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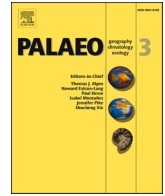
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Plant taphonomy and palaeoecology of Pennsylvanian wetlands from the Erillcastell Basin of the eastern Pyrenees, Catalonia, Spain

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ABSTRACT

The Pennsylvanian flora from the intramontane Erillcastell Basin in the eastern Pyrenees (Catalonia, Spain) is described in a palaeoenvironmental context based on a combined study of sedimentology, plant taphonomy and paleoecology. This basin differs from other Pyrenean basins of this age in comprising a wide array of fluvial channel and floodplain-related facies, with a limited development of peat mire facies. Both late Moscovian and early Gzhelian successions are rich in diverse calamitalean remains (mainly *Calamites cistii* and *C. suckowii*, in addition to *C. undulatus* in the Moscovian) and pectopterid foliage (mainly *Polymorphopteris polymorpha*) corresponding to marattialean tree ferns. An unusual feature of the fluvial channel assemblages is the common occurrence of arborescent lycopsids, especially *Sigillaria brardii*, in association with *Calamites* species, which presumably occupied riparian niches. Palaeotopographic, drainage and climatic constraints of the Erillcastell Basin may explain this unusual ecological distribution of *Sigillaria brardii*, which is mostly associated with peat mires and oxbow lakes in other coeval intramontane South European basins. Findings improve knowledge of intermontane forest ecosystems during the Middle to Late Pennsylvanian transition.

1. Introduction

Middle–Late Pennsylvanian times witnessed a major plant biome turnover in tropical Laurasia (Van Hoof et al., 2013; Falcon-Lang et al., 2018), which has been linked to a global climatic shift towards increasing aridity (Phillips and Peppers, 1984; Cecil, 1990; Winston, 1990; Tabor and Poulsen, 2008). Palaeoenvironmental reconstructions conducted in Pennsylvanian paralic basins in the USA have revealed a decline in the Moscovian wetland flora dominated by lycopsids, and its rapid replacement during Kasimovian times with plant communities dominated by marattialean tree ferns and medullosacean seed-plants, which were more drought tolerant (DiMichele, 2014). In contrast to paralic lowlands, Pennsylvanian vegetation dynamics in intramontane limnic basins of the Hercynian Range (i.e., surrounded by highlands) is relatively less known, but the available data (e.g., Falcon-Lang and Scott, 2000; Martín-Closas and Galtier, 2005; Bek and Opluštil, 2021; Bashforth et al., 2021) suggest a different evolution.

Most of the Pennsylvanian intramontane limnic basins of Central and South Europe occurred in internal zones of the Hercynian Mountain

Range, some of these areas being now located in the Bohemian Massif (Czech Republic; Opluštil and Pešek, 1998), Central French Massif and the Montagne Noire in France (Pochat and Van Den Driessche, 2011), the Cantabrian Mountains in Northern Spain (Ábalos et al., 2002), Southwestern Iberian Massif in Southern Spain (BROUTIN, 1981) and the Eastern Pyrenees in Catalonia (Soriano et al., 1996). To date, only a few palaeoecological studies have been conducted in Moscovian limnic deposits of southern Europe, whereas a larger number of such studies have been performed in analogous sedimentary environments in Gzhelian basins e.g., Graissessac-Lodève in France; (Martín-Closas and Galtier, 2005), Surroca-Ogassa in the Eastern Pyrenees; (Martín-Closas and Martínez-Roig, 2007), Puertollano in the Iberian Massif (Wagner and Álvarez-Vázquez, 2015) and La Magdalena in the Cantabrian Mountains (Bashforth et al., 2010).

In this paper a combination of sedimentologic, taphonomic and palaeoecologic analyses are conducted for the Erillcastell Basin (eastern Pyrenees) to elucidate the composition and palaeoecology of late Moscovian and early Gzhelian plant assemblages. The results reveal that vegetation was heterogenous among the Pennsylvanian intramontane

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basins of the South European Hercynian Range and provide more information about differences and common trends in comparison to coeval lowlands from Euramerica.

2. Geological and palaeobotanical setting

The study area is located 12 km northeast of the town of El Pont de Suert, in the Pyrenean Axial Zone (Catalonia, Spain), between the abandoned village of Erillcastell and the Coll de Fades pass. During the late 19th and early 20th centuries, the coal from this area was exploited in the Malpàs Coalfield (Nagtegaal, 1969).

From a geological perspective, the palaeobotanical localities studied here belong to the Erillcastell Basin, which is Carboniferous-Permian in age (Martí, 1983, 1995; Soriano et al., 1996). The origin of this basin is related to a transtensional tectonic regime during the latter stages of the Hercynian orogeny, from Moscovian to Permian times (Ménard and Molnar, 1988). Thinning of the continental crust produced intense volcanism and subsidence of the Carboniferous–Permian Pyrenean intramontane basins (Martí and Mitjavila, 1988). Four late Hercynian pull-apart basins developed, from west to east, as follows: the Erillcastell (Fig. 1), Estac, Cadí and Castellar de N'Hug-Camprodon basins (Martí, 1995; Soriano et al., 1996).

Located between the villages of Erillcastell and Sas/Guiró (Figs. 1, 2A), the Erillcastell Basin, is a narrow (ca. 15 km long and 3 km wide) intramontane basin, oriented East to West, bounded to the North by strike-slip faults, and internally compartmented by normal faults according to Gisbert (1981), Martí and Mitjavila (1987, 1988) and Martí (1995). During the Moscovian, rapid tectonic subsidence triggered intense volcanic activity, and an accumulation of thick volcano-sedimentary sequences (Martí and Mitjavila, 1988). Volcanism decreased during the Kasimovian and early Ghzelian allowing the development of extensive fluvio-lacustrine systems throughout the basin (Martí, 1981, 1983). This trend continued during the Permian, which is mainly represented by red beds. All these deposits were later involved in the Alpine orogeny and incorporated into the Pyrenean Chain during the Eocene.

Stratigraphic studies of the Erillcastell Basin were first undertaken by Dalloni (1930), Mey et al. (1968) and Nagtegaal (1969). These authors proposed a subdivision of the Carboniferous-Permian deposits based on lithostratigraphy. Later, Gisbert (1981) erected a new subdivision based on allostratigraphic units, i.e., isochronous units limited by stratigraphic unconformities or equivalent paraconformities. These units were termed

the Grey Unit, the Transition Unit, the Lower Red Unit and the Upper Red Unit. Although they are meaningful in terms of basin evolution, it is locally difficult to characterize them in the field. However, these units have generally been accepted and form the stratigraphic scheme followed here. The two first units constitute the object of the present study.

2.1. Grey unit

This comprises a 550 m thick succession that unconformably overlies the folded and foliated pre-orogenic Hercynian deposits. The Grey Unit begins with a sedimentary breccia (Guiró Formation) followed by a thick succession of andesitic tuff, basaltic andesite sheets and volcanic breccia belonging to the Erillcastell Formation (Gisbert, 1981, 1983; Greter et al., 2015). Locally, at Guiró, a coal-bearing clastic succession, rich in plant remains, is intercalated within the volcanic rocks (Nagtegaal, 1969). The upper part of the Grey Unit is characterized by an andesite sheet, on top of which the medieval villages of Erillcastell and Peranera were constructed (Fig. 2). In Coll de Fades, the uppermost part of the Grey Unit is constituted by sedimentary deposits composed of conglomerates, sandstones and shales (lower part of the Malpàs Formation).

The age of the Grey Unit has been a matter of debate. Dalloni (1930) assigned the flora to the late Moscovian (Asturian) based on the plant megafossils found at Guiró. Later, based on the whole Carboniferous-Permian record from the Pyrenees, Gisbert (1981, 1983) concluded that the Grey Unit comprised the late Moscovian (Westphalian D) and the lower part of the Kasimovian (Asturian to Stephanian B). Broutin and Gisbert (1985) revised the flora from Guiró collected by Dalloni (1930) and ascribed it to Kasimovian (Stephanian B). Subsequently, based on the occurrence of *Lepidodendron worthenii* in the same Guiró section, Talens and Wagner (1995) again assigned it a late Moscovian age. A recent palynological study carried out in this plant locality by Juncal et al. (2019) provided a Kasimovian (Stephanian A) age for the plant bearing beds assigned to the Grey Unit. These biostratigraphic results contrast with a radiometric study based on zircons from the ignimbrite of Erillcastell performed by Pereira et al. (2014), whose results provided a lower Permian (Asselian) age (296.1 ± 4.0 Ma). However, the authors acknowledged that this age may be biased by alteration of the rhyolitic pumicite fragments.

2.2. Transition unit

This unit was described by Gisbert (1981, 1983). It corresponds to

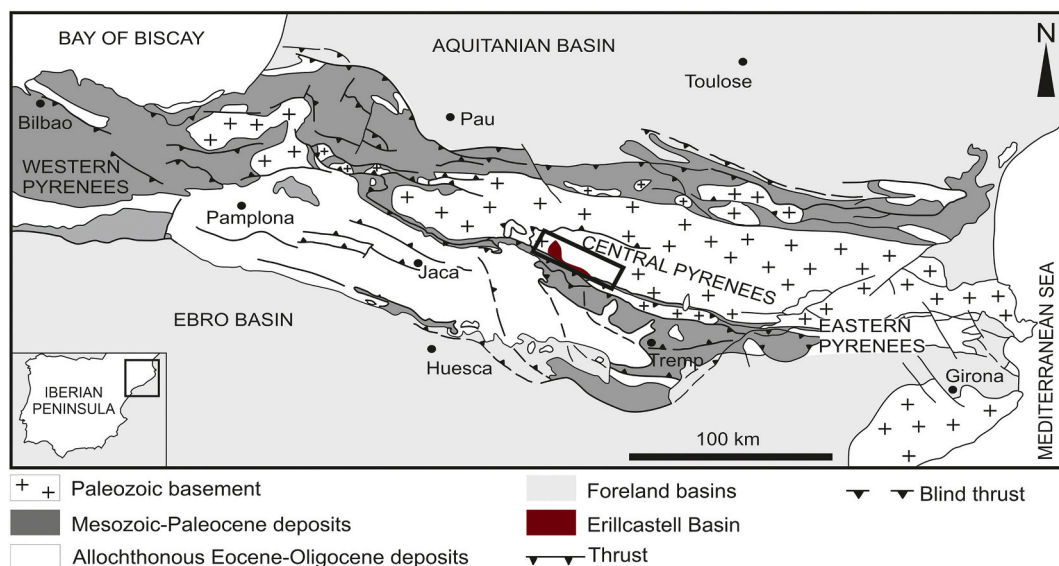


Fig. 1. Geological setting of the Erillcastell Basin in the eastern Pyrenees. Modified from Teixell (1998).

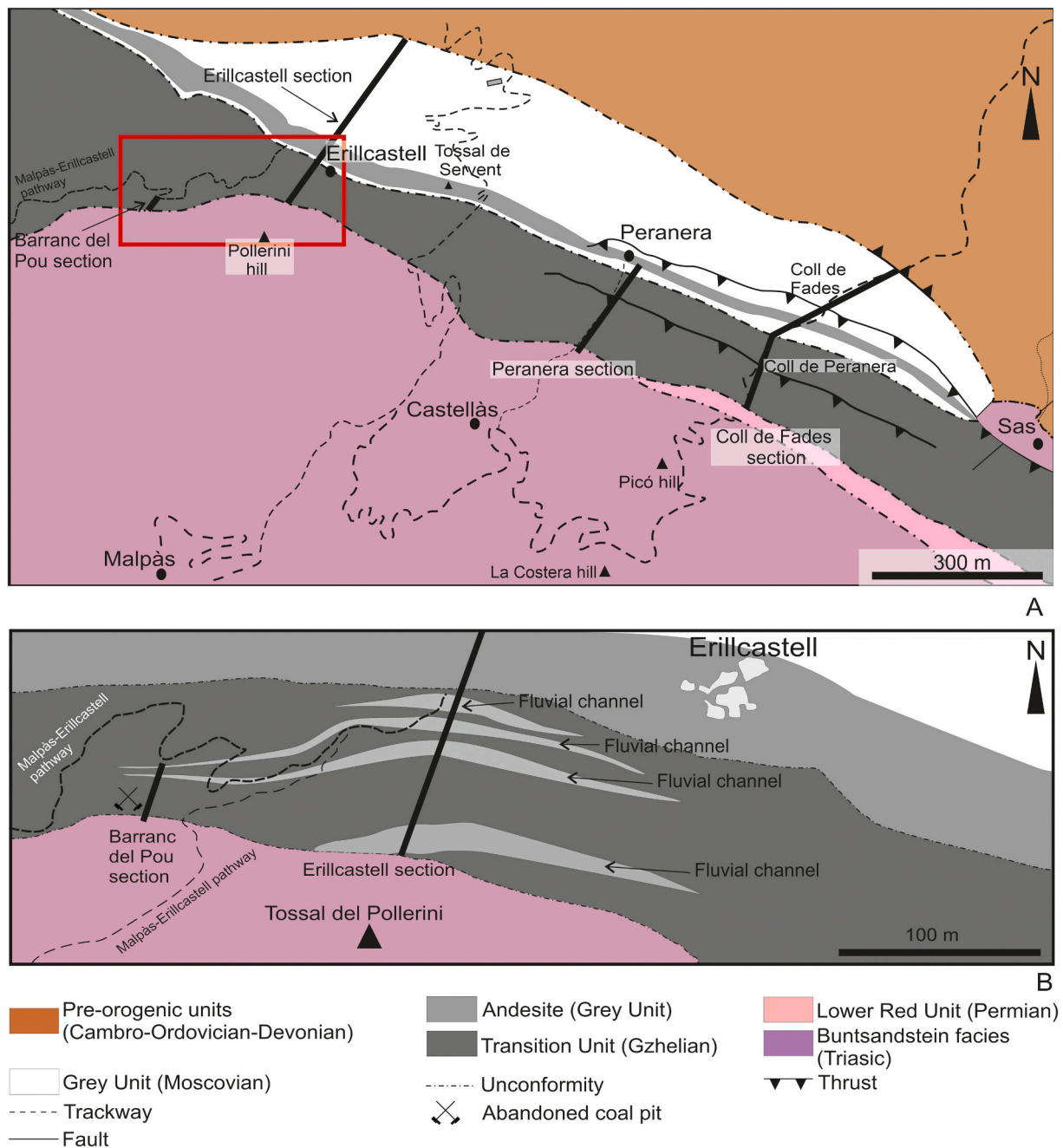


Fig. 2. Detailed geological map of the study area and the position of the stratigraphic logs. A: General map with location of the three sections studied. B: Detailed map of the Erillcastell area showing the correlation of the Barranc del Pou outcrop to the main Erillcastell section.

the upper part of Malpàs Formation of Mey et al. (1968). The thickness of the Transition Unit reaches up to 800 m (Saura and Teixell, 2006). However, in the study area, it is up to 185 m thick, since its top is cut off by the basal Mesozoic unconformity (Figs. 2A–B). It rests unconformably or paraconformably on the Grey Unit and consists of conglomerates, sandstones, black shales and coal (Gisbert, 1981, 1983).

