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Palaeoenvironmental interpretation of the Neogene locality Caranceja (Reocín, Cantabria, N Spain) from comparative studies of wood, charcoal, and pollen

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Abstract

Construction of a highway in Northern Spain uncovered a large amount of plant fossils that were generally in a good state of conservation. In this paper, we specifically analysed 243 small fragments of charcoal and wood that were not totally carbonised, along with seven samples of pollen. We applied Mosbrugger and Utescher's [Palaeogeogr. Palaeoclimatol. Palaeoecol. 134 (1997) 61] "Coexistence Approach" to the results in order to calculate palaeoclimatic parameters.

The presence of some extinct taxa (Taxodiaceae) enabled us to improve the dating from a previous geological study and to date the Caranceja fossil remains at the end of the Pliocene. In the Upper Pliocene, the old Saja Valley was covered by a very dense coniferous forest, with the presence of several angiosperms, with a more or less developed understorey of *Ericaceae*, depending on the period. This forest existed in temperate, fresh, and humid conditions, although it was subjected to a certain continentality that anticipated quaternary climatic oscillations.

This represents one of the richest finds made to date in the Iberian Peninsula, with regard to quantity and diversity of materials, and is the most important one of fossil wood from the Iberian Neogene.

Keywords: Upper Pliocene; fossil wood; pollen; palaeoclimate; Spain

1. Introduction

In the Caranceja site, in Cantabria, Northern Spain, the building works of a highway outcropped numerous fossil plants dated as Neogene. This locality has provided a great quantity of well-preserved materials, especially wood, charcoal, and cones, among other macro- and microfossils. They can contribute valuable palaeobotanical information from a place (Iberian Peninsula) and an age (Mio-Pliocene) of which little was heretofore known. The quantitative and qualitative richness of this discovery can be highlighted. By the kind of materials and their age, they can be related to the studies of Huard and Lavocat

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(1963), Huard and Klingebiel (1965), and Huard (1966, 1967, 1974), or to the studies in the Lower Rhine Basin (Schloemer-Jäger, 1960; Kilpper, 1967, 1968a,b,c; Burgh, 1964, 1973, 1983; Minnigerode, 1986; Figueiral et al., 1999), all of them in lignite mines. Nevertheless, in Caranceja, it is surprising that in a relatively small area so many fossil remains, and especially such well-preserved materials were found. The aim of this paper is to determine the charcoal and woody fossil remains found in the Caranceja site and to contrast them with pollen analysis. These fossils can provide many new data from the palaeoenvironmental reconstruction of the Iberian Peninsula for which neogene floral data are scarce (Álvarez Ramis and Golpe Possé, 1981; Baltuille et al., 1992; Barrón et al., 1996; Barrón and Santisteban, 1999; Bessedik and Cabrera, 1985; Diniz, 1967, Diniz and Sivak, 1979; Geurts, 1977; Médus, 1965; Meléndez Meléndez, 1949; Menéndez Amor, 1955; Michaux et al., 1979; Pais, 1972, 1973a,b, 1978, 1979; Rivas Carballo (1986, 1991); Rivas Carballo and Valle, 1986, 1990; Roiron, 1983; Roiron et al., 1999; Sanz de Siria, 1979–1987; Sole de Porta and Porta, 1976; Suc and Cravatte, 1982; Teixeira, 1943–1973; Valle et al., 1995; Valle and Civis, 1977; Villalta and Crusafont, 1945; Villalta and Vicente, 1972). We used a relatively new technique, the "Coexistence Approach" (Mosbrugger and Utescher, 1997), to calculate palaeoclimate values for this locality. The evolution of forest landscape and the response of the flora to climatic changes can help us to understand the dynamics of forest ecosystems.

2. Study area

Works to build the "Cantábrico" Highway uncovered plant fossil remains that were buried several

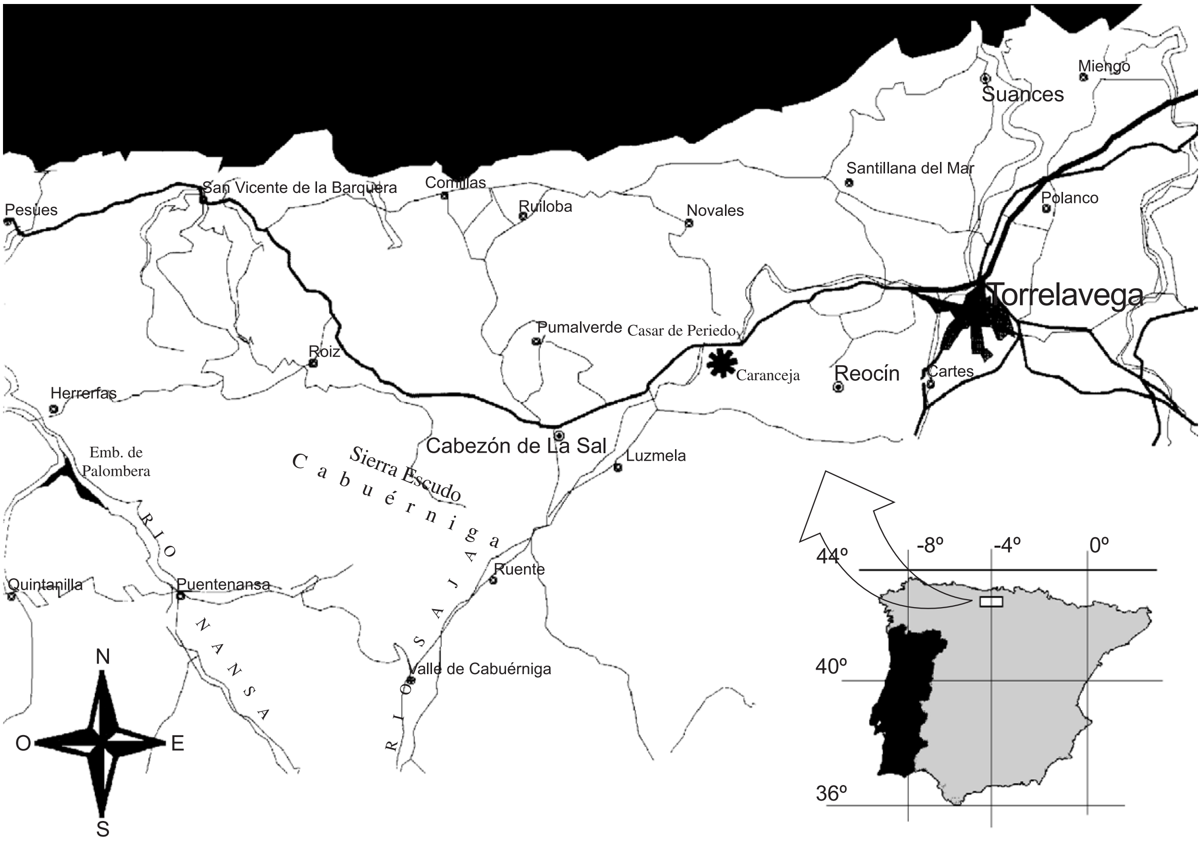

Fig. 1. Location of the Caranceja site (∗).

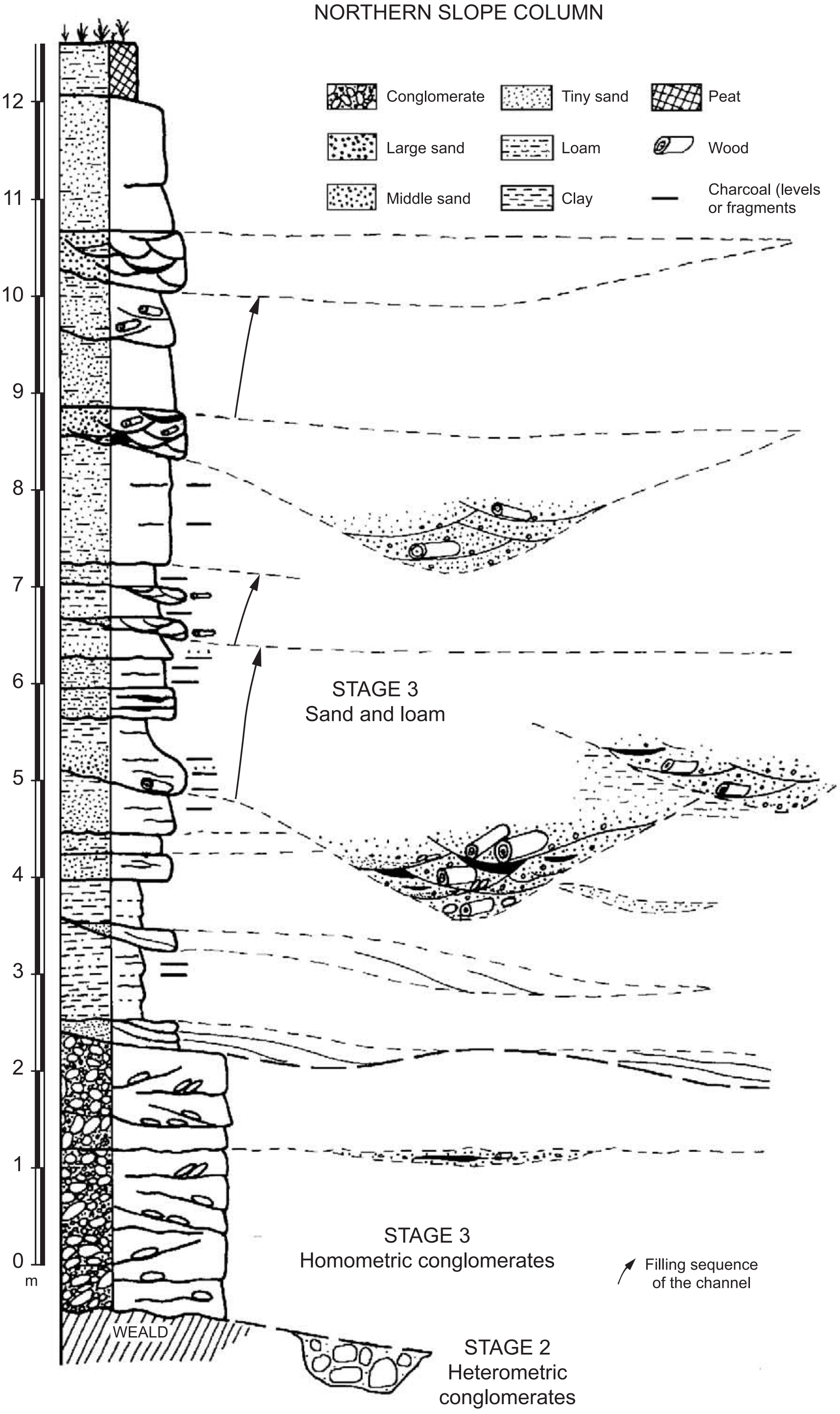

Fig. 2. Stratigraphic column (modified from Alonso et al., 1999).

meters deep, near Caranceja, in the municipality of Reocín (Cantabria, Northern Spain) (Fig. 1). The finding is situated 25 km from Santander on the Torrelavega–Cabezón de la Sal Highway, in the coordinates 49°19′N 4°12′W. Most fossils were collected in situ from the slope made by excavators, whereas the workers had previously extracted others.

