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First report of permineralised plants in the Stephanian of Arnao (Asturias, northwestern Spain)

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ABSTRACT

The first record of an anatomically preserved flora from Stephanian outcrops at Arnao beach (Asturias, Spain) is presented. The stratigraphic section is part of a geological heritage site that preserves exceptional Devonian reef deposits. The Carboniferous succession contains coal seams worked by one of the earliest mines in Spain and its plant-fossil assemblages were reported in the 19th century but scarcely revised later. The new assemblages recovered in the beach, during extreme low tides, represent the first record of permineralised trunks in northwestern Spain. Large cordaitalean specimens are referred to a new species of *Cordaixylon* characterised by non-septate pith, araucarian radial pitting of the tracheids and cross-fields with phyllocladoid pits. Part of the root mantle of *Psaronius* is preserved in water-worn pebbles, indicating the presence of tree ferns in the palaeoflora. The associated compression/impression assemblage includes lycophytes, sphenophytes, pteridosperms and pteridophytes. A comparison of the assemblage confirms its importance for reconstructing the Late Pennsylvanian floral succession in the region.

1. Introduction

Recently, Wagner and Álvarez-Vázquez (2010) published a synthesis of the Carboniferous floras of the Iberian Peninsula, based on a perspective of over fifty years of research. According to these authors the most complete Carboniferous record corresponds to the Cantabrian Mountains, within the Cantabric–Asturian arcuate fold belt. Lists of fossil plants from the Principality of Asturias were published already in the 19th century, including works by renowned palaeobotanists such as Grand'Eury (1877) and Zeiller (1882). However, these early researchers did not provide any illustrations of the Asturian material.

The intricate tectonics of the Cantabric-Asturian fold belt has led to a fragmentation of the stratigraphic record, with numerous smaller or bigger outcrop areas that are fragments of sedimentary basins. At Arnao, on the Asturian coast, a small area with very few coal seams was worked at the turn of the 19th and 20th centuries (see Fig. 1 for location). Paillete was one of the early mining experts who described this area (Paillete et al., 1845). The cliffs west of Cabo Peñas (Asturias) show a Palaeozoic succession from Devonian (Aguión Formation) to various parts of the Carboniferous. The Arnao Platform in Cabo La Vela and Reef to the east of Cabo Peñas (Fig. 1) exhibit a Devonian succession of sufficient importance to be declared a "Lugar de Interés Geológico" (denomination used for geological heritage sites protected under the law). Since the early studies by Méndez-Bedia (1976) the reef deposits at Arnao have been considered as most important for the Early Devonian in Europe. A synthesis of the scientific value of these deposits was published by Arbizu and Méndez-Bedia (2006).

The Carboniferous of Arnao has not been studied in the same detail. Arnao was a centre of coal mining from 1842 to 1915, one of the earliest in Asturias. Most important is a publication by Patac (1932), who dealt with the geological and mining history of Arnao. The coal mine at Arnao was abandoned when the sea threatened to flood the underground workings. The Arnao mine (Fig. 2) was the only coal mine in Spain with undersea galleries. Lorenzo (1977) published some very fragmentary plant impressions, which suggested a late Stephanian B-Stephanian C age. Wagner and Álvarez-Vázquez (2010) assumed a Stephanian B age (late Kasimovian–earliest Gzhelian) for the coal-bearing strata at Arnao, but the plant megafossil record is too poor to sustain this assumption. A Stephanian C (early Gzhelian)/Autunian (late Gzhelian) age cannot be excluded. Further research is necessary to resolve this problem.

Up to now there has been no record of Carboniferous permineralised wood at Arnao or anywhere else in NW Spain. Permineralised plant material is very scarce in the Cantabrian-Asturian fold belt, being restricted to a mention of coal-balls from the upper Westphalian of Lieres in

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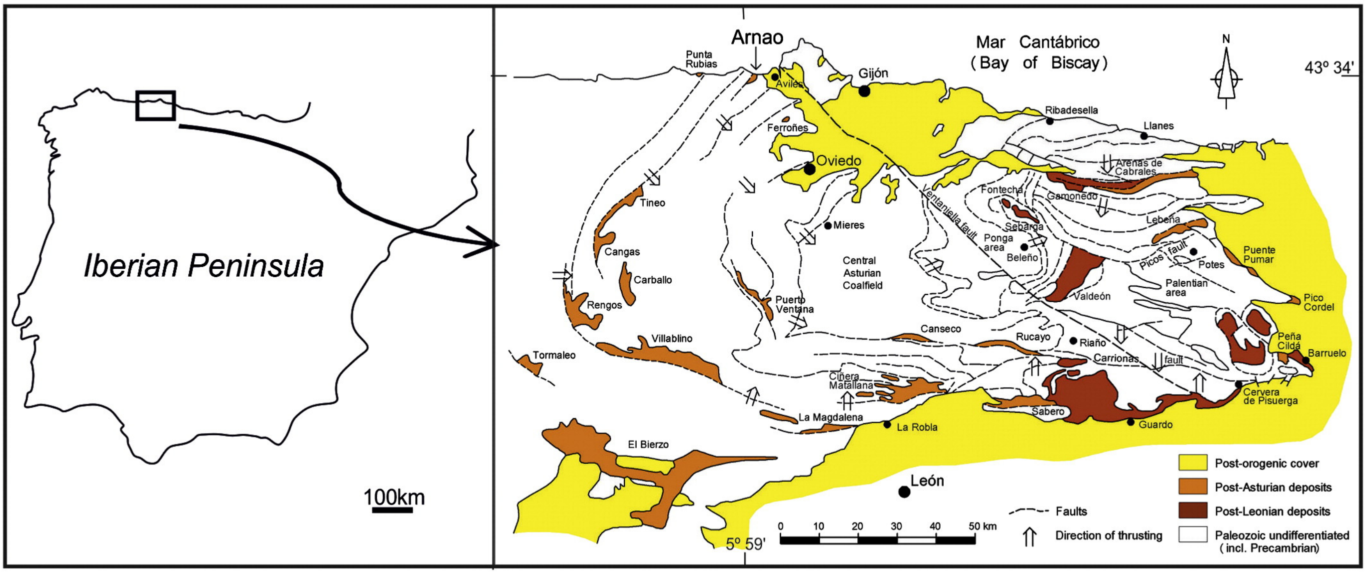

Fig. 1. Map of the Iberian Peninsula showing the main outcrops of Carboniferous deposits in the Asturian area and the location of Arnao (after Knight and Wagner, 2014).

Asturias (Renier, 1926) and well-documented coal-ball specimens at Truébano in the province of León, presumably of late Namurian age (Beckary, 1987a,b; Beckary and Laveine, 1985; Vachard and Beckary, 1989).

