

# CHARCOALIFIED WOOD FROM THE CENOMANIAN OF GARD (SOUTHERN FRANCE): AN INSIGHT INTO EARLY ANGIOSPERM PALAEOECOLOGY

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Girard, V., Philippe, M., Bamford, M., Gomez, B. & Ferry, S. 2012. Charcoalified wood from the Cenomanian of Gard (southern France): an insight into early angiosperm palaeoecology. [Carbón del Cenomaniense de Gard (sur de Francia): paleoecología de las primeras floras de angiospermas]. *Revista Española de Paleontología*, **27** (1), 29-44. ISSN 0213-6937.

## ABSTRACT

The discovery in the Cenomanian (early Late Cretaceous) of Southern France of several localities with abundant charcoal has brought to light several angiosperm wood types. This is the oldest angiosperm wood assemblage discovered yet for Europe. Here we analyse this assemblage, with emphasis on features recognized to be of particular palaeoecological and climatic significance for the Cainozoic according to earlier studies and comparing the inferred results to those from other independent lines of evidence (sedimentology, palynology, isotopic geochemistry, etc.). Vessel diameter and distribution, perforation plates, abundance of vascular tracheids and of septate fibres, presence of diffuse axial parenchyma perhaps should not be used as palaeoecological proxies for the Cretaceous because they do not seem to clearly correlate with other lines of evidence that indicate warm tropical conditions. The abundance of fibre-tracheids fits with the other sources of data, but our results are probably biased by preservation problems. On the contrary, the occurrence of growth-rings, porosity, vessel density, occurrence of vessel groups, occurrence of vasicentric tracheids and of some paratracheal to vasicentric and banded axial parenchyma correlate well with other palaeoclimate indicators. These results show that these features can be used for palaeoclimatological inferences during the early Late Cretaceous.

**Keywords:** Angiosperm woods, Lower Cenomanian, palaeoecological reconstruction, phylogenetic bias.

## RESUMEN

El hallazgo de varias localidades con abundantes depósitos de carbón en el Cenomaniense (Cretácico tardío) del sur de Francia, evidencia la presencia de varios tipos de madera de angiospermas. Esta es la asociación más antigua de maderas de angiospermas descubierta hasta ahora en Europa. Se analiza esta asociación, seleccionando los caracteres reconocidos que tengan algún particular significado paleoecológico y climático, de acuerdo con estudios anteriores y comparando los resultados inferidos con evidencias proporcionadas por otras líneas independientes de investigación (sedimentología, palinología, geoquímica isotópica, etc.). Caracteres como el diámetro y distribución de los vasos, tipos de placas de perforación, abundancia de traqueidas vasculares y fibras septadas, presencia de parénquima axial difusa no pueden ser utilizados como indicadores paleoecológicos debido a que no muestran una correlación clara con otras líneas de evidencia. La abundancia de fibra-traqueidas se ajusta con las otras fuentes de datos, pero estos resultados están sesgados por problemas de preservación. Por el contrario, la presencia de anillos de crecimiento, tipo de porosidad, la densidad de vasos, la presencia de vasos agrupados,

de traqueidas vasicéntricas y de alguna parénquima axial paratraqueal a vasicéntrico y en bandas se correlaciona bien con otros indicadores paleoclimáticos. Estos resultados muestran que estas características pueden ser usadas para realizar inferencias paleoclimáticas durante el Cretácico tardío.

**Palabras claves:** Maderas de angiospermas, Cenomaniense inferior, reconstrucción paleoecológica, sesgos filogenéticos.

## INTRODUCTION

No angiosperm wood record predating the Aptian has yet been found (Crawley, 2001; Philippe *et al.*, 2008). The wood *Aptiana radiata* Stopes is the only Aptian angiosperm wood described so far, but its age is questionable and it likely is younger (Crawley, 2001). By the Albian, angiosperm wood is found worldwide including the morphogenera *Icacinoxylon* Shilkina and *Paraphyllanthoxylon* Bailey (Suzuki, 1982; Wheeler, 1991; Anderberg *et al.*, 2002; Barale *et al.*, 2002; Takahashi & Suzuki, 2003). Nevertheless, angiosperm woods are exceedingly rare in the Albian, and it is only during the Cenomanian that both the number of angiosperm wood species and the proportion of angiosperm wood in fossil assemblages increased significantly (Gryc *et al.*, 2009; Wheeler & Lehman, 2009). In the Iberian Peninsula, only few and badly preserved angiosperm woods have been reported from the Upper Cretaceous (De la Fuente *et al.*, 2008), within the Cenomanian of Segovia area. The sudden increase in the angiosperm wood record by the mid Cretaceous is striking. Why was angiosperm wood unrecorded before the Aptian, while pollen grains, leaves and even delicate flowers of early flowering plants were described from many continents (Wing & Boucher, 1998; Willis & McElwain, 2002; Friis *et al.*, 2006)? Is it simply a taphonomical bias or a more complex and hidden history? Were the earliest angiosperms woody? Was the angiosperm ecology before the Albian such that the wood had little chance to fossilize? These are questions that have puzzled palaeontologists for many years. A detailed palaeoecological study of the mid Cretaceous wood record would contribute to a better understanding of the factors that led to angiosperm wood becoming more frequent among fossil assemblages by the Albian and subsequently.

For a long time it has been recognized that early angiosperm wood is difficult to assign to living families (Bailey, 1924; Page, 1979, 1980, 1981; Wheeler & Baas, 1991). Thus palaeoecological reconstructions based on Cretaceous angiosperm wood can appear precarious when they are only based on hypothetical systematic affinities and the assumption of uniformitarianism. Nevertheless palaeoecological reconstructions could be based on anatomical wood features and on the tight statistical correlations between environmental conditions and the abundance of specific anatomical characters of angiosperm woods (Upchurch & Wolfe, 1987; Wheeler & Baas, 1991, 1993; Wie-

mann *et al.*, 1998, 1999; Poole, 2000; Sakala, 2000; Poole & Van Berghen, 2006).

Charcoals are one of the most common remains in the fossil record (Sander & Gee, 1990), but there are relatively few studies of angiosperm charcoals. Xylogists mainly studied permineralized wood specimens because they generally have a larger size. This bias towards silicified wood is particularly problematic in the case of the study of early angiosperms. Indeed these early angiosperms probably did not develop thick woody logs before the mid Late Cretaceous (Philippe *et al.*, 2008) whereas large logs are much more resistant to degradation and do become silicified (Buurman, 1972). Moreover silicification occurs in a narrow range of environmental conditions (Siurek *et al.*, 2004) and so indicates a strong palaeoecological constraint for the corresponding wood record (Herendeen, 1991). Charcoals can be formed in a broader range of environments and are thus more informative than silicified woods for interpreting palaeoenvironments.