The age of the Transition Unit in the Pyrenees ranges from Kasi-movian to Gzhelian based on Dalloni (1930), Gisbert (1981, 1983) and Mateu-Ibars and Marzo (1985). In the Erillcastell Basin, Talens and Wagner (1995) collected new plant remains that constrained the age of this unit to the early Gzhelian (Stephanian C), which was later confirmed by Wagner and Álvarez-Vázquez (2010).

3. Material and methods

Three stratigraphic sections were measured and correlated to each other in the study area (Figs. 2A–B):

- 1) The Erillcastell section starts 500 m northwest of the Erillcastell village itself and terminates at the base of the Triassic deposits (Buntsandstein facies) at the Pollerini hill (base 42° 25' 39"N; 0° 48' 05"E, top 42° 25' 19"N; 0° 47' 56"E). This section has been complemented at Barranc del Pou, with a short section located 300 m west of Erillcastell village (base 42° 25' 23"N; 0° 47' 42"E, top 42° 25' 22"N; 0° 47' 41"E).

- 2) The Peranera section is located 200 m southeast of the village of Peranera. (base 42°25'12"N; 0°49'00"E, top 42°25'05"N; 0°48'54"E).
- 3) The Coll de Fades section represents the easternmost section and crops out on a mountain pass 900 m east of the village of Peranera (base 42°25'09"N; 0°49'40"E, top 42°24'57"N, 0°49'22"E).

Facies analysis and taphonomic observations of selected outcrops were conducted to elucidate the depositional setting where the plant remains were buried, to evaluate the autochthony, parautochthony or allochthony of these and draw hypotheses about their habitats. Systematic sampling of plant megafossils was conducted. The point quadrat technique developed by Scott (1977) was applied at selected facies in order to quantitatively evaluate the richness and composition of the plant remains. Taphonomic analysis was performed for each leaf bed selected, evaluating the completeness of the plant remains, type and degree of fragmentation, size, orientation and relative abundance within the leaf bed.

The plant remains studied are preserved as adpressions. Twenty-one organ species were recognized (Table 1). Adpressions were photographed using a Nikon 5300 camera and compiled using Helicon Focus 5.3 software (www.heliconsoft.com). The figured plant remains collected are stored at the Museu de Ciències Naturals de Barcelona with quotation numbers MGB 90197 to MGB 90205. The equivalences between regional non-marine stages of Western Europe and global chronostratigraphic units follow the scheme of Heckel and Clayton (2006).

Table 1

Taxonomic list of the Pennsylvanian megafloral species from the studied zone. Int: referred to the interval described in section 4. of the present study. Intervals from 1 to 8 correspond to the Grey Unit while intervals from 9 to 10 belong to the Transition Unit.

Taxonomic list	Barranc del Pou	Erillcastell	Peranera	Coll de Fades
LYCOPSIDA				
<i>Lepidodendron aculeatum</i>				Int. 8
<i>Sigillaria brardii</i>	Int. 9	Int. 9,10	Int. 9,10	Int. 4, 9, 10
<i>Sigillaria sigillata</i>				Int. 10
<i>Stignaria</i> sp.	Int. 9	Int. 9,10	Int. 9,10	
SPHENOPSIDA				
<i>Annularia spinulosa</i>	Int. 9	Int. 9,10		Int. 10
(= <i>Annularia stellata</i>)				
<i>Annularia sphenophylloides</i>		Int. 9		Int. 10
<i>Calamites undulatus</i>				Int. 4
<i>Calamites suckowii</i>	Int. 9	Int. 9,10		Int. 4, 10
<i>Calamites cistii</i>	Int. 9	Int. 9,10	Int. 9	Int. 4, 9, 10
<i>Macrostachya</i> sp.		Int. 9		
FILICOPSIDA				
<i>Pecopteris</i> cf. <i>candolleana</i>		Int. 9		Int. 10
<i>Pecopteris</i> sp.		Int. 9		
<i>Alloiopteris</i> cf. <i>erosa</i>		Int. 9		
<i>Polymorphopteris polymorpha</i>		Int. 9		Int. 10
(= <i>Pecopteris</i> cf. <i>polymorpha</i>)				
<i>Polymorphopteris</i> cf. <i>integra</i>		Int. 9		
PTERIDOSPERMS				
<i>Dicksonites pluckenettii</i>		Int. 9		Int. 10
<i>Callipteridium zeileri</i>		Int. 9		Int. 10
<i>Carpolithus</i> sp.		Int. 9		
CORDAITALES				
<i>Artisia</i> sp.		Int. 9,10		
<i>Cordaites</i> (foliage)		Int. 9		
<i>Cardiocarpus</i> sp.		Int. 9		Int. 4, 10

4. Results

At Erillcastell, the base of the Carboniferous deposits includes the Guiró and Erillcastell formations resting unconformably on pre-orogenic deformed slates and limestones, attributed to the Devonian in the geological map by ICGC (www.icgc.cat). Overlying the Erillcastell Formation, the Malpàs Formation crops out, but its upper part is truncated by an angular unconformity, making the Buntsandstein facies (lower Triassic) cover the late Hercynian deposits (Fig. 3).

At Coll de Fades the contact between the pre-orogenic units and the late Hercynian deposits is by fault and the entire Guiró Formation is missing. In contrast, the overlying Erillcastell and Malpàs formations are well-developed and exposed (Fig. 4; Supplementary Fig. S1). The lithostratigraphic correlation among the sections studied was based on the andesite sheet flow corresponding to interval 6 (Supplementary Fig. S1). For descriptive purposes, the Carboniferous succession in the Erillcastell Basin has been subdivided into 10 lithostratigraphic intervals. The sedimentary features of these intervals are summarized below, and more details are given in Table 2.

4.1. Interval 1

This interval belongs to the Guiró Formation and is only recognized at the Erillcastell section (Supplementary Fig. S1). The base of the interval is constituted by massive, matrix-supported breccia, followed by fining upward microconglomerates and covered by coarse-grained sandstones with trough cross-bedding (Gm and St facies in Table 2). These materials are devoid of plant remains. The breccia is attributed to deposition in debris flows, while the fining upward microconglomerate to sandstone bodies represent river channel infills (e.g., Miall, 1985; Mulder and Alexander, 2001).

4.2. Interval 2

This is a volcanic interval that forms the lower part of the Erillcastell Formation, at Erillcastell and Coll de Fades (Fig. 4). It was the object of exhaustive studies by Martí (1981, 1983) and Martí and Mitjavila (1988). At Erillcastell it consists of whitish pyroclastic rocks characterized by massive, matrix-supported breccias rich in pumice intercalated with laminated cinerites (Vb and Vc in Table 2). This unit is devoid of plant remains. Pumice-rich breccia corresponds to an ignimbrite deposit, while the cinerite deposits represent ash fall following the ignimbrite deposition event (Martí, 1981, 1983).

4.3. Interval 3

This interval only crops out at the Coll de Fades section and belongs to the Erillcastell Formation (Fig. 4). It is composed of grey cinerite (Facies Vc, Table 2), covered by red cinerites. This unit is devoid of plant remains. Cinerites result from air-fall ash deposition (Martí, 1981). Variation in the colour of these cinerites probably represents distinct mineralogical compositions from different volcanic eruptions or different diagenetic alterations.

4.4. Interval 4

This interval only crops out at the Coll de Fades section and represents the base of the Malpàs Formation (Fig. 4, Supplementary Fig. S1). It is constituted by a sedimentary deposit rich in plant remains, which is intercalated with volcano-sedimentary deposits at the base. It is internally organized into three fining upward-sequences, two of them composed of sandstones with epsilon cross-stratification and ripples marks at top, representing the infill of meandering river channels (facies Sr, Table 2), while the third one represents the deposits of a braided river channel (facies St, Table 2). These sequences are topped by shales with plane-parallel lamination, corresponding to floodplain to fluvio-



Fig. 3. Panoramic view of the Erillcastell section, showing the boundary between the Grey Unit and the Transition Unit as inferred from sedimentological and biostratigraphic data (dashed line indicates deduced contact), and the angular unconformity separating Buntsandstein facies and Late Pennsylvanian deposits.

lacustrine deposits (facies Fs, Table 2).

Sandstones representing the infill of meandering river channels contain up to 15 cm long stem casts of *Calamites undulatus* Sternberg (Fig. 4, 5A; Table 2), *C. suckowii* Brongniart (Fig. 5B) and *C. cistii* Brongniart, associated with up to 1 m long logs of *Sigillaria brardii* Brongniart (Fig. 6A). At the top of these sandstones, there are abundant and rounded unidentified axes (5–15 cm long) and well-sorted comminuted plant debris associated with well-preserved *Cardiocarpus* sp. seeds (Figs. 5C, 6B). Floodplain deposits contain *Calamites* adpressions, undetermined axes and rare torn cordaitalean leaves (Fig. 5D, 6C). A specimen of *C. undulatus* (50 cm long and 5 cm wide) was found charred and in an upright position within a pyroclastic bed intercalated in these shales (Fig. 6D). The third sequence, corresponding to the infilling of a braided river channel, was devoid of identifiable plant remains.

Stems of *Calamites undulatus*, *C. suckowii* and *C. cistii* and large *Sigillaria brardii* logs found in the meandering-river channel lag-deposit are interpreted as having been directly incorporated into the river from a riparian vegetation after riverbank erosion and limited water transport that produced some fragmentation, forming a parautochthonous assemblage. *Calamites* growing on the channel margins is a well-known occurrence, e.g., Gastaldo and Degges (2007) in the Moscovian succession of the Mary Lee mine (Alabama, USA). In contrast, the growth of *Sigillaria brardii* on river margins has not previously been reported in the Pennsylvanian Pyrenean basins. However, it has been documented in the Moscovian localities of Indiana (USA) by DiMichele and Nelson (1989) and DiMichele (2014).

Abundant and relatively undamaged stems of *Calamites*, i.e., *Calamites undulatus*, *C. cistii* and *C. suckowii* found in fluvio-lacustrine deposits suggest that the plants grew close to the depositional site. The erect pith cast of *C. undulatus* found charred within a lapilli bed covering a floodplain deposit indicates in situ burial of the living plant in this environment.

4.5. Interval 5

This interval is built up of grey cinerites and crops out both at Erillcastell and Coll de Fades (facies Vc, Table 2). The top is constituted

by greenish shales with plane-parallel lamination (facies Fs, Table 2). These facies are devoid of plant remains.

4.6. Interval 6

This interval is easily visible as a topographic crest in the landscape, allowing for a direct correlation between the three sections studied (Supplementary Fig. S1). It consists of dark grey andesitic basalt (facies Va Table 2). The outcrop of this unit ceases East of Coll de Fades. According to Marti (1983), the andesitic basalt represents a volcanic sheet flow, which migrated from Erillcastell to the East.

