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First report of silicified wood from a late Pennsylvanian intramontane basin in the Pyrenees: systematic affinities and palaeoecological implications

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Abstract: The first anatomically preserved wood specimens of an upland Carboniferous flora from the Iberian Peninsula are reported from the Erillcastell Basin (Eastern Pyrenees, Catalonia, Spain). Two taxa are described, a calamitacean Equisetales (*Arthropitys* sp.) and a Cordaitales (*Dadoxylon* sp.). The *Arthropitys* specimen has fusiform multiseriate rays composed of square parenchyma cells with conspicuous uniseriate or multiseriate simple pits. These pits are located near the transverse walls and occasionally in the tangential walls. The tracheids vary in lumen size, with scalariform-bordered pits on their radial walls and multiseriate pits in their cross-field areas. The *Dadoxylon* specimen commonly has uniseriate fusiform rays. The tracheids are long, with a square shape in transverse section. Their radial walls bear araucarian pitting with a uniseriate to triseriate arrangement. The pits are

circular with a spindle-shaped aperture. Comparison of the Erillcastell specimens with coeval species from Europe indicates that they could belong to new species. The good preservation of the new fossil wood yields significant palaeoenvironmental information. The lack of marked growth rings in both specimens and the presence of tyloses in *Dadoxylon* suggest that the climate in the intramontane basins of the Pyrenees was slightly seasonal towards the end of the Carboniferous. This contrasts with the marked seasonality of coeval lowland basins. Such upland habitats may have enhanced the survival of plants adapted to humid conditions in a global context of increasing aridity.

Key words: *Cordaites*, *Calamites*, silicified wood, upland flora, Pyrenees, Iberian Peninsula.

THE vegetation of the Pennsylvanian palaeotropical wetlands of Euramerica is among the most iconic and well-known in the fossil record. Studies conducted for over two centuries have exhaustively explored the vegetation framework, from the characteristics of individual plant organs to the organization of communities and their dynamics in response to the climate changes of the Late Palaeozoic Ice Age (e.g. DiMichele *et al.* 2009; Bashforth *et al.* 2016; Richey *et al.* 2021). This considerable amount of knowledge about Pennsylvanian floras is based on palynological data and the abundant macro-remains from paralic basins, including both adpressions and anatomically preserved plants. The latter commonly occur in coal balls, carbonate concretions that formed in marine-influenced coal swamps (Scott & Rex 1985). The permineralized plant remains inside coal balls have enabled the

study of the fine anatomical features of lowland Pennsylvanian plants, providing detailed information on their development (e.g. Eggert 1961) and physiology (e.g. Cichan 1986; Baker & DiMichele 1997), as well as their interactions with arthropods (e.g. Scott & Taylor 1983) and microorganisms (e.g. Baxter 1975; Stubblefield *et al.* 1984).

There is significantly less information about the vegetation of intramontane basins such as those that developed in Southern Europe during the late Pennsylvanian (Kasimovian and Gzhelian, 307–299 Ma), here considered equivalent to the Stephanian European regional stage (Heckel & Clayton 2006; Aretz *et al.* 2020). There is general agreement that the elevation of these basins was above 1000 m and their fossil floras represent the upland vegetation of the late Pennsylvanian tropics (Thomas &

Cleal 2017). In Southern Europe, data on the floras of these basins come mostly from palynomorphs (e.g. Juncal *et al.* 2019) and adpressions (e.g. Martín-Closas & Galtier 2005). In the absence of a marine influence, coal balls did not form in intramontane wetlands and, therefore, anatomically preserved plant assemblages are overall rare (Trümpfer *et al.* 2022). The Stephanian A (Kasimovian) silicified plant assemblage of Grand-Croix from the St Etienne Basin (Central France; Fig. 1) is the richest to date, containing 54 plant genera (Doubinger *et al.* 1995; Galtier 2008) and well-preserved associated microorganisms (e.g. Renault 1900; Krings *et al.* 2009; Taylor *et al.* 2012). The assemblage is dominated by Cordaitales and differs from the contemporaneous adpression flora of the same basin, which is dominated by ferns and pteridosperms (Galtier & Phillips 1985; Doubinger *et al.* 1995). In the Graissessac-Lodève Basin, one of the best-known examples of late Pennsylvanian intramontane wetlands in Southern Europe, a few silicified trunks that are up to 50 cm in diameter and 2 m in length have been recovered from Stephanian C fluvial channels (Galtier *et al.* 1997). They correspond to Cordaitales (*Dadoxylon* cf. *brandlingii* and *Dadoxylon* sp.) and a calamitacean Equisetales (*Arthropitys* sp.). The palaeoecology of these plants is

known from adpressions. According to Martín-Closas & Galtier (2005), the Cordaitales would have inhabited the proximal areas of the basin such as the alluvial fans and the banks of braided rivers, while the Calamitaceae would have grown in the floodplains and along the riverbanks. Interestingly, the *Arthropitys* trunks found in the Graissessac-Lodève Basin have a significant amount of wood (at least 10 cm thick), in contrast to the poorly lignified contemporaneous Equisetales from the basin preserved as adpressions and moulds (Galtier *et al.* 1997; Martín-Closas & Galtier 2005). This suggests different growth patterns and/or ecology (Galtier *et al.* 1997; Martín-Closas & Galtier 2005).

In Spain there are well-documented late Pennsylvanian intramontane floras preserved as adpressions (e.g. Wagner 1989 in the Iberian Massif; and Gómez-Alba 2007, Martín-Closas & Martínez-Roig 2007 and Tosal *et al.* 2022 in the Pyrenees), but there has been no report of silicified plants in this type of basin to date. The only other Stephanian silicified plants from Spain belong to the coastal marine (deltaic) facies of the Arnao coalfield (Asturias), with the older records also corresponding to lowland paralic floras such as those found in the coal balls from the Namurian of León and the Westphalian of Asturias

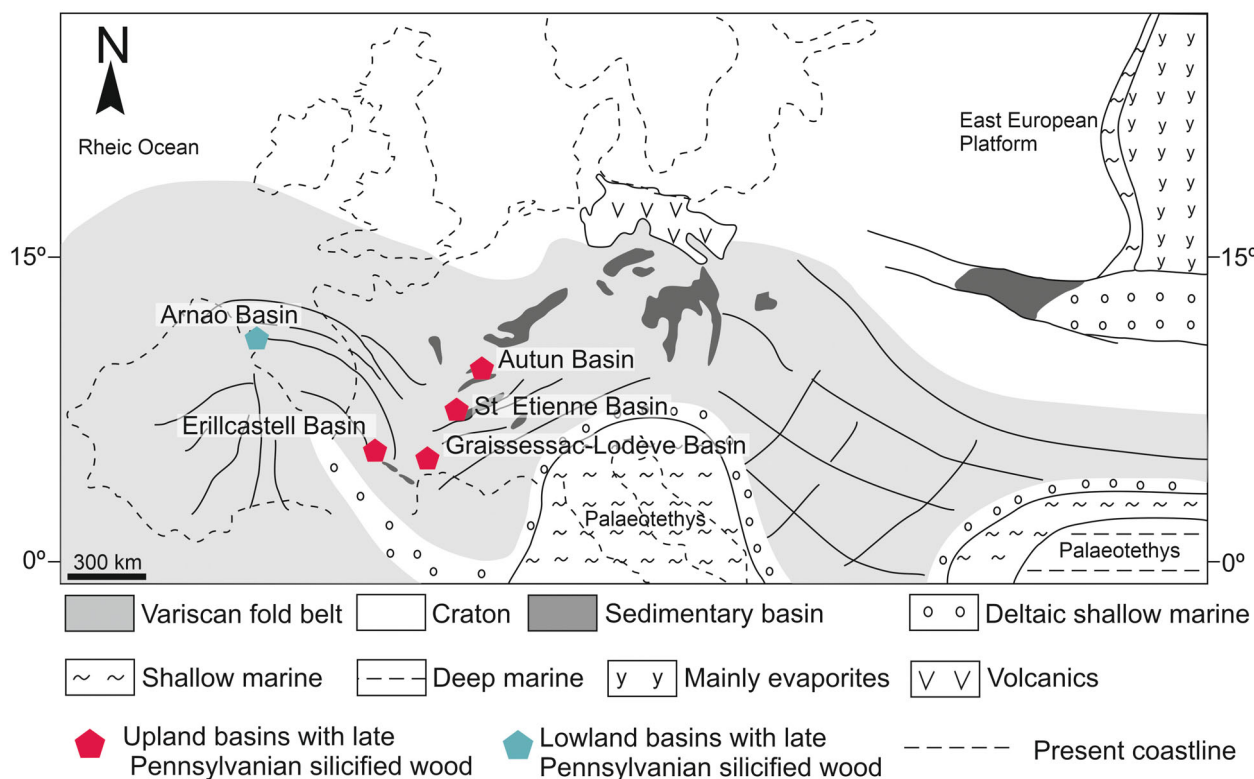


FIG. 1. Geological map of Europe during the Carboniferous–Permian transition. Red pentagons correspond to the upland basins with silicified wood, while the blue pentagon corresponds to a lowland basin with silicified wood. Modified from Roscher & Schneider (2006).