Here, the potential use of mid Cretaceous charcoaled angiosperm wood for palaeoecological reconstruction is demonstrated. The anatomical features of an angiosperm charcoal assemblage from the Cenomanian of Gard (SE France) is studied, without any hypothesis about their systematic relationships. Palaeoecological inferences using Wheeler & Baas' (1991) correlations between anatomical wood characters and ecology are established. These are compared with the palaeoenvironments and the palaeoclimate of the source area at that time as deduced from sedimentology, palynology and isotopic geochemistry.

## GEOLOGICAL AND PALAEOCLIMATIC SETTINGS

Angiosperm wood specimens studied herein were collected at about 40km northeast of the city Nîmes, in the Gard, southeastern France (Fig. 1). Although fossil wood from there was mentioned by Pruvost (1942) and Defretin (1943), this is the first time that angiosperm wood is described from the Cenomanian of southeastern France. Specimens were embedded in siliceous limestones bearing lignite lenses, a local facies formerly named Pauletian (Ducreux, 1982) and dated Lower to Middle Cenomanian. These strata represent margino-littoral sediments, deposited in the western part of the Vocontian basin (Ducreux, 1982). At that time, the Durancian isthmus separated the

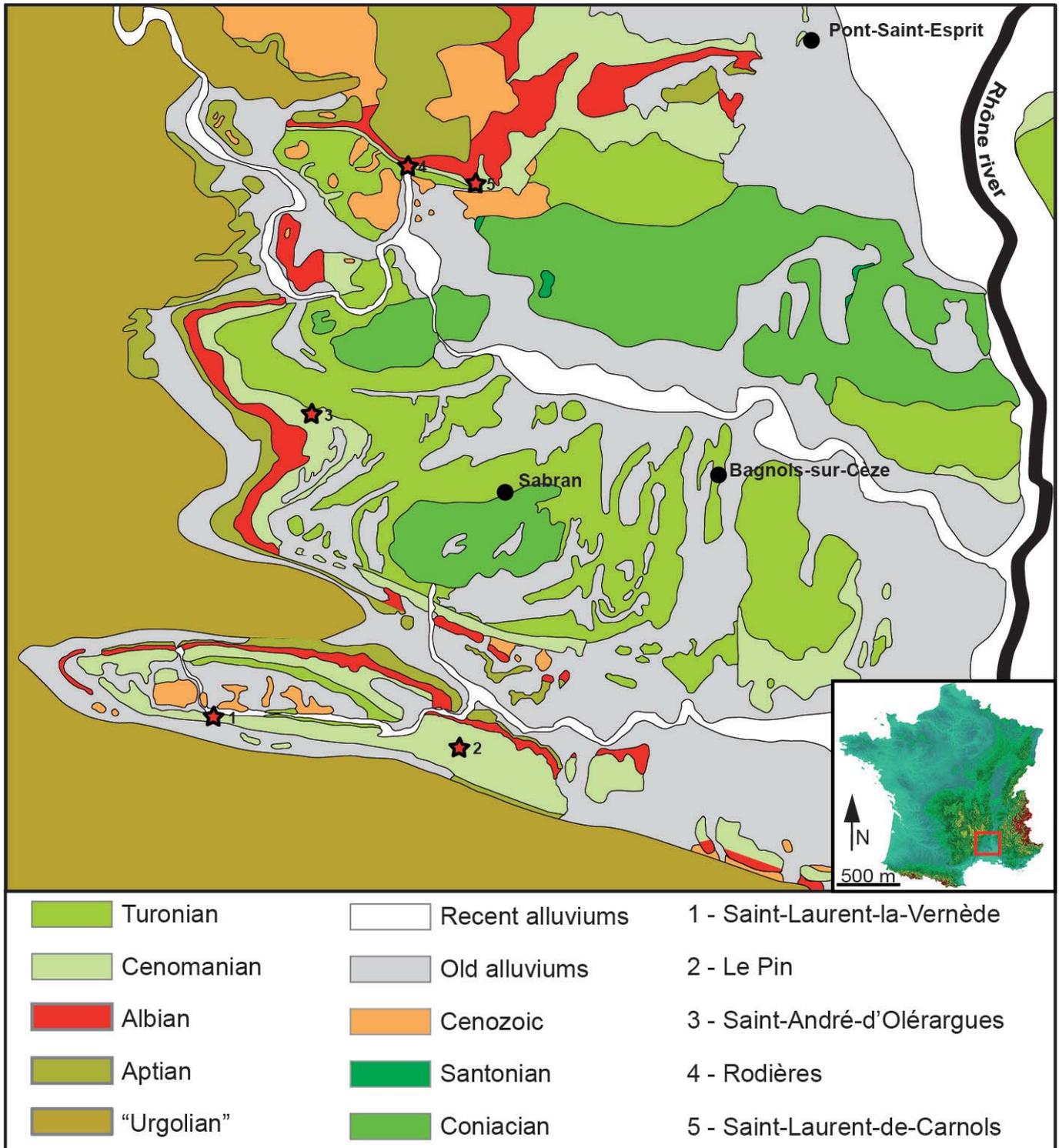


Figure 1. Simplified geological map of the studied area.

Vocontian basin and the south Provençal basin. Important siliciclastic inputs occurred north of the studied area (present day Ardèche) and were driven southward by the western Vocontian coastal current. During the Lower Cenomanian this resulted in the installation of a coastal spit at the level of the present day Rhône valley. The spit pro-

tected the Gard area, and paralic sediments were deposited (Pauletian facies; Ducreux, 1982).

Ducreux (1982) interpreted the lenticular disposition of the Pauletian lignite deposits as puddle infillings, typical of marsh or lagoon environments. This interpretation is also supported by our observations of slickenslides (interpreted

as evidence of vertisols), of clayey palaeosoils (with *in situ* roots) and flaser beddings. During the Early Cenomanian a lagoon isolated by a sandy coastal spit developed in the Gard, and was progressively filled. Thus trophophilous marshes or lagoons could develop in which plant debris and fine-grained sediments accumulated. Occasionally storms or sea level oscillations caused flash-flooding, intercalating lumachelic shell layers with much marine to brackish water bivalve and gastropod debris, especially in the northern part of the study area. These shelly deposits suggest more marine influence in the north compared to the south of the lagoon.

Neither typical fluvial sediments nor evidence of hydrodynamism were identified during the field survey, making it very probable that plant deposits were mostly autochthonous to parautochthonous; that means the materials were locally accumulated. This is supported by the frequent occurrence of intermingled palaeosoils and *in situ* root systems. In conclusion, the Paultian palaeoflora was not a true terrestrial phytocoenosis but rather grew up in and around a lagoon or marsh.

At most localities exposure is limited and it is very difficult to accurately correlate the beds into a general stratigraphic sequence. Paultian facies were deposited from the Albian to the Upper Cenomanian based on micropalaeontological and palynological dating (Ducreux, 1989). Based on sequence-stratigraphic correlation, the age of our charcoalified materials ranges from the Lower-Middle Cenomanian.