4.7. Interval 7

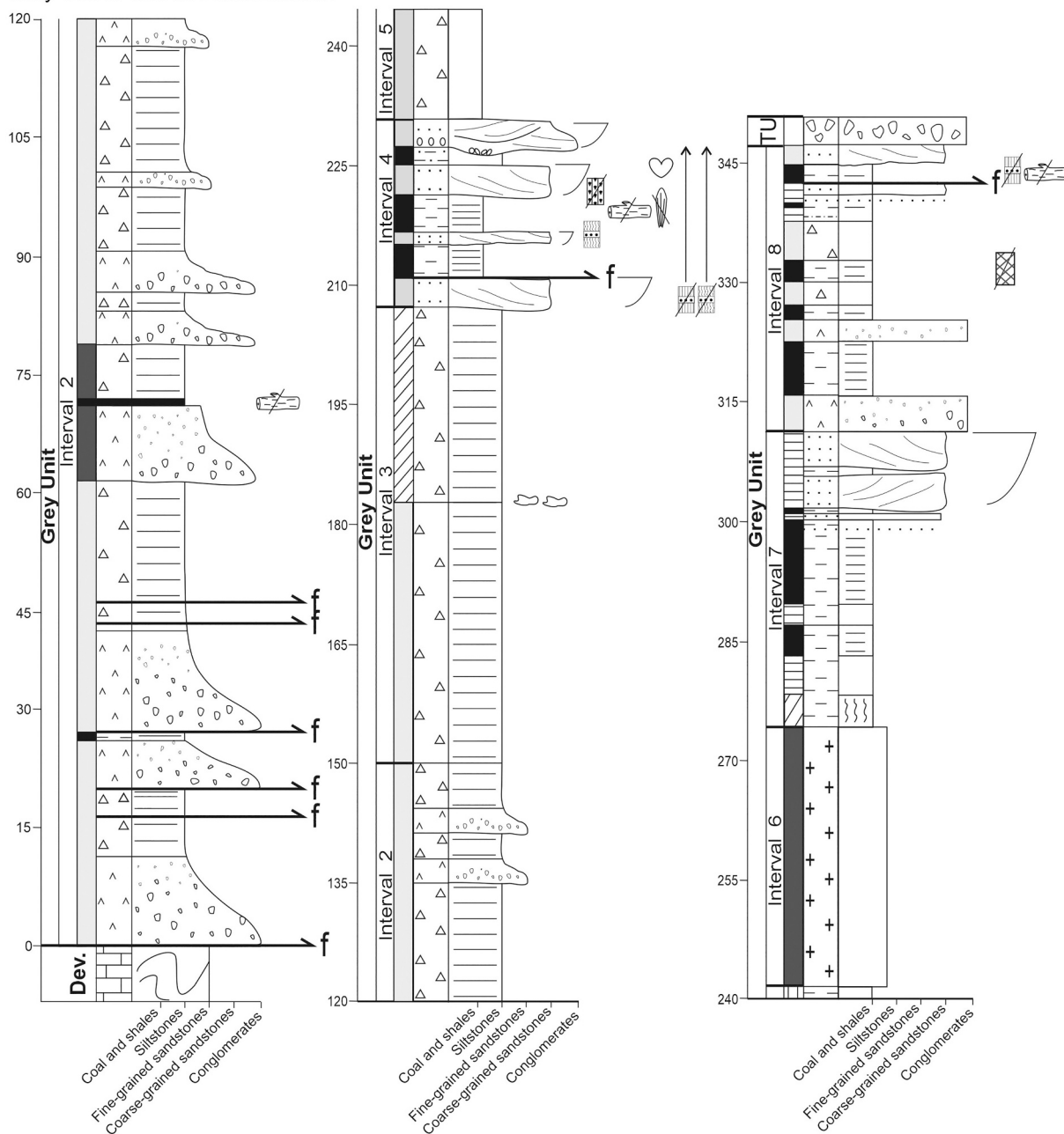
At Coll de Fades, it begins with repeated intercalations of ochre and red mottled claystones (facies Fm, Table 2), which are followed by a succession of laminated dark shales (facies Fs, Table 2), topped by tabular quartz-arenite beds, very well sorted, with epsilon cross-stratification and planar cross bedding (facies Sr, Table 2). The latter includes abundant, highly eroded plant stems. At Peranera the same interval shows some lateral changes of facies, (Fig. 7), to wedge out westwards from this locality (Supplementary Fig. S1).

The ochre and red mottled claystones at the base of the interval at Coll de Fades are interpreted as development of hydromorphic soils with increasing subaerial exposure in the floodplain (facies Fm, Table 2). The overlying, finely laminated dark shales represent deposition in a floodplain to fluvio-lacustrine setting with significant organic matter input under anoxic conditions (facies Fs, Table 2), while quartz-arenites at top correspond to the infill of a meandering river channel (facies Sr, Table 2).

4.8. Interval 8

This interval is better exposed in the Coll de Fades section (Fig. 8), where it shows an intercalation of volcanic deposits (facies Vb and Vc, Table 2) with black shales (facies Fs, Table 2) related to fluvio-lacustrine deposits (Aziz et al., 2003). These shales yield a *Lepidodendron aculeatum*

Grey Unit of Coll de Fades section



Legend

- | | | | | |
|----------------|-----------|---|-----------------------------------|-------------------------|
| Breccia | Slate | Greenish | Fern and pteridosperm adpressions | Cordaitales leaves |
| Conglomerate | Cinerite | Erect <i>Calamites undulatus</i> (fragmented) | Abandoned coalfield | Unconformity |
| Sandstone | Andesite | <i>Lepidodendron aculeatum</i> | Bioturbations | Nodules |
| Limestone | Black | Erect <i>Calamites suckowii</i> and <i>C. cistii</i> (fragmented) | Axes | Fault |
| Siltstone | Dark grey | <i>Sigillaria</i> | <i>Cardiocarpus</i> | Rooting structure |
| Clay and shale | Grey | <i>Artisia</i> | <i>Annularia</i> | FeO Iron oxide crust |
| Coal | Ochre | | | Subspherical alteration |
| Ignimbrite | Red | | | |

Fig. 4. Stratigraphic section of the Grey Unit at Coll de Fades.

Table 2

Summary of the facies described and plant taphonomic features from Pennsylvanian deposits from Erillcastell Basin.

Facies	Code	Interpretation	Interval	Locality	Unit (Gisbert (1981, 1983))	Formation (Nagtegaal, 1969)
Volcano-sedimentary facies	Pyroclastic rocks forming fining upward sequences up to 15 m thick. Base of sequences characterized by massive, matrix-supported breccia of rounded pumice pyroclasts (up to 10 cm across) and sub-angular lithic clasts (up to 15 cm across). Upper part of sequence with pyroclasts. 1–5 cm in size or constituted by lapilli.	Ignimbrite. Fining upward gradation of volcano-sedimentary sequences corresponds to deposition of a dilute, turbulent pyroclastic flow, with deceleration into a laminar flow (Martí, 1981, 1983).	2	Erillcastell	Grey	Erillcastell
			8	Coll de Fades	Grey	Erillcastell
	Greyish or reddish cinerites 15 to 50 m thick.	Ash-fall deposits from a pyroclastic flow. Variation in colour represents distinct mineralogical compositions (Martí, 1981, 1983)	2	Erillcastell	Grey	Erillcastell
			5	Coll de Fades	Grey	Erillcastell
	Dark grey andesitic basalt 40 m thick.	Andesitic sheet flow (Martí, 1981, 1983)	8	Erillcastell	Grey	Erillcastell
			6	Peranera	Grey	Erillcastell
Sedimentary facies	Massive matrix-supported breccia, with poorly sorted clasts. Up to 37 m thick and 400 m in lateral continuity. Clasts up to 30 cm across, angular and mainly composed of Carboniferous black chert (lydite), andesite and volcanic breccia.	Debris flow (e.g., Miall, 1985; Mulder and Alexander, 2001)	1	Erillcastell	Grey	Guiró
			9	Coll de Fades	Transition	Malpàs
			10	Coll de Fades	Transition	Malpàs
	Lenticular (micro-) conglomerates to coarse-grained multistorey sandstones forming fining upward sequences, up to 4 m thick. Conglomerate at base of sequence is rich in quartz and lydite clasts, changing vertically to coarse- sandstones with trough-cross bedding and ripple marks at top.	Braided river channel infill deposit (e.g., Hoey 1992; Lloret et al., 2018). Decrease in flow energy allowed deposition of sands with ripple lamination at top (e.g., Owen et al., 2017).	1	Erillcastell	Grey	Guiró
			9	Erillcastell	Transition	Malpàs
	Repeated sequences (2.5 m thick) of ochre claystone passing upward to red mottled claystone.	Hydromorphic soils. Cyclical flooding of floodplain with increasing subaerial exposure and pedogenesis at top (e.g., Kraus and Aslan, 1993).	7	Coll de Fades	Grey	Malpàs
			4	Coll de Fades	Grey	Malpàs
	Medium to fine-grained sandstones (2–5 m thick and 100 m wide) with epsilon cross-stratification and cross bedding. Epsilon-cross-sets 0.5–1 m thick and intercalated with 10–30 cm-thick dark shales.	Infill of highly sinuous fluvial channels. Epsilon cross-stratification sets correspond to lateral accretion of point-bars. Intercalated dark shales resulted from deposition of suspended load under calm water conditions (e.g., Collinson, 1996; Bridge, 2003; Toonen et al., 2012).	7	Peranera	Grey	Malpàs
			9	Coll de Fades	Transition	Malpàs
			10	Erillcastell	Transition	Malpàs
			9	Peranera	Transition	Malpàs
	Coal-shale partings upon sandstone deposits of facies Sr, intensively bioturbated in the top 20 cm by lycopsid rootlets.	Oxbow lakes colonized by lycopsid peat-mires (e.g., Owen et al., 2017).	9	Erillcastell	Transition	Malpàs
10			Peranera	Transition	Malpàs	
Dark shales and siltstones (0.20–5 m thick) with plane-parallel lamination and siderite nodules (10–30 cm long).	Floodplain or fluvio-lacustrine setting with frequent clastic inputs (e.g., Aziz et al., 2003). Abundant organic matter and siderite precipitation suggests permanent flooding and prevailing poorly oxygenated bottom conditions.	4	Coll de Fades	Grey	Malpàs	
		7	Coll de Fades	Grey	Malpàs	
		8	Coll de Fades	Grey	Malpàs	
		9	Erillcastell	Transition	Malpàs	
		10	Peranera	Transition	Malpàs	

(continued on next page)

Table 2 (continued)

Facies	Code	Interpretation	Interval	Locality	Unit (Gisbert (1981, 1983))	Formation (Nagtegaal, 1969)
			9	Coll de Fades Erillcastell	Transition	Malpàs
Bituminous coal up to 2,5 m thick intercalated with facies Fs. Shales below coal show abundant lycopsid rootlets. Roof shales may contain <i>Sigillaria</i> logs.	C	Peat-mire. Autochthonous peat accumulation in a lycopsid swamp, growing in depressed, calm areas away from clastic influence (e.g., Martín-Closas and Galtier, 2005).	9	Barranc del Pou	Transition	Malpàs

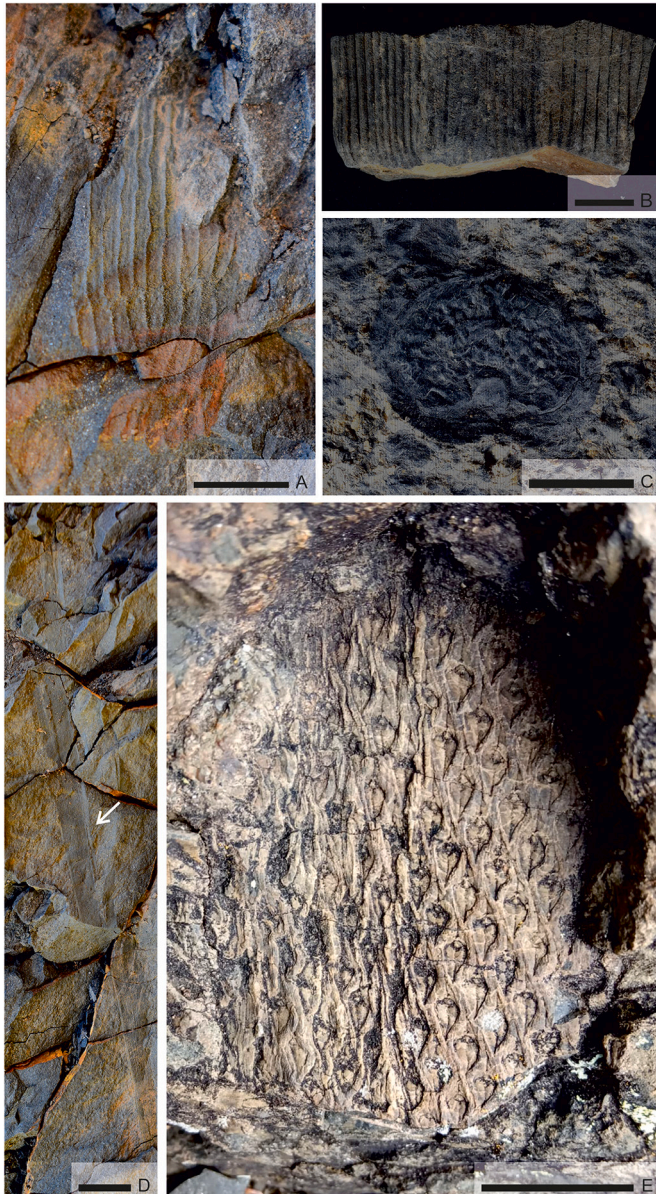


Fig. 5. Moscovian plant taxa found in the Grey Unit at Coll de Fades. A: *Calamites undulatus* stem cast, interval 4 (outcrop picture). B: *C. suckowii* stem cast, in interval 4; MGB 90197. C: *Cardiocarpus* sp., in interval 4; MGB 90198. D: *Cordaites* leaf in interval 4 (outcrop picture). E: *Lepidodendron aculeatum* in interval 8 (outcrop picture). Scale bar: 1 cm.

bark fragment (Fig. 5E), and more abundant *Calamites suckowii* stems, unidentified axes and comminuted plant debris.

Lepidodendron aculeatum bark indicates late Moscovian (Asturian or Westphalian D) age and was deposited as an allochthonous to parautochthonous remain. The *C. suckowii* stems underwent a short transport before burial and thus constitute a parautochthonous assemblage.

4.9. Interval 9(b)(c)(d)(e)

This interval shows a significant variation of thickness, which decreases eastwards (Fig. 8, Supplementary Fig. S1). The following facies associations are the most frequent:

- Matrix-supported breccia (facies Gm, Table 2), with black quartzite (lydite) clasts floating in a sandstone matrix, marks the base of the interval at Coll de Fades (Fig. 8). This breccia is attributed to a debris-flow deposit (facies Gm, Table 2). Plant remains are absent here.
- Lenticular multistratified bodies of coarse-grained sandstones and conglomerates at the base changing vertically to coarse-grained sandstones with trough-cross bedding (facies St, Table 2). These sandstones occur mainly at Erillcastell (5 to 70 m of the section in Fig. 9) and are interpreted as representing the infill of braided river channels. Lag deposits of the sandstone beds include compressed logs of *Sigillaria brardii* (Figs. 10A; 11A), stem casts of *Calamites cistii* and rarely *C. suckowii* (Fig. 11B). *Sigillaria brardii* logs are up to 1 m in length and the bark is torn along the foliage insertion scars (Fig. 12A). Axes of *C. cistii* are about 30 cm long and 15 cm across and display up to 5 nodes. Unidentified and clearly eroded plant axes (up to 2 m long and 0.75 m wide) represent a significant amount of the total assemblage in lag deposits. These remains are considered to form an allochthonous assemblage. Sandstone bodies are dominated by unidentified axes with evidence of rounding and abrasion (Fig. 12B). Identifiable plant remains include eroded *Sigillaria brardii*, *Calamites cistii*, rare *Artisia* sp. pith-casts (Fig. 11H), and *Cardiocarpus* sp. seeds. These remains would form an allochthonous assemblage. However, the association of different organs of cordaitalean plants, such as *Cardiocarpus* seeds and *Artisia* pith-casts, may suggest parautochthony.
- Medium to fine-grained lenticular sandstones with erosive base and epsilon cross-stratification and cross bedding (facies Sr, Table 2). The top sometimes shows thin coal-shale partings (facies Fb, Table 2). The sandstones would represent the infilling of meandering river channels, with the sedimentary sets representing the lateral accretion of point-bars. The coal-shale partings topping these sandstone bodies are interpreted as sedimentation in oxbow lakes during the last channel infilling stages.