Prospection works began in 1996 and fieldwork was carried out until 1997. Collection of materials had to be rushed, as construction of the highway was to continue. Identification of the samples began at that time, but the diversity and quantity of materials caused a considerable delay in this respect.

The deposit is in a hilly area, developed on the siliciclastic Facies Weald of the lower Cretaceous, where the Saja River has traced its course. It is located on a 190-m high plain, in the north of a small elevation running from east to west, at an altitude of 240 m. Situated to the south and separated by a valley are the Ibio Mountains. To the north the plain limits with the present valley of the Saja River.

The substrate here is formed by loam, limonitic clay, and some layers of sandstone. The geological study (Alonso et al., 1999) showed that an old fluvial stream was fitted in the sandy–clay facies from the lower Cretaceous (Weald). The palaeovalley was filled with a sequence of decreasing granulometry running in an upward direction, ranging from gravel to muddy white sands and limes. At these upper levels, we find pieces of wood, charcoal, and other vegetal rests.

The evolution of the system can be separated into four stages (Fig. 2):

1. Stage of torrential regime: small valley or stream that received materials from the slopes, heterometric.
2. Organisation of channel: the river becomes wider and shallower, with a gravel floor.
3. Sandy channel: even wider channel and more meandering. Many trunks beached in the direction of the stream.
4. Reduction of the channel to the south and increase of energy. The northern slope becomes a flood plain with a peat bog.

Alonso et al. (1999) studied the geomorphology of the site and compared it with the regional information, in accordance with other geological research in the area. They conclude that the deposit constitutes an old channel of the Saja River, independent from its present valley and belonging to a different tectonosedimentareous cycle. With the use of stratigraphy and geomorphology, these authors date the sediments between 300,000 years BP and the Pliocene.

3. Materials and methods

Large diameter fossil trunks (up to 70 cm), a great amount of rather well-preserved strobili of different species, and some other fossil remains were found. Among these materials were also 243 pieces of wood charcoal and easily breakable wood, which are the object of the present paper. The study was completed with the analysis of several pollen samples from the same layers as macrofossils.

3.1. Wood analysis

Samples were collected from the upper layers of the third level in the profile. There are whitish silica sands in a lime–clay matrix. All the fragments collected in the same zone were identified with the same code. They were placed among other macrofossils, like big pieces of wood, cones, and twigs.

Most of the wood samples were completely carbonised. Only a small proportion was not totally burnt. The size of fragments is always smaller than 1 cm^3.

In the laboratory, they were washed by immersion in water and afterwards dried by simply leaving them covered with a piece of cloth. In order to identify the pieces of coal, they were just fractured along the three main planes of the wood: transversal, longitudinal radial, and longitudinal tangential. If the wood is well preserved, these planes are very easy to obtain. The planes were observed with reflected light microscope. This method usually provides enough information for a provisional identification. Afterwards, some selected fragments were examined using scanning electron microscopy (SEM).

Some pieces of wood were strongly compressed, and this hindered the diagnosis. Sometimes it was useful to prepare thin slides for microscopic observation of the wood anatomy. The procedure consisted of cutting the samples with the microtome after hydration. Afterwards they were dyed with safranine and placed on a microslide. These sections were observed by means of transmitted light. Dying and mounting are described in Roig et al. (1997).

The identification was made with the aid of common keys for this kind of work: Metcalfe and Chalk (1972), Greguss (1955, 1959), Jacquiot (1955), and Schweingruber (1990), in particular. The software for wood identification from the U.D. Tecnología de la Madera of the Escuela Técnica Superior de Ingenieros de Montes (Madrid, Spain) was also used. Wherever possible, samples were compared with reference collections: Laboratoire de Palèobotanique, Anthracologie et Etude de l'Homme, Institut de Botanique (Montpellier, France) and collections from the U.D. Tecnología de la Madera and U.D. Botánica of the Escuela Técnica Superior de Ingenieros de Montes (Madrid, Spain). Samples are kept in the U.D. Botánica, in E.T.S.I. Montes, in Madrid (Spain). They are identified by numbers PERA11S050397 to PERFS070601.

3.2. Pollen analysis

Seven equidistant samples were taken from the profile, 12 m thick. All of them come from the same layer of wood samples. The method used for the extraction of pollen and spores from these samples was the traditional chemical technique following Faegri and Iversen (1989). Between 350 and 500 pollen grains and spores were counted per sample in order to build a percentage pollen diagram. Calculation of the arboreal, shrubs, and herbs percentages was based on pollen sum. Spores and aquatic plants were excluded from this sum. The pollen diagram was plotted using the programs TILIA 2.0 and TILIA-GRAPH 2.0 (Grimm, 1992).

3.3. Coexistence approach

The "Coexistence Approach" method developed by Mosbrugger and Utescher (1997) was applied to the qualitative results of anthracologic and palynologic analysis. This is not the first time that the "Coexistence Approach" has been applied to both woody rests and pollen data (Figueiral et al., 1999; Figueiral and Mosbrugger, 2000).

This method is based in the assumption that taxa in the Neogen have a "Nearest Living Relative" (NLR) today and the climatic requirements of both taxa are the same. If we want to know the palaeoclima of a certain locality, we need to relate each taxon of the floral list to a NLR. For each climatic parameter, there is an interval in which this NLR can live. If we consider together the intervals for all NLRs, the most common interval for a certain climatic parameter will determine the rank in which all these taxa could coexist. So, this rank includes the value of the climatic parameter at that age of the locality. We have applied the method to both charcoal and pollen data.

4. Results

4.1. Wood identification

Table 1 shows the results of the identification of 243 fragments of charcoal and non-charcoalified wood belonging to 14 different taxa. In Figs. 3 and 4, a summary of the identified taxa and the number of samples for each one is shown.

A short description of the main features used for the identification is now given. Some fossils can only be distinguished at the family level or even higher as a result of poor preservation.

Gymnosperms

Taxodiaceae

Sequoia sp. (Plate I,1–2)

Description: Most of the samples are completely charcoalified and excellently preserved. Two of them have been prepared in thin section. Transversal section (Tr. S.): growth rings distinct, with abrupt transition from early wood to late wood. Tracheids with polygonal section in early wood. Only few rows of flattened tracheids in late wood. Tangential section (Tg. S.): rays 1 to 16 cells high, usually 3 to 9. Exceptionally they are biseriate. Wood parenchyma with smooth transversal walls. Radial section (R. S.): numerous bordered pits in radial walls of tracheids, often biseriate and even triseriate. They are placed in horizontal rows. Cross-field pits taxodioid, sometimes cupressoid. They are very abundant, 2 to 6 (8) per cross field. Frequently they are arranged in one row.

Table 1
Taxa found in the Caranceja deposit

Taxa	Number	Percent wood	Percent pollen
Sequoia sp.	41	16.87	0
cf. *Sequoia* sp.	25	10.29	0
Cryptomeria–*Cunninghamia*	15	6.7	0
cf. *Cryptomeria*–*Cunninghamia*	3	1.23	0
Taxodiaceae	3	1.23	0
cf. *Cupressaceae*	4	1.65	0.45
Cupressaceae–Taxodiaceae	20	8.23	0
Abies sp.	3	1.23	0.52
Picea–*Larix*	52	21.40	1.94
Cedrus	0	0	0.19
Pinus subgen. *haploxylon*	5	2.06	0
Pinus subgen. *diploxylon*	4	1.65	0
Pinus sp.	0	0	30.22
Unidentifiable conifers	22	9.05	0
Acer	0	0	0.04
Ilex sp.	5	2.06	1.05
Alnus	0	0	1.31
Betula sp.	5	2.06	1.91
cf. *Betula* sp.	5	2.06	0
Carpinus	0	0	0.30
Corylus	0	0	0.15
Castanea	0	0	4.86
Fagus sp.	5	2.06	0.93
Quercus sp.	6	2.47	0.75
Salix	0	0	0.04
Ulmus	0	0	0.07
Vaccinium sp.	5	2.06	0
cf. *Vaccinium* sp.	2	0.82	0
Ericaceae	4	1.65	42.99
Ligustrum	0	0	0.04
Phyllirea	0	0	0.04
Rhamnaceae	0	0	0.07
Hedera	0	0	0.07
Unidentifiable angiosperms	3	1.23	0
Unidentifiable	6	2.47	0
Total samples	243	100	87.88

**Pinus* sp.
For each one, number and percentage of woody remains and percentage of ligneous pollen grains are shown.

Identification: The presence of triseriate-bordered pits in longitudinal tracheids is very useful for the identification. This feature, in addition to the presence of taxodioid cross-field pits, is typical of the family Taxodiaceae. The genera, in which bi- and triseriate pits are common, are *Sequoia*, *Sequoiadendron*, *Metasequoia*, *Glyptostrobus*, and *Taxodium*. The latter ones have wood parenchyma with nodular transversal walls. *Metasequoia* has crassulae around the bordered pits when they are biseriate. *Sequoia* usually has higher rays—Huard (1966) does not agree with this feature, and most authors state that it never reaches as many as six pits in the cross field. Nevertheless, their arrangement and the thin walls of tracheids are typical of *Sequoia sempervirens* (D. Don) Endlicher. The descriptions by Greguss (1955) and Palacios (1997) of *Sequoiadendron giganteum* present-day wood are however applicable to the studied samples.