From various geochemical, isotopic and sedimentological evidence, the Cenomanian climate is considered to have been the warmest in recent Earth history, with terrestrial temperatures 6–12°C warmer than present (Sellwood *et al.*, 1993). Voigt *et al.* (2003) estimated the sea surface temperature in Europe during the mid Cretaceous: they calculated 25°C in Spain (sea temperature) while that surrounding England was only 19°C. Over the northwestern Tethys rim the climate was tropical (Pucéat *et al.*, 2003; Amiot *et al.*, 2004) with marked hydrologic seasonality over western Europe (White *et al.*, 2001; Donnadieu *et al.*, 2006). Some palynological investigations (Gaillard, 1982) proposed a climate with rigorous winters for the Cenomanian in the Gard. This however contrasts with other evidence that indicates a tropical climate, probably with hydric seasonality (Ducreux, 1982; Videt, 2004). Studying the black shales of the neighbouring Vocontian basin, Herrle *et al.* (2003a, b) and Bornemann *et al.* (2005) suggested that a monsoonal climate system predominated during the mid Cretaceous in western Europe. As only one study suggested a cold climate, the hypothesis of a warm tropical to sub-tropical climate with possible hydric seasonality is retained for this study.

For more information about the studied area, see Pruvost (1942), Ducreux (1982, 1989), Gaillard (1982), and Ducreux & Gaillard (1986).

## MATERIALS AND METHODS

Charcoals collected from seven localities were examined, but only five provided angiosperm woods. These five localities (Fig. 1) contained fusain as well as other plant remains (e.g., palynomorphs, cuticles, and amber).

Fusain is defined as lignified tissues transformed in a dull, fibrous, pulverulent coal, leaving a black dust on fingers and looking like charcoal (Duparque, 1926). Although production processes for charcoal are always questionable, wildfires are considered to be the major source of charcoal (Herendeen, 1991). Under anoxic conditions, temperatures between 200–400°C induce partial carbonization that prevents decay, limits compaction, and preserves anatomical structures (Scott, 1990; Herendeen, 1991).

Charcoal is usually collected as small pieces, of which the origin is questionable (branch, trunk or root, mature or immature wood). Because of variable anisotropic shrinkage and allometric modifications induced by charring (Slocum *et al.*, 1978; Prior & Gasson, 1993; Figueiral, 1999; Figueiral *et al.*, 2002; Gerards *et al.*, 2007), Wiemann *et al.*'s (1998, 1999) quantitative correlations could not be used, and only a qualitative approach was made. Nonetheless the cells were measured to complete the descriptions. These charcoals were not identified to existing morphogenera because of the limited number of features visible in these small wood fragments under Scanning Electronic Microscope (SEM).

The five localities from which we collected angiosperm charcoals are Saint-André-d'Olérargues, Saint-Laurent-la-Vernède, Le Pin, Rodières, Saint-Laurent-de-Carnols (Fig. 1). Some large (> 2 cm) fragments were collected in the field but most of the specimens were obtained by bulk maceration of the sediments in H<sub>2</sub>O<sub>2</sub> followed by rinsing in tap water through 5-mm, 2-mm, and 1-mm-mesh stainless steel sieves. After drying in a laboratory oven, charcoals were sorted under a stereomicroscope (Wild M3Z) to separate angiosperm woods from other wood types. Sixty supposed specimens were selected and pasted with ordinary glue on aluminum stubs and coated with gold/vanadium for 4.5 minutes at 25eV in a cathode sputtering *Balzers* machine. All examinations were performed at the "Centre Technologique des Microstructures - Université Lyon 1 (Claude Bernard)" under a SEM Hitachi S-800. Software *ANALYSIS* was used to acquire more than 400 microphotographs. SEM observations showed that, among the 60 pre-sorted samples, only 19 have an angiospermous origin. For these charcoals the occurrence of nineteen wood anatomical features was scored (Table 1). These features have been chosen on the model of characters used by Suzuki *et al.* (1996) in a study of Cretaceous angiosperm wood.

Studies by Wheeler & Baas (1991, 1993) and by Wiemann *et al.* (1998, 1999) based on Late Cretaceous and Cainozoic materials demonstrated that some features of secondary xylem in dicotyledonous woods are closely co-

**Table 1.** The nineteen different xylological characters taken into account.

Xylological characters	Observation
General description	Type of wood porosity
Vessel	Presence or absence of vessel clusters or radial multiples
	Orientation of the vessels
	Type of perforation plates
	Presence or absence of helical thickening
	Type of intervessel pits
	Mean diameter of vessels
Fibres	Density of vessels (number per mm <sup>2</sup> )
	Type of fibres
Axial parenchyma	Type and size of pits
	Distribution
Rays	Abundance
	Width measured in number of cells
	Distribution: presence or absence of a special arrangement of the rays
	Height measured in number of cells
	Homogeneity: presence of one or several types of cells per ray
	Shape of the cells (upright, square or procumbent)
	Density (number per mm <sup>2</sup> )
Types of pits (vessel-ray pits or ray-ray pits)	

related to climate but these relationships were not applied to Cretaceous floras as they were for the Cenozoic. The correlations between wood anatomical features of Mesozoic angiosperms and palaeoenvironmental factors are still incompletely known.

Data obtained from our study were analysed to determine whether similar correlations existed for a period as old as the Cenomanian. By comparing palaeoecological inferences obtained from charcoal with those obtained with other methods (geochemistry, palynology, sedimentology), each xylological feature was analysed to determine whether it could be considered as (1) climatic proxy, (2) ecological proxy or (3) unsuitable for our purpose.

## RESULTS

Among the sixty charcoal specimens prepared for SEM examinations, only nineteen show clear affinities with angiosperms. They are not evenly distributed in the five lo-

calities; the percentage of angiosperms in the wood assemblage varies from 1.1 to 9.5 % (Table 2).

**Table 2.** Proportions in angiosperm charcoals in the different localities studied.

	Saint-André-d'Olérargues		Saint-Laurent-la-Vernède	Le Pin	Rodières	Saint-Laurent-de-Carnols
	lower lignitic clay	upper lignitic clay				
Number of examined charcoals	166	95	135	21	25	90
Angiosperm charcoals	8	3	3	2	2	1
Percentage of angiosperms	4.8	3.2	2.2	9.5	8.0	1.1

Among these nineteen specimens, ten groups were recognized. It cannot be ascertained whether the ten morphological types correspond to ten wood morphospecies because only small wood fragments were examined. That also means that it was not possible to determine whether or not these samples correspond to any previously described woods. The descriptions given below only include the features positively determined. Nevertheless the anatomical wood diversity is relatively and unexpectedly high.

