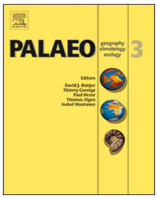
Palaeogeography, Palaeoclimatology, Palaeoecology 495 (2018) 245–258

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo



The late Pliocene palaeoenvironments and palaeoclimates of the western Iberian Atlantic margin from the Rio Maior flora

Manuel Vieira[a,c,*], Matthew James Pound[b], Diamantino I. Pereira[c]

[a] *Shell UK, 1 Altens Farm Road, Nigg, Aberdeen AB12 3FY, Scotland, UK*
[b] *Department of Geography and Environmental Science, Northumbria University, Newcastle upon Tyne NE1 8ST, UK*
[c] *Institute of Earth Sciences, Pole of University of Minho, Campus de Gualtar, 4710-057 Braga, Portugal*

ARTICLE INFO

Keywords:
Piacenzian
Tagus Basin
Pollen and spores
Flora, vegetation
Climate change

ABSTRACT

Using a revised chronology, a new palynological study on the late Pliocene (Piacenzian and earliest Gelasian) Rio Maior site of the Tagus Basin in western Portugal has been undertaken from the F98 core. Combining light microscopy and scanning electron microscopy, a total of 127 different pollen and spore taxa have been identified from the Piacenzian Lake and indicate the presence of a subtropical to warm-temperate mixed forest during the majority of the Piacenzian (3.6–2.8 Ma). It is only in the latest Piacenzian (after 2.8 Ma) that progressive extinctions of climate sensitive taxa and a drop in diversity indicate a cooling and drying climate trend that has also been recorded from high-latitude localities. By the earliest Gelasian (2.58 Ma), a low diversity Ericaceae and *Pinus* dominated vegetation remained. The Piacenzian flora of Rio Maior also shows fluctuations in the presence of climate sensitive taxa and pollen-spore diversity that may be related to Piacenzian glaciations.

1. Introduction

1.1. Rationale

The Pliocene marks the final shift from palaeoclimates warmer than present-day to the glacial – interglacial cycles of the Quaternary (Dowsett and Poore, 1991; Dowsett et al., 1994, 1996, 2016; Haywood et al., 2011; Haywood et al., 2013a, 2013b; Salzmann et al., 2013). Having an interglacial climate warmer than present day and glacial intervals at, or above, present day temperatures makes the Pliocene an excellent natural laboratory for exploring earth systems in a warmer than present climate (IPCC, 2013; Panitz et al., 2016). Earth system reconstructions and palaeoclimate modelling of the Piacenzian (3.6–2.58 Ma) are both well developed and provide a global scale context to our understanding of the late Pliocene (Dowsett et al., 1994, 2010, 2016; Salzmann et al., 2013; Pound et al., 2014; Haywood et al., 2016; Boyd et al., 2018). However, the strength of the Earth System reconstructions and the evaluation of climate simulations are reliant on proxy data (Salzmann et al., 2013). For global scale reconstructions, new proxy data strengthens, refines and changes our understanding of climate and environments during the Pliocene (Salzmann et al., 2013; Pound et al., 2015; Panitz et al., 2016). Whilst for climate modelling of the Pliocene, the need for geographically widespread and high-resolution terrestrial data is necessary for meaningful data-model comparisons (Salzmann et al., 2013; Haywood et al., 2013a). In this paper we present a palynological record from the lower Tagus Basin, Portugal within the context of the new stratigraphical framework that revises the dating of the Rio Maior flora to the Piacenzian. This pollen record includes a level of taxonomic detail that has not been previously reported for the Atlantic margin of the Iberian Peninsula. It clearly demonstrates a more humid vegetation type during the entire Piacenzian than has been reported from the central or eastern regions of the Iberian Peninsula.