(Césari *et al.* 2015 and references therein). Here, we describe permineralized wood specimens recently collected in the Erillcastell Basin (Central Pyrenees, Catalonia, Spain). They represent the first evidence of anatomically preserved plants from a late Pennsylvanian intramontane basin of the Iberian Peninsula. The excellent preservation of the specimens enabled us to assign them to two genera. They provide additional information on the late Pennsylvanian upland vegetation in Europe and highlight the potential for new palaeobotanical discoveries in the region.

GEOLOGICAL SETTING

The study area is located 12 km northeast of the town of Pont de Suert, in the Pyrenean Axial Zone (northwest Catalonia, Spain), near the abandoned village of Erillcastell. From a geological viewpoint, the palaeobotanical locality studied here belongs to the Erillcastell Basin, which is Carboniferous–Permian in age (Martí 1983, 1995; Soriano *et al.* 1996). The origin of the basin is related to a transtensional tectonic regime occurring before the end of the Hercynian orogeny, during the Pennsylvanian (Moscovian–Gzhelian) and Permian (Ménard & Molnar 1988). The thinning of the continental crust produced intense volcanism and the subsidence of the Carboniferous–Permian Variscan intramontane basins (Martí & Mitjavila 1988). In the Catalan Pyrenees

(northeast Spain), four such late Hercynian pull-apart basins were shaped from west to east: Erillcastell (Fig. 2), Estac, Cadí and Castellar de N'Hug-Camprodon (Martí 1995; Soriano *et al.* 1996).

The Erillcastell Basin is a narrow basin (*c.* 15 km long and 3 km wide), oriented east to west, limited to the north by strike–slip faults, and internally compartmentalised by normal faults according to Gisbert (1981), Martí & Mitjavila (1987, 1988) and Martí (1995). During the Westphalian, high tectonic subsidence caused intense volcanic activity, leading to the accumulation of thick volcanic and volcano-sedimentary sequences rich in silica (Martí 1981, 1983; Martí & Mitjavila 1988). The magmatic activity decreased during the Stephanian, enabling the development of fluvio-lacustrine deposits. This trend continued during the Permian, which is mainly represented by red beds of Saxonian facies. However, Permian deposits are locally missing in Erillcastell, where the lower Triassic Buntsandstein facies unconformably overlies the latest Carboniferous deposits. This unconformity is associated with the tilting and erosion of some of the underlying deposits (Mateu-Ibars & Marzo 1985, pp. 1–49) before the beginning of the Mesozoic Iberian rift (Salas & Casas 1993).

Stratigraphic studies in the Erillcastell Basin were undertaken by Mey *et al.* (1968) and Nagtegaal (1969). These authors proposed a subdivision of these deposits based on the lithostratigraphy. Later, Gisbert (1981) proposed a new subdivision based on allostratigraphic units.

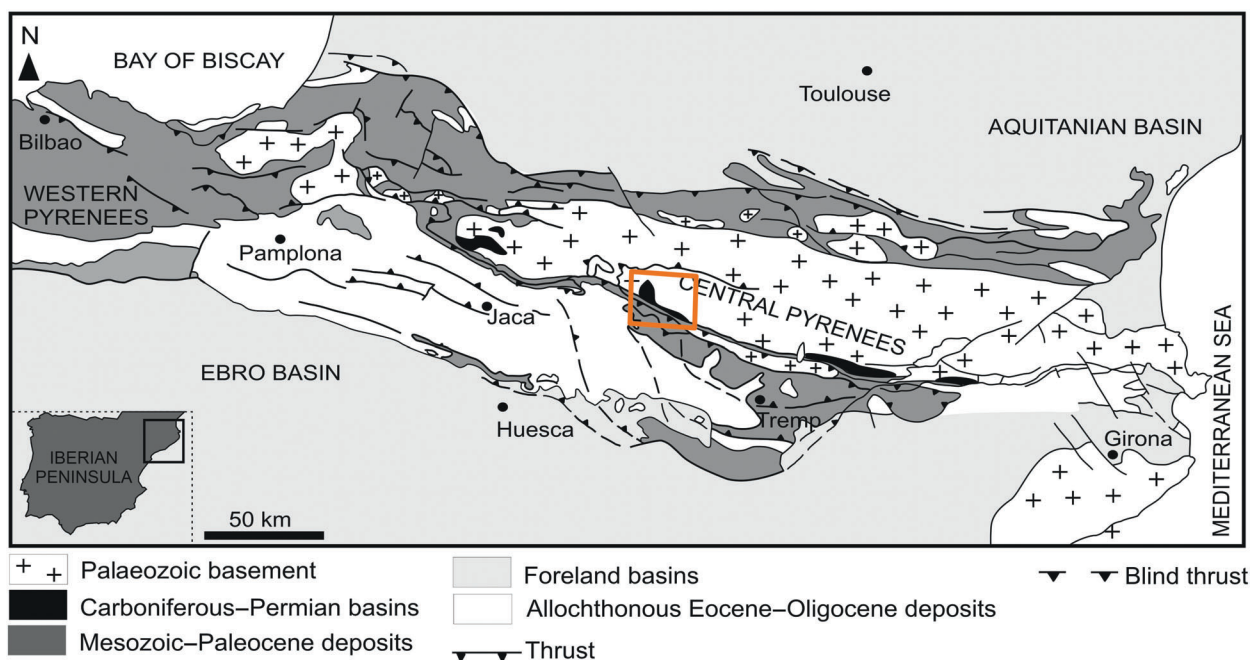


FIG. 2. Geological sketch of the axial zone of the Catalan Pyrenees, showing the location of the study area (orange square). Modified from Teixell (1998).

These units were termed the Grey Unit, the Transition Unit, the Lower Red Unit and the Upper Red Unit. The specimens studied here were found in the lowermost part of the Transition Unit.

The Transition Unit was first described by Gisbert (1981, 1983). Since then, it has generally been accepted that it is Gzhelian in age based on biostratigraphic studies of macroscopic plant remains (Tosal *et al.* 2022 and references therein). In Erillcastell, the Transition Unit is 142 m thick (Fig. 3), rests unconformably on the Grey Unit, and is cut off by the basal Mesozoic unconformity (Gisbert 1981, 1983; Tosal *et al.* 2022). It consists of lenticular conglomerates, sandstones with epsilon stratification and trough cross-bedding, black shales and bituminous coal rich in fossil plant adpressions. The silicified specimens come from a fining-upward sequence composed of conglomerates and coarse-grained sandstones with an erosive base, followed by sandstones with cross-beddings that are covered at the top of the sequence by siltstones (Fig. 3). This sequence is interpreted as an infill of a braided-river channel and the associated floodplain facies (Tosal *et al.* 2022). The silicified wood specimens studied here were found at the top of sandstone bodies, being commonly associated with *Cardiocarpus* seeds and being interpreted as parautochthonous (Tosal *et al.* 2022).

MATERIAL AND METHOD

Two specimens preserved in silica from the late Pennsylvanian were found in Erillcastell. Ten thin sections *c.* 30 μm thick were prepared in transverse, radial and tangential planes. They are stored at the Museu de Ciències Naturals de Barcelona with the collection numbers MGB 90407 LP1–MGB 90407 LP3; MGB 90408 LP1–MGB 90408 LP7. Cellulose acetate peels using HF (Galtier & Phillips 1999) were also prepared at UMR AMAP, Montpellier, to provide complementary information, and are deposited at the Museu de Ciències Naturals de Barcelona under the numbers MGB 90407 P1 and MGB 90408 P1–3. The slides and peels were studied and photographed with a Keyence VHX-7000 digital microscope. For comparative purposes, additional silicified wood specimens from the French limnic basins of Graissessac (Gzhelian) and Autun (early Permian) were studied. These specimens are part of the palaeobotanical collections of the Université de Montpellier; the specimen from Graissessac has accession number G2283; those from Autun have numbers ARX1, ARX2 and ARX3.

At least 50 measurements were taken for each wood character using the free software ImageJ (<https://imagej.net/Welcome>). These data are archived in the Dryad repository (Tosal *et al.* 2023). The measurements

indicated in the text were made on the thin sections. A comparison of the tracheid diameter between the thin sections and the peels showed that although the range was similar, the average size could be slightly different. Such differences were taken into account when comparing the material studied with previous taxonomic descriptions.

Throughout the text, equivalences between global and European regional chronostratigraphic units follow that of Heckel & Clayton (2006), while the higher taxonomic divisions for plants (i.e. Equisetales and Cordaitales) follow that of Taylor *et al.* (2009). The name '*Dadoxylon*' used in the classical literature for some woods attributed to *Cordaites* has been retained in this manuscript but the reader is recommended to see Rößler *et al.* (2014) for a detailed discussion on the use of the names *Dadoxylon* and *Agathoxylon*.