Accretion bars contain abundant *Sigillaria brardii* logs, *Calamites suckowii* and *C. cistii* axes, and undetermined axes (Fig. 10B). Logs of *Sigillaria brardii* are up to 3 m long and 1 m

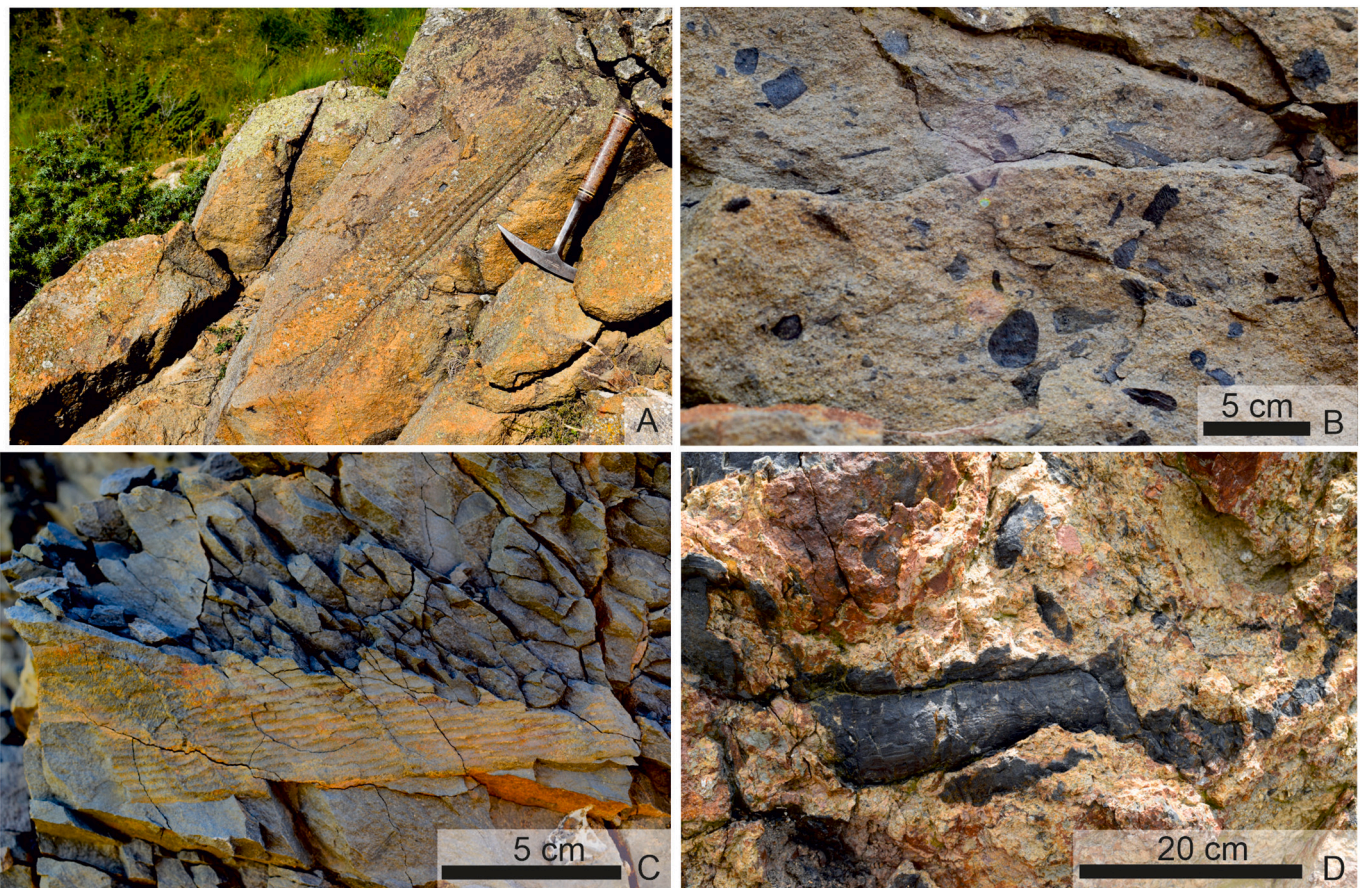


Fig. 6. Plant taphonomic features of the Grey Unit in interval 4 at Coll de Fades. A: Compressed *Sigillaria brardii* log on top of meandering river channel facies. Hammer (28 cm) for scale (outcrop picture). B: *Calamites undulatus* stem cast from floodplain facies (outcrop picture). C: Charred *Calamites undulatus* stem crossing an ignimbrite deposit (outcrop picture). D: Comminuted plant debris and *Cardiocarpus* sp. seed from the last infilling stages of a meandering river channel (outcrop picture).

wide, and randomly oriented (Fig. 12C). The *Calamites* portions are up to 1 m long, 40 cm across and composed of 2–3 nodes (Fig. 12D). An erect stem cast of *C. cistii* was found crossing the lamination. Thin coal-shale partings that top the sandstone bodies yielded abundant *C. cistii* stems and last-order marattialean pinnules of *Polymorphopteris* cf. *polymorpha* and *Pecopteris* sp. These shales are entirely covered by *Stigmara* rootlets forming a palaeosol (Figs. 10B, 12E).

The abundant, well-preserved and large logs of *Sigillaria brardii* from point bars of meandering river channels suggest little transport. In situ burial is attested in the case of the stem of *Calamites cistii* found in life position. In coal-shale partings topping the sandstones, abundant portions of *Calamites cistii* stems suggest short transport and parautochthony while the isolated, torn last order pecopterid pinnules of marattialean tree ferns indicate more intense mechanical fragmentation. Finally, rooting structures of *Stigmara* indicate the development of a lycopsid peat-mire at the final stage of channel abandonment facies (oxbow lake).

- (d) Bituminous coal (facies C, Table 2), are better exposed at Barranc del Pou section (Fig. 13). The coal itself did not provide plant adpressions, but its base is characterized by abundant lycopsid rootlets and occasionally small, compressed rooting structures of *Stigmara* sp. that penetrate the underlying shales up to 70 cm, forming paleosols (Figs. 10D; 14A). The roof shales of this coal yield large compressed logs of *Sigillaria brardii*, displaying random orientation (Figs. 10D, 14B). Almost complete fronds of *Alloiopteris* cf. *erosa* were found in black shale-coal partings

directly underlying the coal, associated with *Stigmara* rootlets, or upon the roof-shales with *Sigillaria brardii* (Figs. 10D, 11D).

Coal facies with abundant lycopsid rootlets at the base and large logs of *Sigillaria brardii* accumulated at top would represent autochthonous peat accumulation in peat mires located beyond clastic inputs (facies C, Table 2). The large lycopsid stems found at the top of the coal, forming a monospecific assemblage, suggest that they were accumulated during the last infilling stages of the peat mire and represent the floor litter of an in situ *Sigillaria* forest (e.g., Martín-Closas and Galtier, 2005). The fine preservation of *Alloiopteris* cf. *erosa*, in the organic shales, both overlaying and underlying the coal, suggests growth in the initial and latest stages of the peat-mire.

- (e) Dark-shale and siltstone intervals with plane-parallel lamination and siderite nodules (facies Fs, Table 2). This facies is occasionally intercalated with fine-grained massive sandstone beds organized in thickening upward sequences (facies Sc, Table 2). Dark shales and siltstones are interpreted as deposited in permanently flooded floodplains to fluvio-lacustrine environments, while sandstone sequences have been attributed to overbank crevasse-splay lobes (facies Sc, Table 2).

Dark shales and siltstone intervals show vertical changes in the composition of plant assemblages. The base, located immediately above sandstone beds (Fig. 10C), shows assemblages dominated by stem casts of *Calamites cistii* that may even be monospecific (Fig. 14C). Most of these remains are 10–30 cm long and 5–10 cm wide. Upwards in the section (i.e. upon sphenopsid-rich beds), shales and siltstones show an increase in marattialean tree-fern

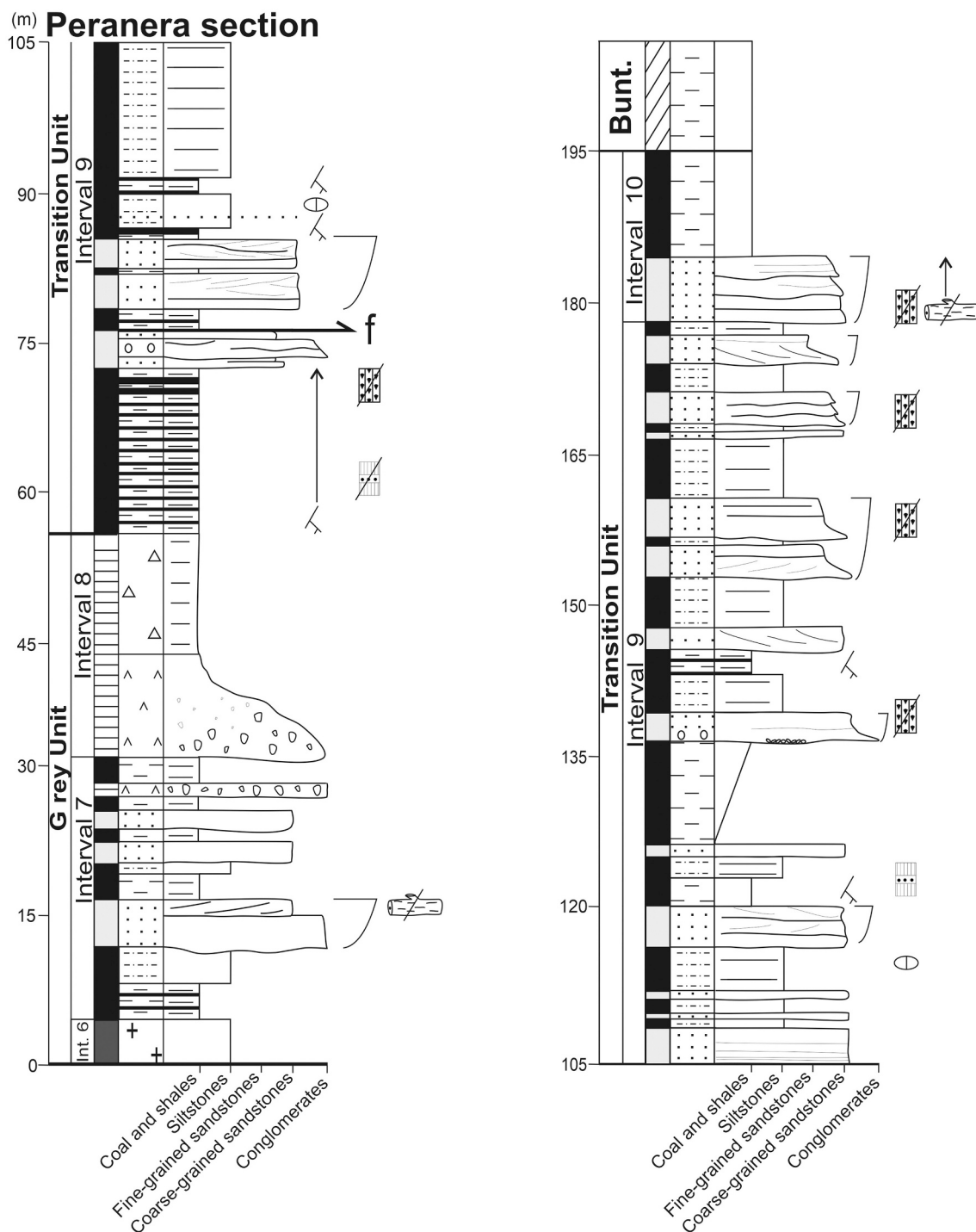


Fig. 7. Stratigraphic section of the Grey and Transition units at Peranera. Legend as in Fig. 4.

foliage (Fig. 10C), generally well-preserved, i.e., *Pecopteris* cf. *candolleana*, *Pecopteris* sp. (Fig. 14D), *Polymorphopteris polymorpha* and rare *Polymorphopteris* cf. *integra* (Fig. 11E), associated with fragmentary foliage remains of pteridosperms including *Dicksonites pluckenettii* (Fig. 11F), *Callipteridium zeilleri* (Fig. 11G) or *Carpolithus* sp. seeds. In turn, there is a significant decrease in the abundance of the sphenopsids. The plant assemblage from these beds indicates a lower Gzhelian (Stephanian C) age. Sandstone beds corresponding to crevasse-splay lobes mainly contain comminuted plant debris and a few *Cordaites* leaves, which are 15 cm long and torn along the venation pattern (Fig. 14E). They

are associated with isolated last order pinnules of *Pecopteris* cf. *candolleana* and *Pecopteris* sp.