1.2. The Rio Maior flora

The palynology of the Rio Maior flora has been investigated since the 1940s when Miguel Montenegro de Andrade studied the first samples from lignites and peats outcropping in this region (Andrade, 1944). In the 1960s, Filomena Diniz started to investigate the Rio Maior basin. Pollen analyses of two drill cores in the axis of the basin allowed Diniz (1984) to recognize nine floristic assemblages (A to I). These attested to a general trend from subtropical (warm-humid) to a cooler, but still humid, climate (Diniz, 1984). An outcrop in the Abum area (Rio Maior) that is stratigraphically equivalent to Diniz's (1984) floristic assemblage G has yielded a partially studied macroflora (mainly documented by fossil leaves) including: *Chamaerops humilis*, *Cinnamomum polymorphum*, *Fagus pliocenica*, *Myrica* sp., *Oreodaphne heeri*, *Osmunda* cf. *parschugiana*,

---

[*] Corresponding author at: Shell UK, 1 Altens Farm Road, Nigg, Aberdeen AB12 3FY, Scotland, UK.
E-mail address: Manuel.Vieira@Shell.com (M. Vieira).

https://doi.org/10.1016/j.palaeo.2018.01.018
Received 18 September 2017; Received in revised form 12 January 2018; Accepted 12 January 2018

Pinus praepinaster, *Pinus* sp., *Pittosporum tavaresi*, *Quercus faginea*, *Sabal* cf. *haeringiana*, *Salix* sp., *Sequoia* cf. *langsdorfii*, *Smilax mauritanica* and *Smilax targionii* (Teixeira, 1942, 1944a, 1944b, 1954, 1973–74; Teixeira and Pais, 1976; Pais, 1987). Detailed carpological analyses from these deposits have not yet been carried out.

With an abundant palynoflora and well-preserved leaf assemblage, Rio Maior is a key location for understanding the Pliocene flora and palaeoclimate of the Atlantic coast of the Iberian Peninsula (Vieira, 2009). The Rio Maior flora has been compared with more northern (France, Germany) and eastern (Spain and Italy) palynological records to resolve regional scale climate development and it has been incorporated into the PRISM3 and PRISM4 global Piacenzian reconstructions (Suc et al., 1995a, 1995b, 1999; Fauquette et al., 1999, 2007; Salzmann et al., 2008; Jiménez-Moreno et al., 2010; Salzmann et al., 2013; Dowsett et al., 2016). However, the majority of these have used the original dating of the palynoflora from Diniz (1984) and not incorporated more recent work in the area that has shown the sediments to be Piacenzian and Gelasian in age (Ramos and Cunha, 2004; Vieira, 2009).

2. Materials and methods

2.1. Geological setting and age

Rio Maior (39°20′ N, 8°56′W) is located close to the Atlantic coast in central Portugal (Fig. 1). The Pliocene deposits fill a sub-basin that is 7.5 km long and 2 km wide, which belongs to the north-west border of the Lower Tagus basin. This sub-basin is limited in the north by a tectonic fault oriented NW-SE and the Mesozoic rocks of Estremadura region (Fig. 1). The Pliocene and Quaternary sediments of the sub-basin overlie an unconformity of Jurassic to Miocene strata. From the bottom to the top, the Rio Maior Pliocene sediments comprise: fine caulinitic sands, lignites and diatomites and, in the uppermost layers, clays and sands (Fig. 2) (Zbyszewski, 1943, 1967). The most complete sedimentary succession is located near the eastern border of the basin (Espadanal area) and constitutes a small anticline with a NW-SE orientation that is 3.5 km long and 1 km wide, with a maximum sediment thickness of around 120 m (Fig. 1). The core selected for this new study was drilled in the central part of this anticline to capture the most complete sequence of sediments (Fig. 1).

The first geological study of this area was conducted by Zbyszewski (1943) who considered the Rio Maior deposits to be Plio-Quaternary in age (Zbyszewski, 1943, 1949). Using climatostratigraphical correlation by the comparison with pollen zones established by Zagwijn (1960), Suc and Zagwijn (1983) and Suc (1984), Diniz (1984) proposed an age for the Rio Maior deposits that spanned the whole Pliocene and the Gelasian (i.e. the Lower Pleistocene). The Diniz (1984) age model has been used subsequently when correlating the Rio Maior flora to others across Europe (Suc et al., 1995a, 1995b, 1999; Fauquette et al., 1999; Jiménez-Moreno et al., 2010). However, these correlating/synthesising studies missed successive sedimentological, palaeontological and isotopic data that have revised this age estimate.