SYSTEMATIC PALAEOLOGY

Two well-preserved silicified wood specimens from Stephanian C (Gzhelian) deposits from Erillcastell are described here. One is 10 cm long and 5 cm wide (Fig. 4A) and corresponds to a secondary xylem portion of a calamite (Fig. 4B–D). The other specimen is 20 cm long and 30 cm wide (Fig. 5A) and corresponds to a secondary xylem portion of a Cordaitales (Fig. 5B–D). Locally, small fissures without preferential orientation infilled by minerals rich in silica (mainly quartz) cross the thin sections. Each specimen is described below in the different planes.

EQUISETALES Candolle ex Bercht. & Presl, 1820

CALAMITACEAE Unger, 1840

Genus ARTHROPITYS Göppert, 1864

Arthropitys sp.

Figure 6

Material. MGB 90407.

Description. In transverse section, the tracheids are rounded, rarely polygonal, with walls 17 μm thick (Fig. 6A). The mean diameter of the tracheid lumen is 49 μm tangentially and 62 μm radially ($n = 33$). In some localized areas of the wood, the average radial diameter of the lumen is reduced to 25 μm (Fig. 6A, B). However, this reduction in size is not associated with the substantial increase in tracheid wall thickness that characterizes latewood. Here, the wall thickness of the tracheids remains constant throughout the wood, and we infer that the specimen lacks true growth rings. Apart from the changes just mentioned, the sample does not show a substantial variation in the radial and tangential diameters of the tracheids outward.

The wood is characterized by two types of rays: large ones that are up to 11 cells wide and narrow ones that are 1–4 (mainly 2) cells wide (Fig. 6C). Both types are separated by

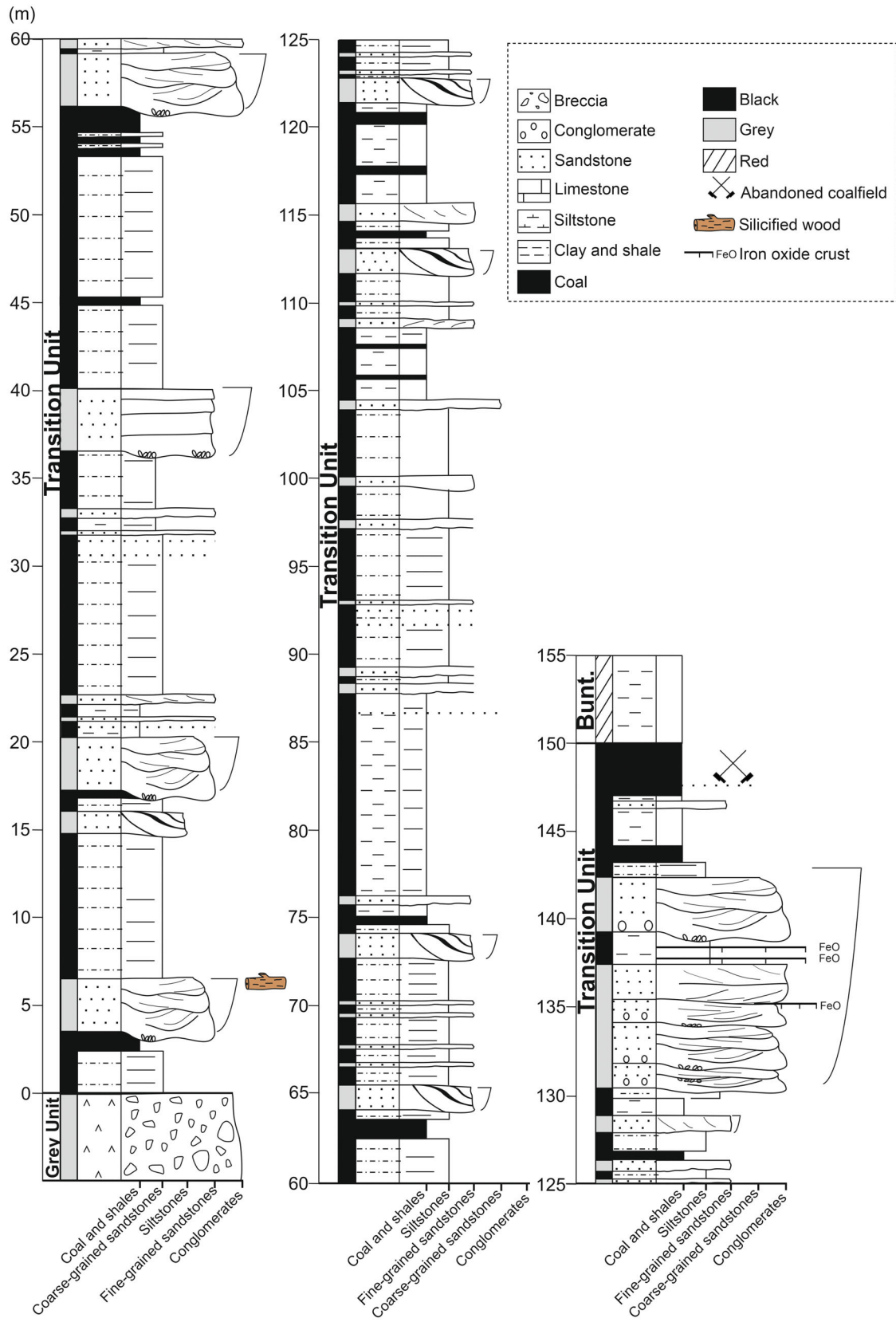


FIG. 3. Stratigraphic section of the Stephanian Transition Unit in Erillcastell. Modified from Tosal et al. 2022.

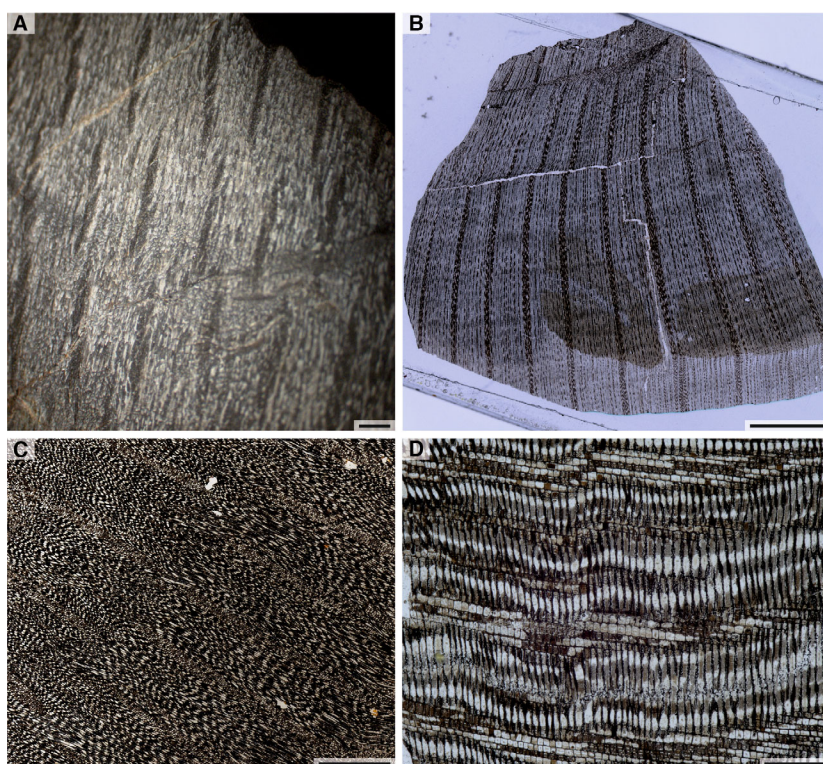


FIG. 4. General view of a permineralized *Arthropitys* sp. specimen from Erillcastell. A, wood in external view showing the longitudinal arrangement of the large rays (MGB 90407). B, transverse thin section (MGB 90407 LP2). C, tangential thin section (MGB 90407 LP3). D, radial thin section (MGB 90407.1). Scale bars represent: 1 mm (A); 5 mm (B); 200 μ m (C); 500 μ m (D).



FIG. 5. General view of the *Dadoxylon* sp. specimen from Erillcastell. A, trunk portion still embedded in the sandstones interpreted as a fluvial channel infill (MGB 90408). B, transverse thin section (MGB 90408 LP2). C, tangential thin section (MGB 90408 LP6). D, radial thin section (MGB 90408 LP1). Scale bars represent: 20 cm (A); 1 mm (B–D).

1–4 rows of tracheids and are composed of parenchyma cells that are square or rectangular and measure 24–51 μm tangentially (mean, 37.5 μm ; $n = 50$) and 49–121 μm radially (mean, 84 μm). Their wall is thin (mean, 6 μm). The ray cells show conspicuous uniseriate or multiseriate (2–10; mean, 4) simple pits. They are spaced and located in the transverse walls and occasionally the tangential walls (Fig. 6C). These pits are rounded or elongated in shape. The diameter of the rounded pits is 5–13 μm (mean, 9 μm ; $n = 50$), while that of the elongated pits is 13–26 μm tangentially and 5–10 μm radially ($n = 50$).