Wood of Taxodiaceae is usually called *Taxodioxylon* Hartig emend. Gothan. This parataxon includes woods related to *Sequoia*, *Sequoiadendron*, *Metasequoia*, *Taxodium*, *Cryptomeria*, and *Athrotaxis*. In the petrified forest of Lesbos (Greece), from the Upper Oligocene to the Lower Miocene, several species of *Taxodioxylon* were described by Süss and Velitzelos (1997). The wood found in Caranceja could be identified with *Taxodioxylon gypsaceum* (Goeppert) Kräusel. In the Upper Miocene in Arjuzanx (Landes, South-Western France), Huard (1966) also identified *T. gypsaceum* (Göppert) Kräuselas as well as Burgh (1973) in the Lower Rhine Basin. All authors relate this species to present-day *Sequoia sempervirens* and the descriptions of the fossil are completely applicable to samples from Caranceja.

Considering that *Sequoia* and *Sequoiadendron* are two taxonomically close genera, our samples share features of both taxa, and in European Tertiary only *Sequoia* or *Sequoioxylon* is described (Fernández

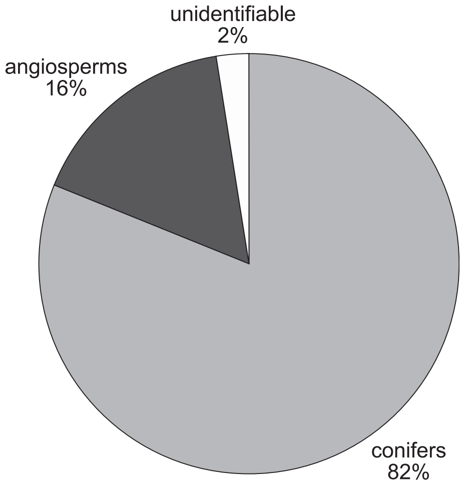

Fig. 3. Relative abundance of gymnosperms/angiosperms.

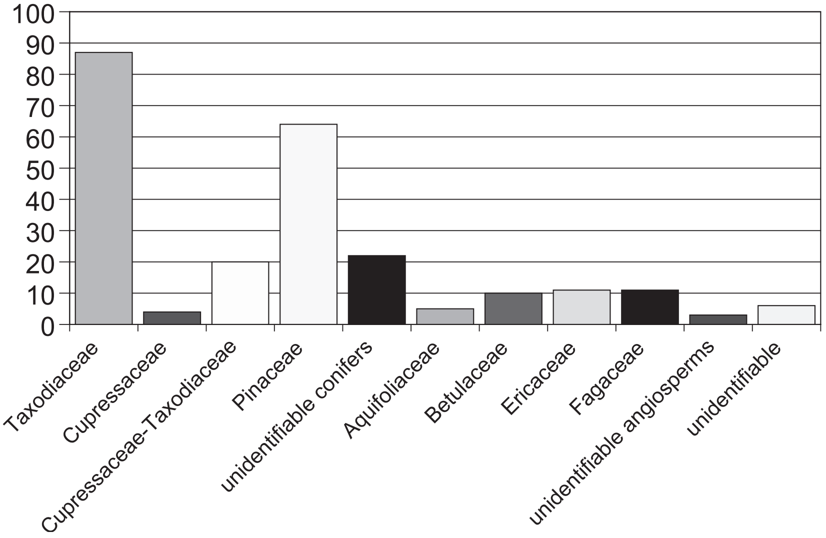

Fig. 4. Taxonomic distribution of analysed samples.

Marrón and Álvarez Ramis, 1967; Palmarev et al., 1991; Barrón and Santisteban, 1999), we have identified them as *Sequoia* sp.

Cryptomeria–Cunninghamia (Plate I,3–6)

Description: Tr. S.: Not completely charcoalified wood. In one sample, a thin section was prepared. Growth rings distinct, rather wide. Late wood in variable proportion, from 1/2 to 1/10 of ring width, even in contiguous rings. Sometimes there are false rings. Gradual transition from early wood to late wood. Tracheids with square section. Rays conspicuous in transverse section. Tg. S.: rays homogeneous, rather long, from 2 to 22 cells. There are some rays partially biseriate. R. S.: bordered pits on tracheids sometimes biseriate. Wood parenchyma with smooth transverse walls. Radial parenchyma with thin horizontal walls. Cross-field pits from 2 to 5, irregularly arranged. These pits are very wide and rounded, surrounded by a small border. Greguss (1955) calls this kind of pit "glyptostroboid".
Identification: The described cross-field pits are in fact a kind of taxodioid pit. They are characteristic of the family Taxodiaceae. These pits can be found in *Glyptostrobus*, *Cryptomeria*, and *Cunninghamia*. The pits of *Glyptostrobus* are very big, which is why we do not consider this genus.

We compared our samples with present-day wood from *Cunninghamia konishii* Hayata (*Cunninghamia lanceolata* var. *konishii*). This species usually has tall rays (up to 18 cells) and more pits in the cross field (2–4) than *Cryptomeria japonica* (L. fil) D.Don. Nevertheless, the form of our cross-field pits is typical of *Cryptomeria*. According to Greguss (1955), *C. japonica* sometimes presents biseriate or triseriate bordered pits. Its rays are frequently short. In cross-fields 1 or 2, exceptionally three pits are found. On the other hand, *C. lanceolata* (Lambert) Hoocker also shows biseriate pits and longer rays (about eight cells, up to 15) than *Cryptomeria*. One to five cross-field pits are rounded and placed in horizontal rows. Although our samples resemble this genus, we did not reject *Cryptomeria*.

Glyptostroboxylon microtracheidale Süss et Velitzelos was compared by its authors with *Cunninghamia lanceolata* (Süss and Velitzelos, 1997). Its description fits very well with the samples from Caranceja.

Taxodiaceae unidentifiable

Description: Tr. S.: Wide growth rings, gradual transition from early wood to late wood. Tracheids generally with square section, rounder in late wood. There are some false rings. Rays conspicuous. Tg. S.: tall rays, between 5 and 12 cells. Parenchyma


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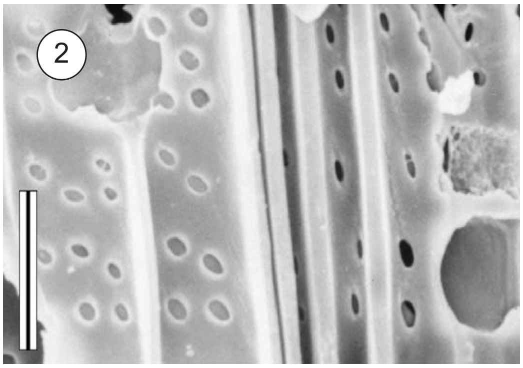
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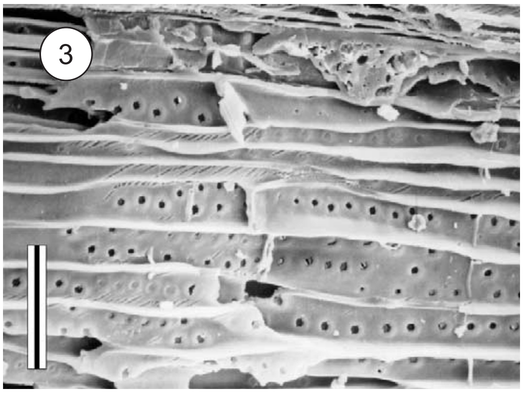
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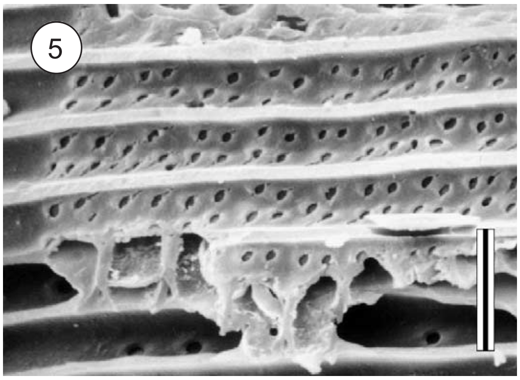
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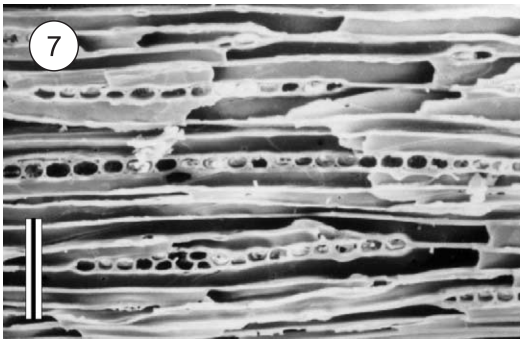
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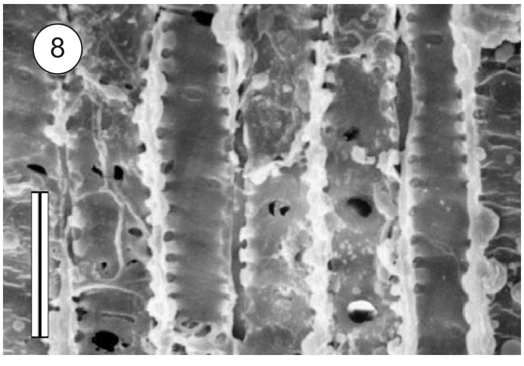
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cells rounded. R. S.: uniseriate-bordered pits in radial walls of tracheids, exceptionally biseriate. Wood parenchyma with smooth horizontal walls. Cross-field pits taxodioid, rather big, (2) 4 (6) per cross field.