The finding of anatomically preserved wood remains in outcrops on the eastern side of Cabo La Vela has allowed adding a different record in NW Spain. The fossiliferous beds are only exposed during extremely low tide. It is noted that permineralised wood remains in Spain are thus far restricted to Autunian (Gzhelian) strata in southern Spain (Guadalcanal and Valdeviar, Sevilla province – Vozenin-Serra et al., 1991) and in central Spain (Rillo de Gallo, Guadalajara province – Sopeña and Sánchez-Moya, 1999). These occurrences are in purely terrestrial basins in parts of Spain that have a very different geological history from the Cantabrian Mountains. This lends certain exclusivity to the Arnao occurrence.

2. Geological context

The small Arnao coalfield and outcrops at La Nieva are apparently in continuity with a string of "Saberian" (middle Kasimovian) and Stephanian B outliers limited by thrust faults in western Asturias and northern León, but this appearance may be misleading. The arcuate disposition of these tectonic outliers is due to the final tightening process of the Cantabric–Asturian arcuate fold belt (Fig. 1). There is no consensus in the literature about the exact nature of the tectonic deformation of Palaeozoic strata in this fold belt and its underlying causes, but extreme tectonic mobility is in evidence. This has led to the generation of three successive basins during Pennsylvanian times, each of which accumulated about 6000–7000 m of strata. Although these basins largely overlap in geographical area, they do not wholly coincide. The successive basins are clearly superimposed with angular

Fig. 2. View of Cabo La Vela with the position of the old mine building (A) and the fossil site (B) with permineralised logs.

unconformities in between. Overall palaeogeographic reconstructions are in Wagner and Álvarez-Vázquez (2010, Figs 3–5).

The arcuate fold belt is overlain, with strongly angular unconformity, by a generally more flat-lying succession of latest Pennsylvanian (Autunian), Permian and Mesozoic deposits. These do not contain coal-bearing strata, but Arnao may be the exception.

Most of the Pennsylvanian sediments in the Cantabrian Mountains are marine with Palaeotethyan faunas, allowing correlation with Eastern Europe, but there is sufficient imbrication with terrestrial, coal-bearing deposits so as to allow correlation with the classical West European chronostratigraphic subunits of the Westphalian and Stephanian stages, based on floral associations. The lower part of the succession at Arnao, seemingly of mixed marine and terrestrial facies (Horvath et al., 1987), occurs separately from a downfaulted coal-bearing part, which has been overthrust by Devonian limestones. The coal-bearing strata at Arnao either belong to the third basinal succession, which extends from upper Barruelian Substage (lower Kasimovian), through "Saberian" into Stephanian B *sensu stricto* (Wagner and Álvarez-Vázquez, 2010), or to the Autunian cover rocks. It is recalled that the Stephanian Stage was proposed by Munier Chalmas and de Lapparent (1892–1894), with A, B and C subdivisions defined by Jongmans and Pruvost (1950) in the eponymous Saint Étienne Basin in the Massif Central, south-central France. The unsatisfactory nature of the A division, incomplete and delimited by unconformities in a strike-slip controlled basin, has led the IUGS Subcommission on Carboniferous Stratigraphy to recognise two lower Stephanian substages, Cantabrian and Barruelian, representing the lower Stephanian, and typified by mixed marine and terrestrial strata of NW Spain (Wagner and Winkler Prins, 1985). Problems with the Stephanian B division at Saint Étienne, where it is floored by an unconformity, have led French authors to have recourse to a Stephanian A-B succession at Carmaux, another intramontane basin in the Massif Central. A "Saberian" Substage has been proposed for "lower" Stephanian B, to precede the Stephanian B *sensu stricto* as represented at Saint Étienne (Wagner and Álvarez-Vázquez, 2010; Knight and Wagner, 2014).

Higher substages, Stephanian C and Autunian form part of the post-tectonic cover of the Cantabric-Asturian arcuate fold belt. Classical Stephanian C and Autunian are in the Saint Étienne and Autunian basins of the Massif Central, France.

3. Description of the stratigraphic section

Horvath et al. (1987) described three sections (megasequences according to those authors) in the Late Pennsylvanian outcrops of Arnao beach. The total succession recorded by Horvath et al. (1987) is less than 80 m, and does not include the underground coal-bearing strata worked in the Arnao coal-mine.

The basal section, 8–9 m thick, was characterised by coarsening-up sequences bearing reworked Devonian fauna. The upper part is composed of fine-grained sandstones and carbonaceous shales bearing plant remains. This section was interpreted by Horvath et al. (1987) as lagoon deposits with progressive fluvial influence.

The middle section (about 65 m) was divided by Horvath et al. (1987) into three intervals. The lower comprises fining-upward cycles, grading from cross-bedded conglomerates at the base, to ripple-laminated coarse and medium-grained sandstones and then interbedded bioturbated shales and siltstones. Plant remains and the permineralised stems described here are found in the middle and upper parts of the cycles, and coal beds were reported from the upper levels. According to Horvath et al. (1987) fining-upward cycles represent deltaic deposits prograding into the lagoon. The middle interval is made up of grain- and coarsening-upward sequences formed of siltstones with linsen-flaser lamination in the lower-half and cross-bedded sandstones in the upper-half. This succession would represent deltaic platform deposits formed during a transgressive event or the abandonment of distributary channels. Similar to the basal interval, the top of the middle section is formed by coarse-grained cross-bedded sandstones and some levels of conglomerates, which indicate a fluvial progradation over platform deltaic deposits.

The upper section (12–15 m) is composed of a monotonous repetition of centimetric to decimetric-scale cycles that begin with algal stromatolites covered by mudstones, shales and fine- to medium-grained sandstones. After a transgressive event, these rocks probably represent sedimentation in coastal plain areas subject to minor oscillatory change in the sea level.

4. Materials and methods

The material analysed in this study was preserved as permineralised logs ranging from approximately 25 cm in diameter to smaller fragments. The trunks were firstly silicified preserving the anatomical structure. However, during a deeper diagenesis the silica was extensively replaced by carbonate (calcite and siderite), which in some cases strongly disturbed the anatomical structure. The carbonate occurs in three different forms: 1) as microcrystalline aggregates that infill the cells partially preserving the anatomical details, 2) as radial growth of prismatic crystals usually replacing the cell walls entirely, and 3) infilling fissures.

Some specimens were prepared by conventional thin sections in transverse (TS), radial longitudinal (RLS) and tangential longitudinal (TLS) orientations. Water-worn pebbles of permineralised logs also occur on the beach. Some of these represent fragments of the rooting system of large tree ferns, which have disintegrated in the intertidal zone. These specimens were eroded from underlying rocks. Some trunks were observed in their original position attached horizontally to the bedrock (Fig. 3B, D), thus indicating local vegetation. The largest of these fallen logs was a trunk 30 cm in diameter and 160 cm long (Fig. 3B).