Sedimentological and lithostratigraphical studies show that a marine transgression took place on the Atlantic coast of Portugal during the latest Zanclean – earliest Piacenzian (Pena dos Reis et al., 1992; Cunha, 1992; Cunha et al., 1993; Ramos and Cunha, 2004). According

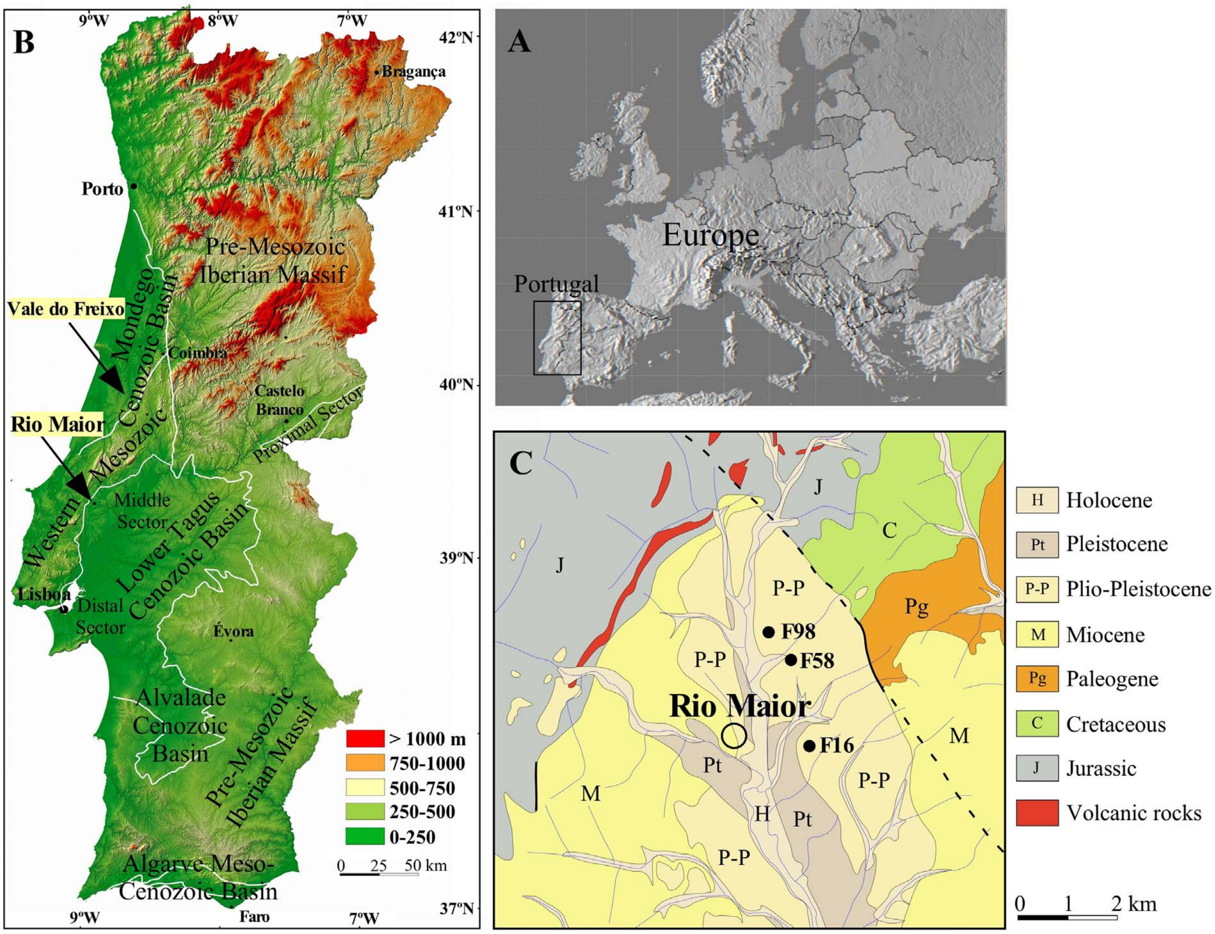


Fig. 1. Geographical location of Portugal (A) and Rio Maior (B) (source: Diamantino Pereira) and a simplified geological map of the Rio Maior sub-basin with the location of borehole F98 (C).
(Modified from Zbyszewski and Almeida, 1959 by Diamantino Pereira)

