

# A new species of *Protaxodioxylon* (Cupressaceae s.l.) from the late Albian of the Aragonian branch of the Iberian Range (Spain). Palaeoclimatic implications

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Vozenin-Serra C.†, Diez J. B. & Ferrer J. 2011. — A new species of *Protaxodioxylon* (Cupressaceae s.l.) from the late Albian of the Aragonian branch of the Iberian Range (Spain). Palaeoclimatic implications. *Geodiversitas* 33 (1): 11-24. DOI: 10.5252/g2011n1a1.

## ABSTRACT

In this paper we describe fragments of silicified wood specimens found in “El Barranquillo” outcrop (Castellote, Teruel, Spain) in the Aragonese branch of the Iberian Range. This new species without any growth ring and with mixed radial pitting could represent an ancestral form of the modern Sequoioideae subfamily. This anatomical study, in association with an observation of the lithological facies, the position and the preservation of the fossil woods, evidences a subtropical climate with abundant precipitation and without seasonal contrasts, during the deposition of the Utrillas Formation.

## KEY WORDS

Cupressaceae s.l.,  
Sequoioideae,  
late Albian,  
Iberian Range,  
Palaeoclimate,  
new species.

## RÉSUMÉ

*Une nouvelle espèce de Protaxodioxylyon (Cupressaceae s.l.) de l'Albien supérieur de la branche aragonaise de la Cordillère Ibérique (Espagne). Implications paléoclimatiques.*

Dans cette étude, nous décrivons des fragments de bois silicifiés trouvés dans les affleurements d'« El Barranquillo » (Castellote, Teruel, Espagne) situés dans la Branche Aragonaise de la Chaîne Ibérique. Cette nouvelle espèce sans cernes de croissance et à ponctuations radiales mixtes, représente vraisemblablement une forme « ancestrale » de la sous-famille des Sequoioideae. L'étude anatomique couplée à une observation des faciès lithologiques, de la disposition et de la conservation des bois fossiles, met en évidence un climat subtropical et humide sans saisons contrastées durant le dépôt de la Formation Utrillas.

## MOTS CLÉS

Cupressaceae s.l.,  
Sequoioideae,  
Albien supérieur,  
Cordillère Ibérique,  
Paléoclimat,  
espèce nouvelle.

## INTRODUCTION

Palaeoxytological studies are still scarce in the Iberian Peninsula. The discovery of fossil wood fragments near Teruel, in northern Spain, joined with sedimentological data could provide important information on the environmental conditions which characterized this area during the early Cretaceous.

### GEOGRAPHICAL LOCATION

The studied palaeontological site is located in the Province of Teruel, within the municipal district of Castellote. It is reached by leaving the town of Mas de las Matas and going 6 km westward (Fig. 1) until arriving at a gully at the foot of a hill known as Pílon de San Pedro. In this area large fragments of silicified wood are scattered on the surface of the site (coordinates: UTM 30TYL268247).

### GEOLOGICAL CONTEXT

The study area is located in the Aragonese branch of the Iberian Range (Lotze 1929), in the southeast zone of the Maestrazgo sector, where the Iberian Range and the Catalanian Coastal Range merge (Guimera 1988). General structural directions are east-west.

The silicified wood remains at the site are situated in the Utrillas Formation (Aguilar *et al.* 1971) (Fig. 1), whose Mesozoic phase is clearly represented in the Iberian Range. The Utrillas Fm consists of continental sediments, mainly sands and sandstones,

alternating with shale, which filled the basins formed during the Jurassic-early Cretaceous tectonic rift phase (Salas 1987), known as the Austrian phase.

At the “El Barranquillo” site the sands are white and fine-grained, distributed in tabular bodies of meter-scale thickness. They exhibit a cross-stratification arranged in sets of decimetrical thickness. Ferruginous crusts and diagenetic structures formed by the migration of iron oxides have been observed. The shales vary in colour and a large number of ferruginous nodules can be found. Remnants of silicified wood are observed in both the sands and shale, with dimensions ranging from a few centimetres to 5 metres (Fig. 2).

The age of the Utrillas Fm is based on the age of the overlying lithostratigraphical units as it lacks biostratigraphic markers. It shows a strong diachronism throughout the Iberian ranges. In the most northwestern zones, where it reaches its maximum development, the Utrillas Fm deposits cover a period between the early Albian and the earliest Cenomanian. However in the Maestrazgo sector, this formation, interpreted as a more distal zone of the progradational system, has a much more restricted temporal distribution. The base of the Mosqueruela Fm, which overlies conformably the Utrillas Fm, contains late Albian orbitolinids (Pardo *et al.* 1991), meaning that in this area the Utrillas Fm represents only a part of the late Albian. The boundary between the Utrillas and Mosqueruela formations is situated about 40 m above the site

