scars is in tune with a higher size insect such as

Palaeodictyoptera, similar scars on *Calamites* in the Gzhelian of France have been related to this same order of insects (Bethoux et al., 2014). Finally, as we discussed before, the galls need a higher grade of specificity (Gonçalves-Alvim and Fernandes, 2001). In other Carboniferous floras (e.g., see Correia et al., 2020) galling evidence has been related with Holometabola and Eriophyoidea, but in our specimens, it does not seem safe to establish the culprits of the galls. More studies on the Carboniferous plant–insect interactions from León are necessary for an accurate interpretation.

In the Carboniferous-Permian boundary, the climate was marked by a global aridification trend (Chumakov and Zharkov, 2002; Roscher and Schneider, 2006). However, the areas around the Rheic Ocean presented onshore winds that bring moisture from ocean to continent (Ziegler, 1990; Roscher and Schneider, 2006). We have not carried out a quantitative analysis of the flora, so we have substantial limitations to interpreting the plant–insect trends of this flora. However, gall-like structures apparently are not uncommon in the area. Only three of the nine DTs found here belong to galling. In both current and fossil ecosystems, galling insects show the highest richness in arid and hot habitats, with sclerophyllous vegetation (Fernandes and Price, 1988, 1992; Lara and Fernandes, 1996; Carneiro et al., 1998; Wright and Samways, 1998; Na et al., 2018; Santos et al., 2021; Moreno-Domínguez et al., 2022). If the apparent relative abundance of galling is confirmed in future quantitative studies this would be consistent with the interpretation of xeric conditions in these Late Pennsylvanian forests, nevertheless, the presence of diversity and abundance of ferns in the flora (such as *Pecopteris*, *Polymorphopteris,* and *Oligocarpia*) that probably need some humid conditions to complete their life cycle is also in tune with moisture input, may due to the previous cited onshore moisture-winds from the ocean (Ziegler, 1990; Roscher and Schneider, 2006).

6. Conclusion

The presence of various ecological interactions, including margin feeding, hole feeding, galling, and oviposition in this Carboniferous palaeoforest suggests a well-establish insect community that found a source of food, lodge, and a protected niche to deposit their eggs. The most affected botanical groups were the Pteridophytes (with interactions on *Polymorphopteris*, *Oligocarpia*, and *Pecopteris*). In this group of plants were found seven of nine identified Damage Types of four different FFGs. Interactions on Coniferophytes (oviposition in *Cordaites*) and Pteridospermatophytes (galling in *Mixoneura*) were less frequent and diverse. Among the possible suspects of causing damage on this plants there are different orders/superorders that have been found in the studied deposits such as Archaeorthoptera, Paoliida, Palaeodictyoptera, Megasecoptera, and Dictyoptera. Possible culprits of the external feeding should need a robust mandibular system to drill the apparent coriaceous tissue and nerves of *Polymorphopteris polymorpha*, *P. pseudobucklandii*, and *P. integra.* These feeding patterns are consistent with (pan)orthopteroid insects, probably of small size. In addition, the apparent diversity of galling could suggest some xeric conditions, at least seasonally or locally. Nevertheless, a future statistical study with more specimens is necessary to clarify the palaeoclimatic implications.

Declaration of Competing Interest

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

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