All thin sections were examined under an Olympus BX53 microscope and images obtained using a DP-26 camera. The material is stored at the Museum of the Department of Geology (DGO) of Oviedo University.

5. Systematic palaeontology

5.1. Fossil-genus Cordaixylon Grand'Eury, 1877

Type species. *Cordaixylon dumusum* Rothwell and Warner, 1984
Cordaixylon andresii sp. nov.
Figs. 4–6
Etymology. Dedicated to the memory of Prof. Andrés Pérez Estaún, an outstanding geologist and dear friend of his Asturian colleagues.
Holotype. DGO 2057
Type locality: 43° 34′ 38″ N, 5°, 58′ 53″W, Arnao Beach, Spain.
Type horizon: c. 40 m from the base of the Carboniferous succession (see Arquer Prendes-Pando et al., 1983, p. 96).
Material. DGO 2057a-i, 2058a-b, 2059a-c.

Diagnosis. Woody tree stem with primary and secondary tissues. Circular eustele with numerous xylem strands. Pith parenchymatous, narrow, homocellular and non-septate. Primary xylem endarch, tracheids with spiral, annular and scalariform/reticulate thickenings. Secondary xylem pycnoxylic without distinctive growth rings. Uniseriate up to rarely triseriate circular bordered to araucarian pits on radial tracheid walls. Rays parenchymatous, mainly uniseriate, one to ten cells high. Cross-fields exhibit one (or, less often, two) obliquely orientated oval simple pit. Scarce axial parenchyma as isolated cells or in short vertical files.

5.1.1. Description

The three specimens analysed, up to 25 cm in diameter, were found to belong to the same type of wood; they are described on the basis of the best preserved specimen.

Fig. 3. A. Fragment of permineralised stem still embedded in the rock. B. Large trunk as exposed on the beach at extremely low tide. C. *Sigillaria brardii* Brongniart. D. *Sigillaria* sp. E. *Calamites* sp.

The permineralised axes are well-preserved with a parenchymatous pith, endarch primary xylem and pycnoxylic secondary xylem. The stem comprises a solid (non-septate) homocellular parenchymatous pith (Fig. 4A), 10–11 mm in diameter, surrounded by a woody cylinder (Fig. 4C). One stem (DGO 2057), although subcircular, is eccentric; the secondary xylem is preserved on one side measuring 60 mm in width and 180 mm on the opposite side. The pith consists of isodiametric cells, 60–180 μm in diameter (Fig. 4B) and 47–148 μm long, arranged in vertical rows (Fig. 4A). The eustele consists of numerous xylem strands at the periphery of the solid pith that show endarch maturation (Fig. 4D, E). Primary xylem comprises tracheids, 15–40 μm in diameter that shows helical, scalariform, reticulate thickenings (Fig. 4G, H). Secondary pycnoxylic xylem composed of tracheids with some occasional axial parenchyma; in transverse section without growth-rings (Fig. 4F); no resin canals have been observed. In RLS the tracheids near the pith exhibit mostly uniseriate contiguous bordered pitting, and then have alternate biseriate and triseriate crowded hexagonal pitting (araucarioid), with narrow diagonal pit apertures (Fig. 4I–K); a small proportion being uniseriate but slightly distant from neighbouring pits and/or biseriate alternate to sub-opposite. Cross-fields with one or two large oculipores (Fig. 5A–C) showing rarely a reduced border; when single, the oculipore is distinctly larger, pyllocladoid (pinoid). Rays in tangential section mostly low, ranging in height from 2 (rarely one) to 10 cells; uniseriate, occasionally biseriate or triseriate (Fig. 5E–F). Scarce axial parenchyma was observed in TLS and RLS (Fig. 5E). An insufficient number of vascular traces were observed, only two, in TS and TLS (Fig. 5J) and one in RLS (Fig. 5G–H), to determine phyllotaxis. They might be interpreted as possible leaf traces or branch traces. In RLS the vascular trace occurs in the wood, 1500 μm away of the pith and is composed of cells with scalariform to reticulate thickenings; the trace passes nearly horizontally through the secondary xylem before disappearing from the plane of section. Branch or foliar scars are not preserved on the external surface of the specimens.

5.1.2. Evidence of tyloses

Evert (2006) described tyloses as outgrowths of the adjacent parenchyma cells, axial parenchyma or ray cells through the pit cavities and into the lumina of the axial tracheids. Within the tracheids of *C. andresii* sp. nov., the tyloses usually are spaced and polygonal or ovoid in shape, occupying part of the tracheid luminae. Occasional single tyloses are observed in cross-section (Fig. 5L). Longitudinal sections show small pyriform structures that protrude from ray cells through the pits (Fig. 5K). These pyriform structures then form balloon-shaped buds, spheroidal to ellipsoidal tyloses (Fig. 6B, G) and septa-like structures similar to those described by Feng et al. (2013, 2015) and Wan et al. (2014). Individual tyloses in *C. andresii* sp. nov. usually have curved ends, different from horizontal true septa. The presence of hyphae close to the tyloses is rare (6A), therefore the possibility that the tyloses have been produced mainly by fungal infection can be discarded.

The presence of tyloses was related to the origin of horizontal septum-like structures in the tracheids of *Xenoxylon latiporosum* by Ogura (1944). This author proposed that the horizontal septa derived from globular tyloses. Philippe et al. (2013) also mentioned the presence of septa-like structures in several Asian specimens related to *Xenoxylon*, but they considered that their origin is uncertain and without taxonomic value. Feng et al. (2015) proposed that septa-like structures, when not related to ray cells, may likely represent host cell