Relatively well-preserved calamitalean remains suggest parautochthony in the fluvio-lacustrine facies. In turn, the relatively well-articulated foliage of marattialean tree ferns only found in the upper part of the fluvio-lacustrine succession, suggest that these plants preferred distal areas as to the sediment supply. In contrast, the intense fragmentation of pteridosperm foliage suggests allochthony. Finally, abundant comminuted plant debris, *Cordaites* sp. leaves and fragmented last order pinnules of pteridosperms found in crevasse splay lobes should be considered an

(m) Transition Unit of Coll de Fades section

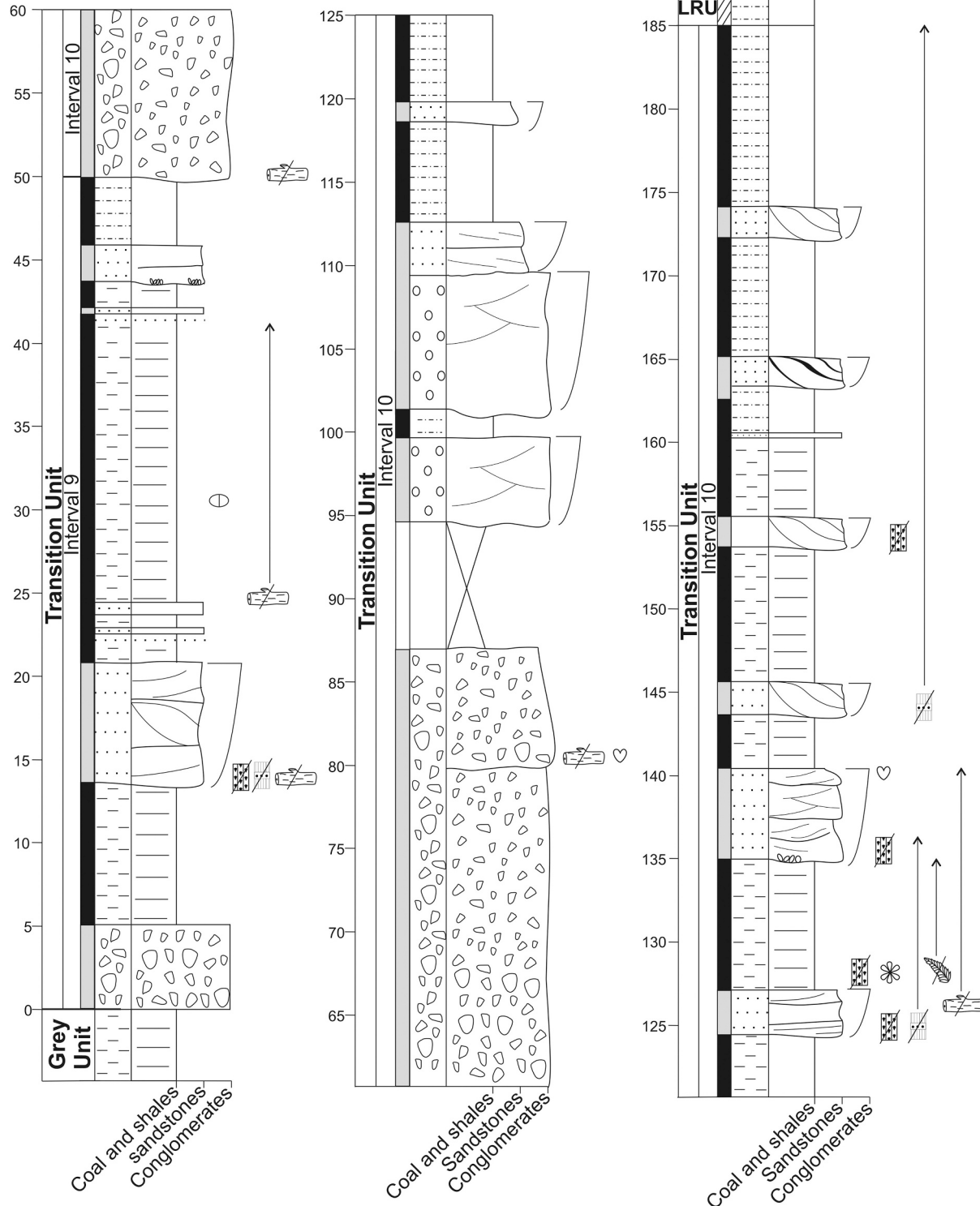


Fig. 8. Stratigraphic section of the Transition Unit at Coll de Fades. Legend as in Fig. 4.

allochthonous assemblage probably transported as suspended load before riverbank avulsion occurred.

4.10. Interval 10

At the Coll de Fades section (Fig. 8), where the interval is better exposed, the base is marked by a massive, matrix-supported breccia that contains a few unidentified torn axes, up to 1 m long. This deposit has

been attributed to deposition in a debris flow, which transported allochthonous woody fragments (facies Gm, Table 2). The section continues with clast-supported conglomerates with erosive base and trough cross-stratification (facies St, Table 2) containing unidentified woody axes at the base, which was attributed to the infill of braided river channels. However, most of interval 10 at Coll de Fades is formed of coarse to medium-grained lenticular sandstone beds with an erosive base and epsilon cross-stratification, attributed to the infill of

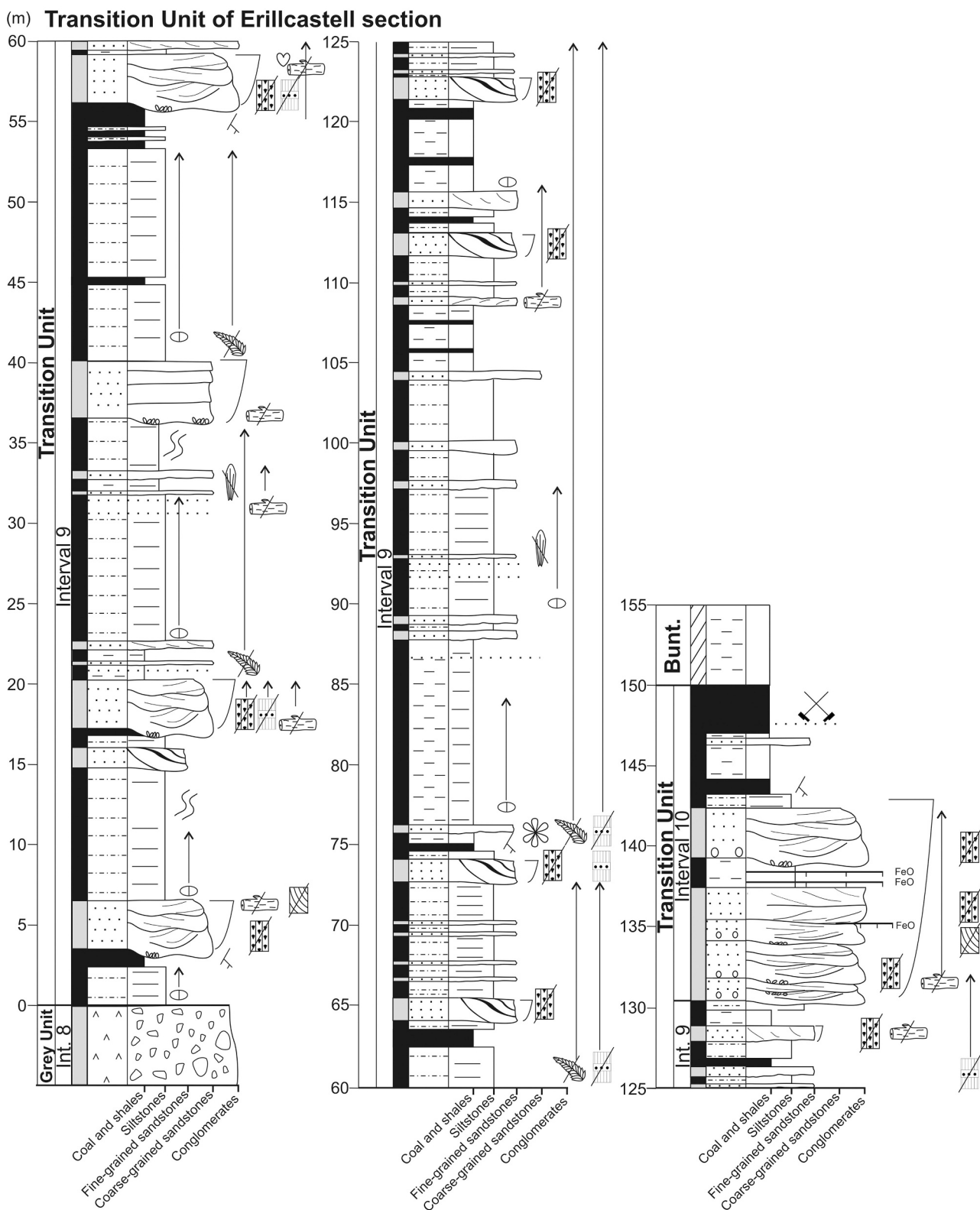


Fig. 9. Stratigraphic section of the Transition Unit at Erillcastell. Legend as in Fig. 4.

meandering river channels (facies Sr, Table 2). Sandstone bodies are intercalated with dark siltstones and shales poor in plant remains, corresponding to floodplain to fluvio-lacustrine facies (facies Fs, Table 2).

The base of the sandstone beds attributed to meandering river channels contains few stems of *Calamites cistii* (0.5 m long), *Sigillaria brardii* logs (1 m long) and rare *S. sigillata* Brongniart barks. The large

stems of *Calamites cistii*, and diverse decortication states of *Sigillaria* indicate transport of these remains from a neighbouring source, suggesting a parautochthonous assemblage. Locally, black shales intercalated with these sandstones contain isolated pteridosperm pinnules (*Dicksonites pluckenettii*, *Callipteridium zeileri*), well-articulated marattialean tree fern foliage (*Pecopteris* cf. *candolleana*, *Polymorphopteris*

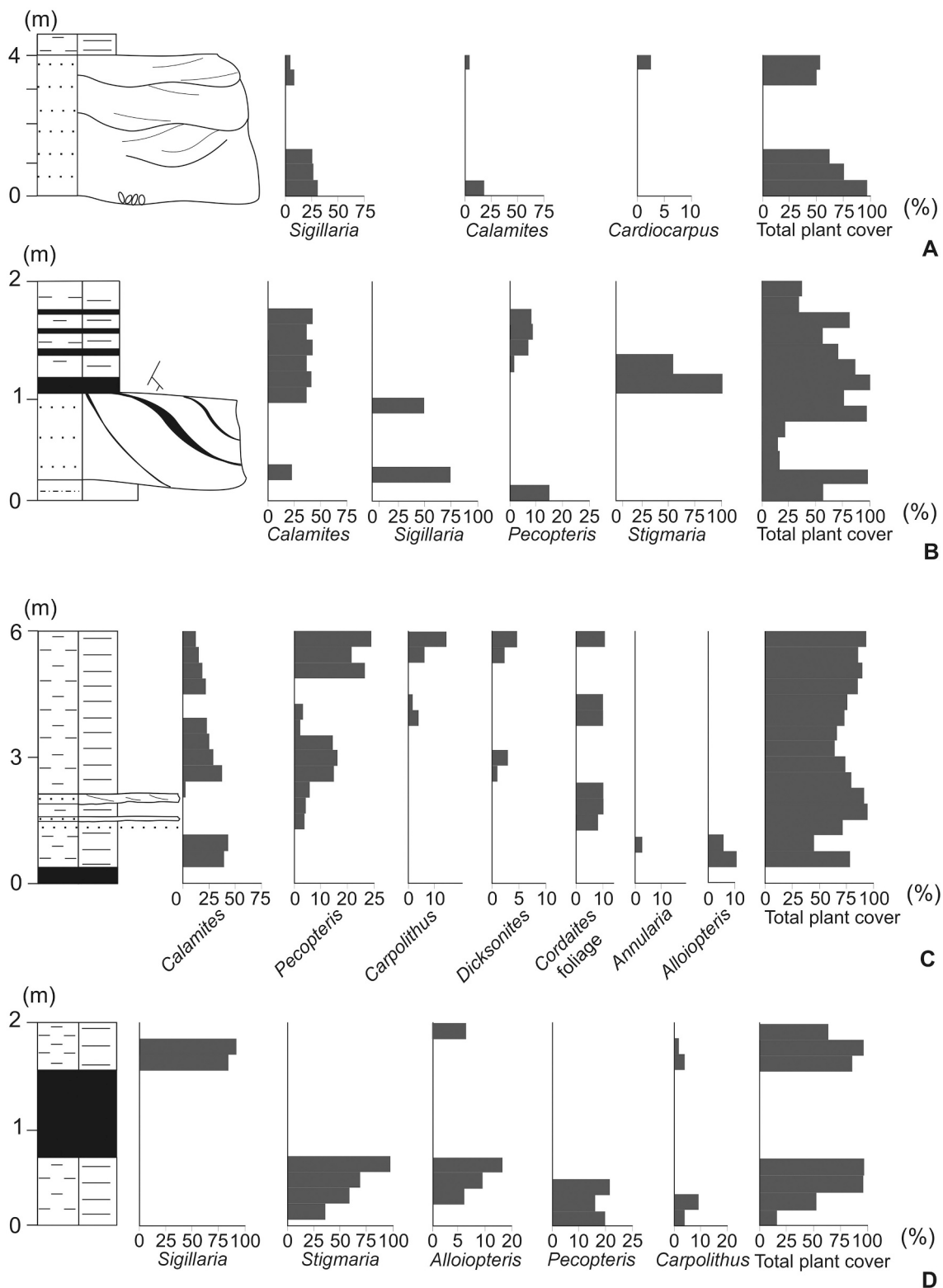


Fig. 10. Point-quadrat counting of plant remains in the different facies of the Erillcastell section based on Scott's method (Scott, 1977). A: Plant assemblages in braided river facies (metres 17–21 in Fig. 10). B: Plant assemblages in meandering river facies (metres 72–75 in Fig. 10). C: Plant assemblages in floodplain (metres 80–86 of Fig. 10). D: Plant assemblages in peat mire facies (metre 18–20 of Fig. 14).

polymorpha) and rarely the sphenopsid foliage *Annularia spinulosa* and *A. sphenophylloides*. The excellent preservation of marattialean tree ferns suggests relatively short transport in suspension forming a parautochthonous assemblage. This contrasts with isolated torn pinnules of pteridosperms found in the same plant beds that show intense

fragmentation due to fluvial transport, thus representing an allochthonous assemblage.