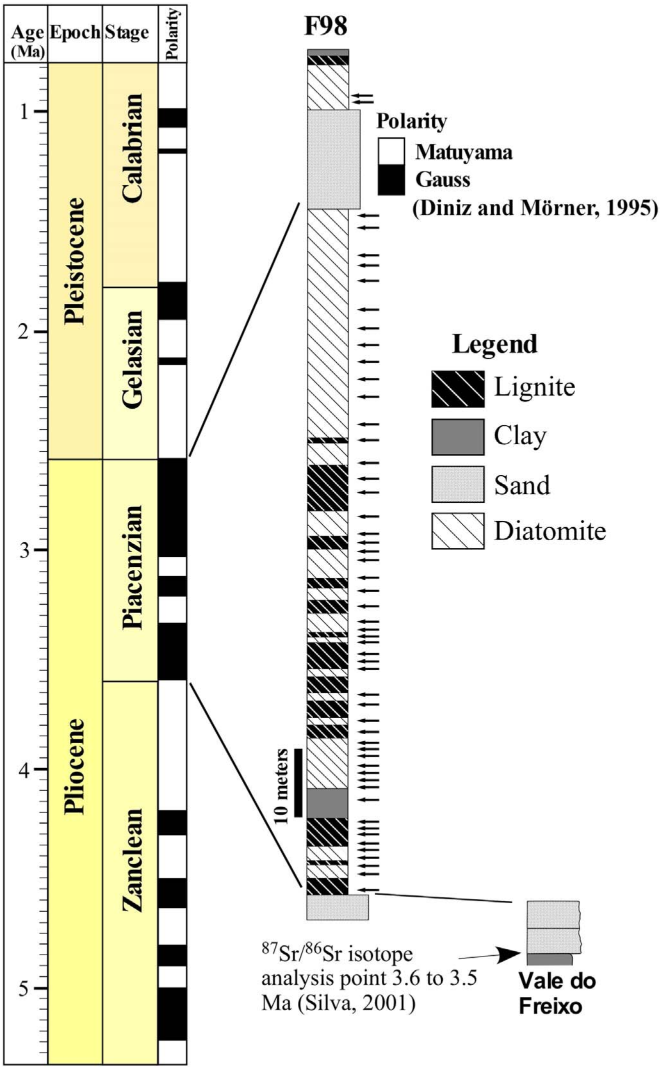


Fig. 2. Lithology of the F98 core and chronostratigraphic interpretation based on correlation with Vale do Freixo (Silva, 2001) for the base of the sequence and Abum area (Diniz and Mörner, 1995) for the top. The small arrows illustrate the position of the studied samples.

to Ramos and Cunha (2004), the transgression reached 28 km inland and deposited a succession of littoral sands. The shallow marine deposits that document this transgression outcrop in the Vale do Freixo (north of Rio Maior) and have been dated using calcareous nannofossils (Cachão, 1990). The presence and abundance of *Discoaster tamalis* allowed correlation with the Biozone CN 12a (Okada and Bukry, 1980) ≈ NN16 of Martini (1971). This latest Zanclean – earliest Piacenzian transgression has also been dated regionally to the same nannofossil biozone (Liu et al., 1996).

The same locality was the subject of a detailed molluscan remains study. This described the occurrence of *Ancilla* sp., *Solariella cincta*, *Solatia piscatorial* and *Tribia uniangulata*, that presently can only be found along the west coast of Africa. Those clearly indicate a shallow marine environment with relatively warm waters (Teixeira and Zbyszewski, 1951; Silva, 2001). Some pectinid shells were analysed for $^{87}Sr/^{86}Sr$ isotopes, which dated this marine transgression that underlies the Rio Maior sediments to 3.79 ± 0.27 Ma (Silva, 2001).