In tangential section, the tracheids measure more than 2.6 cm long (the size of the thin section) and are devoid of pits in the tangential walls. The rays are fusiform (Fig. 6D). The large rays are 2–4.2 mm high, 0.3–0.7 mm wide, and composed of 40–100 parenchyma cells in height. Most cells are polygonal in shape, except those located at the extremities of the rays, which have a rectangular shape. The size of the cells ranges from 24 to 91 μm . The narrow rays are 0.6–1.7 mm high and 52–151 μm wide. They are 14–30 polygonal cells in height, with the width varying from 29 to 78 μm . Pitting is not observed in the wall of the ray cells in the available tangential section. Occasionally, two narrow rays are connected by a thin row of rectangular parenchyma cells (Fig. 6E).

The radial section shows long tracheids with uniseriate to rarely biseriate pits. The pits are scalariform-bordered and the pit aperture is 3–6 μm long (Fig. 6F). Ray cells are rectangular (33–69 $\mu\text{m} \times 31$ –48 μm) with a thin wall (3–7 μm). They bear simple pits distributed sparsely in the cell wall (Fig. 6G). The pits are rounded or elongated in shape and located close to the transverse walls. Cross-field areas show crowded multiseriate pits with an elongated and sub-rounded irregular shape. They measure 12–22 \times 7–13 μm . Often, brownish rounded organic structures are observed in the ray cells. They measure 14 μm in diameter and presumably correspond to fungal spores (Fig. 6H).

Affinities. The most conspicuous character of the specimen is the presence of both small rays and large rays, the latter being interpreted as interfascicular rays. It also shows rectangular or square ray cells in the transverse and radial sections, and a uniform diameter of the tracheids tangentially and radially. These characteristics are consistent with *Arthropitys* (Wang *et al.* 2003; Rößler & Noll 2010; Rößler *et al.* 2012), a genus of the family Calamitaceae that existed from the Pennsylvanian to the Permian. For the specific attribution of the specimen, the anatomical features of the rays and the pitting of the primary and secondary xylem tracheids are considered in more detail hereafter.

Arthropitys comprises 31 species (Wang *et al.* 2003; Neregato *et al.* 2021); however, only 14 have well-developed interfascicular rays in the secondary xylem, as observed in the specimen from Erillcastell. These species are: *A. barthelii* Neregato, Rößler & Noll; *Arthropitys bistrata* (Cotta) Göppert emend. Rößler & Noll; *A. buritiranensis* Neregato, Rößler & Noll; *A. deltooides* Cichan & Taylor; *A. ezonata* Göppert; *A. felixii* Hirmer & Knoell; *A. gallica* Renault; *A. iannuzzii* Neregato, Rößler & Noll; *A. isoramis* Neregato, Rößler & Noll; *A. kansana*

Andrews; *A. medullata* Renault; *A. tocatinensis* Neregato, Rößler & Noll; *A. versifoveata* Anderson; and *A. yunnanensis* (Tian & Gu) ex Wang, Hilton, Galtier & Tian. In addition, the specimen from Erillcastell has scalariform pitting in the tracheid radial walls, a character that is shared only with *A. barthelii*, *A. bistrata*, *A. deltooides*, *A. ezonata*, *A. medullata*, *A. tocatinensis* and *A. yunnanensis* (Table 1). *Arthropitys bistrata* differs from the *Arthropitys* from Erillcastell by shorter and wider ray cells (Table 1). By contrast, *A. barthelii* and *A. tocatinensis* have ray cells of comparable size, which also show circular pits on the horizontal walls. However, unlike the Erillcastell *Arthropitys*, both species lack pits on the radial walls of the ray cells. Furthermore, *A. deltooides* has larger and rounded or sub-rounded ray cells tangentially (Cichan & Taylor 1983), which is in contrast to the polygonal (angular) shape seen in the *Arthropitys* specimen studied here.

The two species with the most similarities to the *Arthropitys* specimen from Erillcastell are *A. medullata* and *A. ezonata* (Table 1). *Arthropitys medullata* is a common species in the lower Permian limnic basin of Autun (France) that Marguerier (1967) described in detail. Although there is a strong resemblance, a slight difference in the wall thickness of the different cell types is observed. While the tracheid wall of the specimen from Erillcastell is thick, that of the specimens from Autun is thin according to Marguerier (1967). Similar differences are observed in the ray cell walls, which are thicker in the specimen from Erillcastell than in those from Autun. The secondary xylem of *A. ezonata* also has similar anatomical features to those of the *Arthropitys* specimen from Erillcastell. However, the tracheid cells are slightly narrower in *A. ezonata* (Table 1). These quantitative differences may be caused by environmental differences during plant growth, as observed by Andrews (1952) in some silicified calamitacean Equisetales specimens from North America, or by abiotic factors, such as the diagenetic processes described by Rößler *et al.* (2021). Therefore, they should not be considered for taxonomic purposes. To further specify the taxonomic attribution of the *Arthropitys* specimen from Erillcastell, it would be necessary to characterize the anatomy of its primary xylem. However, this tissue is missing from the specimen. For this reason, it will be referred to as *Arthropitys* sp. here.

CORDAITALES Scott, 1909

CORDAITACEAE Grand'Eury, 1877

Genus DADOXYLON Endlicher, 1847

Dadoxylon sp.

Figure 7

Material. MGB 90408.

Description. In transverse section, the tracheids are rectangular or square in shape and their lumen size is relatively uniform. They measure 20–46 μm tangentially (mean, 30 μm ; $n = 101$) and 11–41 μm radially (mean, 28 μm ; $n = 101$). The tracheid walls are 6 μm thick ($n = 70$). The regular lumen diameter and the wall thickness indicate the absence of growth rings. 1–7 rows