At Erillcastell (Fig. 9) the interval is truncated by the angular unconformity with the Triassic. The succession and plant assemblages are similar to the lower part of the same interval at Coll de Fades, i.e.,

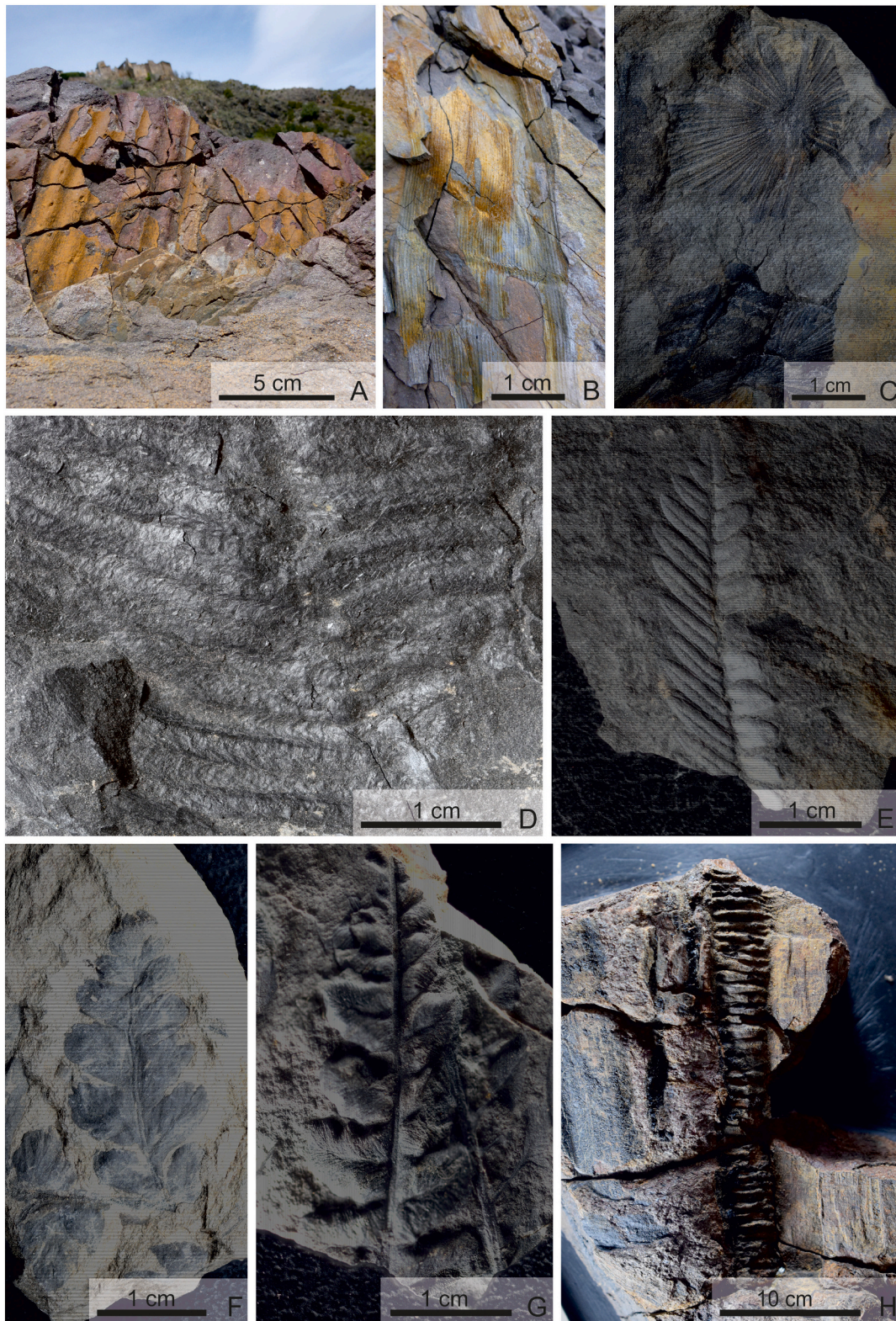


Fig. 11. Stephanian taxa found in interval 9 of the Transition Unit at the Erillcastell section. A: *Sigillaria brardii* (field picture). B: *Calamites cistii* (field picture). C: *Annularia spinulosa*; MGB 90199. D: *Alloiopteris cf. erosa*; MGB 90200. E: *Polymorphopteris cf. integra*; MGB 90221. F: *Dicksonites plukenetii*; MGB 90202. G: *Calopteridium zeilleri*; MGB 90203. H: *Artisia* sp.; MGB 90204.

dominated by braided-river facies (facies St, Table 2), while the top is formed by coal with abundant clastic partings (facies F and Fs, Table 2), similar to the equivalent facies from interval 9.

5. Discussion

The Pennsylvanian stratigraphic record from the Erillcastell Basin (Central Pyrenees) is one of the few successions rich in plant remains in



Fig. 12. Plant taphonomic features in braided and meandering river channel facies from interval 9 of the Transition Unit at Erillcastell (field pictures). A: Torn bark of *Sigillaria* forming the lag-deposit of a braided river channel. B: Rounded fragments of plant axes in braided river channel infilling facies. C: Assemblage of *Sigillaria brardii* bark found in point bar facies. D: Large stem cast of *Calamites suckowii* found in point bar facies. E: *Stigmara* rootlets found in oxbow lake facies. Hammer for scale 28 cm.

the Pyrenees recording at least upper Moscovian and lower Gzhelian assemblages. This has enabled (1) a biostratigraphic revision of the lithostratigraphic framework of the Erillcastell Basin and (2) a characterization of plant communities over time in an intramontane (upland) setting during this interval.

5.1. Stratigraphic and biostratigraphic implications

The chronostratigraphic results obtained for macroscopic plant remains have general consensus concerning the age of the sedimentary and volcano-sedimentary units in the Pyrenean basins, assigning Moscovian to Kasimovian ages to the Grey Unit, and Gzhelian ages to the

Transition Unit (e.g., Broutin and Gisbert, 1985). However, recent studies based on zircon chronostratigraphy (Pereira et al., 2014) and palynomorphs calibrated with them (Juncal et al., 2019) differ in providing much younger ages. Because of divergence in the chronology of the allostratigraphic units, the boundaries between them were also controversial in the Erillcastell Basin.

Here we provide new results that help clarifying the age and the boundaries between the Grey and the Transition units. The occurrence of *Lepidodendron aculeatum* in interval 8 from the Coll de Fades section (Fig. 4, Table 3) indicates a late Moscovian age according to the biostratigraphy described by Álvarez-Vázquez and Wagner (2014) and references herein. Regionally, this falls within the age range of the Grey

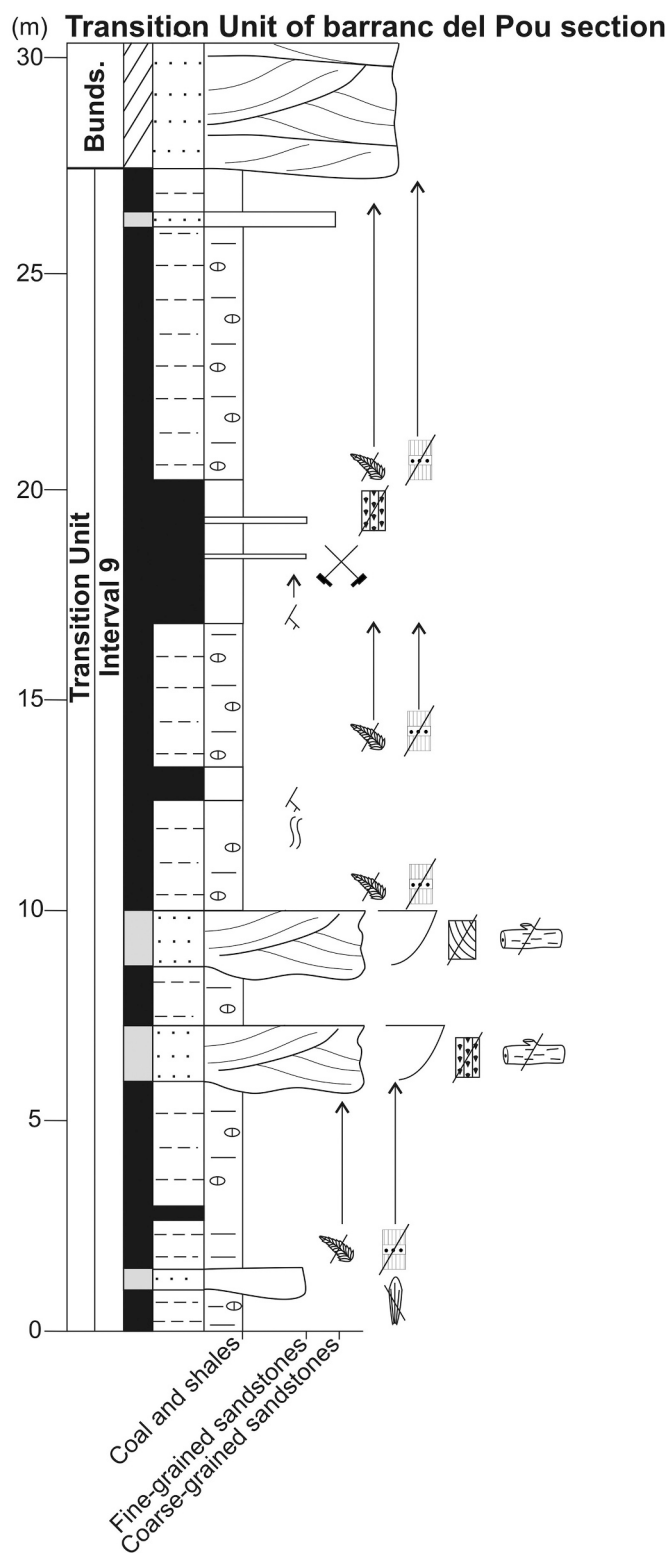


Fig. 13. Stratigraphic section of the Barranc del Pou outcrop. See the correlation of this outcrop with the Erillcastell section in Fig. 2. Legend as in Fig. 4.

Unit according to macroscopic plant remains and suggests that at least intervals 1 to 8 (Guiró, Erillcastell and the lower part of the Malpàs formations) belong to this unit. This rules out the Permian age suggested by Pereira et al. (2014) for the Erillcastell ignimbrite (interval 2).

Stockmans in Nagtegaal (1969) studied several plant beds in the Malpàs Formation at Erillcastell, which would correspond to interval 9

in the present study. Two of these plant beds, located at approximately the middle part of the Transition Unit at the Erillcastell section presented here (Fig. 9; Supplementary Fig. S1), yielded *Sphenophyllum angustifolium* and *Polymorphopteris polymorpha*. These species were also reported by Talens and Wagner (1995) from a bed in the Malpàs Coalfield, the exact stratigraphic position of which is unknown. In any event, both species are characteristic of the early Gzhelian according to Knight and Álvarez-Vázquez (2021) indicating that at least intervals 9 and 10 fall within the regional age range of the Transition Unit (early Gzhelian).

In the present study it has been impossible to characterize the Kasimovian. This may be due either to the lack of record of rocks from this age below the unconformity at base of the Transition Unit or because it was not possible to characterize it biostratigraphically based on mega-plant remains.

In sum, these data suggest that the boundary between the Grey Unit and the Transition Unit in the Erillcastell Basin should be placed at the base of interval 9 (Supplementary Fig. S1, Table 3). As a result, the thickness of the latter unit is significantly thicker than has been proposed by previous authors (e.g. Mujal et al., 2018; Lloret et al., 2018).

Based on this subdivision, the sedimentary record of a third locality called Coll de Sas, studied by Mujal et al. (2018) and located 2 km southeast of Coll de Fades, should be probably reinterpreted as mainly belonging to the Transition Unit. The section of Coll de Sas is cut by a fault at its base. However, at that point it shows an ignimbrite deposit, which is a more characteristic of the Grey Unit. Shortly above this ignimbrite, the base of the log drawn by Mujal et al. (2017) is found, and the greatest thickness (130 m) of the Malpàs Formation develops. These authors report abundant pinnules of *Pecopteris robustissima*, *P. arborescens*, *P. jongmansii* and *Polymorphopteris polymorpha*, which suggest early Gzhelian age, supporting the idea that the greatest thickness of the Malpàs Formation cropping out at Sas belongs to the Transition Unit and is laterally equivalent to the top of interval 9 at Erillcastell, Peranera and Coll de Fades.

When compared with the deposits of the Transition Unit at Coll de Fades or Erillcastell, the succession at Sas is largely dominated by distal facies of the riverine belt (mainly floodplain shales and siltstones), supporting the idea that the most proximal point in terms of the sedimentary processes of the Transition Unit should be positioned near Coll de Fades, where alluvial (debris-flow) deposits and thick coarse breccias related to proximal braided river channels occur.

5.2. Reconstruction of plant communities

5.2.1. Grey unit

A taphonomic analysis of the Moscovian flora at Coll de Fades has enabled a palaeoenvironmental reconstruction of two plant assemblages (Fig. 15A).

Meandering rivers: *Calamites undulatus*, *C. suckowii* and *C. cistii* were found parautochthonous in the lag deposits of meandering river channels, suggesting that the riparian vegetation was dominated by a relatively diverse sphenopsid flora. A similar habitat has been interpreted for several species of *Calamites* in other Moscovian paralic basins in Euramerica including Alabama (Gastaldo, 1986; DiMichele and Phillips, 1996) and Illinois in the USA (DiMichele and Nelson, 1989) or Writhlington in England (Proctor, 1994), all located in lowland settings.

Remains of *Sigillaria brardii* were also found to be parautochthonous in the bed load of the same meandering river channels, associated with sphenopsid remains, adding more diversity to the same riparian community. This is the first time that such a habitat has been reported for *Sigillaria brardii* in the Pennsylvanian of the Pyrenees. However, DiMichele and Phillips (1996), documented the preference of this species for well-drained areas close to rivers in Moscovian lowland wetlands of the USA.