A diverse palynological assemblage was identified from this same outcrop and the presence of the dinoflagellate cysts *Achomosphaera* spp., *Lingulodinium machaerophorum*, *Operculodinium tegillatum*, *Selenopemphix armageddonensis*, *Spiniferites* spp. and *Tectatodinium pellitum*. The presence of *Selenopemphix armageddonensis* and *Lingulodinium machaerophorum* with relatively long processes, supports the palaeoenvironmental reconstruction based on molluscs of a relatively shallow marine environment. (Vieira et al., 2006). According to Louwye et al. (2004), *Operculodinium tegillatum* is recorded in the north Atlantic from 5 to 3.5 Ma, becoming extinct close to the limit between biozones NN15 and NN16 of Martini (1971). Combining the nannofossil, dinoflagellate and the isotopic data we consider a narrowest age range of 3.7–3.52 Ma (widest possible age range: 4.06–3.5 Ma) for the marine transgression that underlies the pollen bearing sediments of Rio Maior. At that time, the sea reached Rio Maior and deposited a succession of littoral sands, which are followed by the diatomites, lignites and clays representing a lacustrine environment that have yielded an abundant pollen flora subsequent to the marine transgression (Cunha, 1992; Ramos and Cunha, 2004). The basal sands present in Rio Maior yielded rare dinoflagellate cysts comparable with the better studied assemblages of Vale do Freixo (Vieira, 2009).

The uppermost sediments of the Rio Maior succession have been dated by magnetostratigraphy of outcrops in the Abum area to the Gauss – Matuyama reversal at 2.58 Ma (Diniz and Mörner, 1995) This provides an upper age estimate of the early Gelasian for the final infilling of the Rio Maior sub-basin (Diniz, 2001, 2003). According to this new dating, the sequence of lacustrine diatomites and lignites were deposited mainly in the Piacenzian (late Pliocence). The previous Zanclean age assigned by Diniz (1984) and extensively quoted in the literature (Suc et al., 1995a, 1995b, 1999; Fauquette et al., 1999; Jiménez-Moreno et al., 2010) should be considered redundant.

2.2. Methods

This study utilises the F98 core, which was taken in the central part of the sub-basin and recovered the entire sedimentary sequence (Fig. 1). This core was drilled in the 1970s and has been well conserved by the Portuguese Geological Survey. A total of 56 samples for palynological analyses were collected over 125 m, mainly from the diatomites and lignites (Fig. 2). From samples initially weighing about 50 g each, 15 g were processed for the diatomites and 5 g for the lignites. Sediments were treated with 30–40 ml of 37% HCl and 30–40 ml of 40% HF to remove carbonates and silicates respectively. Sample residues were sieved at 125 μm and 10 μm to remove course and fine fractions. Due to the high quantities of amorphous organic matter and charcoal fragments, the samples were boiled with 2–3 g of $NaBO_2H_2O_23H_2O$ (sodium perborate) and distilled water for about 5 min followed by three approximately one minute centrifugations in order to remove the chemical from the organic residue. No oxidizing reagents or alkalis, harmful to some pollen grains, were used. The final residues were diluted in liquid glycerine and mounted on slides. Slides were studied with a Leitz Laborlux S and Olympus CK 40 microscopes consulting literature including Erdtman (1971), Sivak (1975), Valdes et al. (1987), Reille (1999), Otero et al. (1996), Kapp et al. (2000) and Stuchlik et al. (2001, 2002). In order to get the most complete assemblage and identify questionable taxa, some pollen grains from all the slides studied, were separated for single grain observations under LM and SEM, according to the procedures outlined by Zetter (1989) and Vieira et al. (2009).

The palynological analyses include counts of pollen grains and spores. Pollen counts ranged from 303 to 521 grains per sample. *Pediastrum* and *Botryococcus* were not included in the counts (Supplementary Table 1). *Botryococcus* is particularly abundant in many samples. Pollen zones were defined using CONISS in StrataBugs.