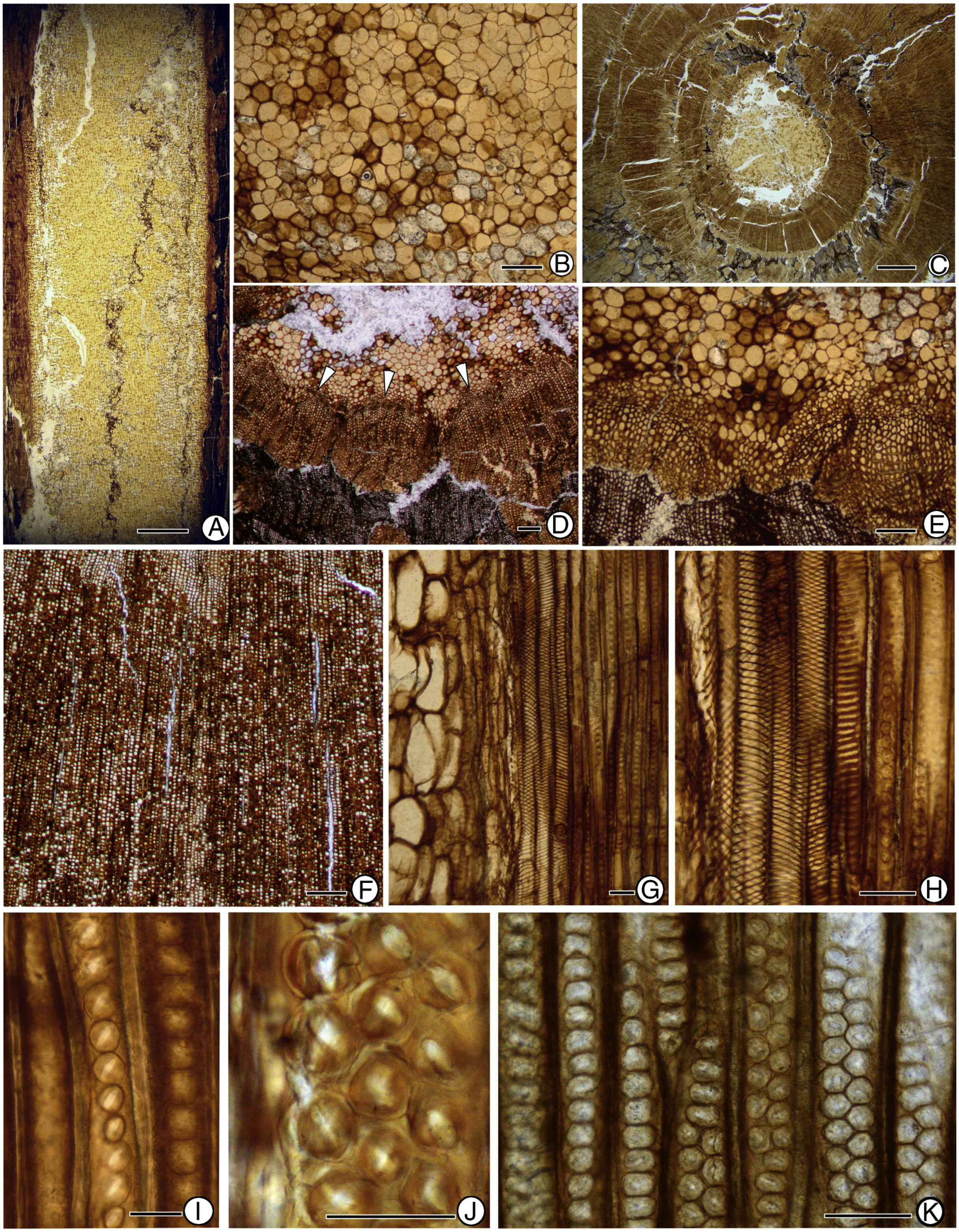

Fig. 4. *Cordaixylon andresii* sp. nov. A. Radial longitudinal section (RLS) showing the solid pith composed of vertically aligned cells, without septa. DGO 2057i. B. TS, close up of the parenchyma cells in the pith. DGO 2057a. C. Transverse section (TS) of the stem showing the pith and xylem. DGO 2057a. D, E. TS, showing the eustele with the secondary xylem demarcating irregular woody wedges (white arrows). DGO 2057a. F. Transverse section of secondary xylem without distinctive growth rings. DGO 2057b. G. Radial longitudinal section showing pith and primary xylem. DGO 2057i. H. RLS, close up of primary xylem cells with helical to reticulate thickenings. DGO 2057i. I. RLS showing uniseriate pits of the tracheids. J. Close-up of the elliptical crossed apertures of the pits in a triseriate tracheid. DGO 2059b. K. RLS section showing uni-biseriate, alternate and contiguous pits. Scale bar: A, C = 3 mm; B, D, E, F = 200 μm; G, H, J, K = 50 μm; I = 25 μm.

reactions to fungal attacks or the remains of metabolic products of fungal enzymatic activity.

The presence of tylosis in extant species may be induced by different causes, including abiotic and biotic factors. Mechanical injuries, flooding, fungal infection and heart-wood formation are some of the known stimuli (see references in Feng et al., 2013).

The Arnao specimens possess evidence of wood injury and fungal hyphae as possible stimuli of the tyloses.

