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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**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.

INTRODUCTION

Palaeoxylological 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 Pilón 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 Catalan 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 decimetric 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 overlains 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.

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

RÉSUMÉ
Une nouvelle espèce de Protaxodioxylon (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.
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Cuenca
Cenozoic
Cretaceous
Triassic + Jurassic
Palaeozoic
Quaternary
Oligocene-Pliocene
Cenomanian-Turonian
Utrillas Fm. Albian
Escucha Fm. Upper Aptian
Hauterivian-Barremian
Jurassic
Site location
Anticlinal
Synclinal
Fault
Thursts Front
Dip

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

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

<table>
<thead>
<tr>
<th>Specimens</th>
<th>Locality</th>
<th>Age</th>
<th>References</th>
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<tbody>
<tr>
<td><strong>Spain</strong></td>
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<tr>
<td>Cupressinoxylon hortii</td>
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<td>Berriasian-Barremian</td>
<td>Lemoigne &amp; Marin 1972</td>
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<tr>
<td>Dadoxylon (Araucarioxylon) sp.</td>
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<td>Xenoxylon sp.</td>
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<tr>
<td>Agathoxylon sp.</td>
<td>Teruel Province</td>
<td>Albian</td>
<td>Gomez et al. 1999</td>
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<tr>
<td>Not identified (described in this work)</td>
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<td>Albian</td>
<td>Diez et al. 1996; Muñoz Barragán et al. 1999</td>
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<td>Dadoxylon (Araucarioxylon) riojense</td>
<td>Igea, La Rioja Province</td>
<td>Valanginian-Hauterivian</td>
<td>Barale &amp; Viera 1991</td>
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<td>Aptian</td>
<td>Del Nido et al. 1998</td>
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<td>Agathoxylon riojense</td>
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<td>? Aptian</td>
<td>Doublet &amp; Garcia 2004</td>
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<td>Hacinas Cameros Basin, Burgos Province</td>
<td>Barremian-Aptian</td>
<td>Garcia Esteban et al. 2006</td>
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<td>Asturias Province</td>
<td>Kimmeridgian</td>
<td>Valenzuela et al. 1998</td>
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<td>Terres and Lastres formations</td>
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<td>Philippe et al. 2010</td>
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<td><strong>Portugal</strong></td>
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<td>Prototaxodioxylon sp. = Prototaxodioxylon sp. in Philipp et al. 2010</td>
<td>Guimarota near Leiria</td>
<td>Kimmeridgian</td>
<td>Mohr &amp; Schultka 2000</td>
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<td>Dadoxylon (Araucarioxylon) teixeirae</td>
<td>Cadriceria</td>
<td>Boundary</td>
<td>Boureau 1949, 1957; Boureau &amp; Moliño de Almeida 1951</td>
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<td>(Boureau)</td>
<td>South of Torres Vedras</td>
<td>Hauterivian-Barremian</td>
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<tr>
<td>Protodadoxylon aveiroense (Lauverjat et Pons, 1980)</td>
<td>Esgueira near Aveiro</td>
<td>Senonian</td>
<td>Lauverjat &amp; Pons 1980</td>
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<td>Beira Littorale Province</td>
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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.

PALAEOXYLOGICAL 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 paleoxylology.

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 recrystalization. (Diez et al. 1997; Muñoz-Barragán et al. 1999).

For this palaeoxylological 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

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.

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**

Homoxyleous 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 mm² 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
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**Fig. 3.** — *Protaxodioxylon turolense* Vozenin-Serra, n. sp. (holotype MPZ 97/2514): **A**, transverse section without growth rings; **B**, tangential section showing uni- or partly biseriate rays and abundant axial parenchyma; **C**, tangential view of smooth transverse end wall in axial parenchyma. Scale bars: 100 μm.
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 Albion of El Barranquillo with fossil and modern species of the Sequoioidae 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 Prototaxodiocolylon 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 Prototaxodiocolylon Kräusel & Dolianiti (1958). Consequently it was impossible to consider the Prototaxodiocolylon genus as valid. Nadjafi proposed the name Metataxodiocolylon 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 Prototaxodiocolylon Bamford & Philippe (2001) characterized by mixed radial tracheid pitting and taxodioid cross-field pits. To our knowledge this genus comprises one single species Prototaxodiocolylon 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 Prototaxodiocolylon romanensis but the absence of growth rings and the ray height (P. romanensis has lower rays) led us to create a new species Prototaxodiocolylon turolense. It is interesting to notice that during the Jurassic, can be found structures with mixed radial pitting and true abietinean radial pitting, so Taxodiocolylon lemoignei Philippe (1994) from the Oxfordian of Bourgogne, France, has a typical abietoid radial pitting, and is very close to Taxodiocolylon gypsaicum (Göppert) Kräusel, 1949. Later on, some wood specimens were attributed to the genus Prototaxodiocolylon (Philippe et al. 2006, 2010, Philippe pers. comm.) (cf. list hereafter):

– Hungary: Pécsbányatelep: Sinemurian or Hettangian given as Taxodiocolylon sp. by Greguss & Kedves (Philippe & Barbacka 1997);
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**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 μm.
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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);
Romain, Doubs: Toarcian (Philippe 1995);
Larzac, Aveyron: Middle Bathonian (Garcia et al. 1998);
Essonne: Middle Callovian (Garcia et al. 1998).
– Portugal: Guimarota: 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 Protaxodioxylon: P. marisii without any mention of the former genus Protaxodioxylon creation by Bamford & Philippe (2001). Protaxodioxylon 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 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, paleolatitude 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 Portas & 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 (Blokhina 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.
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