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A palaeoecological interpretation of the lower–middle Pleistocene Cal Guardiola site (Terrassa, Barcelona, NE Spain) from the comparative study of wood and pollen samples

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Abstract

The Cal Guardiola site, discovered during the construction of an office building in the centre of Terrassa (Province of Barcelona, NE Spain), is home to one of the richest deposits of lower–middle Pleistocene flora in the Iberian Peninsula. The site contains a large quantity of plant macroremains, including non-carbonised wood, in an exceptional state of preservation. In this work, 100 wood fragments were analysed along with 25 pollen samples and 2 coprolites, all from the same horizon. These remains revealed the presence of a mixed deciduous forest with significant numbers of *Quercus* (*Quercetum mixtum*). Thermophilous, meso-hygrothermophilous and river forest species were also present, including some taxa rarely recorded for the Pleistocene, e.g., the mesocratic group of species represented by *Juglans, Carya* and *Platanus.* Fossil wood of *Aesculus* was also identified; this is the first Pleistocene reference of this species in Iberia. In this open Mediterranean forest, several remarkable gymnosperms were present. For example, *Pinus haploxylon*-type pollen was identified, demonstrating the survival of this group of conifers during the lower Pleistocene in the Iberian Peninsula. Pollen of Taxodiaceae was also found — the first reference of this family for the Iberian Pleistocene-showing these taxa survived on the Peninsula until the lower–middle Pleistocene transition. Warm-temperate and humid conditions prevailed during this interval; clear indications of an interstadial episode were observed.
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Keywords: lower–middle Pleistocene; fossil wood; pollen; Iberian Peninsula, Taxodiaceae

1. Introduction

The construction of a building in the centre of Terrassa (Province of Barcelona, Spain) unearthed a large quantity of plant macroremains from the lower–middle Pleistocene transition; this was named the Cal Guardiola site. This site contains large amounts of non-carbonised wood mixed with the remains of fauna (bones

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and coprolites) and a small number of seeds, leaves and phytoliths. The wood shows signs of biodegradation, carbonification, taphonomic distortion and, in some cases, pyritization. However, the tissues are well preserved and the absence of mineralisation allows the wood to be classified as duripartically preserved (Schopf, 1975) or preserved in a basically unaltered state (Spicer, 1991).

The age and the quantitative and qualitative richness of its materials render it one of the best Iberian Pleistocene sites. In fact, no similar site exists in Spain. However, its macroremains can be compared to those of the Tertiary fluvial sediments of Caranceja (northern Spain) (Alcalde Olivares et al., 2004) and those found in lignite mines in central Europe (Schloemer-Jäger, 1960; Huard and Lavocat, 1963; Van der Burgh, 1964; Huard and Klingebiel, 1965; Huard, 1966; Huard, 1967; Kilpper, 1967, 1968a,b,c; Van der Burgh, 1973; Huard, 1974; Van der Burgh, 1983; Minnigerode, 1986; Figueiral et al., 1999). The analysis of the Cal Guardiola macroremains was complemented by pollen studies.

This site is a source of essential information on a less well known period of the early Pleistocene. Little information is available on either the dynamics or the characteristics of the Pliocene–Pleistocene, lower Pleistocene or middle Pleistocene flora. The accurate dating of deposits is often technically difficult and the data obtained fragmentary. The most important studies performed to date in this area have been those of Andrade (1944), Elhaï (1966), Diniz (1972), Teixeira and Pais (1976), De Deckker et al. (1979), Geurts (1979), Julià and Villalta (1984), Antunes et al. (1986), Leroy (1987), García Antón (1989), García Antón and Sainz Ollero (1991), Leroy (1997) and Martín-Arroyo (1998). The present work is the first to be performed with a large number of non-carbonised wood specimens from the lower–middle Pleistocene in Europe, and which contrasts macro-and microfossil data.

Samples were dated by palaeomagnetic analysis at the Jaume Almera Institute (C.S.I.C.), Barcelona. Magnetostratigraphic analysis clearly situated them below the Brunhes-Matuyama geomagnetic boundary, i.e., they are over 0.78 Ma of age (J.M. Garcés, pers. com.). Micromammal remains such as *Mimomys savini* Hinton or *Allophaiomys burgondiae* Chaline suggest the age of the Cal Guardiola site to be between 1.2 and 0.8 Ma.

The aim of this work was to reconstruct the palaeoenvironment of the Cal Guardiola site from the examination of its fossil wood and pollen content, comparing the results obtained in both analyses.

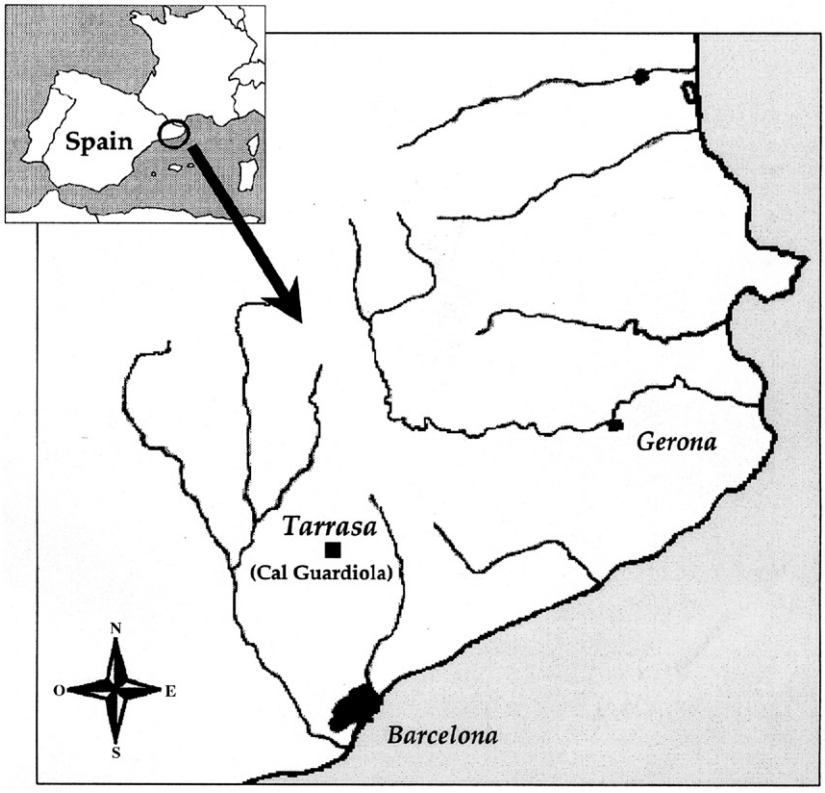


Fig. 1. Location of the Cal Guardiola site in Catalonia (Iberian Peninsula).

2. Study area

The Cal Guardiola site is located in the municipality of Terrassa in northeastern Spain, about 25 km northwest of Barcelona and west of the River Vallparadís (geographical coordinates 2°00′40″ W, 41°34′6″ N, UTM 31TDG1702; altitude c. 310 m; Fig. 1). It lies in the tectonic trough of the Vallés-Penedés region, which forms part of the NE–SW–aligned Costero–Catalana Mountains, a range some 250 km long.

Geologically, the relief of the area is strongly defined by the fault system generated during the pre-orogenic (Mesozoic) and compressive (Palaeogene) phases. The depressions produced were subsequently in-filled with dissimilar materials during the Neogene (Fig. 2). Lithologically, these sedimentary materials consist of continental facies (mainly argillites, sandstones and puddingstones) laid down under conditions similar to those that reigned during the Vindobonian, the deposits of which they overlie. Along the Vallés depression, deposits of quaternary materials can be found. These might be associated with the terraces of the rivers Cardoner, Segre, Llobregat and Besós (Gutiérrez Elorza, 1994).