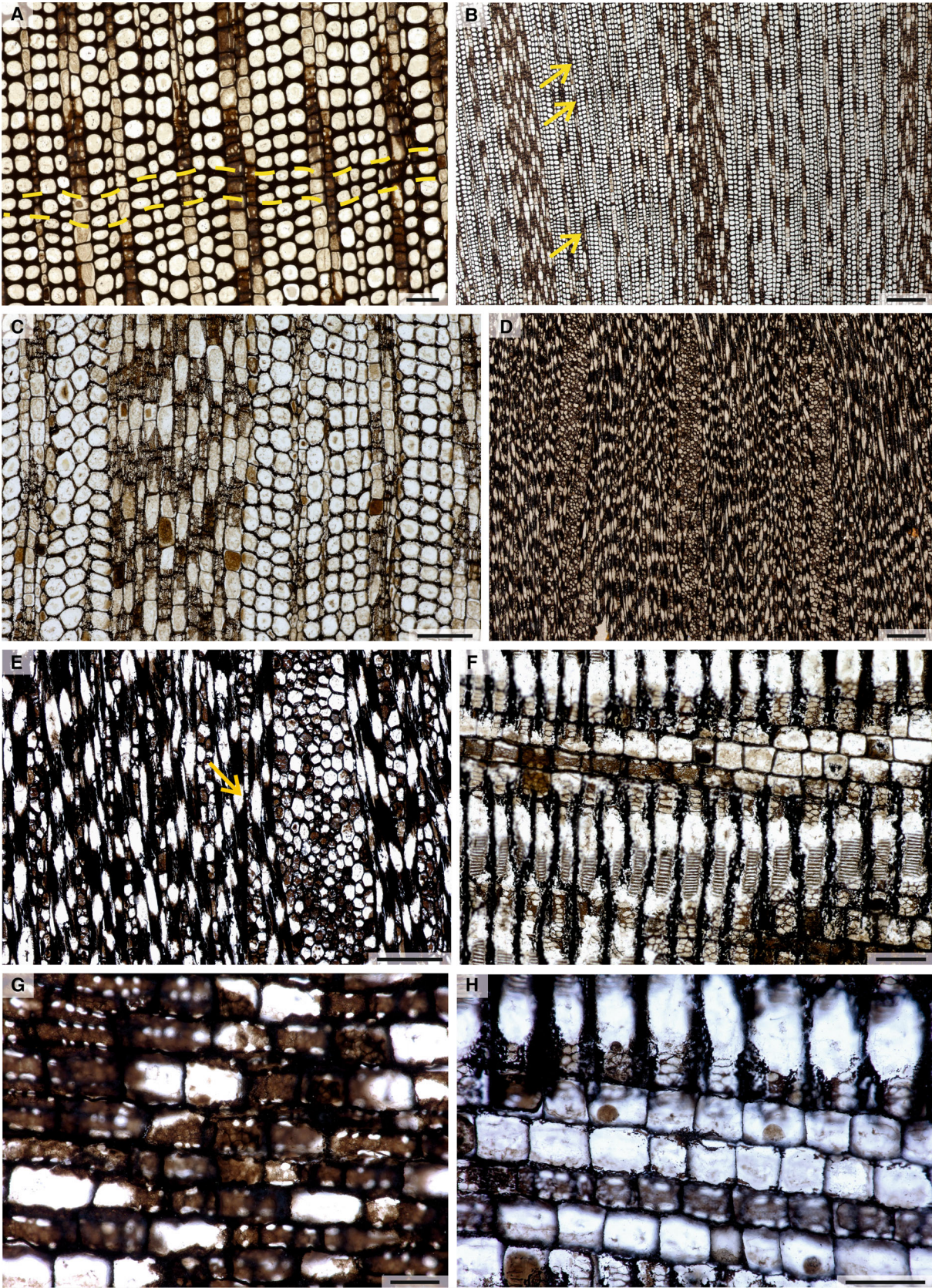


FIG. 6. Thin sections of *Arthropitys* sp. from Erillcastell. A, transverse section showing the rounded shape and thick walls of the tracheids; discontinuous lines mark a tangential zone of the tracheids with a smaller lumen diameter (MGB 90407 LP2). B, transverse section showing variations in the tracheid lumen diameter suggesting changes in growth patterns (arrows) (MGB 90407 LP2). C, transverse section showing large rays with simple pits located in the transverse walls and occasionally at the border of the tangential walls (MGB 90407 LP2). D, tangential section showing fusiform-shaped rays (MGB 90407 LP3). E, tangential section showing a large ray and two narrow rays connected by a thin row of rectangular parenchyma cells (arrow) (MGB 90407 LP3). F, radial section showing the tracheids with scalariform-bordered pits and the cross-fields with characteristic multiserial pits showing an elongated and sub-rounded irregular shape (MGB 90407 LP1). G, radial section with square-shaped ray cells bearing simple pits (MGB 90407 LP1). H, radial section showing ray cells with brown rounded structures that may correspond to fungal spores (MGB90407 LP1). Scale bars represent: 100 μm (A, C, E–H); 500 μm (B, D).

TABLE 1. Comparison of cross-sectional wood characters in late Palaeozoic *Arthropitys* showing scalariform pitting in the radial walls of the tracheids.

	Tracheid features		Ray features			
	Diameter (μm)	Shape	Large ray width (no. of cells)	Cell shape	Cell size (μm)	Pits
<i>Arthropitys</i> sp. from Erillcastell	49–62	Rounded, rarely polygonal	≤ 11	Square to rectangular	37.5 wide, 121 long	Circular pits in transverse and radial walls
<i>Arthropitys bistrata</i>	35–70	Rounded or rectangular	3–7	Square to rectangular	45–120 wide, 15–40 long	Absent
<i>Arthropitys medullata</i>	–	Rectangular	–	Square to rectangular	–	–
<i>Arthropitys ezonata</i>	20–50	Rectangular	< 30	Square to rectangular	30–100 wide, 70–150 long	–
<i>Arthropitys deltoides</i>	72–78	Rectangular	< 6	Rounded or sub-rounded tangentially	16.7 wide, 86.6 long	Absent
<i>Arthropitys yunnanensis</i>	50	Rectangular	< 50	Rectangular	–	–
<i>Arthropitys tocaninensis</i>	49	Rectangular	–	Rectangular	31–135 long	Circular pits in transverse wall
<i>Arthropitys barthelii</i>	34	Rectangular	–	Rectangular	102 long	Circular pits in transverse wall

of tracheids separate the uniseriate to rarely biserial rays (Fig. 7A). The ray cells are 81–160 μm long (mean, 95 μm) and 10–22 μm wide (mean, 14 μm ; $n = 7$) and their tangential walls are oblique. Occasionally, pale brown spherical structures (10 μm in diameter) occur in the ray cells and may correspond to fungal spores (Fig. 7B).

The tangential section shows long tracheids (greater than 2 cm) and fusiform rays. The ray density is 21–27 per mm^2 . Most rays are uniseriate, but may occasionally be biserial in their widest part (Fig. 7C). The rays are 40–210 μm high (mean, 121 μm ; $n = 103$), 20–40 μm wide (mean, 26 μm ; $n = 103$), and composed of 1–7 (mean, 4; $n = 103$) parenchyma cells with a regular rounded or sub-rounded shape.

The radial section shows araucarian pitting (contiguous pits, multiserial alternate pits) in the tracheid walls, with a uniseriate (29%), biserial (48%) or triserial (23%) arrangement (Fig. 7D). The pits are circular or oval in shape and 15–45 μm (mean, 25 μm ; $n = 50$) in diameter. Their aperture is 4.7–

12.1 μm wide (mean, 7.8 μm ; $n = 50$) and spindle shaped. Locally, some tracheids are filled with an ochre–orange content with a polygonal shape that probably corresponds to a late stage of tylose formation (Fig. 7E). Cross-field pitting shows crowded uni- or biserial small circular pits (6 μm) with a spindle-shaped aperture (Fig. 7F).

Affinities. The specimen described above has uni- to biserial rays that separate one to several rows of square to rectangular tracheids with araucarian radial pitting. Based on the work of Marguerier (1971), these features are consistent with the secondary xylem of both the Cordaitales and Coniferales. To date, only the remains of Cordaitales (i.e. *Artisia* pith casts, *Cordaites* leaves and *Cardiocarpus* seeds) have been found in the Erillcastell Basin, while coniferalean specimens are absent (Tosal et al. 2022). We assume, therefore, that the permineralized wood remains studied here are likely to correspond to Cordaitales. At present, three morphogenera are informally accepted as woody axes of

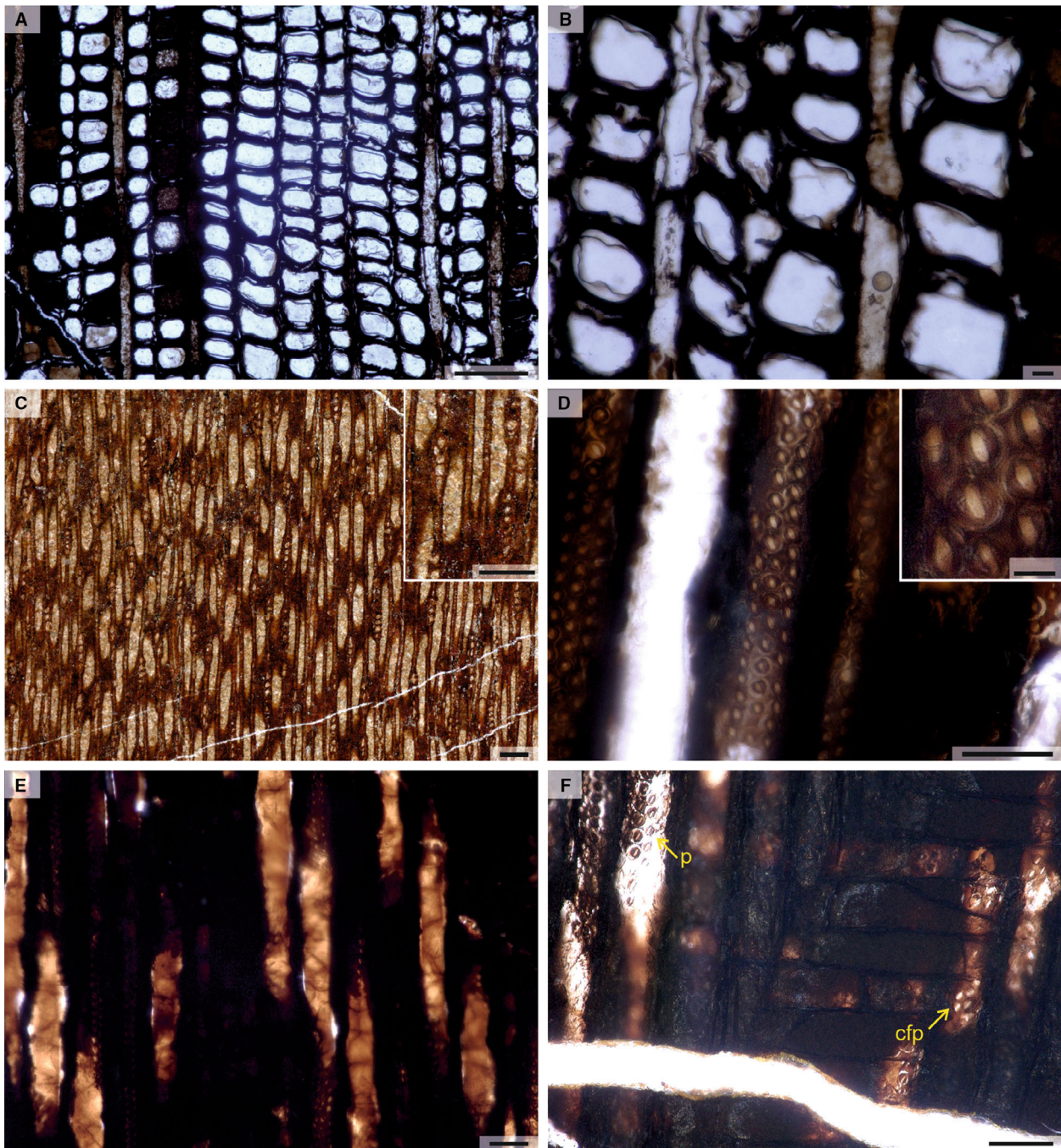


FIG. 7. Thin sections of *Dadoxylon* sp. from Erillcastell. A, transverse section showing rectangular to square tracheids and narrow rays with radially elongated cells (MGB 90408 LP2). B, transverse section showing a brown spherical structure, possibly a fungal spore, in a ray cell (MGB 90408 LP3). C, tangential section showing fusiform uniseriate, rarely occasionally biseriate rays (see inset) (MGB 90408 LP7). D, radial section showing triseriate pits in the tracheid walls; inset: detail of the circular pits with a spindle-shaped aperture (MGB 90408 LP4). E, radial section showing ochre-orange contents with polygonal shapes, possibly tyloses, filling the tracheids (MGB 90408 LP4). F, cross-field pitting with biseriate circular pits (cfp) that are significantly smaller than the tracheid pits (P) (MGB 90408 LP1). Scale bars represent: 100 μm (A, C); 10 μm (B); 50 μm (D–F); 10 μm (C inset, D inset).