Floodplain and fluvio-lacustrine deposits: A charred stem of *Calamites undulatus* was found upright within an ignimbrite intercalated in floodplain to fluvio-lacustrine deposits in interval 4, clearly showing an

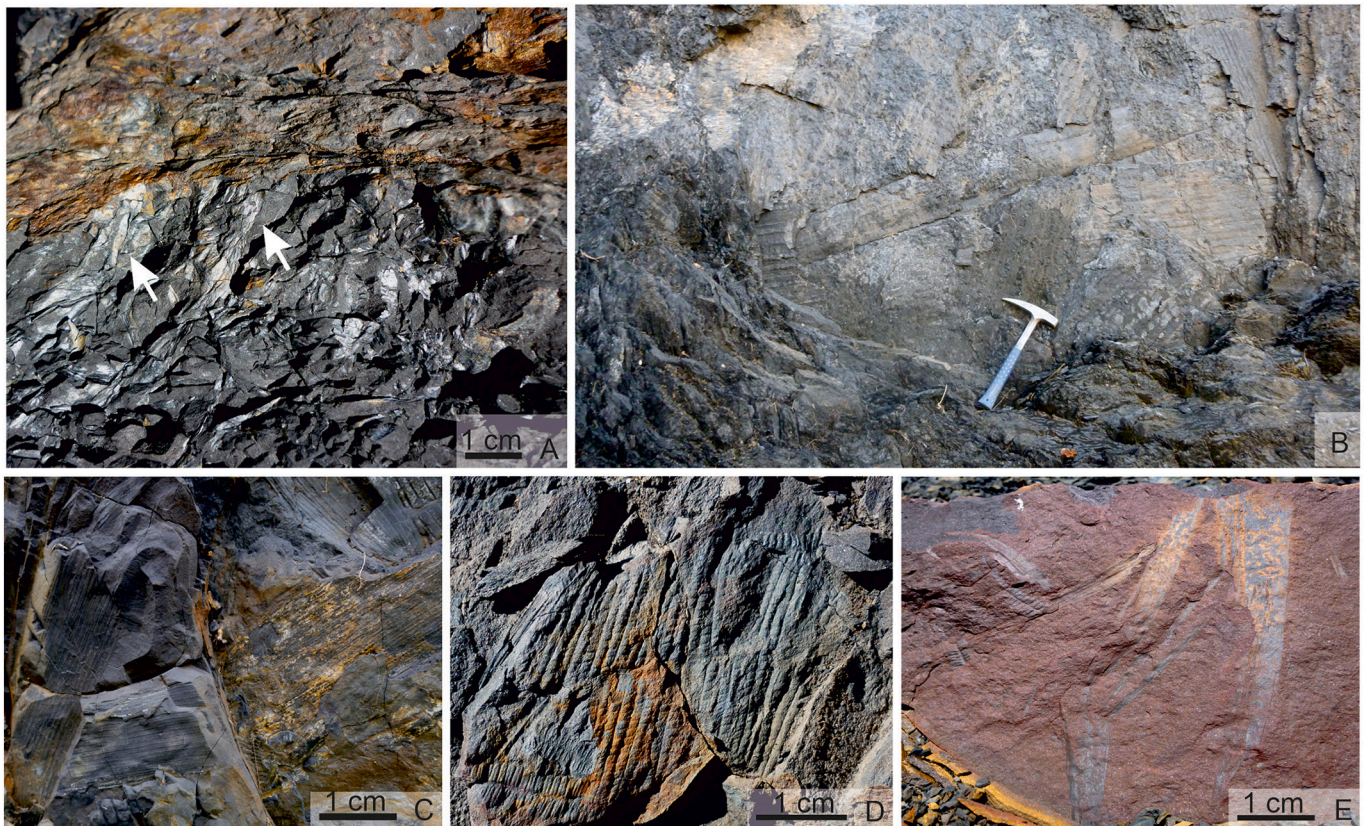


Fig. 14. Plant taphonomic features of floodplain, crevasse-splay and peat-mire facies from interval 9 of the Transition Unit at Barranc de Pou (A – B) and Erillcastell (C – D) A: *Stigmaria* rootlets (marked with an arrow) at the base of peat mire (coal seam 2) forming paleosols (field picture). B: Large logs of *Sigillaria* without orientation in roof-shales of peat mire (field picture). C: *Calamites* from floodplain facies (field picture). D: Well-articulated foliage of *Pecopteris* sp. from floodplain facies (field picture). E: Torn leaf of *Cordaites* observed in crevasse splay deposits (field picture). Hammer for scale 28 cm.

autochthonous habitat of this species in such facies. Other plant remains found within the permanently inundated fluvio-lacustrine deposits all appear to be allochthonous or parautochthonous. Fragments of *Calamites suckowii* and *C. cistii* stems are common in such facies, where they may even form monospecific assemblages, also suggesting growth near or on the floodplain. *Calamites* was already associated to floodplain facies from coeval intramontane palaeo-equatorial basins in the Bohemian Massif (Bashforth et al., 2011) and Maritimes Basin, Canada (Bashforth et al., 2014).

Cordaitaleans are difficult to characterize from a palaeoecological perspective with the available data. Allochthonous *Cardiocarpus* sp. seeds found both in fluvial channels and in floodplain deposits, as well as the isolated leaves of *Cordaites* sp. found in floodplain deposits, suggest that cordaitaleans grew upstream. Fluvial habitats have been reported for this group in other Moscovian localities in Euramerica. For instance, Falcon-Lang and Bashforth (2004, 2005) and Bashforth et al. (2014) found large cordaitalean logs with preserved stumps in alluvial channels of an upland area from the Pennsylvanian of Newfoundland and New Brunswick (Canada), suggesting that these plants would have been growing upstream, relatively close to the riverbanks.

5.2.2. Transition unit

Four plant landscapes have been identified in the depositional settings of this unit (Fig. 15B):

Braided rivers: The vegetation that grew in braided river settings in the Erillcastell Basin is difficult to ascertain since no direct evidence, such as rooting structures, was found. Nevertheless, different organs of the Cordaitales, such as their pith casts (*Artisia* sp.) or seeds (*Cardiocarpus* sp.) were found in the channel infill facies, suggesting that Cordaitales grew close to braided rivers. Furthermore, torn leaves of *Cordaites* were

recognized in crevasse-splay deposits associated with this type of river, indicating that these organs were transported downstream in the suspension load, reaching the floodplain as an overbank deposit. Martín-Closas and Galtier (2005) have described a similar sedimentary process for a monospecific *Cordaites* leaf assemblage found in a crevasse-splay in the Graissessac-Lodève Basin. Based on this taphonomic evidence it appears that cordaitaleans may have been a significant riparian element in braided-type rivers (Fig. 16A). This habitat has also been noted for cordaitaleans in other Upper Carboniferous limnic basins, for example in Nova Scotia or England (Falcon-Lang and Scott, 2000).

Meandering rivers: Large and abundant logs of *Sigillaria brardii* and stems of *Calamites suckowii* and *C. cistii* were found in the lag deposits and point bars of meandering river channels indicating that these plants grew alongside the riverbanks forming a riparian belt. The axes of these plants would have fallen directly into the channel by gravity or by riverbank avulsion and would then have been transported a short distance before sinking and forming a parautochthonous assemblage in the river channel itself. The presence of an erect *Calamites cistii* stem in a point bar deposit supports this hypothesis. Besides, *Sigillaria brardii* would also have grown in oxbow lake facies as indicated by the common occurrence of *Stigmaria* sp. (rootlets and a few axes) in coal with clastic partings topping deposits of high sinuosity channels.

Calamites has long been known to have grown on riverbanks of lowlands (e.g., Thomas, 2013; DiMichele and Phillips, 1994 and references herein), and in intramontane limnic basins of southern Europe (Martín-Closas and Galtier, 2005; Martín-Closas and Martínez-Roig, 2007). However, the occurrence of *Sigillaria brardii* flanking meandering riverbanks is previously unknown in the lower Gzhelian of southern Europe and represents a new habitat for this plant in the region.

Floodplains and fluvio-lacustrine deposits: *Calamites cistii* was found in

Table 3
Chrono- and lithostratigraphic correlation proposed for the Pennsylvanian deposits from Erillcastell Basin.

Stages equivalence (Heckel and Clayton, 2006)		Interval	Lithology of the interval	Locality	Plant assemblage	Formations (Mey et al., 1968; Nagtegaal, 1969)	Allostratigraphic units (Gisbert (1981, 1983))	
Global	Regional							
EARLY GZHELIAN	STEPHANIAN C	10	Conglomerates, sandstones and shales	Erillcastell, Peranera and Coll de Fades	<i>Sigillaria brardii</i> <i>Sigillaria sigillata</i> <i>Annularia spinulosa</i> <i>Annularia sphenophylloides</i> <i>Calamites cistii</i> <i>Pecopteris cf. candolleana</i> <i>Polymorphopteris polymorpha</i> <i>Dicksonites pluckenetii</i> <i>Callipteridium zeilleri</i> <i>Cardiocarpus</i> sp.	Malpàs	Transition	
		9	Conglomerates, sandstones, shales and coal	Erillcastell, Peranera and Coll de Fades	<i>Sigillaria brardii</i> <i>Stigmara</i> sp. <i>Annularia spinulosa</i> <i>Annularia sphenophylloides</i> <i>Calamites suckowii</i> <i>Calamites cistii</i> <i>Macrostachya</i> sp. <i>Pecopteris cf. candolleana</i> <i>Pecopteris</i> sp. <i>Alloiopteris cf. erosa</i> <i>Polymorphopteris polymorpha</i> <i>Polymorphopteris cf. integra</i> <i>Dicksonites pluckenetii</i> <i>Callipteridium zeilleri</i> <i>Carpolithus</i> sp. <i>Artisia</i> sp. <i>Cordaites</i> (foliage) <i>Cardiocarpus</i> sp.	Malpàs	Transition	
	LATE MOSCOVIAN	WESTPHALIAN D	8	Volcanic breccia and cinerites. Locally shales	Erillcastell, Peranera and Coll de Fades	<i>Lepidodendron aculeatum</i>	Malpàs	Grey
			7	Sandstones and shales	Peranera and Coll de Fades	–	Malpàs.	Grey
		6	Andesitic basalt	Erillcastell, Peranera and Coll de Fades	–	Erillcastell	Grey Unit	
		5	Cinerites	Erillcastell and Coll de Fades	–	Erillcastell	Grey	
		4	Sandstones and shales	Coll de Fades	<i>Sigillaria brardii</i> <i>Calamites undulatus</i> <i>Calamites suckowii</i> <i>Calamites cistii</i> <i>Cardiocarpus</i> sp. <i>Cordaites foliage</i>	Malpàs	Grey	
		3	Cinerites	Coll de Fades	–	Erillcastell	Grey	
		2	Volcanic breccia and cinerites	Erillcastell and Coll de Fades	–	Erillcastell	Grey	
		1	Breccias, conglomerates and sandstones	Erillcastell	–	Guiró	Grey	

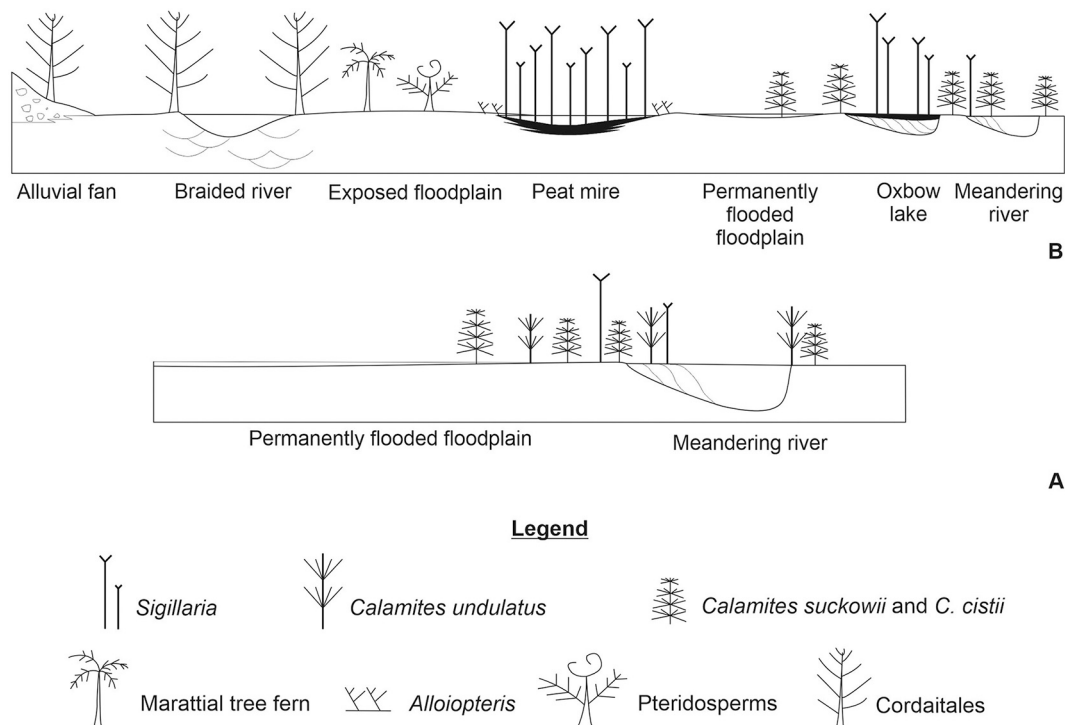


Fig. 15. Palaeoenvironmental reconstruction of the Pennsylvanian in the Erillcastell Basin. A: Late Moscovian palaeoenvironments. B: Early Gzhelian palaeoenvironments.

the coarser deposits of these facies, together with other abundant, well-preserved organs that may be related to this plant, such as *Macrostachya* sp., *Annularia spinulosa*, *A. sphenophylloides*. This suggests that *Calamites* could grow in proximal areas of the floodplain, not far from the river-banks. This facies also contains large and well-articulated fronds of marattialean tree fern foliage including *Polymorphopteris polymorpha*, *Polymorphopteris* cf. *integra*, *Pecopteris* cf. *candolleana*, forming a parautochthonous assemblage. Taphonomic features suggest that these ferns also grew close to the floodplain. The presence of pteridosperms around floodplains from the Erillcastell Basin should be interpreted with caution since their remains always constitute allochthonous assemblages in these deposits. These plants may perhaps have grown distally from the floodplain.