Identification: In one sample, they look more cupressoid, but always with big lumen. Both samples have features like the ones that have been identified as *Cryptomeria–Cunninghamia*. Nevertheless, the conservation has been completely different because these samples are charcoalified. We cannot confirm that they belong to the same taxon, and therefore identified them at family level.

Cupressaceae

Description: Small pieces of poorly preserved coal. Tr. S.: growth rings distinct and narrow, with small proportion of late wood. Tracheids with thick walls. Some scattered cells have dark contents. Tg. S.: small bordered pits on tangential walls of tracheids. Rays short, most of them with 3–5 cells, exceptionally up to 14 cells, partially biseriate. R. S.: bordered pits uniseriate. Abundant wood parenchyma, with smooth transverse walls. Rays homogeneous. Cross-field pits cupressoid, from 1 to 4 per cross field, generally 2. Sometimes they look quite taxodioid, but always disposed in two rows.

Identification: Conifers with cupressoid cross-field pits are *Cupressaceae* and Taxodiaceae. Among these, *Actinostrobus*, *Widdringtonia*, *Chamaecyparis*, *Fokienia*, and *Cupressus* are considered. The other genera have ray parenchyma with thick walls, even nodular, or crassulae. Radial parenchyma in *Diselma* and *Juniperus* has nodular transverse walls, and *Fitzroya* has vestured pits. *Actinostrobus* usually has many pits in each cross field and *Widdringtonia* lives only in the southern hemisphere, so we do not consider these two genera.

Taxodiaceae tends to have biseriate-bordered pits. *Sequoiadendron* and *Taiwania* have neither nodular walls in wood parenchyma, nor common biseriate rays, as other members of the family do. Generally, they have taxodioid cross-field pits, but according to Greguss (1955), all of them, except *Athrotaxis*, can also have cupressoid pits. *Taiwania* commonly has biseriate-bordered pits. *Sequoiadendron* shows very taxodioid pits in the cross field, generally abundant (4–6) and in disarray.

Having rejected all the Taxodiaceae, we can affirm that our samples belong to one of these genera: *Chamaecyparis*, *Fokienia*, or *Cupressus*. Cones of *Cupressus* have been found in the site (Alonso et al., 1999). Wood of *Cupressus* has been described in the Miocene of the Rhine Basin by Figueiral et al. (1999).

Cupressaceae–Taxodiaceae

Description: Tr. S.: Growth rings narrow and distinct, with a small proportion of late wood. There are not resin ducts. Tg. S.: rays between two and eight cells, only higher in PERF27, up to 12. R. S.: bordered pits uniseriate on longitudinal tracheids. Wood parenchyma with horizontal walls smooth. Rays homogeneous. In the cross fields, the pits are not easy to distinguish, sometimes seeming to be cupressoid, but sometimes appearing taxodioid.

Identification: The samples are not sufficiently preserved to identify the cross-field pits. As they have bordered pits that are always uniseriate on radial walls of tracheids and they lack resin ducts, this wood probably corresponds to a *Cupressaceae* or Taxodiaceae.

Plate I

1. PERA45: Transversal section. *Sequoia* sp. Scale bar = 1.000 μm.
2. PERF24: Radial section. *Sequoia* sp. Taxodioid cross-field pits. Scale bar = 200 μm.
3. PERA73: Radial section. *Cryptomeria–Cunninghamia*. Biseriate bordered pits. Scale bar = 500 μm.
4. PERA73: Radial section. *Cryptomeria–Cunninghamia*. Reaction wood. Scale bar = 200 μm.
5. PERA73: Taxodioid cross-field pits of *Cryptomeria–Cunninghamia*. Scale bar = 200 μm.
6. PERA73: Tangential section of *Cryptomeria–Cunninghamia*. Scale bar = 500 μm.
7. PERD35: Tangential section. *Abies* sp. Long biseriate rays. Scale bar = 200 μm.
8. PERD35: Radial section of *Abies* sp. Dentate walls of radial parenchyma. Scale bar = 200 μm.

Pinaceae

Abies sp (Plate I,7–8)

Description: Tr. S.: Wood without vessels and resin ducts. Growth rings rather wide, with a progressive transition from early wood to late wood. Rays are easy to distinguish in transverse section. Tg. S.: rays high, up to 28 cells. Sometimes they are partially biseriate. R. S.: tracheids with bordered pits usually uniseriate, occasionally biseriate. Radial parenchyma with horizontal walls that are very thick and nodular. Tangential walls are also nodular. Radial tracheids are missing. In cross fields, two small pits appear, sometimes 1 or 3, in one horizontal row.
Identification: Genus *Abies* is easy to recognise by its radial parenchyma with nodular horizontal walls. There are other genera with horizontal walls thick, for example, among *Taxales*, but they have spiral thickenings in the tracheids. Sometimes this feature appears in some *Cupressaceae*, but here the horizontal walls are smooth, or rays are never so tall.

Most of the *Pinaceae* have resin ducts. *Cedrus* has bordered pits with scalloped tori and heterogeneous rays. *Keteleeria* and *Pseudolarix* never have such tall rays. This is why we have identified our samples as *Abies* sp.

Pinus subgen. *haploxylon* (Plate II,9–10)

Description: Tr. S.: Wood with resin ducts. The epithelial cells have thin walls, but this feature is not easily distinctive. The transition from early wood to late wood is more or less gradual, and the proportion of late wood is rather big. Tg. S.: this section has been observed only on PERF3B due to deformations of the other samples. There are horizontal resin ducts inside fusiform rays. Uniseriate rays have up to four cells in height. R. S.: bordered pits uniseriate. Rays heterogeneous. Cross-field pits are fenestriform, commonly two per cross field, but most times only one. Radial tracheids are difficult to identify, but their walls are smooth without teeth. These tracheids are usually on a marginal position. Horizontal walls of radial parenchyma are rather thick, while tangential walls are thinner and smoother.
Identification: The unique family with physiological resin ducts is *Pinaceae*. Most of the genera with these ducts have epithelial cells with thick walls, but only *Pinus* has thin walls.

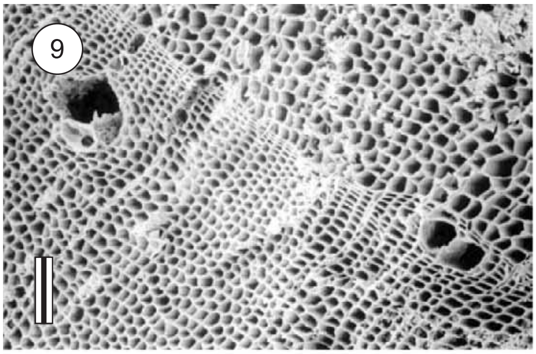
Wood in pines has heterogeneous rays. Radial tracheids with smooth, thin walls are characteristic of *haploxylon* subgenus. Among these species, those belonging to groups *cembra* and *strobus* have fenestriform cross-field pits (Greguss, 1955). According to Burgh's (1973) keys for the genus *Pinus*, our samples could belong to section *Strobus*.

Pinus subgen. *diploxylon*

Description: Some of the samples are not completely charcoalified. Tr. S.: growth rings rather wide and distinctive, with a small proportion of late wood. There are resin ducts placed in the transition from early wood to late wood, the epithelial cells of which have thin walls. Tg. S.: horizontal resin ducts inside fusiform rays. R. S.: bordered pits uniseriate on the radial walls of tracheids. Rays heterogeneous, with marginal and sparse tracheids, probably denticulate, but this feature has not been completely determined, because most of the rays are filled with resin. In any case, teeth are small. Radial parenchyma with thin horizontal walls. There are from one to four pits in the cross fields, pinoid or sometimes fenestriform.