Carboniferous to Triassic Cordaitales: *Cordaixylon* Grand'Eury, *Mesoxylon* Scott & Maslen, and *Dadoxylon* Endlicher (Trivett & Rothwell 1985; Trivett 1992; Philippe 2011). *Cordaixylon* and

Mesoxylon are mainly used for axes with a well-preserved primary xylem, while *Dadoxylon* is mainly used for isolated wood (Philippe 2011). Three morphogenera have actually been used

TABLE 2. Comparison of wood characters in some late Palaeozoic Cordaitales from southern Europe.

	Ray length (µm)	Tracheid lumen (µm)		Ray density (no. rays/mm ²)	Diameter of pits (µm)	Aperture width of pits (µm)	Diameter of cross-field pitting (µm)	Locality
		Tangential	Radial					
<i>Dadoxylon rollei</i>	–	13.9–62.9	16.3–54.6	32–34	20–31	7–16	Not preserved	Autun
<i>Dadoxylon</i> cf. <i>brandlingii</i>	150	26–57	31–57	9–24	8–15	–	–	Graissessac-Lodève
<i>Cordaixylon andresii</i>	–	40–82	72–88	–	12–17	4–9	24	Arnao
<i>Dadoxylon</i> sp. (Erillcastell)	80–160	20–46	11–41	21–27	15–45	5–12	6	Erillcastell

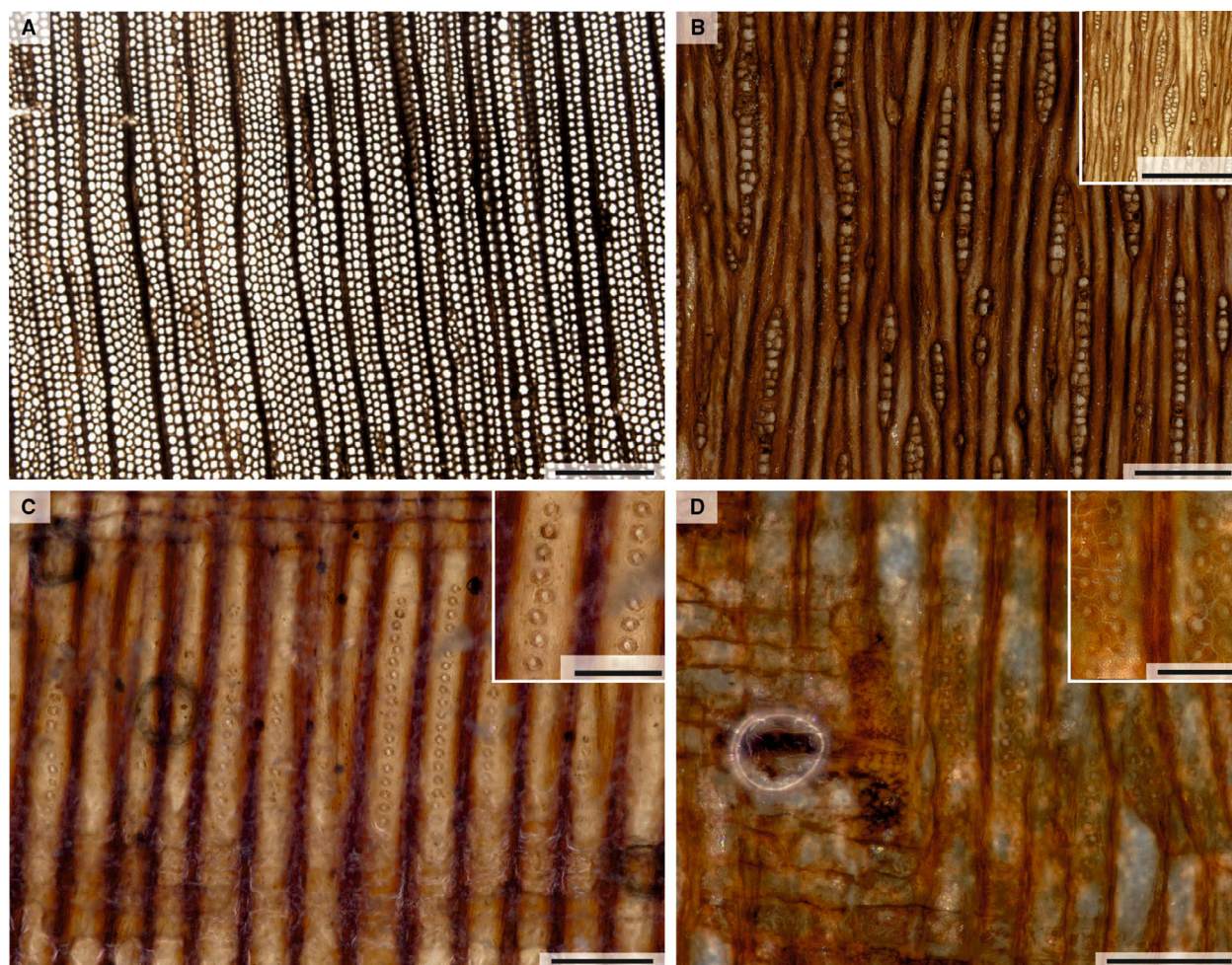


FIG. 8. Thin sections of early Permian *Dadoxylon rollei* from Autun. A, transverse section showing rays separating 2–7 rows of tracheids (ARX1). B, tangential section showing uniseriate and occasionally biseriate rays; inset: detail of a triseriate ray (ARX2). C, radial section showing uniseriate circular pits in the tracheid walls; inset: detail of pitting (ARX2). D, radial section showing rare biseriate pitting in the tracheid walls; inset: detail of pitting (ARX2). Scale bars represent: 500 µm (A, B inset), 200 µm (B), 100 µm (C, D); 50 µm (C inset, D inset).

traditionally for isolated wood specimens with araucarian pitting: *Agathoxylon* Hartig, *Dadoxylon* and *Dammroxylon* Schultze-Motel. However, a discussion on the taxonomy of this

morphological complex is beyond the scope of this study and we refer interested readers to the work of Philippe (2011) and Rößler *et al.* (2014). Here, we provide a comparison of the new specimen