From a stratigraphic point of view, the Cal Guardiola site comprises a 5.5 m thick sequence containing a set of sedimentary bodies, mostly gravels showing little granulometric selection. These are the result of successive alluvial fans alternating with sedimentary units due to water moving at different flow rates (Berástegui et al., 2000). Four main sedimentary bodies can be differentiated. The

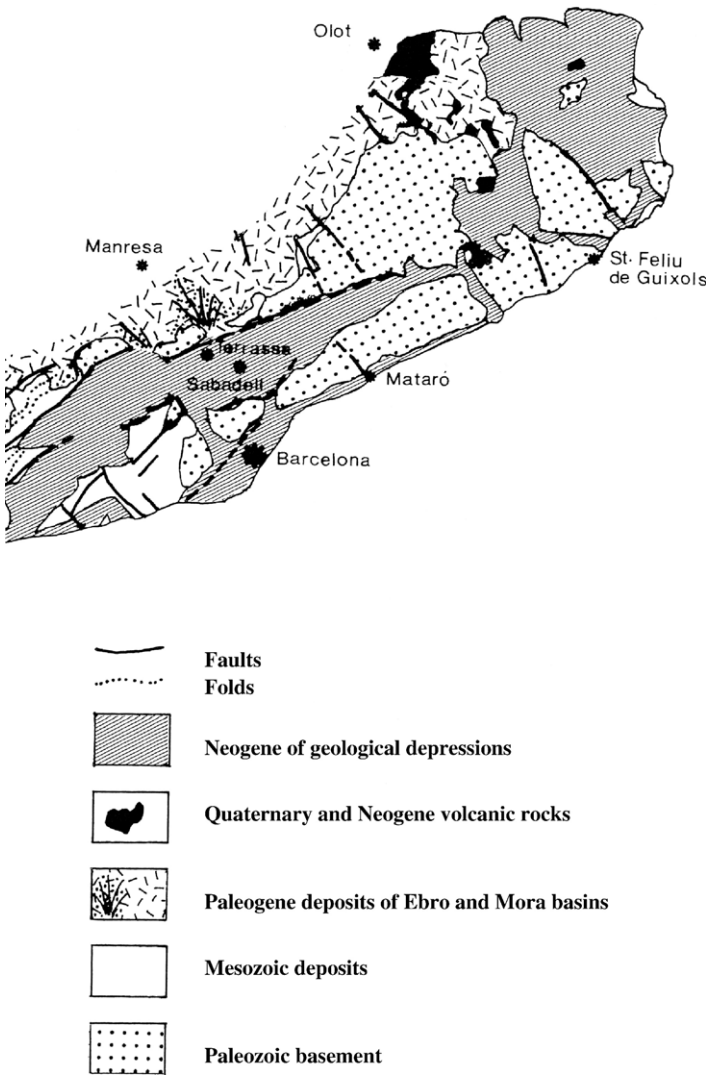


Fig. 2. Tectonics of the eastern zone of the Costero–Catalana Mountains (modified from Sala, 1994).

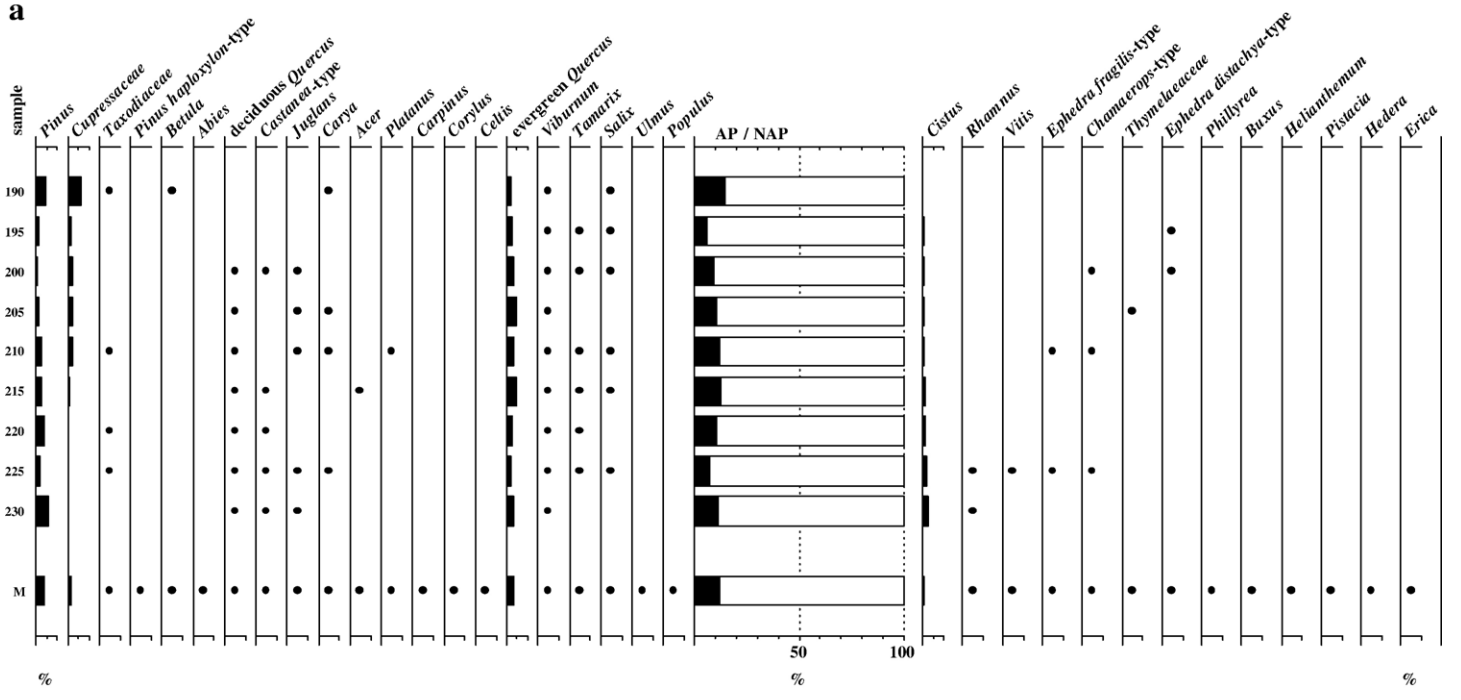


Fig. 3. Composite pollen diagram of the Cal Guardiola site. The sample numbers correspond to one of the sections analysed (S1), while 'M' corresponds to the mean for all the samples analysed from level D2 (n=27). 3a: Tree and shrub taxa. 3b: Herbaceous taxa, hygro–hydrophytes and Pteridophytes.

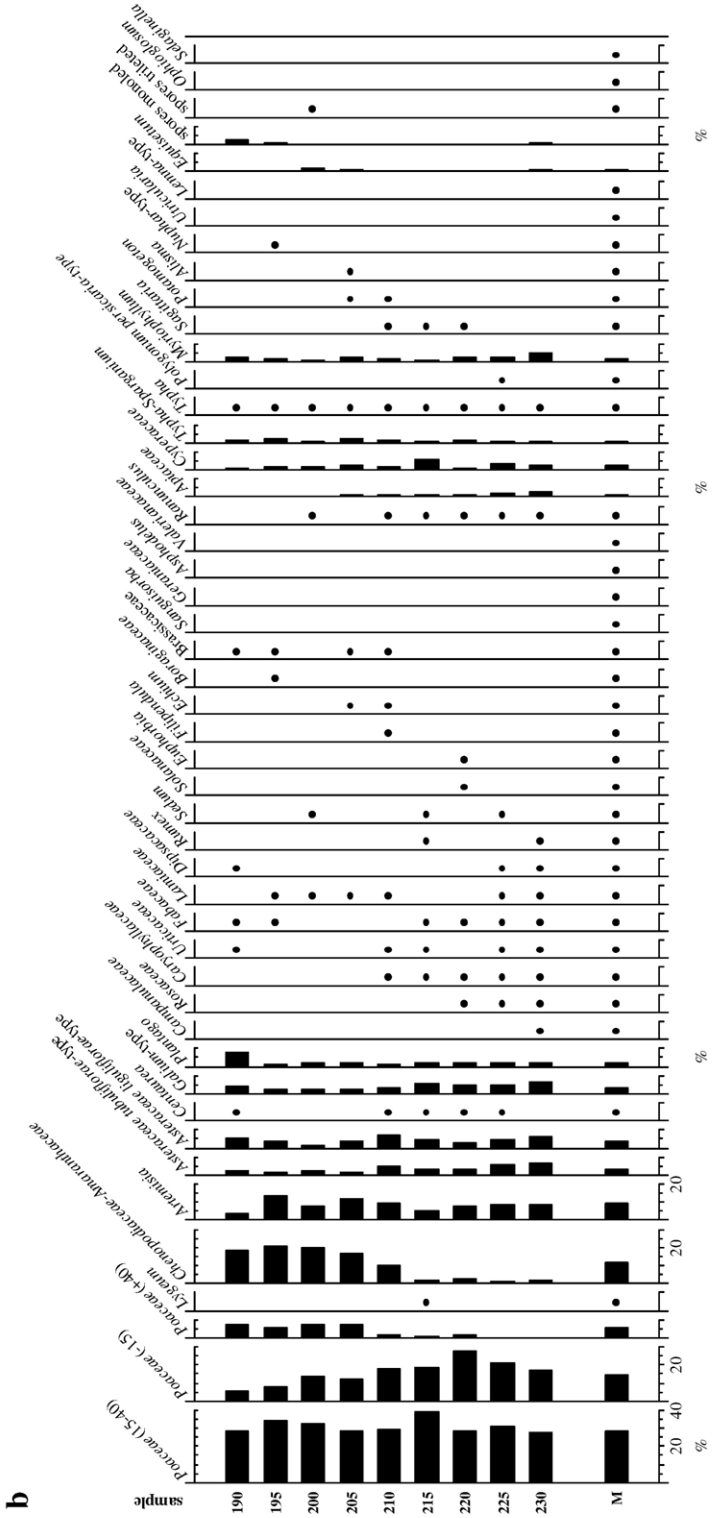


Fig. 3 (*continued*).