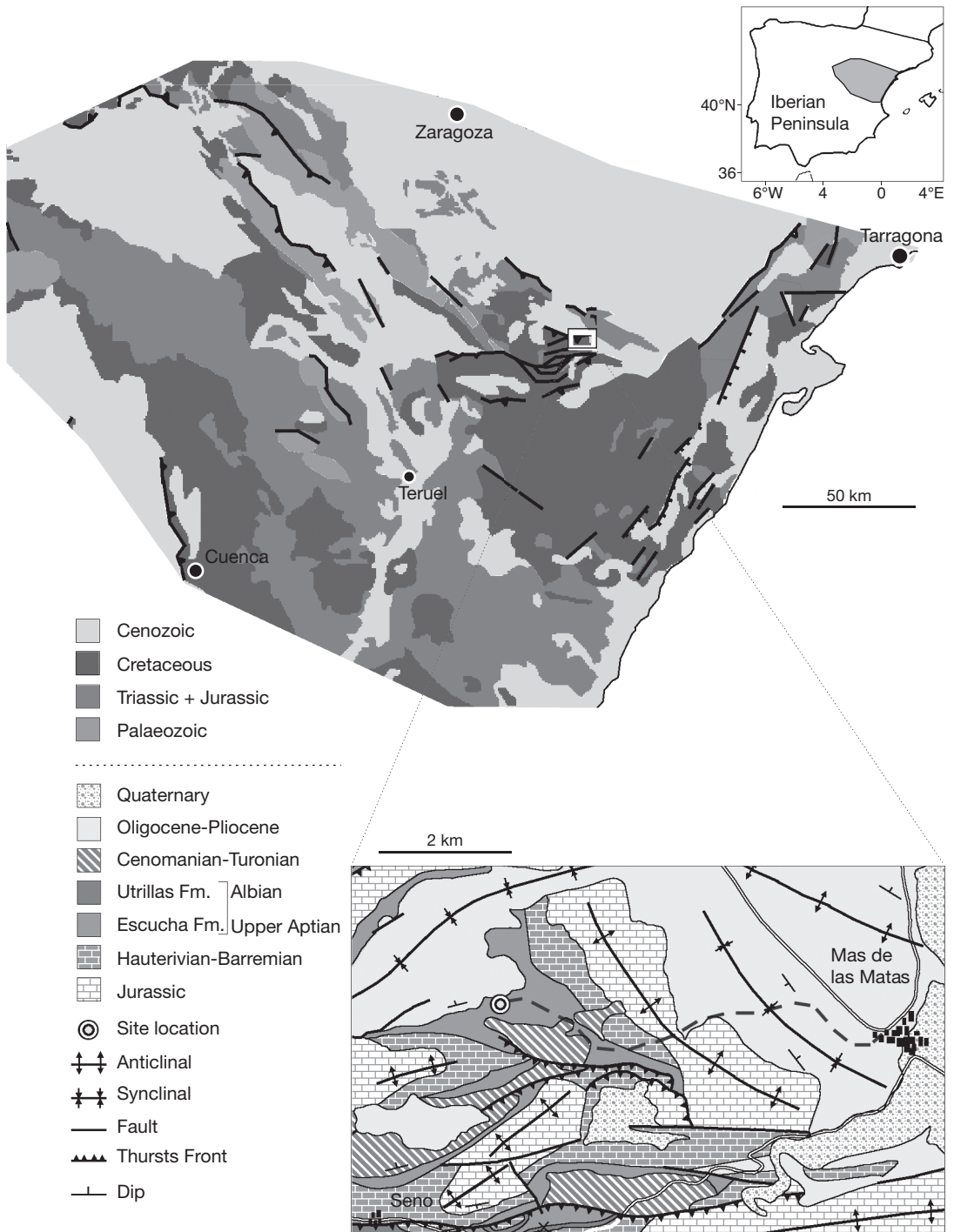


FIG. 1. — Location of the fossiliferous site in a geological sketch of the Aragonian Branch of the Iberian Chain of Teruel, Spain.

TABLE 1. — Kimmeridgian-Cretaceous conifer woods in the Iberian Peninsula.

Specimens	Locality	Age	References
<b>Spain</b>			
<i>Cupressinoxylon hortii</i> Stopes, 1915 <i>Cupressinoxylon</i> sp. <i>Dadoxylon</i> sp. <i>Dadoxylon (Araucarioxylon)</i> sp. <i>Xenoxylon</i> sp.	Ladruñan, Seno and Oliete El Maestrigo - Bajo Aragon Teruel Province	Berriasian- Barremian	Lemoigne & Marin 1972
<i>Agathoxylon</i> sp.	Teruel Province	Albian Escucha Formation	Gomez <i>et al.</i> 1999
Not identified (described in this work)	Castellote Teruel Province	Albian	Diez <i>et al.</i> 1996; Muñoz Barragán <i>et al.</i> 1999
<i>Dadoxylon (Araucarioxylon)</i> <i>riojense</i> Barale & Vieira, 1991	Igea, La Rioja Province	Valanginian- Hauterivian	Barale & Viera 1991
<i>Pinoxylon riojanus</i> Del Nido <i>et al.</i> , 1998	Soto de Cameros Northern Iberian System	Aptian	Del Nido <i>et al.</i> 1998
<i>Agathoxylon riojense</i> Barale & Viera, 1991	Cameros Basin Northern Iberian System	? Aptian	Doublet & Garcia 2004
<i>Protopodocarpoxylon haciniensis</i> García Esteban & Palacios, 2006 <i>Agathoxylon</i> sp.	Hacinas Cameros Basin, Burgos Province	Barremian-Aptian	García Esteban <i>et al.</i> 2006
<i>Agathoxylon</i> <i>Protocupressinoxylon</i> sp. <i>Protocupressinoxylon purbeckensis</i> Francis, 1983	Asturias Province	Kimmeridgian Lastres Formation Terenes and Lastres formations	Valenzuela <i>et al.</i> 1998 Philippe <i>et al.</i> 2010
<b>Portugal</b>			
<i>Prototaxodioxylon</i> sp. = <i>Protaxodioxylon</i> sp. in Philippe <i>et al.</i> 2010	Guimarota near Leiria	Kimmeridgian	Mohr & Schultka 2000
<i>Dadoxylon (Araucarioxylon)</i> <i>teixeirae</i> Boureau, 1949 = <i>Protopodocarpoxylon teixeirae</i> (Boureau) Boureau, 1951	Cadriceria South of Torres Vedras	Boundary Hauterivian- Barremian	Boureau 1949, 1957; Boureau & Moitinho de Almeida 1951
<i>Protopodocarpoxylon</i> <i>aveiroense</i> (Lauverjat et Pons, 1980)	Esgueira near Aveiro Beira Litorale Province	Senonian	Lauverjat & Pons 1980

and can be clearly observed in the nearby hill of the Pilón de San Pedro.

The Utrillas Fm shows a transgressive pattern, which was initiated with fluvial sediments which evolved towards detritic-calcareous sediments typical of transitional environments (Pardo 1979).

#### EL BARRANQUILLO AREA

The precise extent of the El Barranquillo area still remains unknown. The study section corresponds to mixed, sand-shale channel-fill deposits, most likely from a meandering channel.

Four of the wood fragments are notable for their good state of preservation and large dimensions. These specimens, despite being incomplete are from 1.5 to 4.75 m long, with diameters between 0.5 and 0.7 m (Muñoz-Barragán *et al.* 1999: pl. 1). Three of them lay parallel to each other in their original depositional position and are oriented nearly at a right angle with respect to the palaeocurrents. The different orientation of the fourth piece is due to erosional process. Around the largest fossil wood fragments, a multitude of smaller fragments have been found (lengths

from 5 to 40 cm), which are derived from the weathering of larger specimens. All these remains are permineralized and often appear to be torn or split away from a trunk and laid in a parallel direction. No traces of pith, phloem, or bark have been found, and no branches or roots are attached to the large specimens.

#### PALAEOXYOLOGICAL BACKGROUND

Kimmeridgian and Cretaceous conifer wood remains already known in the Iberian Peninsula are listed in Table 1. This study adds an element to the knowledge of the Iberian palaeoecology.

#### MATERIAL AND METHODS

The fossil remains found in El Barranquillo are fragments of decorticated wood. These remnants were moved on a considerable distance, and later underwent complex processes of carbonization, silicification, and subsequent partial recrystallization. (Diez *et al.* 1997; Muñoz-Barragán *et al.* 1999).

For this palaeoecological study 14 specimens were selected, and studied in transverse, tangential and radial sections. The anatomical description is in accordance with the IAWA Softwood List (IAWA Committee 2004). These samples are housed at the Paleontological Department of the University of Zaragoza (Spain), under the numbers MPZ 97/2504 to MPZ 97/2518. All of them are pieces of coniferous pycnoxylic wood. Three of them are well-preserved enough for description and identification by the first author.

#### SYSTEMATIC PART

##### PINOPHYTA

##### Order CONIFERALES

##### Family CUPRESSACEAE Gray *sensu* Farjon, 2005

##### Genus *Protaxodioxylon* Bamford & Philippe, 2001

TYPE SPECIES. — *Protaxodioxylon romanensis* (Philippe) Bamford & Philippe, 2001

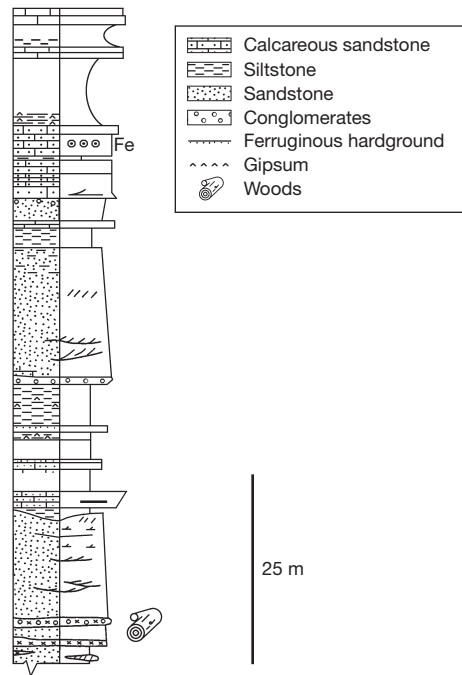


FIG. 2. — Synthetic stratigraphic column of Utrillas Formation in the "El Barranquillo" outcrop (modified from Pardo 1979).