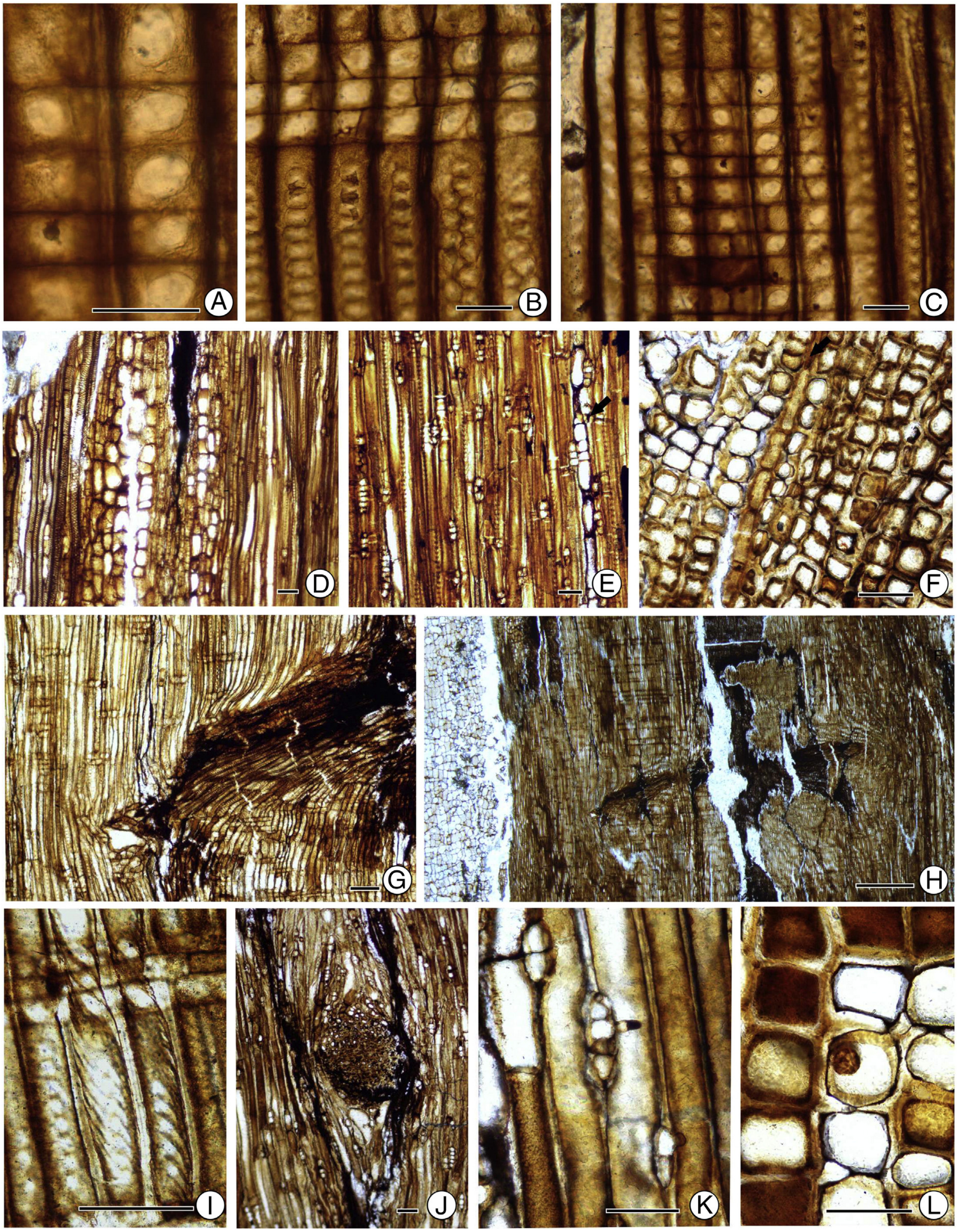

Fig. 5. *Cordaixylon andresii* sp. nov. A. Close-up of oval to circular and oblique cross-field pits. B. Detail of cross-field and tracheid pitting. C. An unusual tall cross-field. D. TLS section at the periphery of the pith showing parenchyma cells limited at both sides by primary xylem. E. TLS of the secondary xylem showing the rays and axial parenchyma (arrows). F. Close-up of TS, black arrow indicating rectangular parenchymatous ray cells. G. Detail of the vascular trace in H. DGO 2057i. H. Longitudinal section showing a vascular trace in its nearly horizontal course through the secondary wood. DGO 2057i. I. Helical thickenings in tracheids. J. TS of subcircular vascular trace identified in TLS of the wood. DGO 2057d. K. TLS showing a small pyriform and rounded tyloses emerging from two ray cells. L. Tyloses in TS of tracheids. Scale bar: A, B, C, E, F, K, L = 50 μm; G, I, J = 100 μm; H = 1000 μm.

5.1.3. Wound evidence

Specimen DGO 2057 preserves a band of tissue at the periphery of the secondary xylem (Fig. 6C) that may be interpreted as wound response where the surviving cambium sealed the scar with new woody tissue. In radial section probable cambial cells are thin-walled, and their tangential width (up to 12 μm) is narrower than that of the

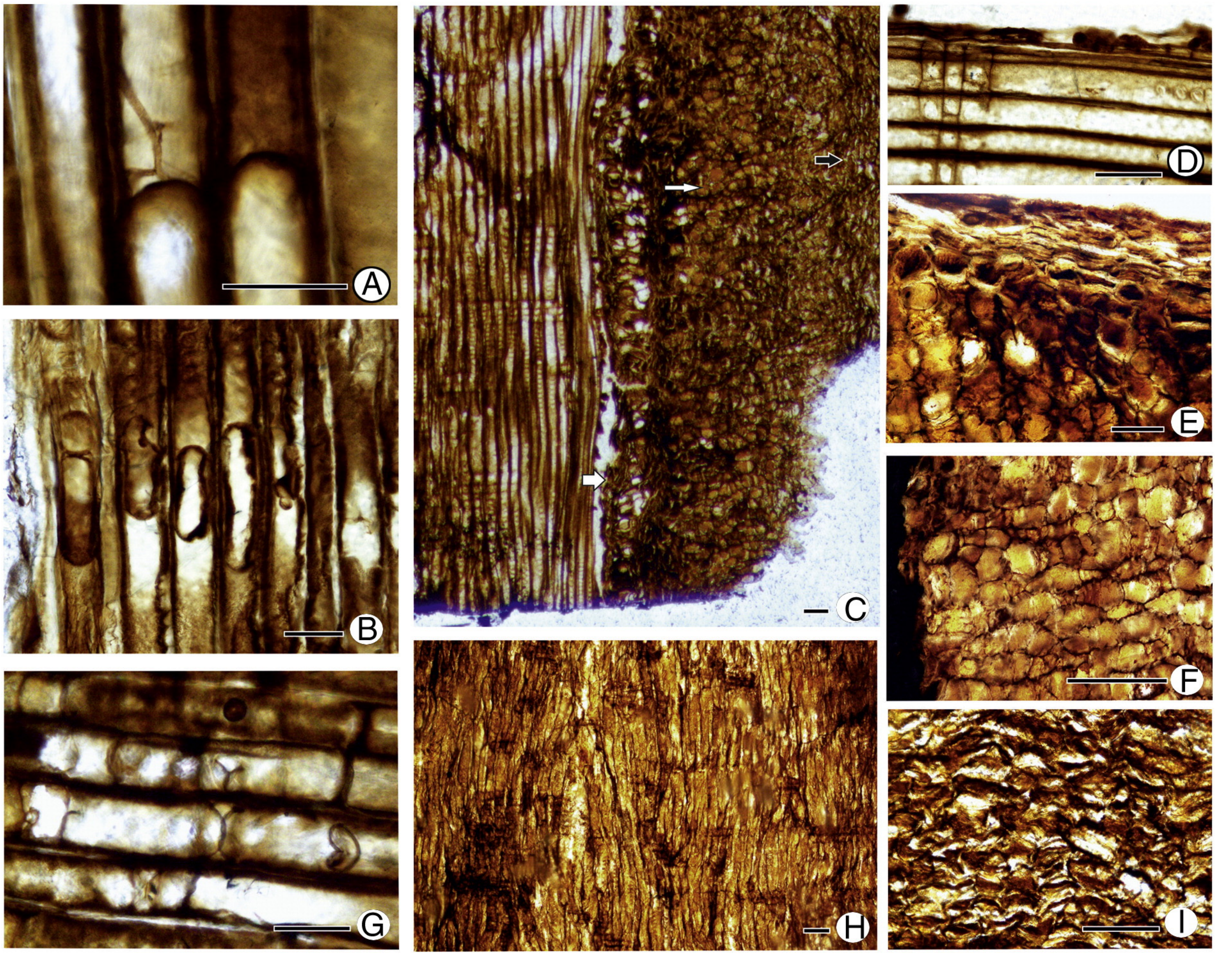

Fig. 6. *Cordaixylon andresii* sp. nov. A. Longitudinal section of tracheids showing a probable hypha. DGO 2057i. B. Tyloses in longitudinal section. DGO 2057i. C. RLS showing the secondary xylem (left) and the abnormal tissue (right) interpreted as hidden injury. DGO 2057i. D. Detail of probable thin cambium cells. DGO 2057i. E. Detail of the narrow zone of cells indicated by the short white arrow in C. DGO 2057i. F. Cells of the zone indicated by the long white arrow in C, showing the reticulate pattern of secondary cell-wall thickenings. DGO 2057i. G. TLS showing tyloses in tracheids. DGO 2057i. H. Secondary xylem sealing the wound tissue. DGO 2057i. I. Collapsed cells of the zone indicated by the black arrow in C. DGO 2057i. Scale bar: A, B, G = 50 μm, C, D, E, F, H, I = 100 μm.