lowermost is situated over the Upper Miocene (Tortonian) series and appears to have been shaped by water flows of varying intensity. Upon this lies a stratum made up of sediments generated by a high-intensity alluvial fan. A subsequent phase involved an environment which gave rise to the main sedimentary unit: Level D2. This level was home to chaotically distributed wood, coprolites and other macroremains, which suggests they were subject to a debris-flow event and that all were deposited in a short period of time. They later would have undergone necrokinesis and fossil-diagenetic processes. Pollen was also extracted from this level and analysed. The results of this and the wood analysis, however, can only be interpreted from the point of view of the presence and numbers of taxa; they should not be interpreted from a sequential point of view given the likely deposition method. The following sedimentary units indicate the continuation of sedimentation (although the water flow appears to have been less intense) with a reduction in the gravel fraction.

3. Methods and materials

An archeaopalaeontological excavation was undertaken over an area of some 691 m^2. Wood and pollen samples were collected from different sections of level D2, the thickness of which varied from 40 to 120 cm. This sampling of wood and pollen samples was undertaken at the excavation site by a team from the *Miquel Crusafont Palaeontological Institute* and the *Universitat Autònoma de Barcelona* during 1997. All fossils were collected from *in situ* resting sites. The same kinds of pollen and wood were found all over level D2.

3.1. Wood analysis

The wood samples – tainted black by the sediments – were all collected from the aforementioned Level D2. All had been preserved under anoxic conditions. This level houses a very diverse series of animal remains, some showing partial anatomical connections. Plant fossils are also abundant. Pieces of wood were obtained from large trunks and even twigs, etc. Most of the fragments were strongly compressed, which led to frequent problems during microscopic analysis.

One hundred wood fossils were analysed using traditional micrographic techniques (Schweingruber, 1978; De Palacios, 1997). Fragments measuring approximately 1 × 1 × 2 cm were processed with a microtome to provide thin sections approximately 15–20 μ thick. These were placed in a watch glass containing distilled water, stained with safranin, and then washed with distilled water and alcohol. They were then submerged in xylol. A few drops of a *Euquit* fixer were then added and the samples observed under transmission light microscopy using an Olympus B × 50 series optical microscope equipped with UIS lenses (magnification × 50, × 100, × 200 and × 500).

To identify the wood samples, anatomical studies were performed according to Greguss (1947), Jacquiot et al. (1973), García Esteban and Guindeo Casasús (1990), and Schweingruber (1990). All samples were compared to those in reference collections of extant wood belonging to the *U.D. Botánica* and *U.D. Tecnología de la Madera* of the *Escuela Técnica Superior de Ingenieros de Montes, Universidad Politécnica de Madrid* (Spain). The studied samples were finally deposited with the *Servei d'Arqueologia de la Generalitat de Catalunya* (Barcelona) and the *U.D. Botánica* of the *Escuela Técnica Superior de Ingenieros de Montes*, *Universidad Politécnica de Madrid* (Spain). Four samples could not be assigned to a specific taxon owing to their state of preservation.

3.2. Pollen analysis

Sixty pollen and 18 coprolite samples were analysed. Of these, only 25 pollen samples and two coprolite samples (all from level D2) provided good results (Burjachs, in press). Three profiles were seen in different parts of the excavated area: S1 (which provided nine samples), P68 (seven samples), profile 25–35 (six samples). Single samples were also taken from three other profiles (profiles 3–8, 34–39 and 37–42). Fig. 3a shows the pollen counts for these profiles, and for those of the coprolites ('M' = mean pollen count for level D2). Each sample was prepared for analysis following the method of Goeury and Beaulieu (1979), as modified by Burjachs (1990) in accordance with the proposal of Girard and Renault-Miskovsky (1969) (Burjachs et al., 2003). The basic pollen count included all pollen except that of aquatic plants (Cyperaceae, *Typha–Sparganium*, *Typha*, *Myriophyllum*, *Polygonum persicaria*-type, *Alisma*, *Sagittaria*, *Nuphar*-type, *Lemna*-type, *Utricularia* and *Pteridophyta*). The pollen diagram was plotted using TGWiev v. 2.0.2 software (Grimm, 2004). The pollen samples were identified using the classic works of Moore et al. (1991) and Reille, (1995, 1998, 1999) as an aid.

4. Results

4.1. Wood identification

Table 1 shows the identification analysis results of the 100 non-carbonised wood fragments. These

Table 1
Taxa found in the Cal Guardiola deposit

Taxa	% Wood	% Pollen	Pollen number
Acer aff. *pseudoplatanus*	19		
Quercus subgen. *quercus*	16		
deciduous *Quercus*		4.6	59
Aesculus aff. *hippocastanum*	15		
Ulmus sp.	14	1.3	16
Acer aff. *campestre*	8		
Fraxinus aff. *angustifolia*	7		
Populus sp.	4	0,2	3
Salix sp.	2	1,7	22
Ligustrum vulgare	2		
Phillyrea sp.		0.5	6
Acer sp.	2	1.6	22
Cornus sanguinea	2		
Quercus sp.	2		
evergreen *Quercus*		24.0	307
Viburnum opulus	1	4.1	52
cf. Fraxinus	2		
Pinus sp.		25.4	324
Pinus type *haploxylon*		0.4	5
Cupressaceae		12.2	156
Cistaceae		5.9	75
Tamarix sp.		3.5	45
Castanea- type		3.3	32
Ephedra sp.		1.9	24
Abies sp.		1.8	23
Juglans sp.		1.2	15
Carya sp.		1.0	13
Rhamnus sp.		0.9	12
Buxus sp.		0.9	11
Vitis sp.		0.8	10
Taxodiaceae		0.6	8
Chamaerops-type		0.5	6
Hedera sp.		0.4	5
Celtis sp.		0.2	3
Thymelaeaceae		0.2	3
Pistacia sp.		0.2	3
Erica sp.		0.2	2
Betula sp.		0.2	2
Carpinus sp.		0.1	1
Platanus sp.		0.1	1
Corylus sp.		0.1	1
Inidentifiable	4		

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

belonged to 11 taxa (all angiosperms) covering seven families. The main diagnostic characteristics observed for each sample are also shown.

Angiosperms

Fagaceae

Quercus subgenus *Quercus* (Plate I, 1–2)

Description: Transverse section (Tr.S.): Growth ring boundaries distinct. Ring-porous with 2 to 3 rows of pores in the earlywood. Average tangential vessel diameter 150–250 μ. Latewood pores solitary or in radially orientated groups. Pore size transition from the early-to the latewood zones abrupt. Tyloses in vessels frequent. Libriform fibres, thick-walled and paratracheal parenchyma present. Tangential section (Tg.S.): rays uni-to multiseriate. Uniseriate, homogeneous rays up to 200 μ in height. Average multiseriate, heterogeneous rays 250–300 μ wide. Septate fibres present. Radial section (R.S.): simple perforation plates. Intervessel pits alternate, often with oval apertures. Spiral thickenings absent.