##### *Protaxodioxylon turolense* Vozenin-Serra, n. sp.

HOLOTYPE. — MPZ 97/2514, Paleontological Museum, University of Zaragoza, Spain.

PARATYPES. — MPZ 97/2504 and MPZ 97/2516, Paleontological Museum, University of Zaragoza.

TYPE LOCALITY. — El Barranquillo site, municipal district of Castellote, Teruel Province, North Spain, coord. UTM 30TYL268247.

TYPE HORIZON. — Utrillas Fm, Lower Cretaceous (late Albian).

ETYMOLOGY. — The specific name refers to the Spanish denomination for the inhabitants of Teruel.

DIAGNOSIS. — Secondary homoxyleous pycnoxylic wood, without distinct growth-rings. Tracheids with polygonal lumen. Dimensions (tangential x radial): 35-66 (55) x 40-76 (70)  $\mu$ m. Uni- and biseriate, locally triseriate rays of 7-42 (12-22) cells in height. Density: 5-6 rays by tangential horizontal mm. Cells height: 20

to 25 µm. Rays homogeneous with smooth horizontal and end walls. Mixed radial pits mostly uniseriate in closely crowded arrangement or contiguous and separate, rarely biseriate, then opposite and surrounded by crassulae. Dimension of pits (height and width) 24–28 × 28–32 µm. 1 or 2 taxodioid pits (occasionally 3) in cross-fields, 13–15 µm in diameter, disposed in one single horizontal line. Abundant axial parenchyma, with smooth transverse end walls.

## DESCRIPTION

### *Transverse section*

Homoxyloous pycnoxylic wood without any growth ring. The tracheids have a polygonal outline (Fig. 3A), with radial diameter comprised between 40 and 76 (70) µm and tangential diameter of 35 to 66 (55) µm, the wall thickness varies between 3 and 5 µm.

There are from 1 to 8 files of tracheids between adjacent rays, mostly 2 to 5. The number of tracheids per mm<sup>2</sup> varies between 224 and 256.

### *Tangential section*

The rays are uniseriate or completely or partially biseriate (Fig. 3B). Triseriate rays can occasionally be seen. They are of average height, between 7 and 26 cells, mostly between 12 and 22. However, rarely the height exceeds 30 cells and can reach as many as 42 cells. There are 5–6 rays per tangential millimetre. The parenchyma ray cells are between 20 and 25 µm high.

The axial parenchyma is abundant (Fig. 3C). The parenchyma cells are rectangular, between 30 and 50 µm wide and have smooth transverse end walls.

Radial section: The tracheids show radial pits of mixed type with clear araucarian tendency. Radial uniseriate pits are predominant, and mostly in closely crowded arrangement (87%, Fig. 4A) others being contiguous or separate (6%, Fig. 4C). Opposite biseriate pits can also be seen surrounded by bars of Sanio (7%) (Fig. 4D). The height of the pits varies between 24 and 28 µm, and the width between 28 and 32 µm.

The rays are homogeneous (Fig. 4B). Both horizontal and end walls of the ray parenchyma cells are thin and smooth; the cell height varies between 20 and 25 µm, and their length between 150 and 290 µm.

The cross-fields are rectangular in shape and show 1 or 2 taxodioid pits (occasionally 3), with a large oblique or horizontal opening included in the areola limits (Fig. 4F, G). The diameter of the cross-field pits varies between 13 and 15 µm, they are arranged in a single horizontal line when there are 2 or 3 pits per field.

## DISCUSSION

The general aspect of the tracheids and rays, the presence of taxodioid cross-field pits and the presence of abundant axial parenchyma, indicate that the structure can be related to the taxodiaceous Cupressaceae. Recent phylogenetic analyses based on molecular and morphological data propose to consider both Cupressaceae and Taxodiaceae as a single family (Cupressaceae *s.l.*), excluding *Sciadopitys* Siebold & Zucc. transferred to a monotypic family *Sciadopityaceae* Luerss. (Gadek *et al.* 2000; Farjon 2005). Within this family Cupressaceae *sensu lato* the greatest affinities are found within extant genera that have smooth terminal walls of the parenchyma cells namely *Athrotaxis*, *Cunninghamia*, *Metasequoia*, *Sequoia*, *Sequoiadendron* and *Taiwania*. Both *Cunninghamia* and *Taiwania* show pitting of variable type in the cross-fields, while the specimens studied present only taxodioid cross-field pits. *Athrotaxis* is characterized by low rays (Phillips 1948).

With the exception of the tracheid radial pitting, the specimens studied show the characteristic of the genera *Sequoia*, *Sequoiadendron* and *Metasequoia*. These genera, mainly differentiated by their leaves and reproductive organs, show very similar wood characteristics. Some differences proposed to differentiate these genera on the wood anatomy are the size of the radial pitting in earlywood, smaller in *Metasequoia* (10–13 µm) than in *Sequoia* and *Sequoiadendron* (14–24 µm) (Gromyko 1982), the maximum height of the rays (higher in *Sequoia*) the number of cross-fields pits (from 2–8, and sometimes 10 in *Sequoia*, and less than 6 in *Metasequoia* and *Sequoiadendron*). The specimens found at El Barranquillo combine the characteristics of these three genera. The fossil woods related to the subfamily Sequoioideae have predominant abietoid radial pitting on the tracheids as does the extant *Sequoia*. However, the structure studied here