### Morphotype A (Figs 2A-C)

*Locality:* Saint-André-d'Olérargues

*Specimen numbers:* AWSE-0001; AWSE-0016; AWSE-0020

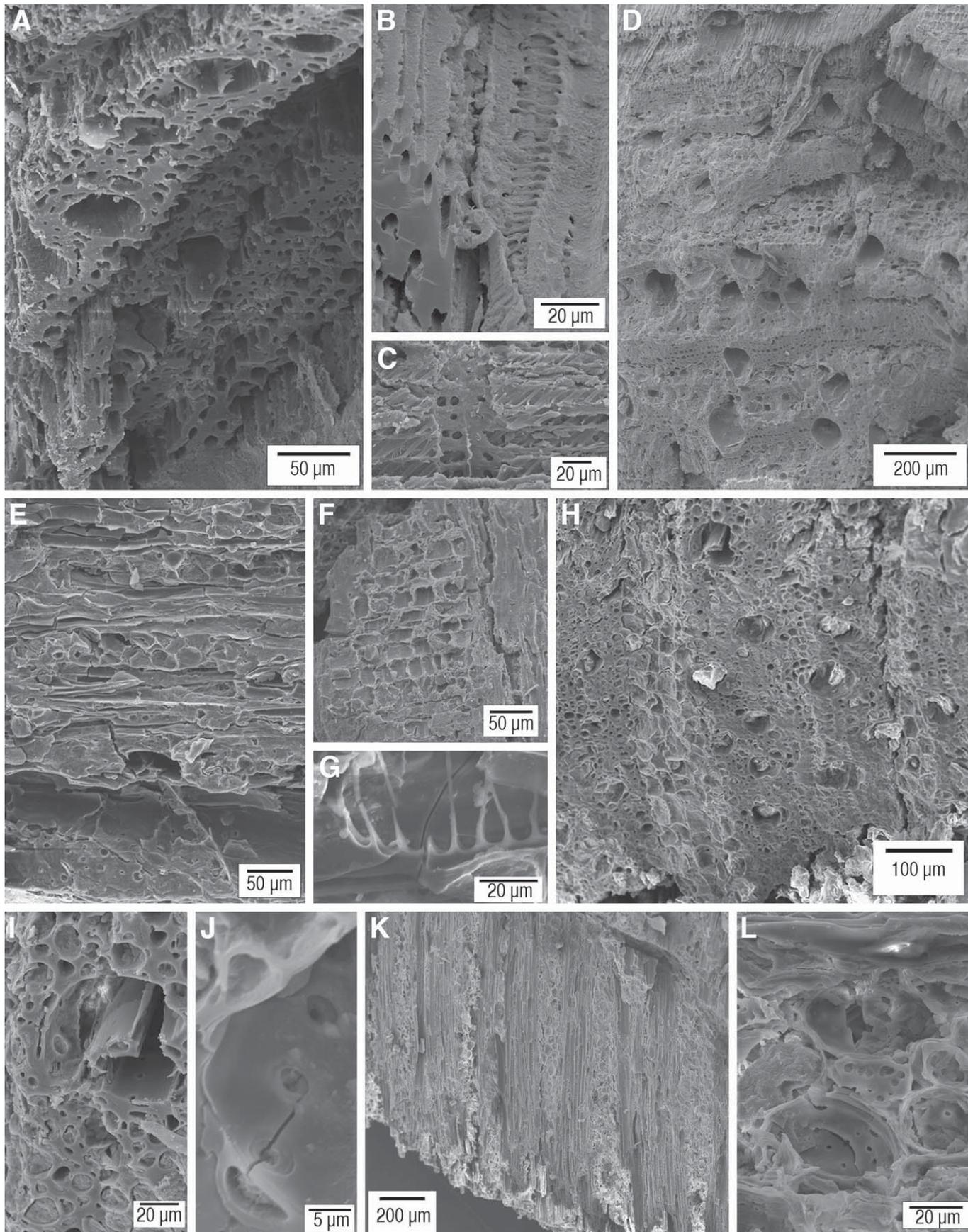
*Description:* Growth ring boundaries are indistinct or absent and wood diffuse-porous (Fig. 2A). Vessels are mainly solitary, some pairs, with scalariform perforation plates of 10–25 bars (Fig. 2B). There are two sizes of vessels: small vessels 25–30 µm in diameter, and large and slightly flattened vessels 70–100 x 100–130 µm in diameter. Intervessel pits are small and alternate (4 µm in diameter). Vessel density is greater than 40 vessels per mm<sup>2</sup>. Fibres have thin walls and simple pits. In longitudinal section spiral thickening of vascular tracheids can be seen. Axial parenchyma is rare, mainly diffuse. Rays are very low, possibly only up to three cells high, and 1–2 seriate. Vessel-ray pits are simple and opposite (Fig. 2C).

### Morphotype B (Figs 2D-F)

*Locality:* Saint-André-d'Olérargues

*Specimen numbers:* AWSE-0002; AWSE-0004; AWSE-0013

*Description:* Growth ring boundaries are indistinct or absent and wood diffuse-porous (Fig. 2D). Vessels are mainly solitary, rarely in radial multiples of 2–3, with simple perforation plates (Fig. 2E). Intervessel pits are small



and opposite (4 µm in diameter). Mean vessel diameter is 80–120 µm but some vessels are as small as 30 µm, a density of 15–20 vessels per mm<sup>2</sup> was observed. Fibres have simple pits 5 µm in diameter and are thin-walled. Axial parenchyma is rare and diffuse. Rays are 1–3 seriate (Fig. 2E), 2–10 cells high (Fig. 2F), and heterocellular with procumbent, square and upright cells. There are 10–15 rays per mm. Vessel-ray pits are centrally positioned on the cells and solitary (3–4 µm in diameter).

#### **Morphotype C** (Figs 2H-L)

*Locality:* Saint-André-d'Olérargues

*Specimen number:* AWSE-0006

*Description:* Wood is diffuse-porous and growth ring boundaries are indistinct or absent. Vessels are 35–60 µm in diameter and mainly solitary or radially grouped in 2's or 3's (Figs 2H-I). Vessels have scalariform perforation plates with 5–10 bars (Fig. 2G) and small intervessel pits 4–5 µm in diameter. Vessel density is 20–25 vessels per mm<sup>2</sup>. Fibres have simple pits (Fig. 2J). Vasicentric tracheids were observed. There is abundant paratracheal vasicentric axial parenchyma. Rays are 4–5 seriate, more than 30 cells high (Fig. 2H) and storeyed (Fig. 2K). Rays are weakly heterocellular with at least 1 row of marginal upright cells and there are small and multiple ray cell-to-ray cell pits (Fig. 2L). Vessel-ray pits were not observed.

#### **Morphotype D** (Figs 3A-C)

*Locality:* Saint-André-d'Olérargues

*Specimen numbers:* AWSE-0007; AWSE-0044

*Description:* Growth ring boundaries are indistinct or absent and the wood is diffuse-porous (Fig. 3A). Vessels are mainly solitary or radially grouped in 2's or 3's. Vessels are oval (60–80 x 130–150 µm) with scalariform perforation plates and a minimum of 10 bars (Fig. 3B). Intervessel pits are small, 4 µm in diameter. Vessel density is 30–40 vessels per mm<sup>2</sup>. Fibres have simple pits, thin walls and some are septate. Abundant axial parenchyma is in narrow irregular bands (1 to 3 cells wide). Rays are heterocellular with procumbent cells and 1–2 rows of marginal upright cells, 1–2 seriate (Fig. 3C) and 8–13 cells high. Ray cell-to-ray cell pits are small and numerous. Vessel-ray pits were not observed.