Identification: Based on anatomical features the samples belong to the genus *Quercus* (Greguss, 1947; Jacquiot et al., 1973; García Esteban and Guindeo Casasús, 1990). The conspicuous growth rings and the abrupt pore size transition from the early-to the latewood are typical of *Quercus* subgenus *Quercus* (Schweingruber, 1990). According to García Esteban and Guindeo Casasús (1990), none of the samples could be assigned to *Quercus robur* or *Q. petraea* because of the high average tangential vessel diameter (350–450 μ) of the earlywood. In addition, *Q. petraea* has multiseriate rays 400–450 μ wide. *Quercus robur*, has uniseriate rays up to 350–400 μ in height, features also absent in the samples. The earlywood of *Q. pyrenaica* has an average tangential vessel diameter of 280–350 μ, and an average uniseriate ray height of 250–400 μ; neither of these characters was observed. *Quercus faginea* Lam., *Q. humilis* Miller and *Q. canariensis* Willd., show strong uniformity in their wood anatomy and are impossible to distinguish from one another at this level. The fossil samples with the above-mentioned anatomical characteristics were therefore assigned to this latter group of species.

Hippocastanaceae

Aesculus aff. *hippocastanum* L. (Plate I, 3–6)

Description: Tr.S.: well-defined growth rings, diffuse-porous. Pores are solitary or in radial rows of 2 – 4 (sometimes 5) elements. The average diameter of the earlywood pores 30–40 μ, 20–25 μ in the latewood. Pits simple with a hexagonal areola. Tyloses occasionally present in vessels. *R.S.*: homogeneous rays and simple perforations present. Fine, spiral thickenings in vessels. Libriform fibres present. Tg.S.: strictly uniseriate rays, with an average height of between 2 and 20 cells. Average ray height 200–300 μ.

Identification: Some of the samples examined might belong to the genus *Aesculus* (Greguss, 1947; Jacquiot et al., 1973; García Esteban and Guindeo Casasús, 1990; Schweingruber, 1990). Since comparative anatomical wood studies of the representatives of this genus are not available, no accurate discrimination

based on anatomical studies is possible. However, the distribution and representation of *Aesculus* in the Tertiary and Pleistocene strongly suggests the samples belong to *A.* aff. *hippocastanum*, which is nowadays restricted to the Balkans. Given this current distribution, the presence of another species belonging to the genus at this point in the Pleistocene on the Iberian Peninsula is unlikely.

Aceraceae

Acer aff. *pseudoplatanus* L. (Plate I, 7–8)

Description: Tr.S.: growth ring boundaries distinct. Diffuse-porous with vessel elements widely spaced, solitary or in small groups (2–4 vessels). Average tangential vessel diameter 45–60 μ. Tyloses in vessels absent. Tg.S.: rays of two distinct sizes, 1–2 seriate and 4–6 (8) seriate. Average multiseriate ray height 500–600 μ, up to 1100 μ. Libriform fibres present. R.S.: distinct spiral thickenings present in narrow and wide vessel elements. Simple perforation plates. Homogeneous rays and intervessel pits alternate.

Identification: The anatomical features of some specimens led to their assignation to the genus *Acer*. According to Schweingruber (1990), *Acer platanoides* and *A. pseudoplatanus* can be differentiated from other *Acer* species by the presence of multiseriate rays 4 to 6 cells wide and, on average, 1 mm high. In all other European species (*A. campestre* L., *A. monspessulanum* L., *A. opalus* Miller and *A. heldreichii* Orph. Ex Boiss.) the rays are smaller. *Acer pseudoplatanus* has an average tangential vessel diameter of 50 μ or greater, an average ray height of up to 1000 μ, and multiseriate rays up to 8 cells wide (Jacquiot et al., 1973). According to Jacquiot et al. (1973) and García Esteban and Guindeo Casasús (1990), some of the samples examined could be identified as belonging to this taxon.

Acer aff. *campestre* L. (Plate II, 9–10)

Description: Tr.S.: growth ring boundaries distinct, diffuse-porous. Pores widely spaced, solitary or in small groups, commonly 2–4 vessels, radial rows. Average tangential vessel diameter 30–40 μ. Tg.S.: rays 1–3 cells wide, seldomly 4 cells. Average multiseriate ray height 200–300 μ. Distinct uniseriate rays. Rays composed of a single cell type. Libriform fibres present. Fibres non-septate. R.S.: spiral thickenings conspicuous in all vessels, perforation plates simple. Intervessel pits alternate and vessel-ray pits with distinct borders.

Identification: Some of the samples were assigned to *Acer* aff. *campestre* L.. According to García Esteban and Guindeo Casasús (1990), *A. campestre* L., *A. opalus* Miller and *A. monspessulanum* show the above-mentioned anatomical characteristics. In agreement with Jacquiot et al. (1973), non-acute rays 1–5 cells wide plus uniseriate rays frequently formed by square cells, typical characteristics of *A. campestre* L. according to these authors, were seen.

Ulmaceae

Ulmus sp. (Plate II, 11)

Description: Tr.S.: growth ring boundaries distinct, ring-porous. Earlywood with 2 to 3 rows of pores. Vessels arranged in tangential bands or diagonal pattern. Tyloses in vessels occasionally present. Tg.S.: Multiseriate rays 3–5 (6) cells wide, occasionally up to 8. Libriform fibres and vascular tracheids present. R.S.: perforation plates simple. Spiral thickenings conspicuous in vessel elements. Rays homogeneous, occasionally slightly heterogeneous with one row of square marginal cells.

Identification: Some samples showed the typical characteristics of the genus *Ulmus*. However, *Ulmus* species cannot be differentiated on the basis of wood microscopic characteristics (Schweingruber, 1990; García Esteban and Guindeo Casasús, 1990).

Oleaceae

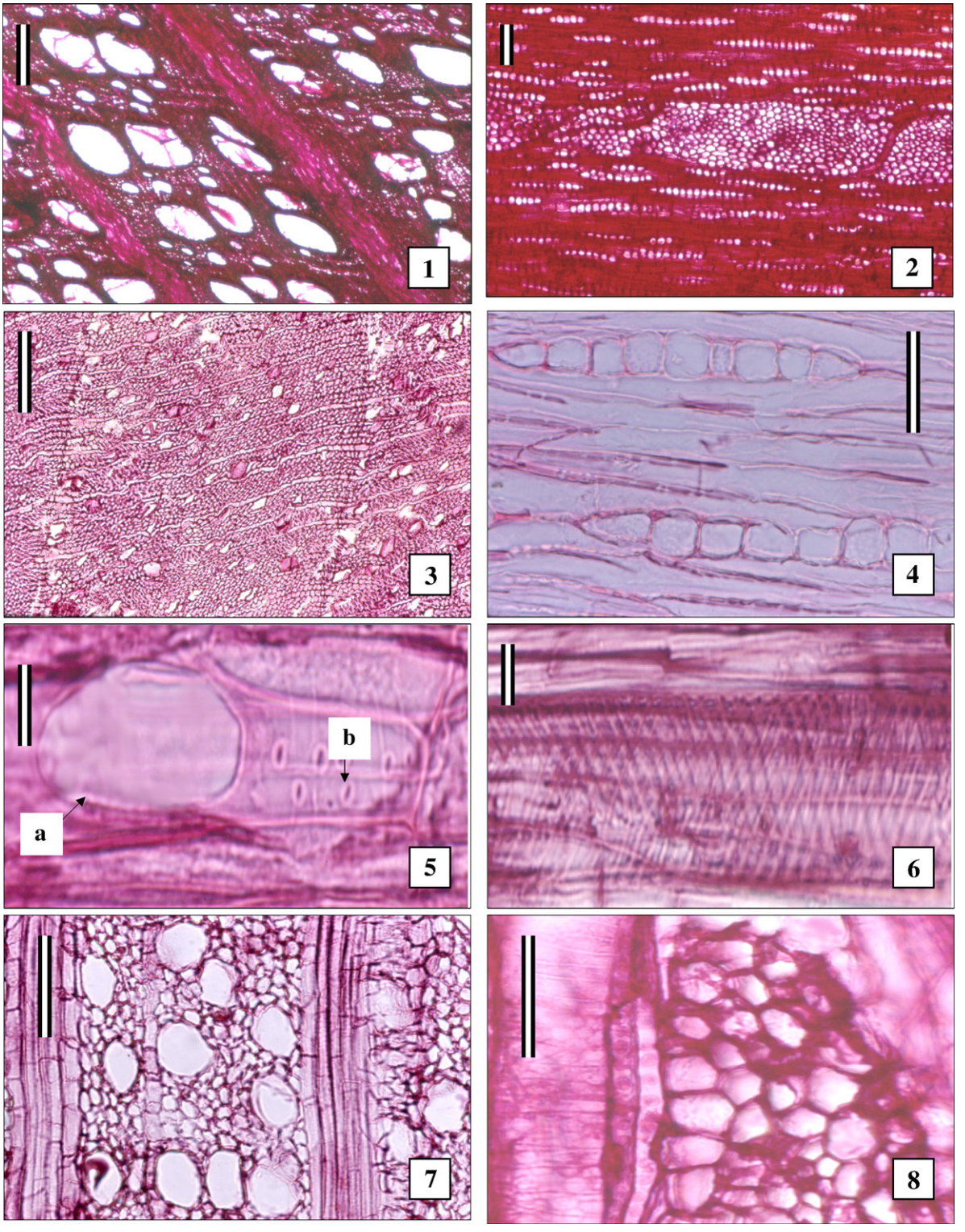
Ligustrum vulgare L. (Plate II, 12–14)