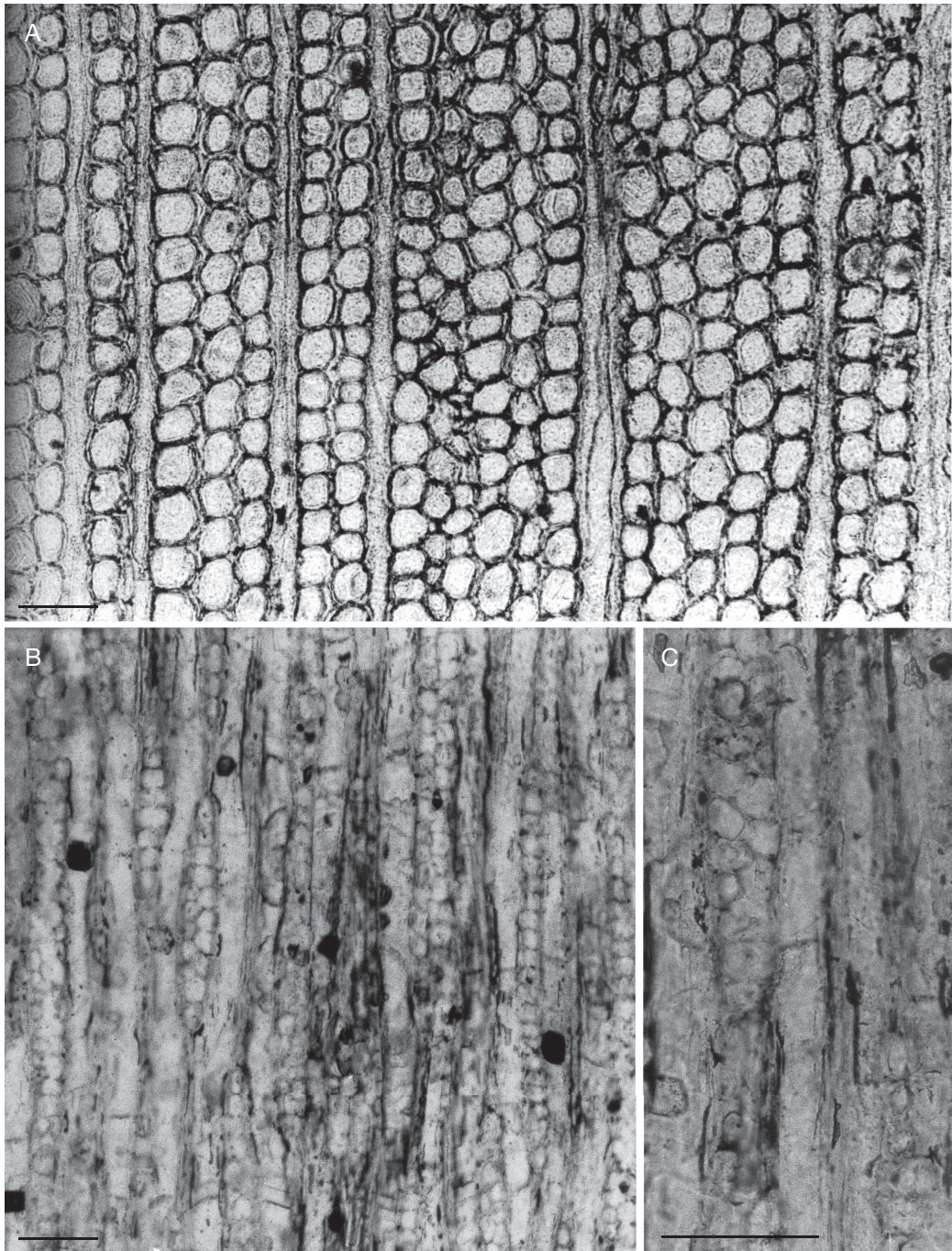


FIG. 3. — *Protaxodioxylon turolense* Vozenin-Serra, n. sp. (holotype MPZ 97/2514): **A**, transverse section without growth rings; **B**, tangential section showing uni- or sometimes partly biseriate rays and abundant axial parenchyma; **C**, tangential view of smooth transverse end wall in axial parenchyma. Scale bars: 100  $\mu$ m.

has a clearly mixed structure with chief araucarian characteristics (87%). Many coniferous fossil genera, especially Jurassic and Cretaceous, show all the characteristics of the modern groups to which they are related, with the exception of their mixed radial pitting

#### AFFINITIES

The presence of mixed radial pits in the tracheids is characteristic of some Mesozoic conifers. These morphogenera are usually named by adding the prefix *proto-* to the name of the modern genus with which they have the most similar characteristics. Kräusel (1917) proposed the artificial group of the Protopinaceae to accommodate these morphogenera, as they were anatomically well defined and localized in time. This point of view has been (and still is) a subject of controversy amongst researchers. Hollick & Jeffrey (1909) claimed that the tracheid radial pitting had a predominant taxonomic value, and considered that the mixed structures were the ancestral forms of modern Araucariaceae. Gothan (1907) on the other hand, rejected the preponderance of this characteristic in comparison to more important ones such as the morphology of the rays and cross-fields and considered that the Mesozoic mixed structures are the ancestral forms of abietineous conifers.

Bailey (1933) and Bailey & Faull (1934) were opposed to the use of the group proposed by Kräusel, arguing that mixed structures with clear araucarian tendency are observed in the roots and axes of the cones of some modern abietineous conifers (*Cedrus*), which means they are within the variation limit of this group. Grambast (1960) affirmed that pitting of a mixed type, far from being characteristic of a particular group of conifers of the Mesozoic era, can in fact be seen not only amongst certain Tertiary and modern conifers, but also amongst many Permo-Carboniferous gymnosperms in southern regions.

Without wishing to enter into these debates about the usage of the Protopinaceae artificial group, the affinities of the wood structure from the Upper Albian of El Barranquillo with fossil and modern species of the Sequoioideae subfamily indicate that, in this particular case of araucarioid pitting clearly

predominant, the mixed type possibly corresponds to an ancestral feature of modern taxodiaceous Cupressaceae.

Fossil woods with mixed radial pitting and closely related to taxodiaceous Cupressaceae were firstly named *Prototaxodioxylon* by Vogellehner (1968). This genus was not based on proper observations by Vogellehner but on an erroneous interpretation of cross-fields pits in the wood *Protocupressinoxylon chouberti* Attims (1965), from Morocco. Moreover this last wood deposited in the “Laboratoire de Paléobotanique-Paris” was reexamined by Nadjafi (1982) who discovered the presence of true spiral thickenings like in the family Taxaceae. So, Nadjafi attributed it to *Prototaxoxylon* Kräusel & Dolianiti (1958). Consequently it was impossible to consider the *Prototaxodioxylon* genus as valid. Nadjafi proposed the name *Metataxodioxylon* for such woods related to the former Taxodiaceae and without spiral thickenings. Unfortunately this last name has never been published, so it is invalid. Following the determination key to morphogenera of Mesozoic conifer-like woods by Philippe & Bamford (2008), we can attribute our Spanish wood to the genus *Protaxodioxylon* Bamford & Philippe (2001) characterized by mixed radial tracheid pitting and taxodioid cross-field pits. To our knowledge this genus comprises one single species *Protaxodioxylon romanensis* (Philippe) Bamford & Philippe (2001), known from the Lower Toarcian of Doubs, France and Lower Pliensbachian of Bas-Rhin, France. Our specimens are close to *P. romanensis* but the absence of growth rings and the ray height (*P. romanensis* has lower rays) led us to create a new species *P. turolense*. It is interesting to notice that during the Jurassic, can be found structures with mixed radial pitting and true abietinean radial pitting, so *Taxodioxylon lemoignei* Philippe (1994) from the Oxfordian of Bourgogne, France, has a typical abietoid radial pitting, and is very close to *Taxodioxylon gypsaceum* (Göppert) Kräusel, 1949. Later on, some wood specimens were attributed to the genus *Protaxodioxylon* (Philippe *et al.* 2006, 2010, Philippe pers. comm.) (cf. list hereafter):

– Hungary: Pécsbányatelep: Sinemurian or Hetangian given as *Taxodioxylon* sp. by Greguss & Kedves (Philippe & Barbacka 1997);