#### **Morphotype E** (Figs 3D-G)

*Localities:* Saint-André-d'Olérargues; Le Pin

*Specimen numbers:* AWSE-0032; AWSE-0041

*Description:* Wood is diffuse-porous and growth ring boundaries indistinct or absent (Fig. 3D). Vessels are solitary to radially grouped in 2's or 3's, with scalariform perforation plates of more than 20 bars (Fig. 3E). Intervessel pits are small and mixed, alternate or opposite to scalariform. There are two sizes of vessels: narrow (30–50 µm in diameter) and large (70–100 µm in diameter). Vessel density is high (30–40 per mm<sup>2</sup>). Fibres have simple pits. Axial parenchyma is rare and badly preserved. Rays are heterocellular and narrow, 1–2 seriate (Fig. 3F). Ray height is 6–15 cells. Vessel-ray pits are simple and multiple (Fig. 3G). The ray density is inestimable (at least > 5).

#### **Morphotype F** (Figs 3H-J)

*Locality:* Saint-André-d'Olérargues

*Specimen number:* AWSE-0010

*Description:* Growth ring boundaries are indistinct or absent and the wood is diffuse-porous (Fig. 3H). Vessels are radially grouped in 3's or 4's, with scalariform plates (Fig. 3I). Opposite to scalariform intervessel pits are present. Vessels are narrow and slightly radially flattened (35 x 20 µm) and resemble tracheids. It is difficult to distinguish fibre-tracheids with alternate to opposite simple pits from vasicentric tracheids (Fig. 3J). Some fibres are septate. Axial parenchyma and rays are poorly preserved. Vessel-ray pits were not observed.

#### **Morphotype G** (Figs 3K-L)

*Locality:* Saint-André-d'Olérargues

*Specimen numbers:* AWSE-0022; AWSE-0025

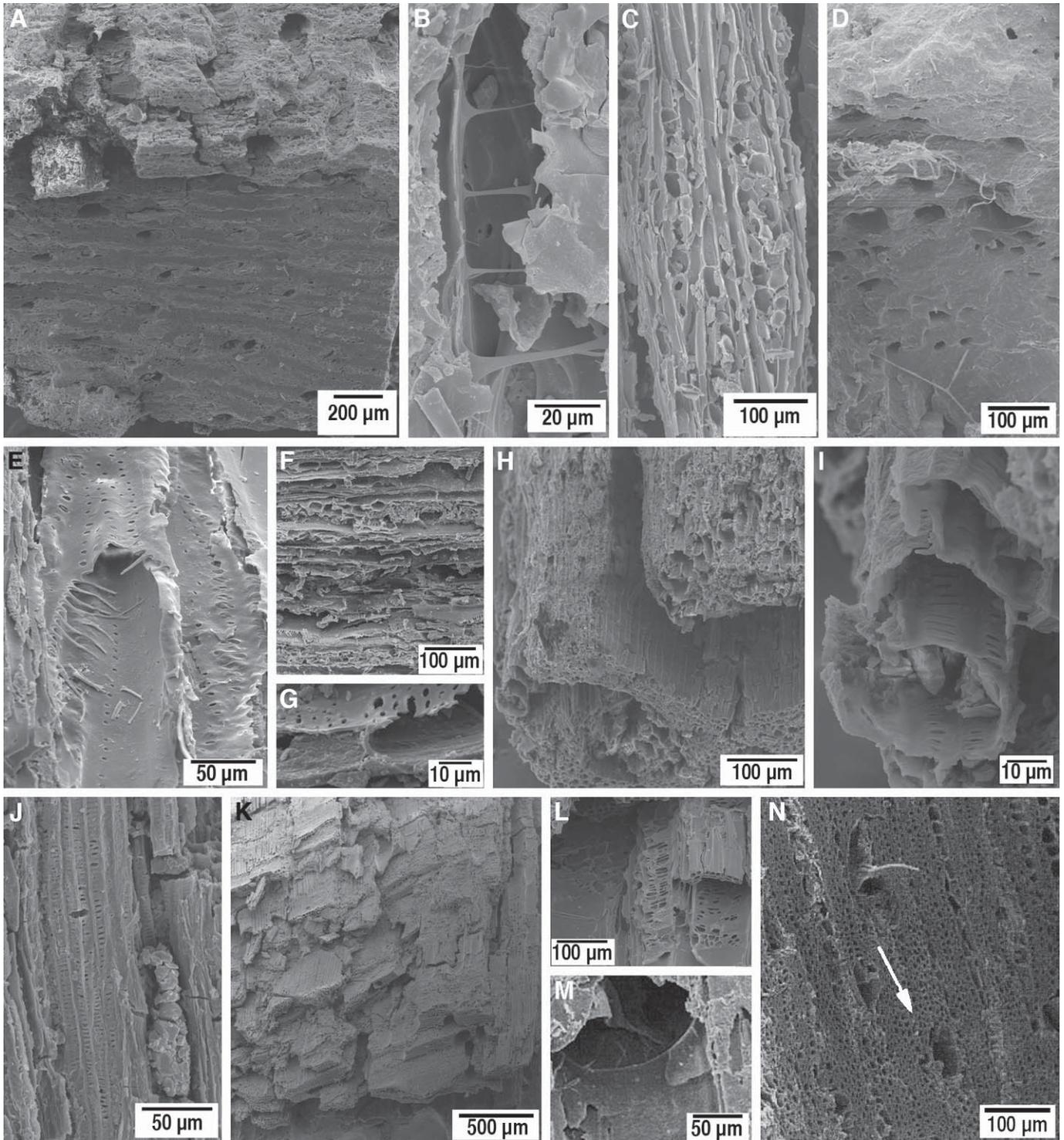
*Description:* Diffuse-porous wood has indistinct or absent growth ring boundaries (Fig. 3K). Vessels are 70–140 µm in diameter, solitary or grouped in 2's or 3's and with simple perforation plates. Reticulate small and large intervessel pits (Fig. 3L), 4–15 µm, are without borders. There are 15–20 vessels per mm<sup>2</sup>. Thin-walled fibres with simple pits are abundant (4 µm in diameter). Some septate fibres are also present. Axial parenchyma is rare and badly preserved. Rays are heterocellular with procumbent and square to upright cells, 2–5 seriate and fairly high (20–30 cells). Ray density was not measurable but appears high. Vessel-ray pits were not observed.

#### **Morphotype H** (Figs 3M-N)

*Localities:* Rodières; Saint-Laurent-de-Carnols

*Specimen numbers:* AWSE-0045; AWSE-0046; AWSE-0056

**Figure 2.** Different anatomical features observed on woods from Gard. **A–C:** Type A. **A:** Transversal view. **B:** Scalariform plate. **C:** Details of ray cells and fibres. **D–F:** Type B. **D:** Transversal view. **E:** Tangential view showing a vessel with a simple perforation (bottom) and uni- to triseriate rays (top). **F:** Radial view of a ray. **G–L:** Type C. **G:** Scalariform plate. **H:** Transversal view. **I:** Detail of a group of 2 vessels. **J:** Detail of the fibre pits. **K:** Tangential view showing the storeyed rays. **L:** Details of the ray cells and of the ray cell-to-ray cell pits.