Description: Tr.S.: growth ring boundaries distinct. Semi-ring to diffuse-porous. Pores generally solitary, mainly distributed in the earlywood. In the latewood, vessels in small groups (2–3 elements) are occasionally seen. Average tangential vessel diameter in earlywood

Plate I

1. CAL631: Transversal section. *Quercus* subgenus *Quercus*. Pore size transition from the early-to the latewood zones abrupt. Scale bar=200 μm.
2. CAL1166: Tangential section. *Quercus* subgenus *Quercus*. Rays uni-to multiseriate. Scale bar=100 μm.
3. CAL1235: Transversal section. *Aesculus* sp. Rings marked with diffuse porous isolated elements or in small radial groups. Scale bar=100 μm.
4. CAL1235: Tangential section. *Aesculus* sp. Uniseriate homogeneous rays. Scale bar=75 μm.
5. CAL1235: Radial section. *Aesculus* sp. a. Simple perforation plate. b. Vessel with inter-vessel pits in which the fine spiral thickenings can be observed. Scale bar=20 μm.
6. CAL950: Radial section. *Aesculus* sp. Detail of vessel with spiral thickenings. Scale bar=10 μm.
7. CAL1563: Transversal section. *Acer* aff. *pseudoplatanus*. Diffuse-porous with vessel elements, solitary or in small groups. Scale bar=100 μm.
8. CAL1563: Tangential section. *Acer* aff. *pseudoplatanus*. Distinct spiral thickenings present and multiseriate ray. Scale bar=50 μm.

40–50 μ, 20–30 μ in the latewood. Tg.S.: rays generally biseriate, although uniseriate rays also frequent. Average ray height 300–500 μ. R.S.: rays conspicuously heterogeneous, with 1 to 4 rows of marginal cells. Spiral thickenings in vessel elements. Simple perforation plates. Fibre-tracheids present.



Identification: Some specimens showed features typical of the genus *Ligustrum* L. Their anatomical characteristics led to their identification as *Ligustrum vulgare* L. (Greguss, 1959; García Esteban and Guindeo Casasús, 1990).

Fraxinus aff. *angustifolia* Vahl. (Plate II, 15–16)

Description: Tr.S.: ring-porous. Pores generally solitary. Average tangential vessel diameter 120–140 μ. Paratracheal parenchyma, vasicentric and confluent. Sometimes there are distinct bands of parenchyma. Tg. S.: rays multiseriate, 3–4 cells wide. Spiral thickenings absent. Tyloses present in vessels. R.S.: rays homogeneous, occasionally heterogeneous with one row of square marginal cells. Simple perforation plates. Libriform and septate fibres present.

Identification: The characteristics of some samples led to their identification as members of the genus *Fraxinus*. However, assignment to species was difficult because of the strong uniformity in wood anatomy shown by *Fraxinus* species, and because of the decay and strong compression shown by the specimens. The single row of pores in the earlywood and the presence of septate fibre are, however, characteristic of *F. angustifolia* Vahl. The samples also showed tangential bands of parenchyma and multiseriate rays 3–4 cells wide, also typical of *F. angustifolia* Vahl. (Schweingruber, 1990).

Caprifoliaceae

Viburnum opulus L. (Plate III, 17–18)

Description: Tr.S.: diffuse porous. Pores generally solitary, very rarely in small groups. Vessels uniform in size over the entire growth ring. Average tangential vessel diameter 40–50 μ. Tg.S.: rays (1) 2–3 cells wide. Average ray height 250–400 μ, up to 600 μ. Average ray width 20–30 μ. R.S.: scalariform perforation plates with more than 20 bars. Rays distinct, heterogeneous with several rows of upright marginal cells. Fibre tracheids present. Spiral thickenings absent.

Identification: The anatomical features of some specimens strongly suggested they belonged to *Viburnum opulus* L. The lack of spiral thickenings in vessel elements or fibre-tracheids is typical of this species. *Viburnum lantana* L. and *V. tinus* L. show this anatomical characteristic (Schweingruber, 1990). In addition, *V. tinus* L. has smaller pores.

Cornus sanguinea L. (Plate III, 19–20)

Description: Tr.S.: growth ring boundaries distinct. Diffuse porous. Vessels generally solitary, uniform in size over the entire growth ring. Tyloses occasionally present. Average tangential vessel diameter 70–80 μ. Tg.S.: rays uniseriate or multiseriate, 3–5 cells wide. Average uniseriate ray height 180–230 μ; average multiseriate height rays 400–600 μ. Spiral thickenings absent. R.S.: fibre-tracheids present. Scalariform perforation plates with more than 15 bars. Distinct heterogeneous, multiseriate rays with 1 to 3 rows of upright marginal cells.

Identification: Two samples were assigned to the genus *Cornus*. The presence of distinct growth boundaries and thin-walled fibre-tracheids identified them as *C. sanguinea* L. (Schweingruber, 1990).

Salicaceae

Salix sp. (Plate III, 21–22)

Description: Tr.S.: growth ring boundaries distinct and diffuse porous. Vessels commonly in small groups of 2–4 (6) elements, sometimes grouped in radial rows. Tg.S.: uniseriate, seldom biseriate rays. R.S.: distinct heterogeneous rays with 1 to 2 rows of square and upright cells. Large, simple ray-vessel pits. Simple perforation plates and libriform fibres present. Spiral thickening in vessel elements absent.

Identification: Some samples were identified as belonging to the genus *Salix*. No identification at the species level was possible; *Salix* species cannot be distinguished from one other on the basis of their wood anatomy (Schweingruber, 1990).

Populus sp. (Plate III, 23–24)

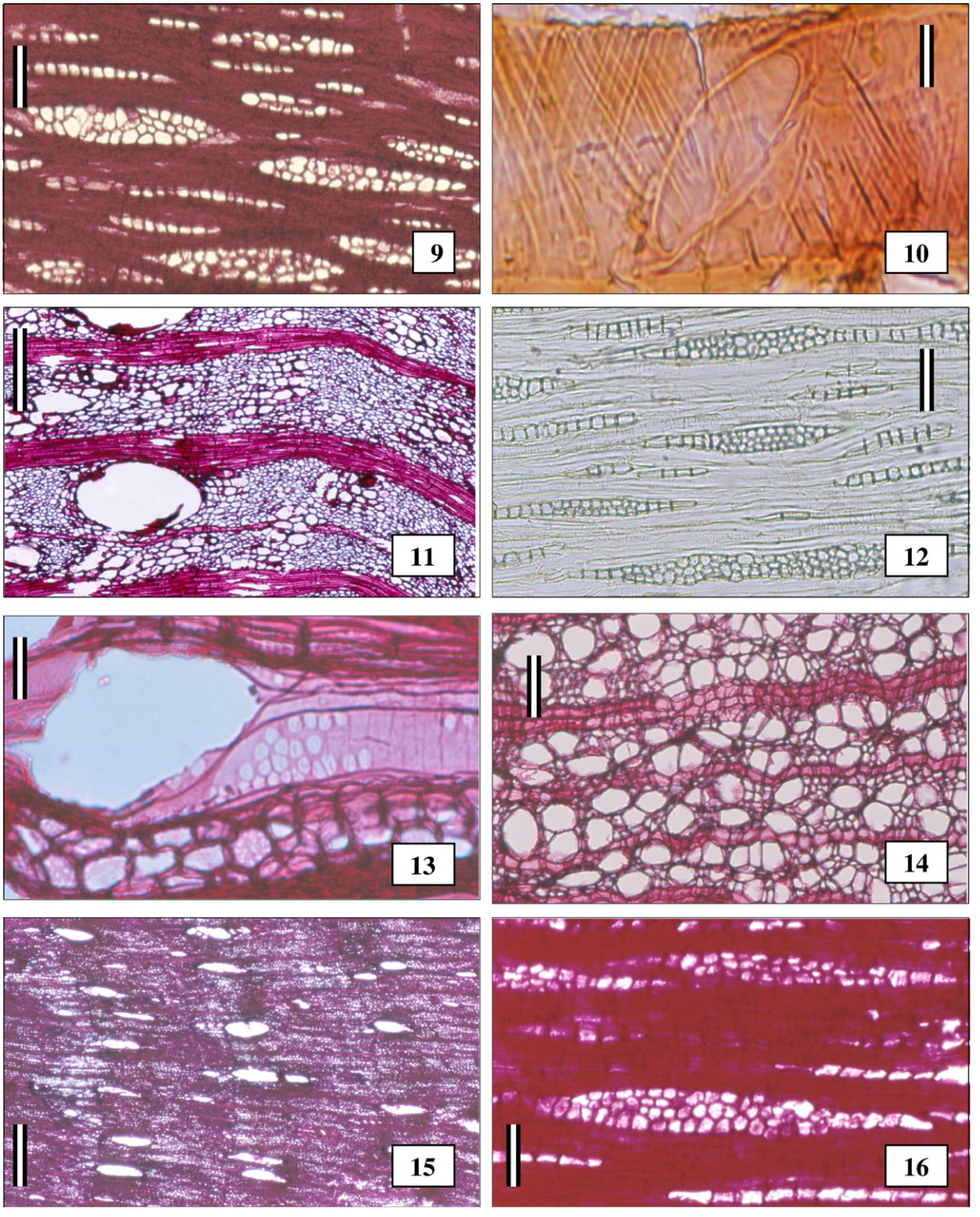
Description: Tr.S.: growth ring boundaries distinct. Diffuse porous with a large number of pores either solitary or in radial groups of 2–3 (sometimes 4) vessels. Tg.S.: uniseriate, seldom biseriate, homogeneous rays.