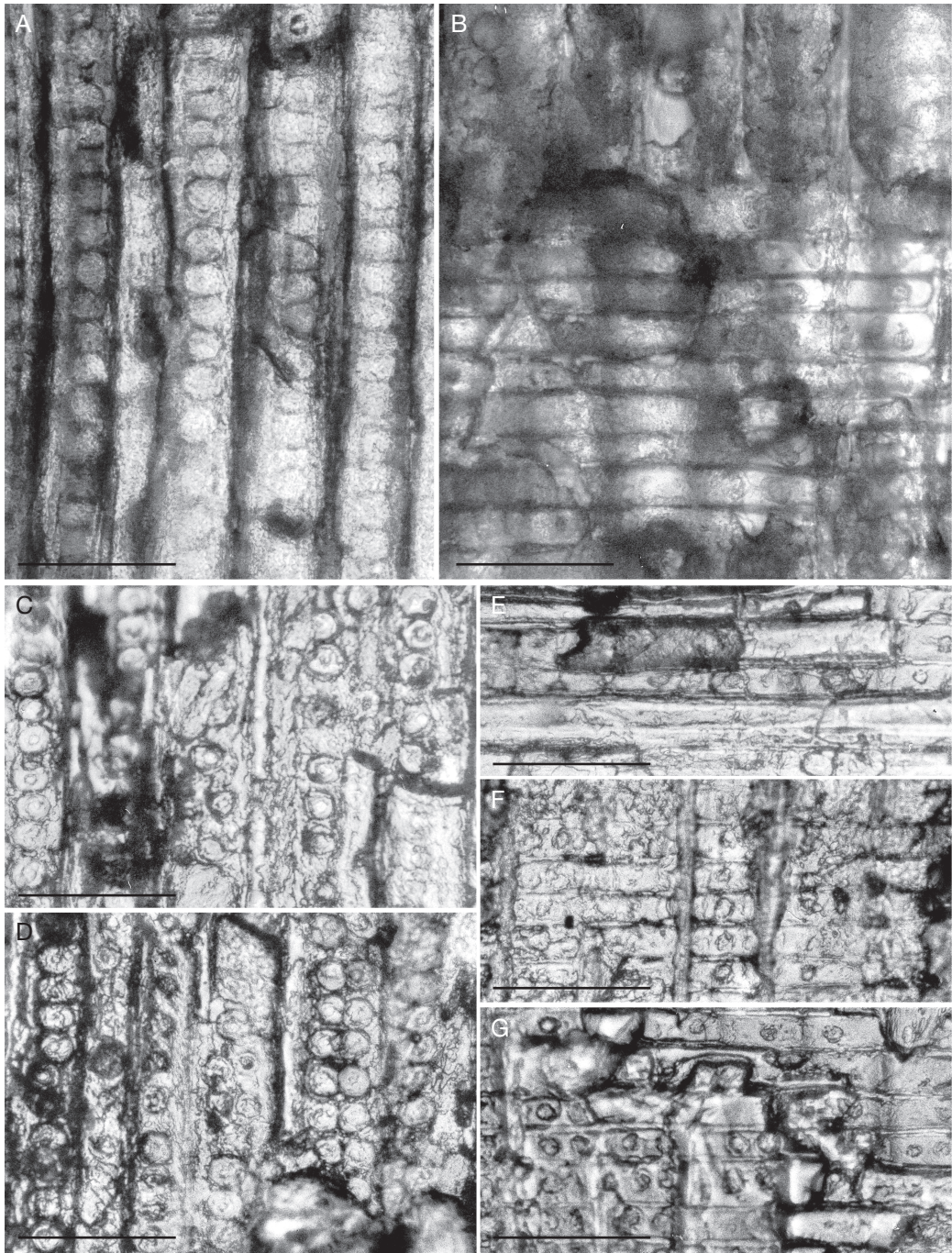


FIG. 4. — *Protaxodioxylon turolense* n. sp., radial sections: **A, B, E, G**, holotype MPZ 97/2514; **C, D, F**, paratype MPZ 97/2504; **A**, araucarioid uniseriate radial pitting; **B**, smooth and thin tangential walls in ray cells and araucarioid uniseriate radial pitting; **C**, mixed radial uniseriate pits with araucarian affinity; **D**, abietoid bordered pits on the radial walls of the tracheids and crassulae; **E**, smooth horizontal walls of ray cells and taxodioid cross-field pits; **F, G**, distribution of taxodioid cross-field pits. Scale bars: 100  $\mu$ m.

Vasas and Pecs: Hettangian (Philippe *et al.* 2006).  
– Poland: Gnaszyn: Bathonian (Philippe *et al.* 2006).

– France: Lixhausen, Bas-Rhin: Bathonian (Süss & Philippe 1993);

La Grandville, Ardennes: Hettangian (Thévenard *et al.* 1995);

Romains, Doubs: Toarcian (Philippe 1995);

Larzac, Aveyron: Middle Bathonian (Garcia *et al.* 1998);

Essonne: Middle Callovian (Garcia *et al.* 1998).

– Portugal: Guimarães: Kimmeridgian (Mohr & Schultka 2000; Philippe *et al.* 2010).

– England: Cleveland Basin, North Yorkshire given as *Taxodioxylon* spp.: late Pliensbachian Cleveland Ironstone Formation to late Bathonian Scalby Formation (Morgans 1999).

The anatomy of these woods could be precised in order to know if they belong to different species. All of them are Jurassic in age.

Otherwise Iamandei & Iamandei (2004) created a new species attributed to the genus *Prototaxodioxylon*: *P. marisii* without any mention of the former genus *Protaxodioxylon* creation by Bamford & Philippe (2001). *Prototaxodioxylon marisii* comes from the late Cretaceous-early Tertiary of Romania and there is an ambiguity between the description and the illustrations: textfig. 3 of Iamandei & Iamandei (2004) shows abietoid and araucarioid radial pitting with cupressoid cross-field pits and not taxodioid, while radial pitting in pl. I is clearly araucarioid and cross-fields pits indistinct. Further precision would be necessary.

Taxodiaceous woods have been mainly identified from Upper Cretaceous to Cenozoic sediments. In addition to the morphogenus *Protaxodioxylon*, some species referred to *Taxodioxylon* were also recorded from the Jurassic and Lower Cretaceous:

– *Taxodioxylon lemoignei* Philippe, 1994 (= *Dadoxylon* sp. of Lemoigne & Thierry 1968) from the Jurassic (Oxfordian) of France with uniseriate or biseriate abietoid radial pitting, and 1-3 (4) taxodioid cross-field pits in the earlywood cross-fields.

– *Taxodioxylon* sp. from the Wealden facies of the Mons Basin, Belgium (Gerards *et al.* 2007).

– *Taxodioxylon szei* Yang & Zheng, 2003, Lower Cretaceous of the Jixi Basin, China shows 1-3 – seriate abietoid pitting, abundant wood parenchyma, rays (1-50 cells high) with some idioblasts and 1-6 taxodioid pits in cross-fields.

– *Taxodioxylon albertense* (Pen.) Shimakura 1937, known from Canada, USA, Japan (Barremian to Santonian) is characterized by abietoid pitting surrounded by bars of Sanio and rays very high (up to 70 cells).

– *Taxodioxylon* sp. (Falcon-Lang *et al.* 2007) discovered in the Lower Cretaceous Chaswood Formation (Canada), preserved as charcoal, is characterized by opposite radial pitting, taxodioid cross-fields and absence of axial parenchyma.

In the high latitudes (78°N), Harland *et al.* (2007) collected permineralized woods from the South Spitzberg (Aptian/Albian). *Taxodioxylon* was the dominant morphogenus amongst the conifers (25% of the sampled set).

In the southern hemisphere, podocarps and araucarian conifer forests associated with some Taxodiaceae are known in the late Albian of SE Alexander Island and Antarctic Peninsula, palaeolatitude 75°S (Falcon-Lang & Cantrill 2000; Falcon-Lang *et al.* 2001). The Alexander Island taxon (*Taxodioxylon*) is fairly similar to *T. lemoignei* described in France.