**Figure 3.** Different anatomical features observed on woods from Gard. **A–C:** Type D. **A:** Transversal view. **B:** Scalariform plate. **C:** Tangential view showing rays and fibres. **D–G:** Type E. **D:** Transversal view. **E:** Scalariform plate. **F:** Tangential view showing uni- to biseriate rays. **G:** Details of ray cells. **H–J:** Type F. **H:** Transversal view. **I:** Detail of a radial multiple of 3 vessels. **J:** Pits of the fibres. **K–L:** Type G. **K:** Transversal view. **L:** Perforation of the vessel plates. **M–N:** Type H. **M:** Simple perforation plate of the vessels. **N:** Transversal view showing vessels and axial parenchyma (white arrow).

*Description:* Growth ring boundaries are indistinct or absent and wood diffuse-porous (Fig. 3N). Vessels are 80–110  $\mu\text{m}$  in diameter, solitary or grouped in 2's to 3's. Perforation plates are simple (Fig. 3M). There are small, opposite intervessel pits (4  $\mu\text{m}$  in diameter) and 10–15 vessels per  $\text{mm}^2$ . Fibres have simple pits. Some septate fibres have been observed. Rare diffuse axial parenchyma is poorly preserved. Rays are 1–3 seriate, 20–25 cells high (Fig. 3N) and heterocellular with one row of marginal upright cells. Vessel-ray pits were not observed.

#### Morphotype I (Figs 4A-B)

*Locality:* Saint-André-d'Olerargues

*Specimen number:* AWSE-0021

*Description:* Semi-ring porous wood has growth ring boundaries indistinct or absent (Fig. 4A). Vessels are solitary or in radial multiples of 2-3-4 cells, with 3 sizes: small (40–50  $\mu\text{m}$  in diameter), medium (80–90  $\mu\text{m}$ ) and large (140–150  $\mu\text{m}$ ). Perforation plates are scalariform and intervessel pits are small (4  $\mu\text{m}$ ). Fibres with simple pits are present but a large proportion of the woody tissue comprises long cells with abundant spiral thickening (vascular tracheids?). Axial parenchyma is rare and diffuse. Rays are homocellular, mainly uniseriate and 3–5 cells high (Fig. 4B). Rays are equally spaced out (150–160  $\mu\text{m}$  between two rays). Ray density is low but could not be measured.

#### Morphotype J (Figs 4C-D)

*Locality:* Saint-Laurent-la-Vernède

*Specimen number:* AWSE-0011

*Description:* Diffuse-porous wood has growth ring boundaries indistinct or absent (Fig. 4C). Vessels are mostly solitary or in pairs and large, 170–200  $\mu\text{m}$ . Perforation plates were not observed. There are 10–15 vessels per  $\text{mm}^2$  and intervessel pits are small, 4  $\mu\text{m}$  in diameter. Fibre-tracheids are badly preserved with large bordered pits (Fig. 4D). Presence of diffuse axial parenchyma was noted. Rays are large, heterocellular, 10–15 seriate and 25–30 cells high.

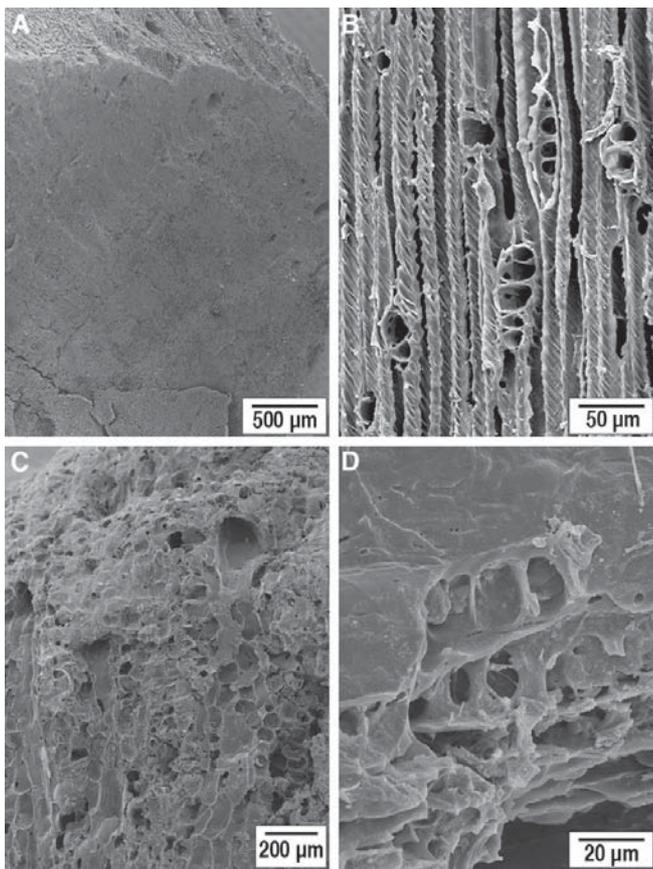
## DISCUSSION

### ANGIOSPERMS IN EARLY-MIDDLE CENOMANIAN PHYTOCENOSSES OF GARD

In the Gard localities the low percentage of angiosperm wood (Table 2) suggests that woody flowering plants probably occupied only a small part of the vegetation. A straightforward interpretation of the relative proportions of angiospermous and gymnospermous wood fragments, however, is risky mainly because of taphonomical and ecological biases (Martín-Closas & Gomez, 2004).

All the angiosperm wood specimens studied were from axes of relatively small diameter (i.e., less than a few centimetres) when judged on ray divergence. Charring is known to induce shrinkage and distortion (McGinnes *et al.*, 1971) so we consider that our specimens are not relevant to address the question of the habit of these angiosperms. Some xylogenological characters of these specimens, however, indicate the existence of already tall (undoubtedly shrubby, perhaps arborescent) angiosperms. Indeed, some woods have simple perforation plates, which was a character related to the development of a shrubby or arborescent habit in flowering plants (Wheeler & Baas, 1991). It has been also observed abundant alternate intervessel pits, which Carlquist (1988) suggested as the consequence of robust vessel walls and interpreted as an indicator of high stature (shrub or arborescent) in angiosperms.

The nineteen angiosperm wood specimens from the Cenomanian of the five localities of Gard reveal a surprising diversity (Girard, 2005). On the basis of the xylogenological key by Suzuki *et al.* (1996), ten morphotypes (A-J above) have been distinguished. This diversity appears quite large as only six Aptian or Albian wood morphospecies were previously described worldwide.



**Figure 4.** Different anatomical features observed on woods from Gard. **A–B:** Type I. **A:** Transversal view. **B:** Tangential view. **C–D:** Type J. **C:** Transversal view. **D:** Pits of the fibres.