Plate II

9. CAL1592: Tangential section. *Acer* aff. *campestre*. Rays 1–3 cells wide, seldom 4 cells. Scale bar=50 μm.
10. CAL450: Radial section. *Acer* aff. *campestre*. Spiral thickenings conspicuous and simple perforation plate. Scale bar=10 μm.
11. CAL1301: Tranversal section. *Ulmus* sp. Vessels arranged in tangential bands or diagonal pattern. Scale bar=150 μm.
12. CAL62: Tangential section. *Ligustrum* cf. *vulgare*. Rays conspicuously heterogeneous. Scale bar=20 μm.
13. CAL62: Radial section. *Ligustrum* cf. *vulgare*. Distinct spiral thickenings in vessel and simple perforation plate. Scale bar=20 μm.
14. CAL62: Transversal section. *Ligustrum* cf. *vulgare*. Pores generally solitary or in small groups. Scale bar=75 μm.
15. CAL274: Transversal section. *Fraxinus* cf. *angustifolia*. Ring-porous and pores generally solitary. Scale bar=200 μm.
16. CAL274: Tangential section. *Fraxinus* cf. *angustifolia*. Rays multiseriate, 3–4 cells Wide. Scale bar=50 μm.

Libriform fibres present, tyloses occasionally present. R. S.: spiral thickenings absent in vessel elements. Simple perforation plates and large ray vessel pits.

Identification: Some samples were assignable to the genus *Populus* (Jacquiot et al., 1973; García Esteban and Guindeo Casasús, 1990; Schweingruber, 1990).



Identification at the species level was not possible due to the lack of known diagnostic characteristics.

4.2. Pollen analysis

Table 1 summarises the identification of both the macro-and microfossils analysed. The pollen diagram (Fig. 3a and b) reveals that the site once had open vegetation, with a low tree density (12.1% AP) and a significant presence of *Pinus* and evergreen *Quercus*. A mesocratic group of species with low pollen values was also present, in particular *Carya,* cf. *Castanea* and *Juglans*. The few grains of *Platanus* and *Celtis* indicate the modest local presence of these genera. Pollen grains of Taxodiaceae were also recorded, but in low percentages. The occurrence of pollen of *Pinus haploxylon*-type is noteworthy. A characteristic group of Mediterranean taxa was also present, including the genera *Phillyrea, Pistacia*, *Cistus, Thymeleaceae* and *Chamaerops*-type.

The high value for Poaceae (up to 49%) renders it the dominant group of the herbaceous pollen flora. This implies the presence of a hygrophilous or mesophilous grassland close to the site, or that there was a neighbouring xerophilous or mesoxerophilous open grassland. Pollen of cf. *Phragmites* (Poaceae with a diameter <15 μ) was represented.

5. Discussion and conclusions

With 23 families of woody plants (56 including the herbs and pteridophytes), the palynoflora of the Cal Guardiola site is evidently more diverse than its macrofossil flora, which was represented by only eight families. There may be several explanations for this. Firstly, wood fragments only reflect the local vegetation, but pollen can be dispersed over large distances and therefore provides information about the regional vegetation. A significant number of species represented in the palynoflora record probably never grow close to the fossilization site. This was likely the case of the Mediterranean taxa *Pistacia*, Cistaceae*, Phillyrea* and *Vitis*, and of *Pinus*, *Abies* or *Ephedra*. Secondly, the wood flora revealed the presence of families such as Hippocastanaceae and Cornaceae that were not represented in the palynoflora. A large number of fossil wood specimens belonging to *Aesculus* were found, but this genus produces small quantities of entomophilous pollen (Subiza, 1980; Strandhede et al., 1984). This might explain its absence in the pollen record but its presence in the macrofossil record. Similarly, the taphonomic potential of *Cornus* and *Ligustrum* might explain their absence in the palynological record, although other factors may be responsible.

The pollen record identified four families of Gymnosperms (Pinaceae, Cupressaceae, Ephedraceae and Taxodiaceae), none of which were represented in the wood remains even though the general preservation potential of gymnosperm wood is greater than that of angiosperms (Hedges et al., 1985; Hatcher and Clifford, 1997). Differences in habitat requirements probably explains their absence from the macrofossil record, although low density in the fossilization area and stochastic processes might also be responsible.

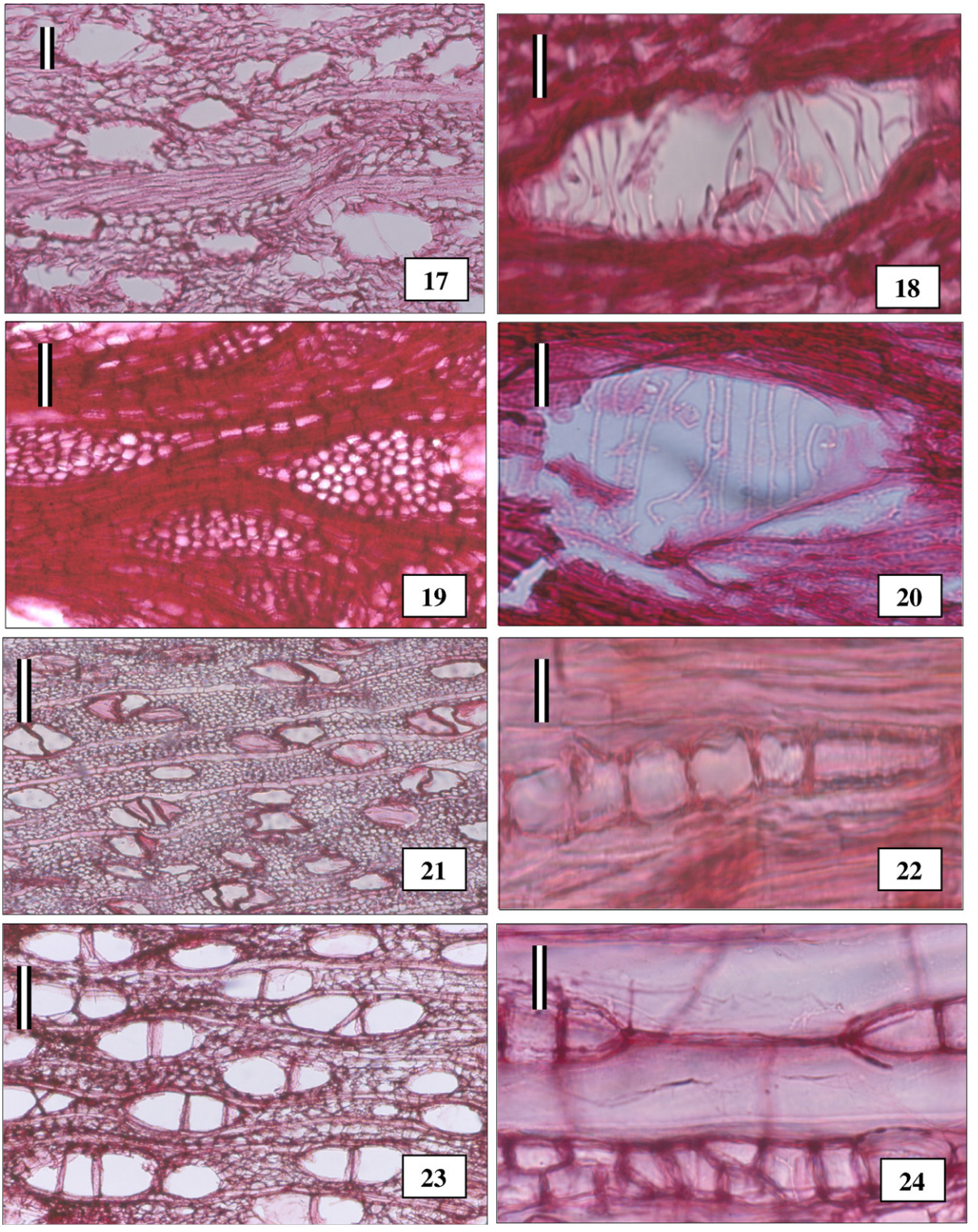
Taphonomic processes such as biodegradation, dispersal, necrokynesis and fossil diagenetic displacements might explain some of the differences between the macro- and microflora records. Finally, stochastic processes might also play a considerable role. Although it is not easy to assess the importance of these processes, they should be taken into account when interpreting palaeoenvironments.