Undeniably, the anatomical characteristics of the “El Barranquillo” specimens fit well into the morphogenus *Protaxodioxylon*. Our wood indicates that *Protaxodioxylon*, known till now from Jurassic only, might have extended at least during the Lower Cretaceous.

## PALAEOGEOGRAPHIC AND PALAEOECOLOGICAL CONTRIBUTIONS

It is known that the Cretaceous was an era of warm climate, especially in the equatorial zones (Vakhrameev 1991). The position of the Iberian Peninsula during this epoch, as an arm of the Tethys between 20 and 30°N (Masse *et al.* 1993), lies in the subtropical climatic band in the northern hemisphere, according to Smiley (1967) and Vakhrameev (1991). In the early Albian, a general

occurrence of coal deposits reflected a humid climate (Vakhrameev 1991).

During the Albian, the deposits of the Escucha and Utrillas formations took place. In the case of the Escucha Fm, the sedimentological (Pardo 1979; Querol & Salas 1988; Pardo *et al.* 1991) and palaeontological data (Solé de Porta & Salas 1994) indicate that the climate was subtropical, warm and humid during that time.

The climatic conditions prevailing in the area of deposition of the Utrillas Formation appear as a persistence of the subtropical climate that characterized the deposit of the underlying formations. This climatic interpretation has been confirmed by studies of pollen grains and spores carried out by Solé de Porta & Salas (1994), and backed up by the petrological characteristics of the sediments. As a matter of fact, a subtropical, warm and humid climate, is deduced from the presence of large quantities of iron oxides and the high percentage of kaolinite in the formation (Marfil & Gómez-Gras 1992) resulting from the change in the original feldspars.

In palaeogeographic terms the fossil wood found in El Barranquillo provide valuable information. None of the studied samples shows growth rings, that is to say, their tracheids have a constant diameter throughout the entire growth process. The formation of growth rings in the wood of vascular plants is directly related to environmental conditions in which the plants grow (Creber & Chaloner 1985; Creber & Francis 1999).

The absence of growth rings in the woods found in El Barranquillo indicates that throughout the life cycle of the trees, the dominant climate during the deposit of the Utrillas Formation in the northwestern sector of the Maestrazgo was not distinctly seasonal.

Modern representatives of the Sequoioideae are restricted to very limited areas in the northern hemisphere, where the climate is humid, the temperature is low and the seasons are marked. *Sequoia* and *Sequoiadendron* are limited to the west coast of the USA, and *Metasequoia* to southern China. In both cases the genera are part of humid forests close to mountain chains. This specific location is due to the displacement that

the conifers have undergone since the middle of the Cretaceous when the angiosperms began their explosive radiation.

Fossil wood related to the subfamily Sequoioideae are well known during the Late Cretaceous. Their distribution is restricted to the northern hemisphere, along the west coast of the USA and Canada, Europa, and Eastern Asia (Blokchina 1995, 1997). No representative of the Sequoioideae has been described previously from the Iberian Peninsula for this age. The finding in the Iberian Range of *Protaxodioxylon turolense*, which may be an ancestral form of the subfamily of Sequoioideae Saxton (Farjon 2005), would indicate that in the late Albian this subfamily had already individualized within the Cupressaceae.

The development of vegetation in the study zone, favoured by the influence of a subtropical climate without marked seasons, and by high levels of precipitation along the river banks, must have been of great importance. The selection that occurred during the taphonomic processes was responsible for the finding in the site of the taxon represented by silicified fossil wood and led to the identification of the subfamily Sequoioideae. This taxon may have formed part of a large conifer forest.

## CONCLUSIONS

The xylological study of the silicified fossil wood fragments found in the site has allowed us to propose a new taxon *Protaxodioxylon turolense*, which could be an ancestral form of the Sequoioideae clade. Fossils of this subfamily are known since the Barremian, therefore the findings of *P. turolense* confirm the appearance of the Sequoioideae during the Lower Cretaceous.

The extinct Sequoioideae would have been an element of a forest located along river banks (riparian forest). The site formed part of a region where vegetation might have been abundant, but whose remains need to be found.

Histological study of the fossil wood indicates that the subtropical climate in which they grew had no contrasted seasons, because the samples do not exhibit growth rings.

## Acknowledgements

This article is a contribution to projects CGL2008-00809/BTE. We thank Catherine Privé-Gill, Jean Broutin (Université Pierre et Marie Curie, Paris) and the two reviewers Jakub Sakala (Charles University, Prague) and Denise Pons (Université Pierre et Marie Curie, Paris) for their very useful comments on the manuscript. We wish to thank Marta Pérez Arlucea (Universidade de Vigo) for the corrections of the English text. Authors also thank the Grupo de Estudios Masinos y Museo de Mas de las Matas (Teruel) for their assistance and support in the fieldwork activities.