corresponding radial file of tracheids (Fig. 6D). No more than three cells were noted in the cambial zone. A thin fissure filled by mineral separates a first narrow zone of cork-like cells that are seen as thick-walled squat brick-shaped cells in radial section (Fig. 6E). Adjacent to this band is a zone of irregularly shaped cells aligned in irregular rows perpendicular to the secondary xylem tracheids. These have a poorly preserved reticulate pattern of secondary cell-wall thickenings and may be interpreted as dead phloem or callus cells (Fig. 6F) with abnormal pits (Schweingruber, 2007). The surrounding tissue includes thick-walled collapsed cells, which are hard to interpret because they are strongly crushed and deformed (Fig. 6I). Finally, poorly preserved secondary xylem is observed at the periphery, with tracheids exhibiting uniseriate bordered pits and cross-fields (Fig. 6H) oriented in the same way as the inner wood. This abnormal association of cells might be interpreted as the result of hidden cambium injuries that led to the production of callus tissue.

5.1.4. Remarks

The largest specimen, 25 cm in diameter, could probably represent the main stem of a small tree. The few identified vascular traces are consistent with this interpretation, considering the numerous leaf traces present in *Cordaites* twigs. The estimated tree heights calculated on the basis of regression equations (Niklas, 1994) reach approximately 20 m.

The internal asymmetry of the trunk does not seem to be the result of taphonomic processes. The eccentric position of the pith in TS may be interpreted as the result of mechanical stress. Trees usually compensate for physical instability during height and volume increase by the production of more cells on the loaded side (Schweingruber et al., 2006). The recognition of tracheids with helical cell wall grooves in radial section (Fig. 5I) suggests the presence of compression wood, typical of tree stems affected by mechanical stress. Another possibility is that the fragment corresponds to a large branch of a bigger trunk.

5.1.5. Comparisons

A useful tool for distinguishing woods is the pitting of cross fields. Philippe and Bamford (2008) defined phyllocladoid (Kräusel, 1917) as fenestroid pit, usually single in a cross field, with pointed to subpointed tips, without areola. These authors characterised the Mesozoic conifer-like woods including genus *Protophyllocladoxylon* Kräusel in Group B, with araucarian or xenoxylean radial pitting and cross fields with oopores phyllocladoid, usually somewhat bordered in the latewood. This type of oopore corresponds to the “window-like” oopore defined by IAWA with usually 1–2 large simple or apparently simple cross-field pits. *Protophyllocladoxylon* Kräusel (Lepekhina, 1972; Pant and Singh, 1987) include pycnoxylic woods (only secondary xylem preserved) with araucarian radial pitting and simple and large (typically one, two, rarely three) cross-field pits.

Some Palaeozoic morphogenera of gymnospermous woods have been described, showing a *Protophyllocladoxylon*-type secondary xylem: *Phyllocladopitys* Kräusel (with a homogeneous pith and mesarch primary xylem), *Medullopitys* Kräusel (characterised by pith with sclerenchymatous strands and mesarch primary xylem), *Septomedullopitys* Lepekhina (with endarch primary xylem and large heterocellular pith with secretory ducts) and *Megaporoxylon* Kräusel (endarch primary xylem and heterocellular pith). The specimens from Arnao beach, with endarch primary xylem and homogeneous pith, do not conform to those genera. Several genera of Stephanian age displaying solid pith have been described, e.g. *Phyllocladopitys* Kräusel and *Abietopitys* Kräusel. However, these are characterised by a mesarch primary xylem, which is different from the endarch primary xylem in specimens from Arnao.

These Asturian specimens could represent diverse gymnosperms including cordaitaleans and conifers. Noll et al. (2005) proposed to distinguish the wood of cordaitaleans from that of conifers by the arrangement and outlines of bordered pits in radial tracheid walls of secondary xylem, the transition between the primary xylem and the pith, external and internal disposition of the pith, leaf traces and branching.

A cordaitalean affinity seems most likely for the Arnao specimens. Usually, the pith of the cordaitalean stems has been characterised as septate (Stewart and Rothwell, 1993; Taylor et al., 2009). However, in the basal part of stems and young shoots, with an incompletely developed diaphragm, the pith is usually solid (Falcon-Lang, 2007). *Metacordaites rigolloti* Renault, 1896 was one of the first cordaitalean stems described from the Autunian of France with endarch xylem. Although it possesses simple pits in the cross-fields, it differs from the Asturian specimens in the solid and heterocellular pith, with parenchyma, secretory ducts and resiniferous cells. Later, the genus *Mesoxylon* was established for stems with mesarch xylem, whereas *Cordaixylon* was characterised by endarch traces. A detailed discussion about the validity and original definition of *Cordaixylon* was provided by Hilton et al. (2009). These authors remarked that Grand'Eury (1877) established the genus for specimens from the Grand Croix locality in the Saint Étienne basin with *Artisia*-like piths and wood of *Dadoxylon*-type, which were later described in detail by Renault (1879).

The Asturian specimens are referred to the fossil-genus *Cordaixylon* even though this name was expanded to characterise the whole plant on the basis of the more complete remains from North America (Rothwell and Warner, 1984). Considering the near geographic and time relation with the original material described by Grand'Eury (1877) and the probable affinity of these large trunks, it is considered superfluous to define a new taxon. This option is coincident with the proposal of the International Code of Nomenclature (2012, Art. 11.1, Ex. 1). Although scarce axial parenchyma is present in the Asturian specimens, the systematic value of its presence is equivocal and it is difficult to judge its absence in a fossil wood as was discussed by Rößler et al. (2014). It is also important to note that most specimens described as *Cordaixylon* do not exceed 6 cm in diameter (Trivett, 1992; Hilton et al., 2009) and probably represent the anatomy of small plants. The anatomy of large trees is less known including, among others, specimens up to 26 cm in diameter assigned to Cordaitales by Wang et al. (2003) and large stumps from Newfoundland described by Falcon-Lang and Bashforth (2005).