5.1. Reconstruction of the vegetation and landscape

The results of the analyses performed allow a reconstruction of the Cal Guardiola palaeoenvironment. The wood fossils offer information on the river vegetation and/or mesophilous forests of the fossilization area, and the pollen data provide both local and regional palynological information. Streamside and river forest plants– Salicaceae (*Populus* and *Salix*), Fagaceae (deciduous *Quercus*),

Plate III

17. CAL1512: Transversal section. *Viburnum* cf. *opulus.* Diffuse porous. Pores generally solitary. Scale bar=50 μm.
18. CAL1512: Radial section. *Viburnum* cf. *opulus.* Scalariform perforation plates with more than 20 bars. Scale bar=20 μm.
19. CAL1485: Tangential section. *Cornus* cf. *sanguinea.* Distinct heterogeneous, multiseriate rays with 1 to 3 rows of upright marginal cells. Scale bar=40 μm.
20. CAL1485: Radial section. *Cornus* cf. *sanguinea.* Scalariform perforation plates with more than 15 bars. Scale bar=20 μm.
21. CAL65: Transversal section. *Salix* sp. Diffuse porous. Vessels grouped in small groups. Scale bar=100 μm.
22. CAL65: Tangential section. *Salix* sp. Distinct heterogeneous rays. Scale bar=20 μm.
23. CAL934: Transversal section. *Populus* sp. Diffuse porous with a large number of pores either solitary or in radial groups. Scale bar=100 μm.
24. CAL934: Tangential section. *Populus* sp. Uniseriate homogeneous rays. Scale bar=20 μm.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Aceraceae (*Acer*), Caprifoliaceae (*Viburnum*), Ulmaceae (*Ulmus*) and Oleaceae (*Fraxinus*)– were represented in both the macro-and microfossil record.

The area appears to have been home to a river or river-marsh ecosystem with a variety of plant environments. The dominant species of the river habitat were the aquatic macrophytes, including *Typha–Sparganium*, cf. *Phragmites* (Poaceae with a diameter <15 μ), *Myriophyllum*, *Sagittaria*, *Potamogeton, Alisma*, *Utricularia*, *Lemna*, *Polygonum* and *Nuphar.* A first and second riparian bands were detected, probably with taxa such as *Tamarix, Populus, Salix, Fraxinus, Sambucus, Viburnum, Cornus, Ligustrum* and *Ulmus*. In addition, a meso-hygrophilous forest developed over damp soils near the river. The foremost taxa in this broad-leaved deciduous forest were *Quercus* subgenus *Quercus*, *Acer* (*A. pseudoplatanus* type and *A. campestre* type) and *Carpinus.* Among the trees in the immediate surroundings of the site were the mesocratic *Aesculus, Platanus, Carya, Juglans* and *Celtis.* The presence of these species provides valuable palaeoecological information for the interpretation of the palaeoenvironment and palaeoclimate.

Away from the riverside, on the sunny slopes and in the drier parts of the fossilization site, a Mediterranean shrubland and forest vegetation developed. In this type of more or less open community, fragmented patches of *Quercus* were dominant. A characteristic group of Mediterranean taxa was present, including the genera *Phillyrea, Pistacia*, *Cistus,* Thymeleaceae and *Chamaerops*-type. Coniferous taxa such as *Pinus* and Cupressaceae were also present. Grasslands with members of the family Poaceae, including *Lygeum*, and Asteraceae, Chenopodiaceae, Amaranthaceae and Brassicaceae, were dominant in open dry areas, and were the main components of the herbaceous vegetation.

Finally, in the highest areas with higher levels of precipitation and a cooler climate, a *Betula–Abies–Pinus sylvestris*-type forest was established. These taxa may also have grown at lower altitudes where similar climatic conditions were present. Taxodiaceae may also have been present along the moist river margins of the riparian forest, or at higher altitudes with continuously high moisture levels. In these higher areas, there was no markedly dry summer and a mixed *Betula–Abies–Pinus*-Taxodiaceae forest would have existed.

5.1.1. The Taxodiaceae family

The disappearance of Taxodiaceae from Europe is probably related to the climatic changes of the Pliocene–Pleistocene, although the reasons for its complete extinction are unknown. Pronounced thermal contrasts or interspecific competition may have had an influence on its members' distributions. However, the family's demanding water requirements (Fauquette et al., 1998) were probably the most important cause of their decline; certainly, Quaternary climatic oscillations gave rise to changes in air and soil moisture levels which could have encouraged their demise. The ensuing summer droughts may have had a profound effect on hygrophilous taxa belonging to family Taxodiaceae and other Tertiary relicts in the Mediterranean area.

According to Zagwijn (1974), in the Netherlands the extinction of the Taxodiaceae took place at the Reuverian–Praetiglian boundary. In central and southern Europe, the family disappeared somewhat later. Thus, Taxodiaceae pollen is recorded in the Pliocene–Pleistocene and lower Pleistocene sites of Fornace Tini, Rio Ferraio, Piedrafitta and Stirone (Lona et al., 1969; Lona and Bertoldi, 1972) is considered by some authors to mark the Plio-Pleistocene boundary "the Tiberian boundary" (Lona et al., 1969). According to Michaux et al. (1979), this family disappeared from central Italy in the Early Pleistocene.

In France, the distribution of the Taxodiaceae was drastically reduced during the Pliocene–Pleistocene transition, although its members existed in the lower Pleistocene in different regions of the Massif Central, e.g., in the Velay and Mont Dore lower Pleistocene sites, where these taxa are recorded for some episodes (Brun, 1976). They were also present in the Bourgogne region in the middle Tiglien (Jan Du Chene, 1976).

Although in Europe Taxodiaceae occurs in the lower Pleistocene record, this family is exclusively related to the Tertiary series in the Iberian record. The earliest pollen and macroremains date from the lower Miocene (Fernández Marrón and Álvarez Ramis, 1988; Barrón and Diéguez, 2001). During the Pliocene, a significant reduction in their populations took place, although it is still possible to find fossils in the Iberian record. The occurrence of Taxodiaceae pollen in the northeastern Iberian Peninsula (Suc and Cravatte, 1982; Suc, 1997) and Pampilhosa do Botao (where *Sequoia*, *Taxodium* and *Sciadopitys* pollen has been recorded) is noteworthy (Diniz, 1972). Moreover, a leaf impression fossil of Taxodiaceae has been identified at the Lepe Pliocene site (Barrón et al., 2003). Finally, wood of the Taxodiaceae genera *Sequoia* and *Cryptomeria* or *Cunninghamia* has been recorded in the northern Iberian Peninsula (Alcalde Olivares et al., 2004).