## REFERENCES

- AGUILAR M. J., RAMÍREZ DEL POZO J. & ORIOL RIBA A. 1971. — Algunas precisiones sobre la sedimentación y la paleoecología del Cretácico Inferior de la zona de Utrillas-Villaroya de los Pinares (Teruel). *Estudios geológicos* 27 (6): 497-512.
- ATTIMS Y. 1965. — *Contribution à l'étude des flores fossiles du Maroc*. PhD thesis, Faculty of Sciences, University of Paris, 190 p. (unpublished).
- BAILEY I. W. 1933. — The cambium and its derivative tissues, VII. Problems in identifying the wood of the mesozoic Coniferae. *Annals of Botany (London)* 47 (1): 145-157.
- BAILEY I. W. & FAULL A. F. 1934. — The cambium and its derivative tissues IX. Structural variability in the redwood, *Sequoia sempervirens*, and its significance in the identification of fossil woods. *Journal of the Arnold Arboretum* 15: 233-254.
- BAMFORD M. K. & PHILIPPE M. 2001. — Jurassic-Early Cretaceous Gondwanan homoxylous woods: a nomenclatural revision of the genera with taxonomic notes. *Review of Palaeobotany and Palynology* 113 (4): 287-297.
- BARALE G. & VIERA L. 1991. — Description d'une nouvelle paléoflore dans le Crétacé inférieur du Nord-Ouest de l'Espagne. *Munibe, Ciencias naturales* 43: 21-35.
- BLOKHINA N. I. 1995. — Petrified wood of *Metasequoia* from the Miocene of Kamchatka (Korfa Bay). *Paleontological Journal* 29 (1A): 103-112.
- BLOKHINA N. I. 1997. — Fossil wood of *Sequoioxylon chemrylicum* sp. nov. (Taxodiaceae) from the Paleogene of Chemurnaut Bay, Kamchatka. *Paleontological Journal* 31 (2): 235-238.
- BOUREAU E. 1949. — *Dadoxylon (Araucarioxylon) teixeirae* n. sp. bois fossile du Jurassique supérieur portugais. *Comunicações dos Serviços geológicos de Portugal* 29: 187-194.
- BOUREAU E. 1957. — Sur le *Protopodocarpoxyylon teixeirae* Boureau. Affinités. Répartition géographique. Signification stratigraphique. *Comunicações dos Serviços geológicos de Portugal* 38 (2): 423-430.
- BOUREAU E. & MOITINHO DE ALMEIDA F. 1951. — Sur l'âge du *Dadoxylon (Araucarioxylon) teixeirae* Boureau de Cadriceira (Portugal). *Comunicações dos Serviços geológicos de Portugal* 32: 5-6.
- CREBER G. T. & CHALONER W. G. 1985. — Tree growth in the Mesozoic and Early Tertiary and the reconstruction of palaeoclimates. *Palaeogeography, Palaeoclimatology, Palaeoecology* 52 (1-2): 35-60.
- CREBER G. T. & FRANCIS J. E. 1999. — Tree ring analysis: Palaeodendrochronology, in JONES T. & ROWE N. (eds), Fossil plants and spores: modern techniques. *Geological Society, Special publication*: 245-250.
- DEL NIDO J., GÓMEZ MANZANEQUE F., MASEDO F., MORLA C., ROIG S. & SÁNCHEZ HERNANDO L. J. 1998. — Identificación de un dendrolito en Cretácico inferior (Aptiense) del Sistema Ibérico Septentrional (La Rioja, España). Consideraciones paleoambientales. *Revue de Paléobiologie* 17: 513-523.
- DIEZ J. B., CANUDO J. I., FERRER J., MUÑOZ-BARRAGÁN P., RUIZ-OMENACA J. I. & SORIA A. R. 1996. — Transporte y resedimentación de tramos silicificados en el Albiense (Fm. Utrillas, Castellote, Cordillera Ibérica). Comunicación de la II Reunión de Tafonomía y Fossilización, Zaragoza: 97-102.
- DIEZ J. B., FERRER J., MUÑOZ-BARRAGÁN P., GÁMEZ-VINTANED J. A. & SORIA A. R. 1997. — Interés científico, sociocultural y didáctico del yacimiento paleontológico de troncos petrificados de "El Baranquillo" (Castellote, Teruel). *Mas de las Matas* 16: 89-110.
- DOUBLET S. & GARCIA J. P. 2004. — The significance of dropstones in a tropical lacustrine setting, eastern Cameros Basin (Late Jurassic-Early Cretaceous, Spain). *Sedimentary Geology* 163: 293-309.
- FALCON-LANG H. J. & CANTRILL D. J. 2000. — Cretaceous (Late Albian) coniferales of Alexander Island, Antarctica. 1: wood taxonomy; a quantitative approach. *Review of Palaeobotany and Palynology* 111 (1-2): 1-17.
- FALCON-LANG H. J., CANTRILL D. J. & NICHOLS G. J. 2001. — Biodiversity and terrestrial ecology of the mid-Cretaceous, high-latitude floodplain, Alexander Island, Antarctica. *Journal of the Geological Society* 158 (4): 709-724.
- FALCON-LANG H. J., FENSOME R. A., GIBLING M. R., MALCOLM J., FLETCHER R. & HOLLEMAN M. 2007. — Karst-related outliers of the Cretaceous Chaswood Formation of Maritime Canada. *Canadian Journal of Earth Sciences* 44: 619-642.
- FARJON A. 2005. — *A Monograph of Cupressaceae and Sciadopitya*, Royal Botanic Gardens, Kew, 648 p.
- GADEK P. A., ALPERS D. L., HESLEWOOD M. & QUINN

- C. J. 2000. — Relationships within Cupressaceae sensu lato: a combined morphological and molecular approach. *American Journal of Botany* 87 (7): 1044-1057.
- GARCÍA J.-P., PHILIPPE M. & GAUMET F. 1998. — Fossil wood in Middle-Upper Jurassic marine sedimentary cycles of France: relations with climate, sea-level dynamics, and carbonate-platform environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 141: 199-214.
- GARCÍA ESTEBAN L., PALACIOS P. DE, PHILIPPE M., GUINDEO A. & GARCIA FERNANDEZ F. 2006. — New xylogenetic data and the biogeography of the Iberian Peninsula during the Early Cretaceous. *Geobios* 39: 805-816.
- GERARDS T., YANS J. & GERRIENNE P. 2007. — Quelques implications paléoclimatiques de l'observation de bois fossiles du Wealdien du bassin de Mons (Belgique) – Résultats préliminaires, in STEEMANS P. & JAVAUX E. (eds), *Recent Advances in Palynology. Notebooks on Geology*, Brest. Mémoire 2007/01, Résumé 04 (CG2007\_M01/04).
- GOMEZ B., BARALE G., MARTIN CLOSAS C., THÉVENARD F. & PHILIPPE M. 1999. — Découverte d'une flore à Ginkgoales, Bennettiales et Coniférales dans le Crétacé inférieur de la Formation Escucha (Chaîne Ibérique Orientale, Teruel, Espagne). *Neues Jahrbuch für Geologie und Paläontologie*, Monatshefte 11:661-665.
- GOTHAN W. 1907. — Die fossilen Hölzer von König-Karls Land. *Kungliga svenska Vetenskapsakademiens Handlingar* 42 (10): 1-44.
- GRAMBAST L. 1960. — Évolution des structures ligneuses chez les Coniférophytes. *Bulletin de la Société botanique de France, Mémoire* 107: 30-41.
- GROMYKO D. V. 1982. — [A comparative-anatomical study of wood in the family Taxodiaceae]. *Botanichesky Zhurnal* 67 (7): 898-906 (in Russian).
- GUIMERÁ J. 1988. — *Estudi estructural de l'enllaç entre la Serralada Ibérica i la Serralada Costanera Catalana*. PhD thesis, University of Barcelona, 600 p. (unpublished).
- HARLAND M., FRANCIS J. E., BRENTNALL J. S. & BEERLING D. J. 2007. — Cretaceous (Albian-Aptian) conifer wood from northern hemisphere high latitudes: forest composition and palaeoclimate. *Review of Palaeobotany and Palynology* 143: 167-196.
- HOLLICK A. & JEFFREY E. C. 1909. — Studies of Cretaceous coniferous remains from Kreischerville, New York. *Memoirs of the New York Botanical Garden* 3: 1-137.
- IAMANDEI E. & IAMANDEI S. 2004. — New conifer in late Cretaceous lignoflora from the South Apuseni. *Acta Palaeontologica Romaniaae* 4: 137-150.
- IAWA COMMITTEE 2004. — IAWA list of microscopic features for softwood identification. *IAWA Journal* 25: 1-70.
- KRÄUSEL R. 1917. — Die Bedeutung der Anatomie lebender und fossiler Hölzer für die Phylogenie der Koniferen. *Naturwissenschaftliche Wochenschrift, Jena* 16: 305-311.
- KRÄUSEL R. 1949. — Die fossilen Koniferen-Hölzer (Unter Ausschluss von *Araucarioxylon* Kraus). II Teil. Kritische Untersuchungen zur Diagnostik lebender und fossiler Koniferen-Hölzer. *Palaeontographica*, Abteilung B, 89 (4-6): 83-203.
- KRÄUSEL R. & DOLIANITI E. 1958. — Gymnospermenhölzer aus dem Paläozoikum Brasiliens. *Palaeontographica* B 104 (4-6): 115-137.
- LAUVERJAT J. & PONS D. 1980. — Le gisement sénonien d'Esgueira (Portugal): stratigraphie et flore fossile. *103<sup>e</sup> Congrès national des Sociétés savantes*, Nancy 1978, sciences, fascicule II: 119-137.
- LEMOIGNE Y. & THIERRY J. 1968. — La paléoflore du Jurassique moyen de Bourgogne. *Bulletin de la Société géologique de France* 10: 323-333.
- LEMOIGNE Y. & MARIN P. 1972. — Bois silicifiés du Crétacé inférieur continental de la province de Teruel (Espagne). *Bulletin mensuel de la Société linnéenne de Lyon* 10: 201-214.
- LOTZE F. 1929. — Stratigraphie und Tektonik des keltiberischen Grundgebirges (Spanien). *Abhandlungen der K. Gesellschaft der Wissenschaften zu Göttingen, Mathematisch-physikalische Klasse*, Neue Folge 14 (2): 320 p.
- MARFIL R. & GÓMEZ-GRAS D. 1992. — Procedencia y modelo diagenético de las areniscas de facies Utrillas en la Cordillera Ibérica (Umbrales de Ateca) y la Meseta Norcastellana. *Revista de la Sociedad Geológica de España* 5 (3-4): 101-115.
- MASSE J. P., BELLION Y., BENKHELIL J., BOULIN J., CORNEE J. J., DERCOURT J., GUIRAUD R., MASCLE G., POISSON A., RICOU L. E. & SANDULESCU M. 1993. — Lower Aptian (114-112 Ma), in DERCOURT J., RICOU L. E. & VRIELYNCK B. (eds), *Atlas Tethys Palaeoenvironmental Maps*. BEICIP-FRANLAB, Rueil-Malmaison, 307 p.
- MOHR B. & SCHULTKA S. 2000. — The flora of the Guimarota mine: 27-32, in MARTIN T., KREBS B. (eds), *Guimarota: a Jurassic Ecosystem*. Verlag Dr Friedrich Pfeil, Munich, 155 p.
- MORGANS H. S. 1999. — Lower and middle Jurassic woods of the Cleveland Basin (North Yorkshire), England. *Palaeontology* 42 (2): 303-328.
- MUÑOZ-BARRAGÁN P., DIEZ J. B., FERRER J. & SORIA A. R. 1999. — Tafonomía de los troncos silicificados albienses del yacimiento de "El Barranquillo" (Castellote, Provincia de Teruel, España). *Revista Española de Paleontología* 14 (2): 165-172.
- NADJAFI A. 1982. — *Contribution à la connaissance de la flore ligneuse du Jurassique d'Iran*. PhD thesis, University of Paris VI, 110 p. [unpublished].
- PARDO G. 1979. — *Estratigrafía y sedimentología de las*