Charcoal studies have been underrepresented for the investigation of early angiosperm evolution and systematics (Herendeen, 1991). Many of our specimens were only a few millimetres in size so some rare cell or perforation types may have been overlooked. This and the possible allometric modifications of cell dimensions during charring processes suggest that interpretation on diversity is not prudent.

### Angiosperm palaeoecology

This study aimed to determine the potential of angiosperm charcoal for palaeoecological reconstruction, using narrow statistical correlations evidenced by Wheeler & Baas (1991, 1993) and by Wiemann *et al.* (1998, 1999) between environmental conditions and qualitative to semi-quantitative anatomical characters of angiosperm woods. Given the limitations mentioned above, inferences are discussed, considering wood characters one by one.

### Growth rings

The absence of growth rings in the angiosperm wood specimens observed might indicate that a climate without marked seasons existed during the Early-Middle Cenomanian in Gard. Indeed, only living plants of rather uniform environments do not have growth rings (Wheeler & Baas, 1991; Brison *et al.*, 2001). However, we observed in the same localities similar-sized charcoal specimens that we identified to the Coniferales (*Taxodioxyton* Hartig, *Podocarpoxyton* Gothan) and the Ginkgoales (*Ginkgoxyton* Saporta), a small proportion of them having well-marked growth rings (6 out of 32 specimens, i.e., 15%) (Fig. 3A). Three reasons can explain such a discrepancy during the Early-Middle Cenomanian in Gard: (1) although growth

rings were produced by gymnosperms (endogenous control hypothesis), environmental conditions were uniform over the year; (2) although early angiosperms did not record a seasonality, there was a seasonality in temperature or rainfall (seasonal climate hypothesis); (3) the growth rings were not observed in angiosperm wood because of the small dimension of specimens (taphonomical bias hypothesis). Gymnosperm charcoal specimens found in the same fossil wood assemblage exhibit growth rings, while they are of similar size to the angiosperm charcoal specimens. This observation makes it plausible that the absence of growth rings in angiosperm charcoal is a primary signal, i.e., early angiosperms formed no rings, having a continuous growth (Poole, 1994).

The occurrence of growth rings in other woody plants (i.e., conifers or ginkgos) supports the seasonal climate hypothesis. Brison *et al.* (2001), however, showed that by the Mesozoic *Taxodioxyton* Hartig always produced growth rings, whatever the climate it was experiencing. Moreover, as the proportion of homoxyloous wood specimens with growth rings is low compared to normal Mesozoic figures, we favour the endogenous control hypothesis for explaining the discontinuous growth observed in some gymnosperm specimens.

Falson-Lang *et al.* (2001) described similar wood assemblages from the upper Middle Cenomanian of Czech Republic, gymnosperm charcoal having growth rings and

**Table 3.** Summary of the different studied anatomical characters and the palaeoecological inferences that can be made from each one.

Wood features	State	Climatological inferences in modern floras	Climatically informative	Probable interpretation
Growth rings	mainly absent	tropical with low seasonality	partly (seasonality)	rainfall seasonality possible if the plants grew up on a well-watered soil
Porosity	mainly diffuse	tropical	yes	
	low density	tropical	yes	
Vessels	small diameter	temperate	no	Phylogenetically biased? <sup>1</sup>
	scalariform perforation plates	temperate to cold	no	Phylogenetically biased? <sup>1</sup>
	mainly isolated	temperate to cold	no	Phylogenetically biased? <sup>1</sup>
	occurrence of radial groups of 2-3 pores or clusters	hydic seasonality	yes	
Fibres/tracheids	weak abundance of fibre-tracheids	tropical	yes	preservational biases
	occurrence of vasicentric tracheids	hydic seasonality	yes	
	septate fibres rare	temperate	no	phylogenetical or preservational biases
Axial parenchyma	mainly apotracheal diffuse	temperate	no	Phylogenetically biased? <sup>1</sup>
	some paratracheal to vasicentric	tropical	yes	

(Footnotes)

<sup>1</sup> Inferred as phylogenetically biased for the Cretaceous (Wheeler & Baas, 1991)

angiosperm charcoal having none. They suggested that angiosperms grew in areas where water was usually available, such as riparian or amphibious vegetation, whereas gymnosperms occupied drier areas. The same explanation cannot stand for the Pauletian wood assemblage of Gard because of its peculiar depositional environment (i.e., a protected marsh or lagoon). Takahashi & Suzuki (2003) observed distinct growth rings in most of the 266 gymnosperms and none in most of the 144 dicotyledonous angiosperms from the Cretaceous of Hokkaido. They concluded that the ability to form wood growth rings might have evolved quite late in the majority of the dicotyledons.

These growth ring results are not incompatible with some seasonality. Thus, should a clear thermal seasonality have occurred, both angiosperms and gymnosperms would have developed growth rings. However, a marked seasonality in rainfall climate is compatible with our observations, as long as soils remained well-watered (but not asphyxiating) year-round.

#### Porosity

The high percentage of diffuse porous angiosperm wood (18 out of 19 specimens) fits well with the image of a tropical climate in Gard during the Early-Middle Cenomanian. Today most tropical floras have a similar percentage, but it has been demonstrated that temperate southern hemisphere woody plants are also overwhelmingly diffuse porous (Wheeler *et al.*, 2007). In cool temperate and cold floras a notable proportion of wood is characterised by ring or semi-ring porosity (Wheeler & Baas, 1991; Boura & De Franceschi, 2007), but Boura & De Franceschi (2007) indicated that 28% of the 193 European species wood they studied were only diffuse porous. The occurrence of semi-ring porosity in one specimen (Fig. 3B) is not paradoxical. Even within the tropical belt, some angiosperms develop this feature when they are exposed to seasonal water stress (Wheeler & Baas, 1991). Boura & De Franceschi (2007) showed that most of the ring porous woods from tropical belt belong to deciduous species and that, in 90% of the woods, the character “ring porous” is associated with the character “simple perforation plates”.

The low vessel density (between 15 and 25 vessels per mm<sup>2</sup>) of fossil angiosperm wood from the Lower-Middle Cenomanian of Gard also suggests a tropical climate at that time. Living angiosperms from temperate to cold environments generally have a higher density (more than 100 vessels per mm<sup>2</sup>) than those of tropical angiosperms (except for those growing in high altitude) (Wheeler & Baas, 1991). The charring process may have increased the apparent vascular density, thus limiting the interpretation.

#### Vessels: Diameter, lateral pitting and grouping

Although the three characters considered previously point to a tropical climate (with probable seasonality of precipitation), other wood characters are contrary to this interpretation. Thus, we observe relatively small vessel diameters (on average). In extant floras warm-climate an-

giosperms have larger vessels than those of cold climates (Wheeler & Baas, 1991). In this respect shrinkage from charring is obviously inducing a certain bias (difficult to estimate). Statistical studies showed that narrow vessels ( $\leq 100 \mu\text{m}$ ) were more frequent during the Cretaceous (Wheeler & Baas, 1991) and various data indicate that the Cenomanian was a warm period (Fluteau, 2003). Our observations confirm that for the Early-Middle Cenomanian floras, it is advisable not to use the character “vessel diameter” as a palaeoclimatic indicator.