Mencl et al. (2009) analysed Late Pennsylvanian (Barruelian) silicified wood from the Czech part of the Intra-Sudetic Basin where Goeppert (1857) described for the first time the species known today as *Dadoxylon brandlingii* (Lindley and Hutton) Frentzen, and *Dadoxylon schrollianum* (Goeppert) Frentzen, characterised only by the structure of the secondary xylem. The specimens were later referred to *Agathoxylon* by Mencl et al. (2013). However, Reymanowna (1962) described stems with preserved pith from the Intra-Sudetic Basin that she assigned to *Dadoxylon schrollianum* (Goeppert) Frentzen. The few characters preserved in the specimens described as *Agathoxylon* prevent a close comparison with the species analysed here. However, the three specimens described by Reymanowna (1962) from the Kwaczala Arkose are similar to *C. andresii* sp. nov., in having non-septate pith, endarch primary xylem, tracheids with contiguous pits, cross-fields with one or two oculipores. They differ in the presence of secretory ducts and sclerenchyma nests in the pith of *D. schrollianum*.

Vozenin-Serra et al. (1991) described the secondary xylem of a large specimen (70 cm diameter) from Río Viar (Sevilla province, southern Spain) as *Dadoxylon* (*Cordaixylon*) *brandlingii* (Lindley et Hutton) Frentzen. The wood differs from the specimens described here in the taller rays (usually 2-19 cells) and the cross-fields with one to four cupressoid- or taxoid-type pits. From the nearby locality of Gualdacanal (Sevilla province), Vozenin-Serra et al. (1991) described a wood fragment as *Dadoxylon* (*Araucarioxylon*) *douglaense* Steidtman. This specimen resembles the material from Arnao in the araucarioid pitting of the tracheids but differs by the presence of 1–6 oculipores in the cross-fields.

5.2. Fossil-genus Psaronius Cotta 1832

Type Species: *Psaronius helmintholithus* Cotta 1832
Psaronius sp.
Fig. 7
Material. DGO 2060

5.2.1. Description

The roots are irregularly arranged (Fig. 7C). Roots are small and predominately oval in cross section, measuring 2.45–3.6 mm in their longest axis. Individual roots exhibit a prominent peripheral sclerenchyma ring, 386–690 μm thick (Fig. 7D). Cells of the sclerenchyma ring are isodiametric, usually 65–70 μm in diameter with a wall of 12 μm thick cell layers thick. Within the sclerenchyma ring the root cortical tissue is poorly preserved (Fig. 7E). A parenchymatic interstitial tissue fills the space between roots (Fig. 7F).

5.2.2. Comparisons

These roots, embedded in parenchymatic tissue, most likely correspond to the inner root mantle (Ehret and Phillips, 1977) of the marattialean tree fern *Psaronius* Cotta. *Psaronius* is one of the best known fossil tree ferns (e.g. Morgan, 1959; Rothwell, 1999). It has been reconstructed as a plant about 10–15 m tall (Morgan, 1959), with stems being surrounded near-base by a wide adventitious root mantle. At a higher level, the stem increases in diameter and the root mantle is reduced or absent. Roots of *Psaronius* typically show an actinostelic tracheidal bundle, which is not preserved in our specimens.

The most common vegetative foliage associated with *Psaronius* is of the *Pecopteris*-type (Morgan, 1959; Rothwell, 1999), which is recognised in the palaeoflora of Arnao (*Pecopteris cyathea*, *P.* cf. *monyi*) reinforcing the botanical affinity of the studied roots. However this is a general morphogenus devoid of precise stratigraphic value.

More than 100 species of *Psaronius* have been described from the Carboniferous and Permian low-latitudinal floras of Euramerica and Cathaysia as well as the southern low latitude Permian floras of Gondwana (Rößler, 2006; additional references in He et al., 2013). *Psaronius* was most widespread in the Late Pennsylvanian (Stephanian) and Lower Permian.

The peculiar form of preservation of this fern (Fig. 7A, B) as water-worn pebbles is also common in other parts of the world. Pebbles of Carboniferous silicified gymnospermous wood were described from the drift of south-eastern Massachusetts (Kaye, 1964) and the inter-tidal zone of Montford, Scotland (Falcon-Lang et al., 2010) among other places.

Fig. 7. *Psaronius* sp. A, B. Views of the pebble which preserves part of the *Psaronius* root mantle. C. Cross section showing the shape and arrangement of roots. DGO 2060a. D. Detail of the sclerenchyma ring tissue in cross section. DGO 2060a. E, F. Cross section of roots showing poorly preserved inner cortex. DGO 2060a. G. Interstitial parenchyma between roots in cross section. DGO 2060a. H. Longitudinal section of root, showing sclerenchyma ring and interstitial parenchyma tissue. DGO 2060b. I. Longitudinal section of root, showing some tracheids of primary xylem with scalariform to reticulated thickenings. DGO 2060b. J. Longitudinal section of root showing parenchyma of the cortex. DGO 2060b. Scale bar: A, B = 1 cm; C = 1 mm, D, E = 100 μm; F = 200 μm; I, J = 50 μm.

6. Floral comparisons

Palaeoequatorial forests as found in NW Spain were the source of important coal deposits that were most intensively worked in the 20th century, but knowledge of the floral contents of the Carboniferous of Arnao is incomplete. Zeiller (1882) revised the list of species published by Geinitz (1867) and mentioned for the first time the Stephanian age of the flora. The first palaeobotanical studies were presented by Patac (1932), Jongmans (1951), and Lorenzo (1977). The last author was the only one who illustrated (fragmentary) plant remains. The following species were recognised as impressions from Arnao: *Barthelopteris germarii* (Giebel) Zodrow & Cleal, *Callipteridium* cf. *zeilleri* Wagner, *Odontopteris brardii* Brongniart, *Linopteris gangamopteroides* (De Stefani) Wagner, *Pseudomariopteris cordato-ovata* (Weiss) Gillespie et al., *Helenopteris paleaui* (Zeiller) Krings & Kerp, *Lescuropteris genuina* (Grand'Eury) Remy & Remy, *Diplazites emarginatus* Goeppert, *Nemejcopteris feminaeformis*

(Schlotheim ex Sterzel) Barthel, *Oligocarpia leptophylla* (Bunbury) Grauvogel-Stamm & Doubinger, *Pecopteris cyathea* Schlotheim ex Brongniart, *Pecopteris* cf. *monyi* Zeiller, *Cordaites borassifolius* (Sternberg) Unger, *Calamites suckowii* Brongniart, *Calamostachys tuberculata* (Sternberg) Weiss, *Sphenophyllum angustifolium* Germar and *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger. Specimens of *Sigillaria brardii* Brongniart (Fig. 3C) and *Sigillaria* sp. (Fig. 3D) have been recognised in Arnao beach during the present study. This floral record was regarded as attributable to the *Sphenophyllum angustifolium* Zone by Wagner and Álvarez-Vázquez (2010).