Calamites species forming small stands in floodplain and fluvio-lacustrine facies have been reported in other intramontane limnic basins in southern of Europe, such as Graissessac-Lodève (Martín-Closas and Galtier, 2005) and Surroca-Ogassa (Martín-Closas and Martínez-Roig, 2007). In contrast, the habitat of marattialean tree ferns differs a little between these three basins. In the Graissessac-Lodève Basin, Martín-Closas and Galtier (2005) found rooting systems attributed to tree ferns associated with their logs (*Caulopteris* sp.) in the last infilling stages of a peat mire (Martín-Closas and Galtier, 2005), whereas Martín-Closas and Martínez-Roig (2007) found rooting systems attributed to tree ferns associated with abundant *Polymorphopteris polymorpha* foliage in the last infilling stages of a meandering river channel of the Surroca-Ogassa Basin (Fig. 16B). In conjunction, these data suggest that marattialean tree ferns were able to adapt to different conditions in each environmental context and may have been an opportunistic element in Upper Pennsylvanian lowlands of Euramerica (Knight, 1983; Willard and Phillips, 1993; DiMichele and Phillips, 1996).

Peat mires: In the Barranc del Pou outcrop, close to the Erillcastell section, rooting structures of *Stigmara* occur at the base of coal seams with abundant shale partings, while large logs of *Sigillaria brardii* occur in roof shales, suggesting that this plant was the main component of peat mires and supplied most of the peat (Fig. 16C). Stagnant water, low pH and anoxic conditions probably explain the monospecific character of

this biome (e.g., Phillips and DiMichele, 1992). *Sigillaria brardii* has frequently been documented in peat mires in other latest Pennsylvanian intramontane limnic basins in Southwest Europe. In the case of Graissessac-Lodève, Martín-Closas and Galtier (2005) interpreted *Sigillaria brardii* as usually forming a monospecific community in forested peat-mires, locally accompanied by the zygopterid fern *Alloiopteris erosa* and pecopterid tree-ferns, in the last infilling stages of these mires. In the Erillcastell Basin well-articulated fronds of *Alloiopteris* cf. *erosa* were also found associated with *Sigillaria brardii*, forming a parautochthonous assemblage within the black coal-shale partings, which underlie and overlie the coal (Fig. 16C).

5.3. Palaeoecology of *Sigillaria brardii* in the Pennsylvanian of the Pyrenean basins

Lycopsid-dominated peat-mire plant communities underwent a loss of diversity during the Late Pennsylvanian in Eurasia (DiMichele, 2014; Montañez, 2016). The dramatic contraction and change in composition of the lycopsid-dominated coal forests is widely accepted to be related to a global increase in aridity at the Moscovian-Kasimovian boundary, accompanied by the limited ability of arboreous lycopsids to grow in environments other than peat-mires (Phillips and Peppers, 1984; DiMichele et al., 2001). However, this floristic turnover was diachronous worldwide (Roscher and Schneider, 2006; Tabor and Poulsen, 2008; Bashforth et al., 2021). *Sigillaria brardii* which is considered a prominent component of the Upper Pennsylvanian coal forests in Eurasia diminished its diversity from paralic basins of USA at the late Moscovian, when tree lycopsids were almost completely substituted by marattialean tree-ferns (*Psaronius*) and less-abundant medullosacean pteridosperms, *Sigillaria brardii* remaining as the sole tree-lycopsid in more clastic environments (DiMichele and Phillips, 1996). In coeval lowland basins in Europe, e.g., the Ruhr Basin in Germany (Uhl and Cleal, 2010) or in the Villablino Basin, in Spain (Wagner and Álvarez-Vázquez, 2010), these changes appear to occur later, although this may be in part due to a relatively limited Kasimovian and lower Gzhelian plant fossil record, e.g., in the case of the Ruhr Basin (Uhl and Cleal,

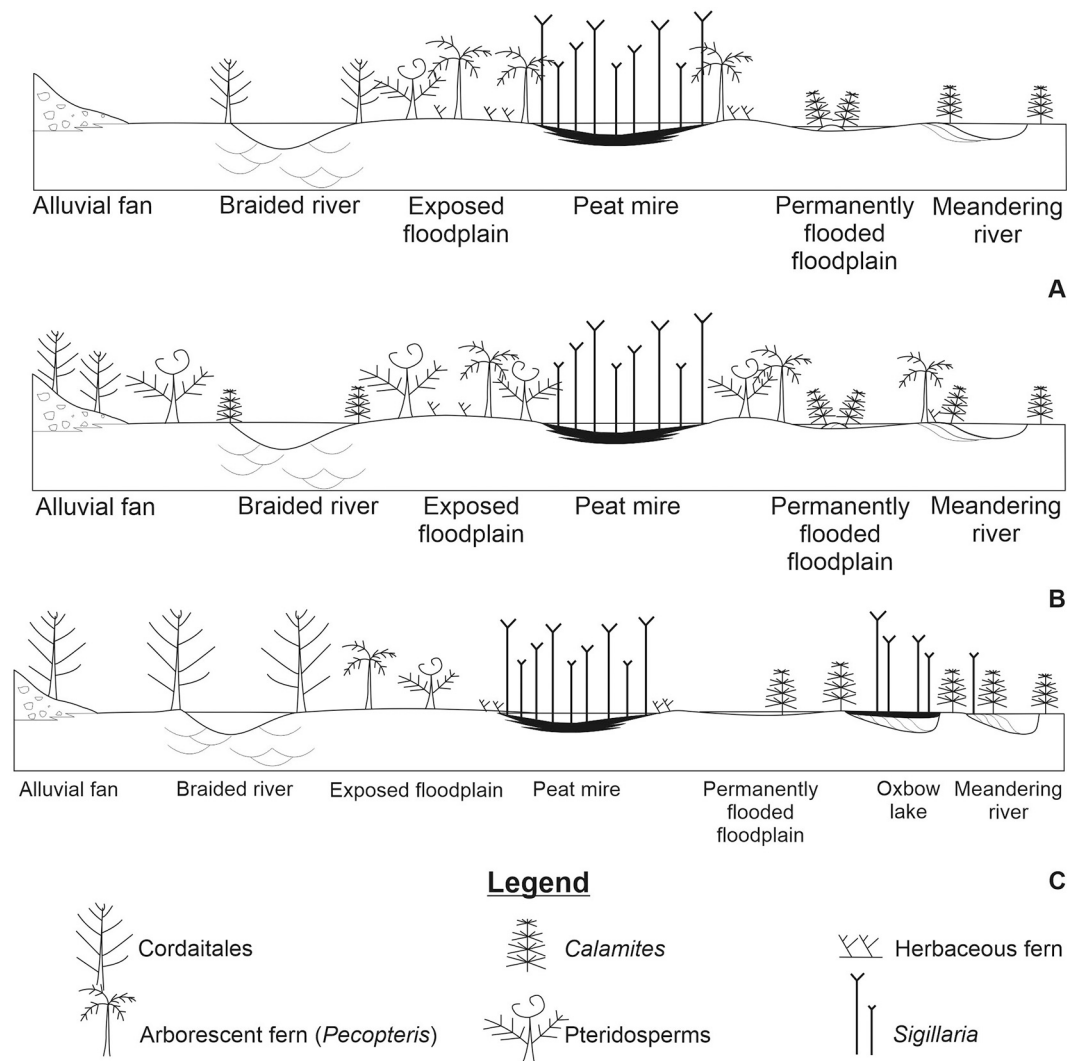


Fig. 16. Comparison of plant distributions in early Gzhelian intramontane limnic wetlands from southern Europe. A: Graissessac-Lodève Basin (Languedoc, France). Modified from [Martín-Closas and Galtier \(2005\)](#). B: Surroca-Ogassa Basin (Catalonia, Spain). Modified from [Martín-Closas and Martínez-Roig \(2007\)](#). C: Erillcastell Basin (Catalonia, Spain).

2010). In contrast, *Sigillaria brardii* is abundant and persisted for a longer time, until the lower Gzhelian, in the intramontane basins from the Variscan Chain ([Schindler et al., 2004](#); [Martín-Closas and Galtier, 2005](#); [Martín-Closas and Martínez-Roig, 2007](#)) and even into the lower Permian in particular areas of Europe ([Schindler et al., 2004](#)). A similar situation is found in Cathaysia ([D'Antonio et al., 2021](#)). This evidence suggests that *Sigillaria brardii* had high capacity to adapt to changing environments and withstand increasing aridity during the Upper Pennsylvanian. Similar ecological conditions are interpreted for *Sigillaria asiatica* from China, which shows anatomic root adaptations for moisture limitation ([Pfefferkorn and Wang, 2009](#); [Chen et al., 2022](#)).

In line with this conclusion, the results presented here show that *Sigillaria brardii* had a broad palaeoecological tolerance in the lower Gzhelian of the Variscan intramontane Erillcastell Basin. However, the abundant occurrence of this species in riverbanks and point-bars of the Erillcastell Basin, contrasts with its exclusive distribution in peat-mires of coeval limnic intramontane basins from Variscan Range i.e. Maritimes Basin, Canada ([Bashforth et al., 2014](#)); Bohemian Massif, Czech Republic ([Opluštil et al., 2017](#)); Graissessac-Lodève Basin in the Montagne Noire, France ([Martín-Closas and Galtier, 2005](#)) and Surroca-Ogassa Basin in the Pyrenees, Catalonia ([Martín-Closas and Martínez-Roig, 2007](#)), where such fluvial facies were equally well represented, but devoid of *Sigillaria*. In comparison to other South European basins

from the same age and similar latitude, this may be related to the particular environmental conditions of the Erillcastell Basin, where (1) peat mires were not abundant, and were short lived and often perturbed by clastic partings; (2) the seasonality in precipitation was high, as evidenced by frequent alternation of oxidized and reduced horizons in finely laminated deposits from floodplain settings or (3) a strong drainage pattern occurred, as attested by a well-developed fluvial network, ranging from proximal alluvial fans into braided rivers and more distal meandering rivers, which hindered the development of large peat-mires. The capacity of *Sigillaria brardii* to colonize these varied fluvial environments suggests that, even during a regressive phase of its history, it kept significant physiological plasticity to withstand adverse environmental situations.

5.4. Possible driving controls of the Pennsylvanian plant distribution

The conditions that controlled the Late Paleozoic plant distribution especially in the tropics is still under debate. For instance, [Kerp \(1996\)](#); [Cleal and Thomas \(1999, 2005\)](#) and [Thomas and Cleal \(2017\)](#) highlighted that in paleotropical areas the climate was permanently humid and proposed that topography and clastic inputs were the main mechanisms that controlled the formation of stagnant water and, as a consequence, the distribution of plants in wetlands. An alternative

hypothesis considers that the main driving force of the vegetation was the climate because in some areas, like in the Bohemian Massif, floral changes do not match the tectonic events, which are considered to enhance clastic inputs and the topography (Opluštil et al., 2017). Recently, another hypothesis popped up which is a combination of the two aforementioned hypotheses (Tabor and Poulsen, 2008; Bashforth et al., 2021). The results presented here range rather in the latter view, since even under similar climatic, tectonic and topographic conditions in the Pennsylvanian of Southwest Europe, differences in plant distribution persisted between the different basins.

6. Conclusions

The Pennsylvanian deposits in the Erillcastell Basin (NE Iberian Peninsula) were studied to determine stratigraphy, biostratigraphy and plant palaeoecology. Identification of *Lepidodendron aculeatum* in interval 8 (late Moscovian) and *Sphenophyllum angustifolium* (early Gzhelian) in interval 9 (both taxa determined by Dr. C. Álvarez-Vázquez, Real Jardín Botánico de Córdoba) at Erillcastell places the boundary between the Grey and Transition units at the base of interval 9, clarifying previous controversies. The lithostratigraphic framework confirms that the Grey Unit is mainly volcano-sedimentary at Erillcastell whereas eastwards it is composed of intercalations of terrigenous and more distal volcano-sedimentary facies, suggesting a West to East drainage pattern. In contrast, the Transition Unit shows a more radial drainage pattern, with the proximal areas mainly located near Coll de Fades, grading to distal facies both to the West (Peranera and Erillcastell) and to the East (Coll de Sas).

Sedimentology and plant taphonomy in the Erillcastell Basin have provided new palaeoecological data about a previously unknown southern European upland flora. Two plant landscapes were found in the Moscovian fluvial deposits: (1) *C. undulatus*, *C. cistii* and *C. suckowii* grew in meandering riverbanks, while *Sigillaria brardii* grew in abandoned channels and (2) *C. cistii* and *C. suckowii* grew sparsely on the floodplains and fluvio-lacustrine areas. Five plant landscapes were recognized in lower Gzhelian deposits: (1) *Sigillaria brardii* inhabited peat mires with *Alloiopteris* cf. *erosa* growing in the peat swamp margins. (2) *Calamites cistii* and *C. suckowii* grew on the floodplain to fluvio-lacustrine areas while medullosacean pteridosperms and marattialean tree ferns would grow in less inundated marginal areas. (3) *Sigillaria brardii* and calamitalean sphenopsids grew on meandering riverbanks and point bars, which is unusual in other Pennsylvanian intramontane basins of southern Europe. Its growth in fluvial habitats was probably enhanced by clastic influxes in peat-mires, strong fluvial drainage and soil high humidity fluctuation. (4) *Sigillaria brardii* also inhabited rare oxbow lakes and peat mires. (5) *Cordaites* and sphenopsid stands might have constituted a riparian element of braided rivers.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2022.111234>.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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