Plate II

9. PERA46: Transversal section with resin ducts. *Pinus* subgen. *haploxylon*. Scale bar = 1.000 μm.
10. PERA46: Detail of rays of *Pinus* subgen. *haploxylon*. Scale bar = 50 μm.
11. PERA21: Transversal section. Root from *Larix–Picea*. Scale bar = 1.800 μm.
12. PERF1A: Transversal section. *Quercus* sp. Scale bar = 2.000 μm.
13. PERF1A: Tangential section. *Quercus* sp. Multiseriate ray in the lower part. Scale bar = 1.000 μm.
14. PERA36: Transversal section. *Vaccinium* sp. Scale bar = 1.000 μm.
15. PERA36: Radial section. Scalariform perforation pates and spiral thickenings from *Vaccinium* sp. Scale bar = 300 μm.
16. PERA36: Detail of scalariform intervascular pits of *Vaccinium* sp. Scale bar = 50 μm.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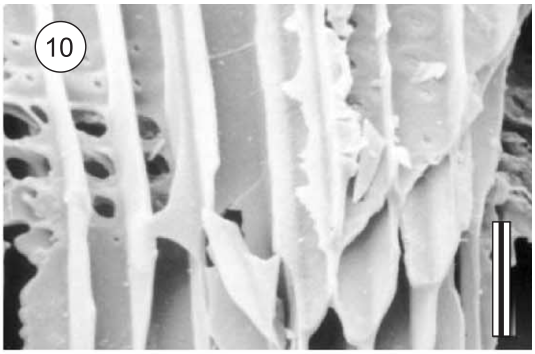
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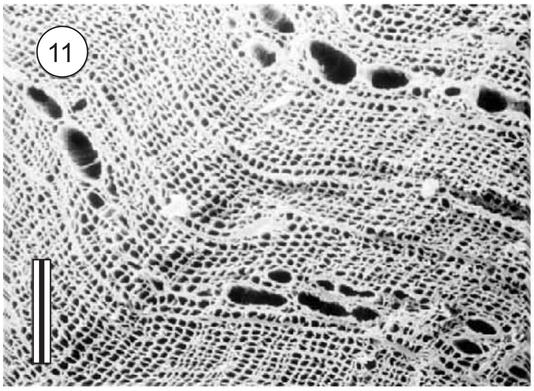
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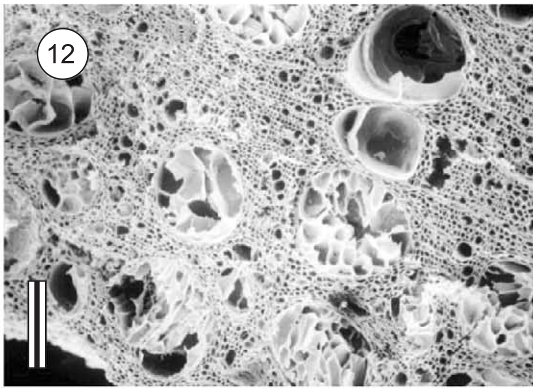
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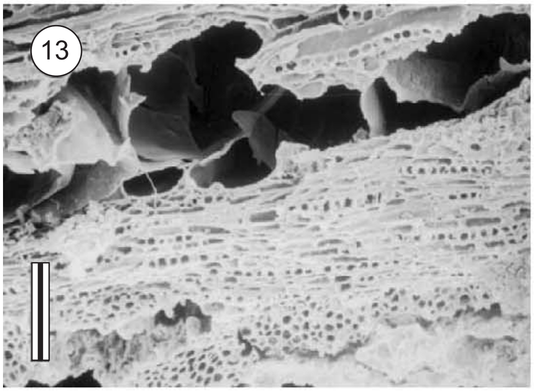
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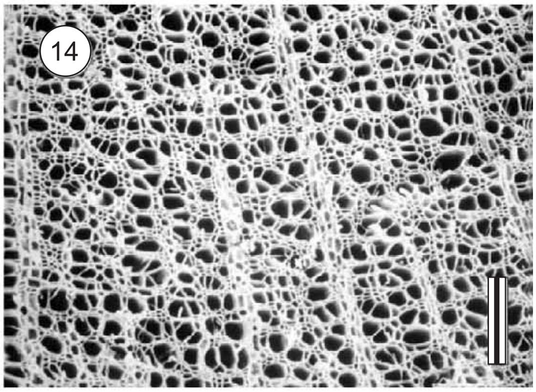
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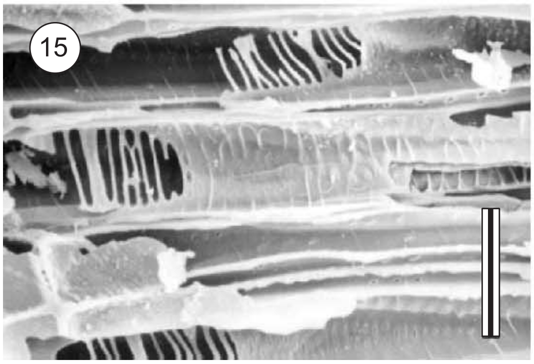
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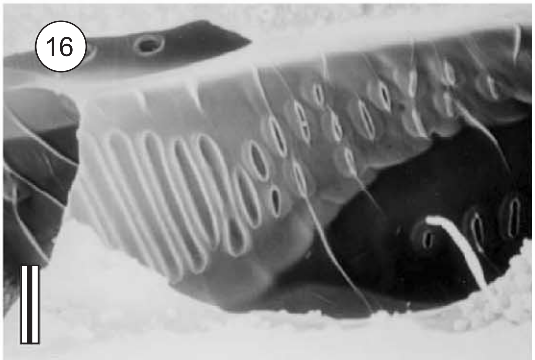
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Identification: Among pines, Burgh (1973) identifies sections *Pinaster*, *Sula*, *Parrya* (subsect. *Nelsonii*), *Leiophylla*, and *Lumholzii* that present heterogeneous rays, not very strongly dentate walls and pinoid cross-field pits. All of them, except *Parrya*, are diploxyl pines. *Pinus nelsonii*, the unique member of this subsection, presents radial parenchyma with thick horizontal walls. That is why we can exclude it. Thus, our sample could be related to many different species among the *diploxylon* subgenus.

Larix–Picea (Plate II,11)

Description: Some samples are rather big fragments of charcoal. Tr. S.: traumatic resin ducts are abundant and even form tangential bands. Growth ring limits are wavy. Tracheids with rounded section. Tg. S.: rays short, from one to seven cells in height. One ray with 11 cells was found. There are very few rays. Radial resin ducts are missing. Wood parenchyma frequent, with transverse walls smooth. R. S.: this section is very difficult to see. Bordered pits are uniseriate. Cross-field pits seem to be taxodioid.
Identification: These samples are rich in traumatic resin ducts and show an exceptional lack of rays. These strange features show similarities with the anatomy of a root. According to Schweingruber (1978), roots cannot be identified, except in very few cases. Its typical features are abundance of parenchyma, small proportions of late wood, and lack of pith. In any case, the presence of resin ducts with thick-walled cells is characteristic of *Picea*, *Larix*, and *Pseudotsuga*. This last genus never has rays as tall as 11 cells.

It is very difficult to distinguish between *Picea* and *Larix*. According to Talon (1997), they can be separated through the form of bordered pits. Our samples are not so well preserved as to recognise this feature. Schweingruber (1990) remarks some differences among these genera, such as the transition from early to late wood, softer in *Picea* than in *Larix*, and the frequency of paired bordered pits, higher in *Larix*. Figueiral et al. (1999), who adopted a cautious nomination as *Larix–Picea*, noted the differences between both genera. Our samples probably belong to the fir, as some cones of this genus have been identified in the locality (Alonso et al., 1999). Pollen grains of *Picea* have also been found, but not *Larix*.

Conifer unidentifiable

Description: All these samples are very badly preserved and, therefore, could not be identified. We can only say that they belong to conifers because of their homogeneous tissue and their lack of vessels.

Angiosperms

Betulaceae

Betula sp

A large proportion of the samples corresponds to bark. One sample has been prepared in thin section.
Description: Tr. S.: All features are very difficult to recognise. Pores are scattered or in small radial groups. Vessels are small, with thick walls. In this section, we can easily observe scalariform perforation plates. Tg. S.: bi- and triseriate rays. They are not very tall, up to 10–15 cells, homogeneous. There are also uniseriate rays. Abundance of fibres. R. S.: vessel pits are rounded, bordered, very abundant, and arranged alternate. Scalariform perforation plates.
Identification: The genera of angiosperms with scalariform perforation plates and bi- or triseriate homogeneous rays are *Alnus*, *Betula*, *Carpinus*, and *Corylus*. According to Greguss (1959), both *Alnus* and *Corylus* and *Carpinus* show aggregate rays. This feature is not present in our samples. According to Schweingruber (1990), *Alnus* and *Corylus* only have multiseriate rays belonging to aggregate rays, and the others are exclusively uniseriate. In *Carpinus*, rays are uniseriate or biseriate, but always very thin. On the other hand, several species of *Betula* show generally triseriate or tetraseriate rays. Intervascular pits are also very characteristic, rounded, very abundant, and small. That is why we have assigned our samples to *Betula* sp. Extant species more similar to our samples are *Betula Pendula* Roth, *Betula alba* L., and *Betula aetnensis* Rafinesque-Schmaltz.

Sample PERA11 shows special features. Its vessels seem to have expanded and the transverse section is completely occupied by these. Perforation plates can be easily observed. In both radial and tangential sections, heterogeneous rays can be distinguished. Vessel pits are minute and rounded. It was so distorted that it appeared impossible to identify. However, in another site (Alcalde Olivares et al., 2003), we found another piece of the same wood, with the remains of its bark, that can clearly be assigned to birch. The structure of its wood is exactly the same as in sample PERA11. It could be a distortion produced by long-term immersion in water.

Fagaceae

Fagus sp

Description: Samples are not well preserved, which hindered identification. Tr. S.: wood with vessels, more or less small. It is diffuse porous, although pores are more concentrated in some zones. Rays can be observed in this section. Tg. S.: there are two sizes within the rays: some of them are uniseriate and other ones are from 3 to 12 (14) wide. The section of its cells is rounded. Rays fusiform. R. S.: vessels with simple and scalariform perforation plates. Intervascular pits are small, bordered, and elongated. Vasicentric tracheids are abundant. Rays are tall, heterogeneous, with procumbent inner cells, and some rows of erect marginal cells.
Identification: The presence of rays with two sizes is characteristic of family Fagaceae. Among it, the only genus with both simple and scalariform perforation plates is *Fagus*.

Quercus sp. (Plate II,12–13)

Description: Tr. S.: Porous ring. Solitary big vessels. There are some pores rather bigger than others. Tg. S.: rays are uniseriate or biseriate in their majority. There are also very wide fusiform multiseriate rays. R. S.: perforation plates are simple. Intervascular pits are small. Vasicentric tracheids are abundant.
Identification: The combination of uniseriate and multiseriate rays is very typical in the genus *Quercus*. The presence of simple perforation plates and vasicentric tracheids is also characteristic.

Aquifoliaceae

Ilex sp

Description: Tr. S.: Ring-porous wood. Pores are in radial clusters, with three, five, or more elements. Tg. S.: rays are very tall and two to five seriate. They are heterogeneous. There are also some uniseriate rays with upright cells. Vessels have wide spiral thickenings. R. S.: perforation plates scalariform. Vessel walls have abundant opposite small pits. Heterogeneous rays have both upright and procumbent cells.
Identification: Radial groups of pores are typical of very few species. In fact, in accordance with Schweingruber (1990), we only found one species with scalariform perforation plates, spiral thickenings, and triseriate rays, with this arrangement of pores: *Ilex aquifolium* L. We cannot affirm that this is the same species because the sample is very old, but it undoubtedly belongs to the genus *Ilex*.

Ericaceae

Vaccinium sp (Plate II,14–16)

Description: Tr. S.: With abundant minute vessels, very abundant, and solitary. They are diffuse porous. Scalariform perforation plates. Growth rings are difficult to distinguish but elements form tangential bands. Fibres with thin walls, very similar to apotracheal parenchyma. Tg. S.: rays uni- to triseriate, up to five cells wide. Most of them are biseriate. They are heterogeneous, short, and fusiform, except uniseriates, which contain erect cells. R. S.: vessels have spiral thickenings on the walls. There are very distinct scalariform perforation plates. Intervascular pits scalariform or rather rounded. Pits between rays and vessels are also big.
Identification: The identification of these samples was very difficult and must even be confirmed due to the fact that, a priori, none of current woody species of the Iberian Peninsula has the same wood. Looking at the descriptions of Metcalfe and Chalk (1972) for angiosperms all over the world, there are not many taxa with spiral thickenings, scalariform perforation plates, and small pores.