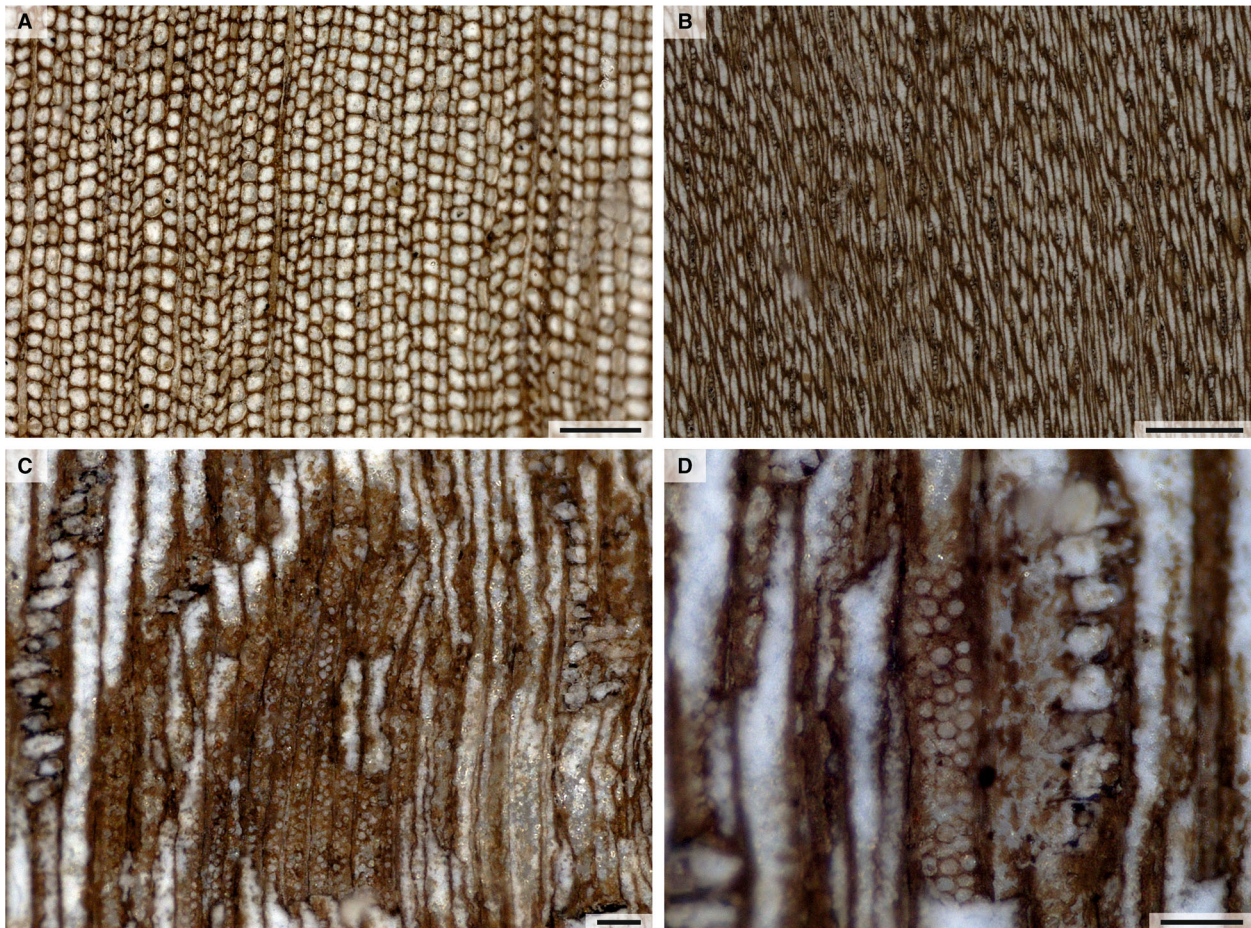


FIG. 9. Peel preparations of a Stephanian *Dadoxylon* cf. *brandlingii* specimen from Graissessac (G2283). A, transverse section showing square-shaped tracheids and narrow rays. B, tangential section with uniseriate and locally biseriate rays. C, radial section showing pitting in the tracheid walls. D, radial section showing the triseriate and alternate arrangement of pits in a tracheid wall. Scale bars represent: 200 μm (A), 500 μm (B), 50 μm (C, D).

from Erillcastell with other late Palaeozoic silicified wood specimens of Cordaitales from southwest Europe (i.e. from the Graissessac-Lodève, St Etienne and Autun basins in France, as well as Arnao in the northwest Iberian Peninsula). Several Cordaitales have been described from these localities: *Dadoxylon rollei* Unger from the lower Permian deposits of Autun (Massif Central, France; Marguerier 1971), *Dadoxylon* cf. *brandlingii* from the Stephanian C deposits of Graissessac-Lodève Basin (Massif Central, France; Galtier *et al.* 1997) and *Cordaixylon andresii* Césari, Álvarez-Vázquez, Méndez-Bedia, Álvarez-Laó, Turrero & Arbizu from the Stephanian C deposits of Arnao Basin (Cantabrian Mountains, northwest Iberian Peninsula, Césari *et al.* 2015), and a specimen from Stephanian C deposits near Saint Etienne that resembles *Dadoxylon subrhodeanum* Grand'Eury. Comparison with the *Dadoxylon* sp. from Erillcastell, using six anatomical characters of wood that are considered diagnostic by Marguerier (1977), is provided below and summarized in Table 2.

Dadoxylon rollei and the specimen from Erillcastell show small uni- to partly biseriate rays that separate one to several rows of tracheids. Their tracheids are square to rectangular in the

transverse section and have thick walls with circular pits radially (Fig. 8A, B). However, three main differences are observed: (1) the *Dadoxylon* specimen from Erillcastell has a multiseriate pitting arrangement in the tracheid walls, unlike the uniseriate (Fig. 8C) or rarely biseriate pitting of *D. rollei* (Fig. 8D); (2) the pit apertures of the *Dadoxylon* specimen from Erillcastell are spindle shaped, which contrasts with the circular pit apertures of *D. rollei* (Fig. 8C, D); and (3) the rays of the *Dadoxylon* specimen from Erillcastell are narrower and have a lower density than those of *D. rollei* (Table 2).

Dadoxylon cf. *brandlingii* as described by Galtier *et al.* (1997), is relatively poorly preserved and some delicate characters, such as the type of the pit aperture, are missing. Like the *Dadoxylon* sp. from Erillcastell, *D. cf. brandlingii* also has square-shaped tracheids in the transverse section (Fig. 9A). The tracheids are long and show multiseriate pitting radially (Fig. 9C). The rays are uniseriate to locally biseriate (Fig. 9B) and the cross-field pits are circular in shape (Fig. 9C, D). However, the *Dadoxylon* sp. from Erillcastell has smaller tracheid lumens and smaller rays than *D. cf. brandlingii* from Graissessac (Table 2).

The well-preserved wood of *Cordaixylon andresii* described by Césari *et al.* (2015) is characterized by tracheids with uniseriate or alternate biseriate and triseriate pitting of the araucarian type. These features are also observed in the *Dadoxylon* sp. from Erillcastell. However, two remarkable differences in the pitting features are observed between them that are significant for taxonomy: (1) the radial pits of the *Dadoxylon* sp. from Erillcastell are circular in shape, while those of *C. andresii* are hexagonal (Césari *et al.* 2015); and (2) the cross-field pits of the *Dadoxylon* sp. from Erillcastell are numerous, small and circular, with spindle-shaped apertures, which contrasts with the 1–2 large pits of *C. andresii*.

Dadoxylon subrhodeanum as briefly described by Grand'Eury (1877) differs from the Erillcastell specimen by the uniseriate pitting of the tracheid radial walls and by its higher rays (10–30 cells high). The specimen resembling *Dadoxylon subrhodeanum* according to Lemoigne (1965) possesses tracheids with uniseriate to triseriate pits of the araucarian type on their radial walls. It differs from the Erillcastell specimen by tracheids that are larger (up to 90 µm in diameter) and mostly hexagonal in transverse section. Its rays are uniseriate but occasionally bi- or even triseriate and higher, with 20 cells in height on average.

To summarize, the wood from Erillcastell is consistent with the morphogenus *Dadoxylon*. However, its anatomical features do not correspond exactly to those of previously reported wood specimens from southwestern Europe from that time. As with *Arthropitys*, finding new specimens with a preserved primary xylem will be crucial in further specifying the affinities of *Dadoxylon* from Erillcastell.

DISCUSSION

Anatomically preserved plants from the Pennsylvanian and lower Permian of Spain

The silicified wood specimens from Erillcastell add data to the sparse record of anatomically preserved plants from the Pennsylvanian to lower Permian deposits of the Iberian Peninsula. The oldest Pennsylvanian record is from the province of León (northern Spain). It consists of coal balls containing marine fauna and terrestrial plants that are late Namurian (= Bashkirian) in age (Gómez de Llerena & Arango 1946; Beckary 1987; Vachard & Beckary 1989). These coal balls have yielded a taxonomically diverse floral assemblage containing 54 species, most of them corresponding to pteridosperms (Beckary 1987; Galtier 1997). In the province of Asturias, Renier (1926) reported a Westphalian coal ball found in a building of the Lieres coal mine company (p. 1291). The coal ball contains *Stigmaria* (Lepidodendrales), *Sphenophyllum* (Equisetales), *Myeloxylon* (Medullosales) and some gymnosperm wood. More recently, Césari *et al.* (2015) described well-preserved silicified trunks of *Cordaixylon* as well as roots of *Psaronius* (Marattiales) from Stephanian C deposits in Asturias (Cantabrian Mountains; northern Spain). To date, these are the only known anatomically

preserved plants from the Carboniferous in Spain. However, they represent plants from a lowland (paralic) setting that would have grown in transitional environments, which makes it difficult to compare them with the upland (limnic) floras from Erillcastell.

For the earliest Permian record, anatomically preserved plants from Spain consist mostly of silicified logs from volcanic deposits. In the province of Seville (southern Spain), silicified wood specimens from the Viar Basin were assigned by Vozenin-Serra *et al.* (1991) to three taxa: *Dadoxylon* (*Araucarioxylon*) *douglasense* Steidtmann (interpreted as coniferalean), *Dadoxylon* (*Cordiaoxylon*) *brandlingii* (interpreted as cordaitalean) and *Dadoxylon* (*Eristophyton*) *ibericum* (attributed to the pteridosperms). Near Aragoncillo, in the Guadalajara province (central-eastern Spain), numerous trunks measuring up to 1.25 m in diameter are preserved *in situ* (Sopeña & Sánchez-Moya 1999 and references therein). They have been assigned to *Dadoxylon* sp. and co-occur with the leafy shoots of walchian conifers (Tricalinos 1928; Sacher 1966 in Sopeña & Sánchez-Moya 1999).