Most perforation plates observed are scalariform. Today this type is encountered mostly from temperate to cold floras (Wheeler & Baas, 1991). However, during the Cretaceous, scalariform perforation plates were clearly more widespread than today. About 60% of Cretaceous angiosperm wood morphospecies described have scalariform perforation plates compared to only 10% of angiosperms today (Wheeler & Baas, 1991). Wheeler & Baas (1991, 1993) interpreted this Cretaceous high percentage as a result of a phylogenetic bias, scalariform perforations being considered as primitive. We also observed specimens with simple perforation plates, which is a character state considered to be derived and which might fit well with a seasonally dry climate. Accordingly the development of simple perforation plates was correlated in some cases with water stress (Wheeler & Baas, 1991).

Fossil angiosperm wood specimens studied have mostly solitary vessels, which may be formed in temperate and cold floras. Wheeler & Baas (1991) demonstrated, however, that all Cretaceous angiosperm wood assemblages share a high proportion of isolated vessels. These results confirm that vessel grouping cannot be used for palaeoclimatic inferences for the Early-Middle Cenomanian and its high proportion observed may be considered as a phylogenetic bias.

Radial groups of 2–4 vessels are observed in twelve angiosperm specimens. Grouped vessels were rare during the Cretaceous and only reached significant importance during the Eocene (Wheeler & Baas, 1991). According to Carlquist (1984), grouped vessels could correspond to “a device for hydraulic safety”, thus ensuring a better sap transport during the dry season. Their relative abundance in the angiosperm woods from the Lower-Middle Cenomanian of Gard compared to other Cretaceous wood assemblages may indicate some seasonality.

#### Fibres and Tracheids

Fibres are badly preserved in most of the wood specimens described here. We observed septate fibres in only three morphotypes (D, G and H) and only in six specimens (31% of the specimens). The lack of septate fibres among the other samples is surprising as those fibres are today more common in tropical environments and they were more frequent during the Cretaceous than today (Wheeler & Baas, 1991). Two possibilities may explain this weak occurrence: (1) Early-Middle Cenomanian angiosperm flora of Gard was phylogenetically unusually low in sep-

tate fibres; and (2) septate fibres were present originally but either not preserved or under-recognized (by the fact they are difficult to recognize under SEM in charcoals). It is advisable not to use septate fibres in our palaeoclimatic interpretation. Vasicentric and vascular tracheids are rare in the wood assemblage described here. Vasicentric tracheids have been observed in only one wood (morphotype C). Vascular tracheids are more common, being found in three specimens of three different morphotypes. These two kinds of tracheids were relatively rare during the Cretaceous (4% of occurrence in the Northern Hemisphere only) but became more common in modern floras subjected to seasonal drought conditions (Wheeler & Baas, 1991). This xylological character fully argues for a tropical climate with alternations of rain and dry seasons during the Early-Middle Cenomanian in Gard. The weak occurrence of bordered pits (only two specimens of two different morphotypes exhibit fibre-tracheids) may indicate a relatively warm climate since the abundance of fibre-tracheids is a characteristic of a cool environment (Wheeler & Baas, 1991).

#### **Axial parenchyma, rays**

Parenchymatous tissues of fossil angiosperm woods are difficult to interpret in terms of palaeoclimate (Kribs, 1935; Wheeler & Baas, 1991, 1993). Ray parenchyma anatomical characters are not statistically correlated with environmental parameters for both modern and extinct wood assemblages (Wheeler & Baas, 1991). We only noted the presence of one specimen with homocellular rays (morphotype I) and the presence of 1–2 rows of upright cells around the rays in three of the morphotypes (C, D, H).

In the specimens studied axial parenchyma is rare and mainly diffuse (Fig. 3D). Today such an axial parenchyma distribution is more frequent in temperate environments than in tropical environments. Nevertheless diffuse parenchyma was very frequent (presence in 50% of the studied woods) during the Upper Cretaceous (Wheeler & Baas, 1991). It may be due to a phylogenetical bias. However, the few occurrences of more elaborate parenchyma, paratracheal to vasicentric (Fig. 3E) and in narrow irregular bands, might indicate a tropical climate. These two types of parenchyma distribution, which are uncommon during the Cretaceous, are mainly found in the wood of tropical angiosperms today (Wheeler & Baas, 1991).

## **SYNTHESIS**

From our study, the image arises of a plant community, in a well watered (phreatic or meteoritic) environment, with angiosperms and gymnosperms growing together and endogenous cyclicity forming growth rings only in gymnosperms. It cannot be completely excluded, however, that early angiosperms had continuous growth in a changing environment. Very little is known about the physiology of

continuous growth, but it was documented even in tropophilous environments where variation is in a warm range, 16 to 25°C, see Jacoby (1989) and references therein.

The palaeoclimatic interpretations deduced from the anatomical study of angiosperm charcoal from the Lower-Middle Cenomanian of Gard (south France) match sedimentological and isotopic studies in seven characters, whereas they differ in the five remaining characters (Table 3). The vessel diameter, the occurrence of scalariform plates, the mainly isolated vessels, the rare septate fibres and the mainly apotracheal diffuse axial parenchyma were already used and interpreted by Wheeler & Baas (1991, 1993) as being linked to a strong phylogenetic bias, at least during the Late Cretaceous. This study verifies that these five wood characters should not be applied to palaeoclimatic reconstructions for the early Late Cretaceous. In contrast, growth-rings, porosity type, porosity density, occurrence of vessel groups, occurrence of vasicentric tracheids and of some paratracheal to vasicentric and banded axial parenchyma suggest a tropical climate with low temperature seasonality and marked water seasonality. This matches well with sedimentological and isotopic evidence. The low abundance of fibre-tracheids also fits with sedimentological and isotopic studies. However, their abundance in our wood assemblage could be biased because of some preservational factors.

Many palaeofloras have been recently discovered in the Upper Cretaceous of Iberian Peninsula, among which angiosperms have a significant share (Friis *et al.*, 2006; Villanueva-Amadoz *et al.*, 2010). It would be of interest to search specifically for angiosperm wood within these strata. Their interpretation would help to investigate relationships between palaeoclimate and early angiosperm evolution, a much debated issue for which the Iberian Peninsula is a key-area.

## **ACKNOWLEDGEMENTS**

The authors very gratefully thank Prof. Elisabeth Wheeler, Prof. Peter Baas and Dr. Jakub Sakala for their valuable help and comments on an earlier draft. Prof. In-Sung PAIK (South-Korea) helped us to interpret the sedimentology of several localities. The authors thank Dr. Silvia C. Gnaedinger (Argentina) for helping to translate the abstract into Spanish.

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*Manuscrito recibido:* 18 de abril, 2011

*Manuscrito aceptado:* 3 de noviembre, 2011