We also used the software for wood identification of the U.D. Tecnología de la Madera of the E.T.S.I. de Montes. We consulted reference collections and the identification was derived to some *Vaccinium* species, but none of the present ones from the Iberian Peninsula. It also shows similarities with *Ericaceoxylon parenchymatosum* van der Burgh, related by its author to *Vaccinium* (Burgh, 1973). The anatomy of this genus is similar to some species of families Theaceae and Symplocaceae.

cf. Erica

Description: All fragments were strongly compressed. Sample PERD25 has been prepared in thin sections to a transmitted light observation. It was treated with sodium hipochlorit (bleach) and the effect has been an expansion of the wood. Tr. S.: minute and sparse vessels in diffuse porous. Growth rings are difficult to distinguish. Density of pores is 120 pores/mm^2. Tg. S.: rays from two to five cells wide, not tall (up to 15–20 cells), fusiform. There are also uniseriate rays. Marginal cells are elliptic, while inner cells are rounded. R. S.: simple perforation plates. Intervascular pits are minute and numerous. There are one or two rows of upright marginal cells and inner cells are procumbent. Pits between vessels and radial parenchyma are small and rounded.
Identification: Following Greguss' (1959) keys, we find two genera with this description: *Erica* and *Vaccinium*. Among extant iberian *Erica*, there are many with rays wider than tri- or tetraseriate rays (Queiroz and Burgh, 1989). *Vaccinium* usually has both perforation plates simple and scalariform.

According to Metcalfe and Chalk (1972), *Ericaceae* shows numerous very small vessels, generally solitary. *Erica* has simple perforation plates, sometimes scalariform in some species. Intervascular pits are opposite and rather small. Rays usually have two sizes, bigger with four or more cells wide. Among *Ericaceae*, there are species with rays 10 cells wide. Uniseriate rays are numerous and constituted by upright cells. They are heterogeneous type II of Kribs, with up to four rows or marginal cells.

Our samples are very similar to the descriptions of *Erica cinerea* L., *Erica umbellata* Loefling ex L., and *Erica terminalis* Salisbury among extant Iberian species (Queiroz and Burgh, 1989).

4.2. Pollen analysis

Results from the seven analysed palynological samples are shown in the pollen diagram (Fig. 5). Quantitatively, trees and shrubs account for over 80%, with *Pinus* and *Ericaceae* (incl. *Calluna*) the taxa with more influence in these percentages. This forestry landscape of conifers (*Pinus*, *Picea*, *Abies*, *Cupressaceae*) and Angiosperms (*Alnus*, *Betula*, *Carpinus*, *Corylus*, *Fagus*, *Quercus*) presents a rich undercanopy with *Ericaceae*. Herbs are scarce in all samples.

The distance between the profile samples is long, so changes of vegetation over time cannot be analysed in detail. Nevertheless, it is possible to remark some qualitative or quantitative differences between the taxa found in the sample sequence. Thus, in the three basal samples (5, 6, and 7), *Ericaceae*, with 50% representation, is the main component of the landscape together with *Pinus* and *Picea*. The two intermediate samples (3 and 4) present a great diversity of angiosperms. *Castanea* and *Ilex* play an important role as the principal ones. The total sum of arboreal taxa accounts for 72% of the total, which indicates a denser forest. Finally, the two upper samples once again show a more open landscape, consisting mainly of conifers accompanied by many shrubby angiosperms. This fact is remarkable on sample 1, where *Ericaceae* values rise to nearly 75%.

With regard to trees and shrubs, there are qualitative similarities with the results of wood and charcoal studies (Table 1). There is a noteworthy absence in the pollen record of an important group such as Taxodiaceae. On the contrary, other arboreal taxa have been found in pollinic samples, but not as macrofossils.

4.3. Climate

The "Coexistence Approach" has been applied on the fossils of Caranceja. The mean annual temperature, the calculation of which was based on charcoal, should be between 9.1 and 20.8 °C. Based on pollen, the results are between 11.6 and 18.1 °C. If we consider only cones (Alonso et al., 1999) 9.1 to 15.8 °C. Considered together, the results will be from 11.8 to 15.8 °C with a probability of 96.3%.

Using the same method, the mean temperature of the coldest month will be between 0.4 and 1.1 °C with a probability of 100%. The interval is delimited by *Pinus peuce* Grisebach and *Pinus sylvestris* L. The mean temperature of the warmest month is between 22.3 and 26.4 °C with a probability of 96.3%. Finally, the mean annual precipitation would have a value of between 641 and 994 mm/year, calculated with a probability of 100% with the

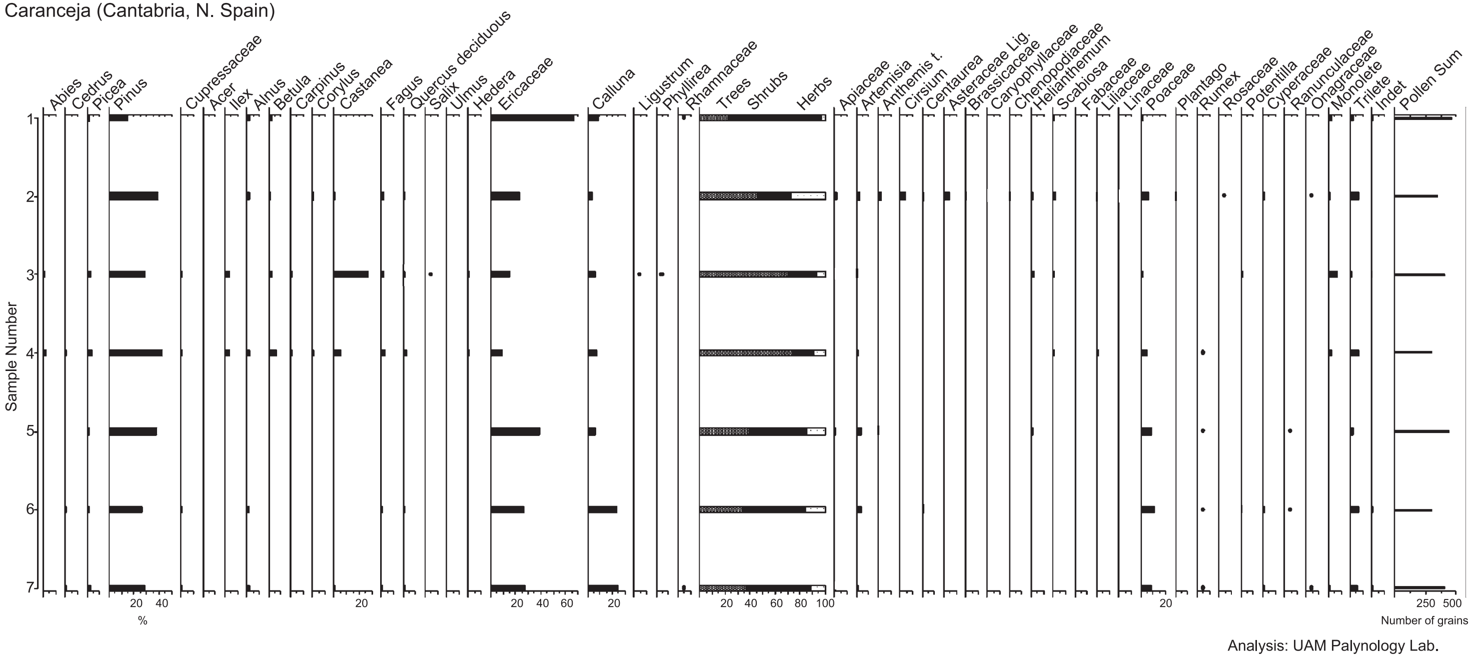

Fig. 5. Pollen diagram of Caranceja site.

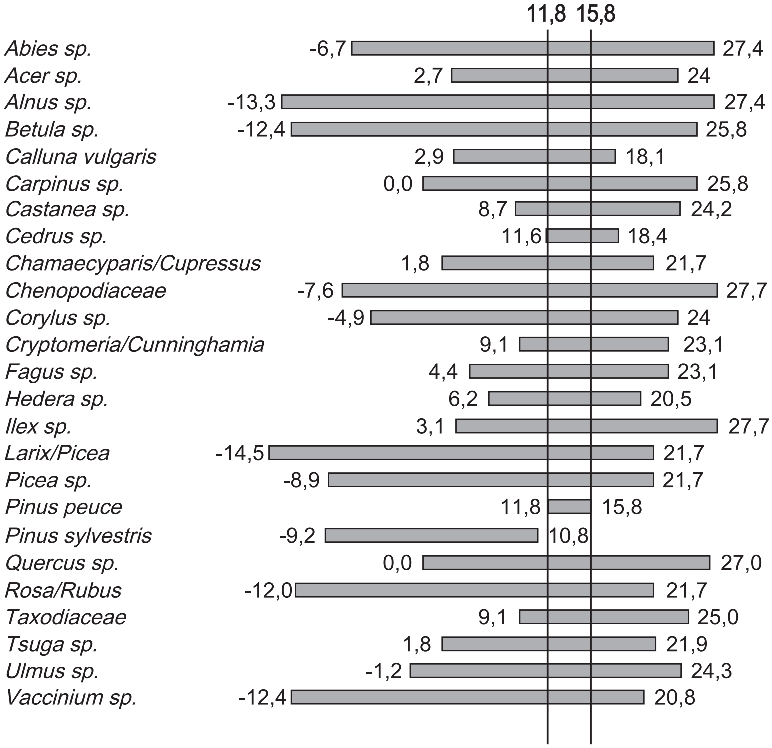

Fig. 6. Example of coexistence intervals for mean annual temperature.

"Coexistence approach". A graphical example of the method for the mean annual temperature is shown in Fig. 6.