Palaeodiversity and palaeoecology of the upland flora from the Erillcastell Basin

Calamitacean trees are one of the iconic components of Pennsylvanian and Permian floras. The good preservation of the wood found at Erillcastell enables the determination of the occurrence of pits in the transverse walls of ray cells (Fig. 6A). A similar feature has been reported in the rays of some Palaeozoic Calamitaceae such as *Archaeocalamites*, *Arthropitys* and *Calamitea* (= *Calamodendron*) (Marguerier 1970), but has not been documented for all calamitacean taxa. This character may have been advantageous for fluid circulation in these genera (Marguerier 1970).

Late Palaeozoic Calamitaceae have been reported from various habitats, indicating their adaptation to diverse ecological conditions. For instance, some species with little wood would have inhabited permanently flooded environments, similar to those of present-day *Equisetum*. Some other taxa have succulent stems and/or deep root systems that would be adapted to reach the phreatic water during seasonally dry conditions (e.g. Barthel & Rößler 1994; Naugolnykh 2005). Finally, others have abundant wood and a well-developed root system (Taylor *et al.* 2009), which have been linked to growth in disturbed settings (Gastaldo 1992). The *Arthropitys* specimen from Erillcastell has a well-developed secondary xylem, suggesting that this plant inhabited an environment with significant clastic inputs close to watercourses. This result fits with the palaeoenvironmental interpretation proposed by Tosal *et al.* (2022) based on a taphonomic study of

the early Gzhelian flora from Erillcastell. The authors concluded that *Calamites* was a riparian element there and grew in point bars and river margins.

The proportions of parenchyma in the Calamitaceae can also be used to infer the climatic conditions in which the plants grew. In extant *Equisetum* species, water stored in the wood parenchyma can indeed sustain the functioning of the vascular system under dry conditions, notably by preventing embolism or by facilitating the refilling of the xylem conduits (Morris *et al.* 2016 and references therein). The *Arthropitys* specimen from Erillcastell is characterized by abundant parenchyma (46%; Fig. 6A). Such high proportions of parenchyma (up to 50% of the total silicified tissue) have also been documented in calamitacean wood specimens from other intramontane basins in Europe (e.g. Rößler *et al.* 2012; Mencl *et al.* 2013), which have been interpreted as an adaptation to dry conditions (Barthel & Rößler 1994; Rößler *et al.* 2012). Indeed, seasonal precipitation has been recently proposed for the early Gzhelian in Erillcastell Basin by Tosal *et al.* (2022), based on the frequent alternation between oxidized and reduced horizons in the floodplain deposits.

Calamitaceae were also capable of adapting their secondary growth to environmental factors, resulting in the development of growth rings. The analysis by Luthardt *et al.* (2017) of an *in situ* early Permian plant community growing around a wet spot under a generally semi-arid climate showed that the Calamitaceae had a higher sensitivity to environmental stress than seed plants. The specimen from Erillcastell shows small changes in the tracheid diameter (Figs 4B; 6A, C), similar to those of the indistinct type 2 rings interpreted by Luthardt *et al.* (2017) as drought-induced false rings. This feature suggests that the plant was growing in relatively favourable conditions, but with variations in the precipitation and/or the water table depth.

The second group of plants represented in the silicified wood specimens from Erillcastell is the Cordaitales, which is regarded as the sister group of the conifers and is also an important component of Pennsylvanian–Permian tropical floras (Anderson *et al.* 2007). Like the Equisetales, the Cordaitales were morphologically diverse and occurred in various habitats. Some Cordaitales, mainly from limnic basins (lowland vegetation), grew in peat swamps and clastic wetlands, where they were represented by shrubs and trees of relatively small stature (<10 m high) (Rothwell & Warner 1984; Costanza 1985; Trivett & Rothwell 1985; Raymond 1988). Other taxa produced large trunks and have been reconstructed as trees up to 30–40 m high. These larger Cordaitales are typically reported to have grown in well-drained substrates at higher altitudes (‘uplands’, Falcon-Lang & Bashforth 2005) and/or during drier, sub-humid to semi-arid climatic episodes (‘drylands’, e.g. Bashforth

et al. 2016). However, some may also have grown in more humid conditions (Wan *et al.* 2020).

The silicified cordaitalean trunk described in this study is relatively large (more than 30 cm across; Fig. 5A), suggesting a height of at least 20 m based on the approach of Niklas (1994). Its wood anatomy is different from that of *Arthropitys*, with a much lower proportion of parenchyma and smaller tracheids. However, like *Arthropitys*, it does not show any evidence of growth rings in the part studied (Fig. 5B). This suggests that the *Dadoxylon* tree grew under relatively equal environmental conditions, as *Arthropitys*. Cordaitalean adpressions are frequently found in the lower Gzhelian fluvial deposits from Erillcastell. They are represented by different plant organs, such as foliage and pith casts (*Artisia*) or seeds (*Cardiocarpus*) (Tosal *et al.* 2022). These remains have been found in association with *Calamites* (mainly *C. suckowii*) and have been interpreted as growing alongside braided rivers (Tosal *et al.* 2022), supporting the hypothesis that both plants grew under similar environmental conditions.

The presence of tyloses in the *Dadoxylon* wood from Erillcastell could be linked to normal heartwood formation. It could also represent a response to an environmental stimulus such as fungal infections or injury-induced or drought-related embolism of the conducting cells (De Micco *et al.* 2016; Decombeix *et al.* 2022). Interestingly, tyloses have also been reported in the late Pennsylvanian *C. andresii* from Asturias, where they may have formed as a response to a fungal infection or wounding (Césari *et al.* 2015). Unlike the specimen from Asturias that shows early stages of tylose formation in the form of isolated bubble-like structures in the tracheid lumina, the *Dadoxylon* sp. wood from Erillcastell shows only the late stages in which the tracheid lumen appears completely filled with tylose walls (Fig. 7E).

Intramontane vegetation and environmental changes in the late Palaeozoic palaeotropics

The late Pennsylvanian and early Permian was an important time for plant evolution in the palaeotropics of Euramerica. A general aridification trend caused a change in the composition of lowland vegetation, with a switch to a dominance by plants adapted to more arid environments (DiMichele 2014). By the end of the Stephanian C (Gzhelian), the coal swamp vegetation is considered to have been restricted geographically to isolated wetter spots (DiMichele *et al.* 2007). This period, sometimes called the ‘Carboniferous rainforest collapse’ (e.g. Sahney *et al.* 2010), corresponds to one of the main extinction events in the plant fossil record (Cascales-Miñana & Cleal 2014). In this context, intramontane basins are likely to have formed refugia, where the effect of the

global climate change towards aridity was less marked due to more favourable temperatures and/or higher precipitation. While DiMichele & Phillips (1996) showed that there was a shift to mires dominated by tree ferns and pteridosperms in the late Pennsylvanian in North America, coeval mires of European intramontane basins typically remained dominated by arborescent lycopsids (Wagner 1989; Martín-Closas & Galtier 2005; Martín-Closas & Martínez-Roig 2007). This is also the case for the Erillcastell Basin, where *Sigillaria brardii* prevailed in peat-mires, while medullosacean pteridosperms and marattialean tree ferns grew in the distal areas of the floodplain (Tosal *et al.* 2022). The silicified specimens described in this study indicate the presence of large woody calamitacean Equisetales and Cordaitales in the basin. Despite their different systematic affinities, wood anatomy and putative physiology, both apparently grew under fairly favourable local conditions. The results obtained here indicate a weakly marked seasonal climate in Erillcastell, which did not vary widely enough to deeply influence the ecology of plant groups such as the Calamitaceae and Cordaitales. However, this seasonality would have been strong enough to influence the palaeoecology of the lycopsids, with *S. brardii* from Erillcastell growing in fluvial environments, as noted by Tosal *et al.* (2022).

CONCLUSION

Silicified wood specimens from Erillcastell represent the first occurrence of anatomically preserved plants from a late Pennsylvanian (Gzhelian) intramontane wetland of the Iberian Peninsula. The specimens correspond to two types of arborescent plants, a calamitacean Equisetales (*Arthropitys* sp.) and a Cordaitales (*Dadoxylon* sp.). They provide information not available from the adpression flora found in this locality, such as growth patterns, interactions with fungi, and the presence of tyloses, which enables us to better understand the plants and their environments. The lack of marked growth rings in the wood of both specimens suggests that they grew under stable local conditions, with possible drier episodes reflected in the reduction of the tracheid lumen size in the *Arthropitys* wood. The data provided here indicate a slightly seasonal climate, at least in terms of precipitation in the intramontane basins of the Pyrenees close to the Carboniferous–Permian boundary. These conditions would have been favourable for most palaeotropical plants, such as sphenopsids, ferns, pteridosperms and cordaitaleans. However, the seasonality in Erillcastell would have been strong enough for lycopsids such as *S. brardii*, which would have spread into fluvial environments during this time span. Future exploration of the area to recover new silicified

plants is expected to lead to a better understanding of the palaeotropical upland floras of Euramerica and their response to the late Pennsylvanian and early Permian aridification and floral turnover.

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DATA ARCHIVING STATEMENT

Data for this study (including cell measurements and full-resolution versions of the individual photos used in the plates) are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.w3r2280vb>

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