Horvath et al. (1987) described two palynological assemblages from the middle and uppermost part of the Carboniferous succession at Arnao, referring them to the lower part of Stephanian B. The palynofloras were characterised by the abundance of *Thymospora pseudothiessenii* (Kosanke) Alpern & Doubinger, the presence of *Spinosporites spinosus* Alpern, *Angulisporites splendidus* Bharadwaj, *Polymorphisporites laevigatus* Alpern and the absence of bisaccate pollen. These two samples seem insufficient evidence for a precise dating and a more detailed sampling may be necessary.

The assignment of the flora of Arnao to Stephanian B *sensu stricto* (Wagner and Álvarez-Vázquez, 2010) invites an immediate comparison with the flora of Saint-Étienne in the Massif Central, France. The Saint Étienne flora has been studied since the 19th century, and a synthesis of the palaeofloristic contents was provided by Doubinger et al. (1995), on a revision of c. 2000 specimens.

Stephanian silicified plants have been recorded from Grand-Croix in the Saint-Étienne basin, as mentioned first of all by Grand'Eury (1873). Hilton et al. (2009) noted that when Grand'Eury (1877) defined the genus *Cordaixylon*, he illustrated the first silicified remains from the Grand Croix locality, particularly a section of a silicified cordaitalean twig (Grand'Eury, 1877, pl. 29.1). This was later described in detail as *Cordaites* by Renault (1879) and referred to cf. *Cordaixylon* by Doubinger et al. (1995). Galtier (2008) provided a revision of specimens from the late Stephanian A (Barruelian?), including cordaitaleans as the most common elements. *Dadoxylon* cf. *brandlingii*, as described by Doubinger et al. (1995) and cf. *Cordaixylon* are the cordaitaleans stems recognised by Galtier (2008) in the plant assemblage. Galtier (2008) also illustrated root mantle of *Psaronius* from the Grand-Croix locality.

Martín-Closas and Galtier (2005) described other European Late Pennsylvanian palaeofloras from the Graissessac-Lodève Basin as dominated by monospecific stands of the arborescent lycopsid *Sigillaria brardii*, whereas the tree fern *Psaronius* is recorded during the later stages of mire accumulation. Isolated thickets of sphenopsids represented by *Calamites* and *Sphenophyllum* grew in the floodplain as well as along secondary channels. Parautochthonous foliage assemblages of ferns and pteridosperms, which grew in exposed areas near the floodplains, also were part of the community. Cordaitaleans, represented by large logs and *Cordaites* leaves preserved in fluvial sediments, were considered riparian elements in the basin. These stems, described briefly by Galtier et al. (1997) as *Dadoxylon* cf. *brandlingii* Lindley and Hutton and *Dadoxylon* sp., differ from the wood remains from Arnao in the pitting of the tracheids and taller rays.

The Barruelian plant assemblages from the Czech part of the Intra-Sudetic Basin are another example of European remains of permineralised wood analysed by Mencl et al. (2009, 2013). Whereas Goeppert (1857) referred this material to the conifers, Mencl et al. (2009) suggested a cordaitalean affinity.

7. Palaeoenvironmental conditions

The Arnao palaeoflora is part of the tropical biome that flourished during the Late Pennsylvanian in Euramerica. DiMichele (2014) emphasized that to conceive the existence of an exclusive wetland coal forest is incorrect because seasonally dry vegetation dominated periodically the low tropics. At the beginning of the late Mid-Late Pennsylvanian, the presence of tree ferns in the wetland palaeoflora became dominant. The Marattiales, today with a tropical distribution, were the main group of tree ferns and *Psaronius*, one of its most known components, is present in the Arnao flora. These plants, supported by a mantle of adventitious roots, colonized wet substrates in areas ranging from large swamps to isolated wet areas into drier landscapes (DiMichele, 2014).

The cordaitaleans were other important group in the wetlands, although these plants are also recognized in diverse habitats including seasonally dry areas. The group encompasses large trees, such as the Arnao specimens, and small scrambling plants. Sphenopsids are also components of the wetland palaeoflora and are, like the cordaitaleans, diverse in size. Calamitaleans are the larger plants of the group and inhabited swamps and riparian corridors whereas some species of *Sphenophyllum* have been interpreted as occupying ponded areas. Stems of *Calamites* sp. and *Sphenophyllum* leaves are also plants recognized in the Arnao succession.

Pteridosperms, a group of seed plants of the wetlands, are abundant in the palaeoflora preserved in La Magdalena Coalfield (Northwestern Spain), "Saberian" or lower Stephanian B in age (Bashforth et al., 2010; Wagner and Castro, 2011). Some taxa are shared with the Arnao flora: *Lescuropteris genuina* and *Pseudomariopteris cordato-ovata*, which have been interpreted as climbing plants and *Callipteridium*, reconstructed as small trees. Small ferns are represented in both floras by *Oligocarpia*, *Nemejcopteris feminaeformis* and *Diplazites* forming part of the groundcover.

Arborescent lycopsids are represented in the Arnao flora by *Sigillaria brardii*, species dominant in the Stephanian wetlands of Graissessac in France (Martín-Closas and Galtier, 2005), and the Stephanian B coals in the Villablino Coalfield of northern León (Wagner and Castro, 2011).

Despite the relatively low number of species at present recognized in the Arnao palaeoflora, the co-occurrence of the above mentioned plants, including lycopsids and tree ferns, suggests that humid conditions with adequate water supply prevailed during the development of the vegetation. Future detailed palaeoecological studies are necessary to reconstruct the dynamics of the vegetation.

8. Conclusions

Late Palaeozoic permineralised plants from Arnao beach in Asturias are the first record of anatomical preserved stems for north-western Spain. The fossil-bearing strata belong to the succession worked by one of the earliest coal mines in Spain. The outcrop is part of a geological area that exhibits also a Devonian succession of sufficient importance to be declared a protected geological heritage site. Thus, the finding of Late Pennsylvanian plants with excellent anatomical preservation increases the geological area value.

Associated compressed plant assemblages include lycophytes, sphenophytes, pteridosperms, pteridophytes and cordaitales. A first analysis of some permineralised specimens has confirmed the presence of Cordaitales and tree-ferns. Cordaitales are represented by large trunks characterised by solid pith, endarch primary xylem, radial araucarian pitting and pyllocladoid cross-fields that allow a new species to be defined. The wood of *Cordaixylon andresii* sp. nov., preserves evidence of tylosis and callus formation with new woody tissue sealing a wound. Tree ferns are identified by roots belonging to the *Psaronius* adventitious inner root mantle.

The characteristics of the flora promote a comparison with the flora of Saint-Étienne (France) but additional field collecting during extremely low tides certainly will allow more precise correlations.

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