5. Discussion and conclusions

5.1. Taxonomic diversity of Caranceja

The Appendix summarizes references to European neogene woods for each taxon that we have found and Iberian references to any other fossil forms. The site of Caranceja has revealed the richest fossil flora to date based on cones, woods, and great quantities of wood charcoal, plus pollen grains in the Iberian Peninsula from the Pliocene. The importance of this finding can be highlighted not only because most references to neogene Iberian woods are new, but also because this is the first palaeobotanical site of the northern slope of the Cordillera Cantábrica in the Neogene. The study of these materials has provided a floral list comprising many common elements of the Neogene in southwestern Europe. From the point of view of vegetation, in Caranceja, a mixed forest existed with many conifers (Taxodiaceae, *Cupressaceae*, and *Pinaceae*) and angiosperms such as *Betula*, *Castanea*, *Quercus*, and *Fagus*. Some different species of *Ericaceae* lived under the canopy.

Some taxa can be given particular mention, as it is the first time that they have been found as wood in the area. Some of them currently live in the Iberian Peninsula, while others have been extinct for a long time.

Abies now exists in the Pyrenees and in the Betic Mountains in Spain, although cones, seeds, and leaves of this genus are common in the neogene deposits. This is the first time that neogene woods of fir are found in the Iberian Peninsula. The same can be said of *Haploxylon* pines, extinct from the Iberian Peninsula during the Pleistocene. The nearest *Pinus* species of this subgenus are

Pinus cembra L., located in the Central Alps, as well as *Pinus peuce* Grisebach, which can be presently found in the eastern part of the Alpine chain.

Picea and *Larix* do not live at present in the Iberian Peninsula, and neogene woods had never been found until now, although there is a great abundance of pollen grains in many pollen diagrams. Woods of *Larix–Picea* were found in the Lower Rhine Basin (Burgh, 1973; Figueiral et al., 1999), but its description does not correspond exactly to the samples of Caranceja, because these are considered to come from roots.

This is also the first time that woods of Taxodiaceae (*Sequoia*, *Cryptomeria–Cunninghamia*) have been identified in the Spanish Neogene. Woods of different species of Taxodiaceae are common in the Miocene of southern and southwestern France.

All the Angiosperms found are extant in the Iberian Peninsula. Among them, the unique genus from which wood has been previously identified is *Quercus*. Carvalho (1958) and Pais (1972) discovered fragments of silicified wood of *Quercus suber* L. in Alentejo, in the Miocene in Portugal. References to any macrofossils of *Erica* in the Iberian Peninsula during the Neogene have not been found. The charcoal from Caranceja could therefore be the first.

It is worth mentioning that wood of *Castanea* was not found in Caranceja, but surprisingly pollen is very abundant, especially in sample P-10. This taxon is frequent in other neogene deposits, both as pollen and as leaves.

5.2. Climatology of Caranceja

The family Taxodiaceae generally indicates high and continuous levels of humidity. *Cryptomeria* needs warmer weather, but can survive with three to six cold months. *Cunninghamia* grows in subtropical and tropical mountains in Southeast Asia. *Sequoia* is typical of temperate climates, not subjected to dry seasons (Michaux et al., 1979). Thus, the environment in Caranceja must have been temperate, with an absence of frost, humid with no dry season.

The "Coexistence Approach" has been applied to the fossil floral list to calculate the most probable interval of mean annual temperature. This interval is between 11.8 and 15.8 °C, very similar to the current mean annual temperature (14.1 °C for Santander, Instituto Nacional de Meteorología). This is rather cold for normal values for the Lower and Middle Pliocene, which supports the hypothesis of an Upper Pliocene age for the locality. Nevertheless, winters were much colder, about 7° lower, but summers were much warmer, an average of 10° higher. Temperatures were therefore much more extreme during that period.

Few places now remain in the world with a similar climate temperate, humid, and contrasted. They can be found especially in Eastern China, on the eastern coast of North America, and in the western Caucasians. Indeed, Taxodiaceae can now be found in China and North America.

5.3. Chronology of Caranceja related to the history of Taxodiaceae

The extinction of Taxodiaceae began during the Middle Pliocene in southeastern France and later in northwestern Europe and Italy. The cause for this lies not only in temperature but also in precipitation changes. In the Pliocene, there were also short cool or even cold phases, but not as intense as the Pleistocene glaciations. Summer drought probably had a greater effect on species belonging to this family, especially in the Mediterranean area.

In southeastern France and northeastern Spain, Taxodiaceae were extinct in the Middle Pliocene, although they occurred in central France and Catalonia in the Late Pliocene (Michaux et al., 1979; Suc and Cravatte, 1982; Suc, 1997). Extinction in the Netherlands was studied by Zagwijn (1974) and took place in the Reuverian–Praetiglian boundary.

In pollen diagrams of Piedrafitta and Stirone, in Central Italy, a rough decrease in *Taxodium* type (or *Sequoia*) is considered by authors to be the Plio-Pleistocene boundary "Límite Tiberiano" (Lona et al., 1969; Lona, 1971). Beyond this limit, some grains of Taxodiaceae can appear only sporadically. According to Michaux et al. (1979), in fact, Taxodiaceae were absent from Central Italy from the Early Pleistocene.

According to Huard (1965), forests of *Taxodium* with *Sequoia* and *Sequoiadendron* could live at the

Pyrenean chain during the Miocene. *Taxodioxylon gypsaceum* has been found specifically in Arjuzanx (SW France). The kinds of deposits and flora found in this site look rather similar to those found in Caranceja. The authors give as a possible date, the Upper Miocene, but Gregor and Velitzelos (1987) and Mai (1995) dated it at Lower Miocene. Both datings are in contradiction with the age set for Caranceja. Previous studies had considered the age of Caranceja to be between 300,000 years old and the Pliocene age (Alonso et al., 1999). The chronology of extinctions of Taxodiaceae leads us to think that, if they were extinct from the northwestern Mediterranean in the Middle Pliocene and from Central France in the Upper Pliocene, Caranceja must be considered to be from the Upper Pliocene age or older. The temperatures calculated by the "Coexistence Approach" are relatively cold for the Lower or Middle Pliocene. This supports the hypothesis of an Upper Pliocene dating.

Acknowledgements

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Appendix A

Taxon that we have found at Caranceja (in bold) and references of European neogene fossils. For pollen, we have only shown some Iberian references.

Taxon	Age	Material	Site	Reference
Sequoia/Taxodioxylon				
Sequoia abientina (*S. langsdorfii*)	Lower Miocene	Twigs	Rubielos de Mora (E Spain)	Barrón and Diéguez (2001)
3 unidentifiable Taxodiaceae (*Cryptomeria*, *Glyptostrobus europaea/ Sequoia abietina*, *Sequoia/Taxodium*)		Cones		
Sequoia cf. Taxodium	Lower Miocene	Pollen	Rubielos de Mora (E Spain)	Fernández Marrón and Álvarez Ramis (1988)
Taxodioxylon. taxodi, *T. distichoides*, *T. gypsaceum*, *T. giganteoides*	Upper Miocene	Wood	Arjuzanx and Hostens (SW France)	Huard (1966, 1974)
Taxodiaceae	Upper Miocene	Cones	Arjuzanx (SW France)	Huard and Lavocat (1963)
Taxodioxylon taxodii	Upper Miocene	Wood	Orignac (S France)	Huard (1965)
Taxodiaceae	Lower Miocene	Wood	Lower Rhine Basin (W Germany)	Burgh (1973); Figueiral et al. (1999)
Cryptomeria				
Cryptomeria sp.	Lower Miocene	Cone	Rubielos de Mora (E Spain)	Barrón and Diéguez (2001)
Taxodioxylon cryptomerioides	Lower Miocene	Wood	Lower Rhine Basin (W Germany)	Burgh (1973)
Cryptomeria rhenana	Upper Miocene	Cones	Satovca, (SW Bulgaria)	Palmarev et al. (1991)
Cryptomeria rhenana	Upper Miocene	Cones	W Germany	Kilpper (1968a,b,c)
Crytomeria anglica	Lower Pliocene	Cones	Derbyshire (C England)	Boulter (1969)

Appendix A (*continued*)

Taxon	Age	Material	Site	Reference
Cupressaceae				
Calocedrus, *Juniperus*, *Thuja/Chamaecyparis*	Lower Miocene	Cones, twigs, compressions	Rubielos de Mora (E Spain)	Barrón and Diéguez (2001)
Cupressaceae (2 sp.)	Pre-pontian	Leaves	Arjuzanx (SW France)	Huard and Lavocat (1963); Huard and Klingebiel (1965)
Cupressus–Chamaecyparis	Upper Serravalian	Wood	Garzweiler (W Germany)	Figueiral et al. (1999)
Abies				
Abies	Upper Oligocene or Aquitanian	Seed	As Pontes (NW Spain)	López Martínez et al. (1993)
Abies saportana	Miocene	Twigs, cones, leaves	La Cerdaña (NE Spain)	Menéndez Amor (1955)
Abies	Miocene–Pliocene	Macrofossils	France	Dubois-Ladurantie (1941)
Abies spectabilis	Upper Pliocene	Leaves	Pichegu (SE France)	Roiron (1981)
Pinus				
Pinus subgen. *haploxylon*	Lower Miocene	Pollen	Rubielos de Mora (E Spain)	Roiron et al. (1999)
Pinus subgen. *haploxylon*	Middle Miocene	Pollen	Povoa de Santarem (C Portugal)	Pais (1978)
Pinus				
Pinus subgen. *haploxylon*	Middle–Upper Miocene	Pollen	Duero Basin	Rivas Carballo and Valle (1986, 1990)
Pinus subgen. *haploxylon*	Neogene	Pollen	Spain	Baltuille et al. (1992)
Pinus subgen. *haploxylon*	Aquitanian	Macrofossils	Lisbon (C Portugal)	Pais (1979)
Pinus aff. *palaeostrobus*	Pliocene	Macrofossils	Papiol, Barcelona (NE Spain)	Sanz de Siria (1983–1984)
Larix/Picea				
Picea	Middle Miocene	Pollen	Povoa de Santarém (C Portugal)	Pais (1978)
Picea	Lower Miocene	Cone	Rubielos de Mora (E Spain)	Barrón and Diéguez (2001)
Larix/Picea	Miocene	Pollen	Rubielos de Mora (E Spain)	Rivas Carballo and Valle (1986); Barrón and Santisteban (1999)
Larix/Picea	Pleistocene	Pollen	Mogardinho (S Portugal)	Antunes et al. (1986)
Picea	Plio/Pleistocene	Pollen	Crespià (NE Spain)	Geurts (1977); Suc anda Cravatte, 1992
Larix/Picea	Lower–Middle Miocene	Wood	Garzweiler (W Germany)	Figueiral et al. (1999)
Piceoxylon	Miocene	Wood	Lower Rhine Basin (W Germany)	Burgh (1973)
Betula				
Betula	Sennonian	Pollen	Iberian Peninsula	Barrón (1996b)
Betula insignis	Lower Miocene	Macrofossils	Rubielos de Mora (E Spain)	Roiron et al. (1999)
Betula insignis	Upper Miocene	Leaves	La Cerdaña (NE Spain)	Menéndez Amor (1955)
Betula prisca	Upper Miocene	Leaves	La Cerdaña (NE Spain)	Álvarez Ramis and Golpe Possé (1981)
Betula cuspidens	Upper Miocene	Macrofossils	La Seo d' Urgell (NE Spain)	Sanz de Siria (1980a,b)
Betula cf. *prisca*	Plaisancian	Impression	Gerona (NE Spain)	Sanz de Siria (1982a,b)
Betula alba	Plaisancian	Macrofossils	Tortosa (NE Spain)	Sanz de Siria (1987)
Carpinus				
Carpinus	Serravalien	Macrofossils	Tagus basin	Pais (1979)
Carpinus	Upper Miocene	Fruits, leaves	Arjuzanx (SW France)	Huard (1974)