- formaciones detríticas del Cretácico inferior terminal en el Bajo Aragón Turoloense. PhD thesis, University of Zaragoza, 470 p. (unpublished).
- PARDO G., ARDEVOL L. & VILLENA J. 1991. — Informe sedimentológico de las formaciones Utrillas y Escucha., *Memoria del Mapa Geológico de España 1:200.000* (Daroca) 40, IGME, 101-112.
- PHILIPPE M. 1994. — Radiation précoce des conifères Taxodiaceae (Coniférales) et bois affines du Jurassique de France. *Lethaia* 27 (1): 67-75.
- PHILIPPE M. 1995. Bois fossiles du Jurassique de Franche-Comté (nord-est de la France): systématique et biogéographie. *Palaeontographica B* 236: 45-103.
- PHILIPPE M. & BAMFORD M. K. 2008. — A key to morphogenera used for Mesozoic conifer-like woods. *Review of Palaeobotany and Palynology* 148: 184-207.
- PHILIPPE M. & BARBACKA M. 1997. — A reappraisal of the jurassic woods from Hungary. *Annales historico-naturales Musei nationalis hungarici* 89: 11-22.
- PHILIPPE M., BARBACKA M., GRADINARU E., IAMANDEI E., IAMANDEI S., KAZMER M., POPA M., SZAKMANY G., TCHOUMATCHENCO P. & ZATON M. 2006. — Fossil wood and Mid-Eastern Europe terrestrial palaeobiogeography during the Jurassic-Early Cretaceous interval *Review of Palaeobotany and Palynology* 142: 15-32.
- PHILIPPE M., BILLON-BRUYAT J.-P., GARCIA-RAMOS J. C., BOCAT L., GOMEZ B. & PIÑUELA L. 2010. — New occurrences of the wood *Protocupressinoxylon purbeckensis* Francis: implications for terrestrial biomes in southwestern Europe at the Jurassic/Cretaceous boundary. *Palaeontology* 53 (1): 201-214.
- PHILLIPS E. W. J. 1948. — Identification of softwoods by their microscopic structure. *Forest Product Research Bulletin* 22: 101-107.
- QUEROL X. & SALAS R. 1988. — El sistema deposicional deltaico del Albiense medio de la cuenca del Maestrazgo-Cordillera Ibérica Oriental. *Resúmenes y Comunicaciones del II Congreso de Geología de España, Granada, Sección de Estratigrafía-Sedimentología I*: 173-176.
- SALAS R. 1987. — *El Malm i el Cretaci inferior entre el massis de Garrafi la Serra d'Espadà. Anàlisi de Conca*. PhD thesis, University of Barcelona, 345 p. (unpublished).
- SHIMAKURA M. 1937. — Studies on fossil woods from Japan and adjacent lands, Contribution II. The Cretaceous woods from Japan, Saghalian and Manchoukuo. *The Science reports of Tohoku Imperial University, Ser. 2, Geol.* 19 (1): 1-73.
- SMILEY C. J. 1967. — Paleoclimatic interpretations of some Mesozoic floral sequences. *American Association of Petroleum Geologist Bulletin* 51 (6), 849-863.
- SOLÉ DE PORTA N. & SALAS R. 1994. — Conjuntos microfiorísticos del Cretácico Inferior de la Cuenca del Maestrazgo. Cordillera Ibérica Oriental (NE de España). *Cuadernos de Geología Ibérica* 18: 355-368.
- SÜSS H. & PHILIPPE M. 1993. — Holzanatomische Untersuchungen an einem fossilen Holz *Circoporoxylon grandiporosum* Müller-Stoll & Schultze-Motel, aus dem Unteren Jura von Elsass (Frankreich). *Feddes Repertorium* 103: 411-456.
- THÉVENARD F., PHILIPPE M. & BARALE G. 1995. — Le delta hettangien de la Grandville (Ardennes, France): étude paléobotanique et paléocéologique. *Geobios* 28 (2): 145-162.
- VAKHRAMEEV V. A. 1991. — *Jurassic and Cretaceous floras and climates of the Earth*, Cambridge University Press, Cambridge, 318 p.
- VALENZUELA M., DIAZ GONZALEZ T. E., GUTIERREZ VILLARIAS I. & SUAREZ DE CENTI C. 1998. — La Formación Lastres del Kimmeridgiense de Asturias: sedimentología y estudio paleobotánico inicial. *Cuadernos de Geología Ibérica* 24: 141-171.
- VOGELLEHNER D. 1968. — Zur Anatomie und Phylogenie mesozoischer Gymnospermenhölzer, Beitrag 7: Prodromus zu einer Monographie der Protopinaceae. II: Die Protopinoiden Hölzer der Jura. *Palaeontographica* 124 B: 125-162.
- YANG XIAO-JU & ZHENG SHAO-LIN 2003. — A new species of *Taxodiioxylon* from the Lower Cretaceous of the Jixi Basin, eastern Heilongjiang, China. *Cretaceous Research* 24: 653-660.

Submitted on 5 March 2010;  
accepted on 2 February 2011.