The appearance of Taxodiaceae pollen in the lower–middle Pleistocene site of Cal Guardiola is significant: this is its first mention for the Iberian Pleistocene record and is one of its latest occurrences in the European Pleistocene record. Huard (1965) indicated the possibility of a continuous Taxodiaceae forest in the Pyrenees

during the Miocene. If this were so, the family may have been continuously present from the Miocene to the lower–middle Pleistocene in the northern Iberian Peninsula. This area of Spain may therefore be one of the most interesting for the palaeoecological and palaeogeographical study of this family with respect to the European Cenozoic period.

5.1.2. Palaeoclimatic reconstruction of the Cal Guardiola site

The Cal Guardiola site was home to a noteworthy group of thermo-hygrophilous and meso-hygrophilous taxa such as *Carya*, *Platanus*, *Juglans*, *Aesculus* and *Carpinus*. The pollen grains and macrofossils of these species suggest a low representation in the broad-leaved forest of the area, although the group was relatively well diversified. The finding of *Carya* represents its latest occurrence in the fossil record of the Iberian Peninsula. Previously, *Carya* has been recorded at the lower Pleistocene sites of Bañolas (Julià and Suc, 1980; Leroy, 1987), Crespiá (Roiron, 1983), Dosquers (De Deckker et al., 1979), and Mas Miguel and Mas Grill (Geurts, 1977). The present results provide the only record of the genus *Aesculus* for the Iberian Peninsula. This reference is also one of the most recent for the genus in Europe, before the radical reduction in its distribution to the Balkans (Postigo Mijarra, 2003). In addition, this is the first reference for this genus in Europe based on the microscopic characteristics of wood.

The above-mentioned taxa are well represented in the European Neogene series. They form part of the deciduous, mesophilous communities characteristic of the warm-temperate episodes of the Pliocene and lower-Pleistocene (Zagwijn, 1967; Renault-Miskovsky and Girard, 1978; Maley, 1980; Urban et al., 1983; Van der Burgh, 1983; Bertoldi et al., 1989, Mariotti Lippi, 1989; Ravazzi and Rossignol, 1995; Ferguson and Knobloch, 1998; Van der Burgh and Zetter, 1998). The appearance of this group of species in the Iberian Pleistocene record is, however, very rare (Geurts, 1979; García Antón, 1992; Leroy, 1997). Its presence at Cal Guardiola suggests a warm-temperate episode.

The presence of the mesocratic taxa Taxodiaceae and *Pinus haploxylon*-type in the lower–middle Pleistocene at Cal Guardiola confirms the importance of the Peninsula as a refuge area. The survival of Tertiary taxa in the Iberian Peninsula over long periods during the Pleistocene is supported by numerous studies (García Antón et al., 1990; Carrión and Sánchez-Gómez, 1992; Martínez-Atienza and Morla, 1992; Morla, 1996; Costa Tenorio et al., 1997; Carrión et al., 2003; Postigo Mijarra, 2003).

5.2. Comparisons with other Pleistocene sites of the Iberian Peninsula and neighbouring areas of Europe

The age of the Cal Guardiola site renders it comparable to others of the Iberian Peninsula. Its chronology is comparable with that of the Gran Dolina deposit of the lower–middle Pleistocene Atapuerca site (García Antón, 1989, 1992; Parés and Pérez González, 1995). The pollen diagram for the latter site shows high percentages of deciduous and evergreen *Quercus,* although *Pinus* and Cupressaceae may have existed in large numbers in certain phases. In the lower Pleistocene TD2 stage, deciduous *Quercus* appeared, but a cold, dry climate became established and *Artemisia, Betula, Pinus* and Cupressaceae became more significant. In TD4, there was a high percentage of arboreal taxa, e.g., *Pinus* and *Quercus*. It should be noted that a major group of taxa such as *Fagus*, *Betula*, *Juglans* and *Olea* was also present during this phase. A transition period between a warmer and a colder climate is inferred. Both the Cal Guardiola and Atapuerca sites have similar floral patterns: a high percentage of mesophilous taxa and a dominant *Quercus–Pinus* mixed forest. The presence of Taxodiaceae and *Pinus haploxylon*-type taxa in the Cal Guardiola site is, however, a remarkable difference. Further, mesocratic taxa are well represented in the Cal Guardiola deposit (quite different from that seen at the Atapuerca site); particularly noteworthy is the first citation of *Aesculus* for the Iberian Peninsula.

The Cal Guardiola site can also be compared with the Buenavista Superior sequence, dated just after the Matuyama-Bruhnes boundary during isotopic Stage 19 (Martín-Arroyo, 1998). In Zone I of the Buenavista site an evergreen *Quercus–Olea* forest with Ericaceae and *Juniperus* is represented, but at the beginning of the middle Pleistocene (zones IIa and IIb) a Mediterranean evergreen *Quercus–Olea* forest is again seen. Species such as *Salix, Juglans, Ulmus, Alnus* and *Pinus* occur throughout the pollen diagram. Buenavista shows a more typical Mediterranean community than Cal Guardiola, which lacks a well-developed thermohygrophilous group. Neither Taxodiaceae nor *Pinus haploxylon*-type are represented in the Buenavista pollen diagram.

The assemblages of the lower–middle Pleistocene sites of the northern Iberian Peninsula strongly resemble those of the Cal Guardiola site. The lower Pleistocene Molli Vell deposit (Geurts, 1977, 1979; De Deckker et al., 1979) includes three phases showing a continuous *Pinus* forest and a strong presence of deciduous *Quercus*. Occasional meso-thermohygrophilous species such as *Carya*, *Juglans*, *Castanea*, *Carpinus* and *Ostrya* were also present. Similarly, a *Pinus–Quercus* forest developed at the lower Pleistocene Mas Grill site (Geurts, 1977, 1979). Meso-

thermohygrophilous taxa including *Fagus*, *Ostrya*, *Carya* and *Juglans* are also represented. Both deposits show a Mediterranean coniferous-broadleaved mixed forest with the presence of Tertiary species, some of which persist in central-eastern Mediterranean refuges. Nevertheless, the Gal Guardiola site has a higher diversity of mesocratic species, and a notable presence of Taxodiaceae and *Pinus haploxylon*-type. The presence of *Aesculus* at Cal Guardiola is an equally significant distinction. In addition, Cal Guardiola stands out for the large quantity and wide diversity of its recorded materials compared to these other sites. It is worth emphasizing the importance of the information inferred from the Cal Guardiola assemblage, which is essential for understanding the development of the Pleistocene flora in the Iberian Peninsula.

With respect to other Western European sites, Cal Guardiola can be compared to the Waalian site at La Vallonnet (Renault-Miskovsky and Girard, 1978) in the Maritime Alps. The pollen sequence of the latter site shows a series of different stages belonging to the lower and middle Pleistocene. The lowermost part of the section reflects a dense, mixed forest (55–75% AP). *Pinus diploxylon*-type species were accompanied by Mediterranean deciduous taxa belonging to the genera *Quercus*, *Ligustrum*, *Fraxinus*, *Salix*, *Ulmus* and to the Oleaceae. Thermophilous trees including *Aesculus*, *Juglans, Pterocarya*, *Carpinus* and *Platanus* are also represented. According to the above authors, the pollen record reveals a temperate-warm and dry climate. The Cal Guardiola site has evident similarities. The Waalian-Menapian Mont-Dore (Brun, 1976) deposit also bears some floristic resemblance to Cal Guardiola. The former shows evidence of a *Quercus* forest with other broad-leaved trees such as *Ulmus*, *Betula*, *Tilia* and *Corylus*, with conifers also well represented. Finally, the Saint-Martial site has analogous flora (Suc, 1976).

The lower-Pleistocene sites of northern and central Europe show different assemblages to those of the Mediterranean peninsulas. In colder times, the percentage of mesocratic species decreased severely in all parts of Europe (they eventually disappeared completely) to the benefit of steppe species (Elhaï, 1969; Suc, 1978; Leroy, 1990; Ablin, 1991). After analysis of the 81/26 deposit located in the North Sea, Ekman (1999) suggested a cold-adapted, hygrophilous flora. According to Leroy et al. (1994), latitudinal and altitudinal differences might explain these differences. In Southern Europe, thermo-hygrophilous taxa were relatively common during the lower and the lower–middle Pleistocene. A good series of them can be seen in Italy at Fornace Tini (Urban et al., 1983), in the Leffe Basin (Ravazzi and Rossignol, 1995), and at the Rio Ferraio, Piedrafitta and Stirone sites (Lona and Bertoldi, 1972). Similar results have been obtained at other sites in France, e.g., Bresse (Jan Du Chene, 1976), Saint-Martial, and Durfort (Suc, 1976).

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