(*continued on next page*)

Appendix A (*continued*)

Taxon	Age	Material	Site	Reference
Carpinus spp.	Upper Miocene	Macrofossils	La Cerdaña (NE Spain)	Villalta and Crusafont, 1981; Menéndez Amor (1955); Álvarez Ramis and Golpe Possé (1981); Barrón (1996a,b)
Carpinus orientalis	Tortonien	Macrofossils	Lisbon (C Portugal)	Pais, 1981
Carpinus grandis	Pliocene	Macrofossils	Vale de Santarém (C Portugal)	Teixeira (1952a,b,c)
Carpinus spp.	Plio/Pleistocene	Macrofossils	Crespià (NE Spain)	Roiron (1983)
Carpinus	Lower Miocene/ Plio-Pleistocene	Pollen	Galice (NW Spain)	Médus (1965)
Carpinus	Lower Miocene/ Plio-Pleistocene	Pollen	Duero Basin	Rivas Carballo (1991)
Carpinus	Lower Miocene/ Plio-Pleistocene	Pollen	SW France	Suc et al. (1986)
Carpinus	Lower Miocene/ Plio-Pleistocene	Pollen	Portugal	Diniz (1967)
Carpinus	Lower Miocene/ Plio-Pleistocene	Pollen	Catalonia (NE Spain)	Suc and Cravatte (1982)
Fagus				
Fagus ferroniae	Miocene	Leaf	Libros (Teruel, NE Spain)	Meléndez (1949)
Fagus spp.	Vallesian	Macrofossils	La Cerdaña (NE Spain)	Villalta and Crusafont (1945); Menéndez Amor (1955); Álvarez Ramis and Golpe Possé (1981)
Fagus pristina, *F. gussonii*	Upper Miocene	Leaves	La Cerdaña (NE Spain)	Barrón and Diéguez (1994)
Fagus pliocenica var. *ceretana* (*F. gussonii*), *F. castaneafolia*, *F. pristine* (*F. castaneafolia*)	Vallesian	Macrofossils	Seo de Urgell (NE Spain)	Sainz de Siria (1980a,b)
Fagus pliocenica	Pliocene	Leaves	Papiol (NE Spain)	Sanz de Siria (1983–1984)
Fagus pliocenica	Plaisancian	Leaves	Ciurana (NE Spain)	Sainz de Siria (1982a,b)
Fagus pliocenica	Pliocene	Leaves	Vale de Vacas (S Portugal)	Teixeira (1952a,b,c)
Quercus				
Quercus suber	Tertiary	Wood	Vale de Vacas, Alentejo (S Portugal)	Pais (1972)
Quercus suber	Miocene	Wood	Ponte de Sor, Alentejo (S Portugal)	Carvalho (1958)
Quercus elaena, *Q. neriifolia*	Burdigalian	Macrofossils	Martorell (NE Spain)	Sanz de Siria (1981a,b, 1982a,b)
Quercus drymeja, *Q. elaena*, *Q. penedesensis*	Upper Miocene	Macrofossils	Sant Sadurni d'Anoia (NE Spain)	Sanz de Siria (1983–1984)
cf. *Quercus rhenana*	Lower Miocene	Leaf	Rubielos de Mora (E Spain)	Barrón and Diéguez (2001)
Quercus spp.	Upper Miocene	Leaves	La Cerdaña (NE Spain)	Menéndez Amor (1955)
Quercus spp.	Vallesian	Leaves	La Seo d'Urgell (NE Spain)	Sanz de Siria (1980a,b)
Quercus drymeja, *Q.* aff. *ilex*, *Quercus* spp.	Vallesian	Macrofossils	La Bisbal (NE Spain)	Sanz de Siria (1981a,b)
Quercus spp.	Upper Miocene	Macrofossils	Montjuïc (NE Spain)	Almera (1894); Vicente i Castells (1988)

Appendix A (*continued*)

Taxon	Age	Material	Site	Reference
Quercus	Upper Miocene	Leaves, cupules	Arjuzanx (SW France)	Huard and Lavocat (1963)
Quercus	Pliocene	Macrofossils	Papiol. Ciurana (NE Spain)	Sanz de Siria (1982a,b, 1983–1984)
Quercus ilex	Pliocene	Macrofossils	Tortosa, Ballestar (NE Spain)	Sanz de Siria (1987); Gregor (1990)
Quercus ilex, *Q. lusitanica*, *Q. cerris*, *Q. pyrenaica*, *Q. sessiliflora*	Upper Pliocene	Leaves	Crespià (NE Spain)	Villalta and Vicente (1972)
Castanea				
Castanea	Miocene	Leaves	Baños de Mula	Royo Gómez (1922)
Castanea	Lower Miocene	Pollen	Rubielos de Mora (E Spain)	Barrón and Santisteban (1999)
Castanea sativa	Serravalian	Leaves	Portugal	Pais (1979)
Castanea	Upper Miocene	Leaves	Arjuzanx (SW France)	Huard and Klingebiel (1965)
Castanea	Upper Miocene	Leaves	Lower Tagus Basin	Teixeira (1973a,b); Pais (1986)
Castanea				
Castanea spp.	Upper Miocene	Leaves	La Cerdaña (NE Spain)	Villalta and Crusafont (1945); Menéndez Amor (1955); Álvarez Ramis and Golpe Possé (1981)
Castanea sativa	Pliocene	Leaves	Portugal	Teixeira (1947a,b,c, 1952a,b,c)
Ilex				
Ilex aff. *I. aquifolium*	Serravalien–Tortonian	Leaves	Sant Sadurní d'Anoia (NE Spain)	Sanz de Siria (1979, 1985)
Ilex golpei, *I. canariensis*	Middle Pliocene	Leaves	Papiol (NE Spain)	Sanz de Siria (1983–1984, 1985)
Ilex	Middle Pliocene	Pollen	Papiol (NE Spain)	Suc and Cravatte (1982); Valle and Civis (1977)
Ilex cyclophylla	Vallesian	Macrofossils	La Cerdaña (NE Spain)	Menéndez Amor (1955); Álvarez Ramis and Golpe Possé (1981)
Ilex aff. *aquifolium*, *I. canariensis*	Plaisancian	Leaf	Ciurana (NE Spain)	Sanz de Siria (1982a,b)
Ilex aff. *falsani*	Pliocene	Macrofossils	Tortosa (NE Spain)	Bataller, 1951
Ilex aquifolium, *I. boulei*, *I. studeri*	Plio-Pleistocene	Leaves	Crespià (NE Spain)	Villalta and Vicente (1972); Roiron (1983)
Ilex	Aquitanian	Pollen	Lisbon (C Portugal)	Roiron et al. (1999)
Ilex	Ramblian–Lower Aragonian	Pollen	Rubielos de Mora (E Spain)	Roiron et al. (1999)
Ilex	Aragonian	Pollen	Torremormojón (CN Spain)	Rivas Carballo and Valle (1986)
Ilex	Lower Pliocene	Pollen	Arjuzanx, Hostens (SW France)	Suc et al. (1986)
Ericaceae				
Ericaceae	Upper Oligocene	Pollen	Galice (NW Spain)	Baltuille et al. (1992)
Ericaceae	Lower Miocene	Pollen	Rubielos de Mora (E Spain)	Roiron et al. (1999); Barrón and Santisteban (1999); Baltuille et al. (1992)
Ericaceae	Lower Miocene	Pollen	Catalonia (NE Spain)	Besedik and Cabrera, 1985

(*continued on next page*)

Appendix A (*continued*)

Taxon	Age	Material	Site	Reference
Ericaceae	Middle and Upper Miocene	Pollen	Duero Basin	Valle et al. (1995); Rivas Carballo (1991)
Ericaceae	Upper Miocene	Pollen	Galice (NW Spain)	Médus (1965)
Ericaceae	Upper Miocene–UpperPliocene	Pollen	Garraf (NE Spain)	Suc and Cravatte (1982); Valle and Civis (1977)
Ericaceae	Lower Pliocene	Pollen	SW France	Suc et al. (1986)
Ericaceae	Lower Pliocene	Pollen	Portugal	Diniz and Sivak (1979)
Ericaceae	Lower Pliocene	Pollen	SW Spain	Sole de Porta and Porta (1976)
Ericaceae	Lower Pleistocene	Pollen	Pyrinees, Algarve	Baltuille et al. (1992); Antunes et al. (1986)

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