Palaeoclimate reconstructions of seven variables: Mean Annual Temperature (MAT), Cold Month Mean Temperature (CMMT), Warm Month Mean Temperature (WMMT), Mean Annual Precipitation (MAP), Mean Precipitation of the Driest Month (MPdry), Mean Precipitation of the Wettest Month (MPwet) and Mean Precipitation of the Warmest Month (MPwarm) were produced using the co-existence approach (Mosbrugger and Utescher, 1997; Utescher et al., 2014). The co-

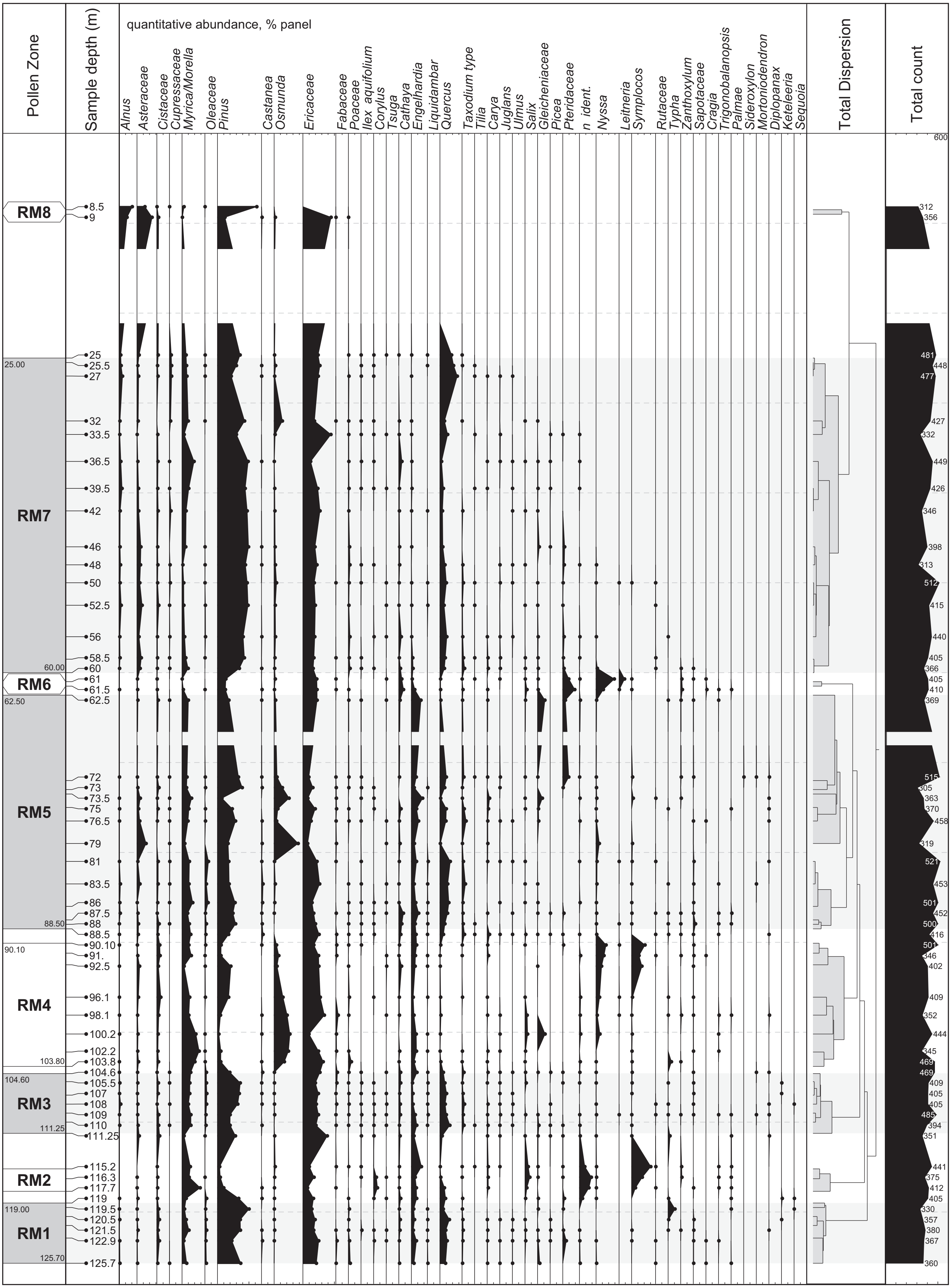


Fig. 3. Summary pollen chart of the most abundant taxa and selected relevant species (in percentage values) and highlighted pollen zones. Full pollen counts are available in Supplementary Table 1.

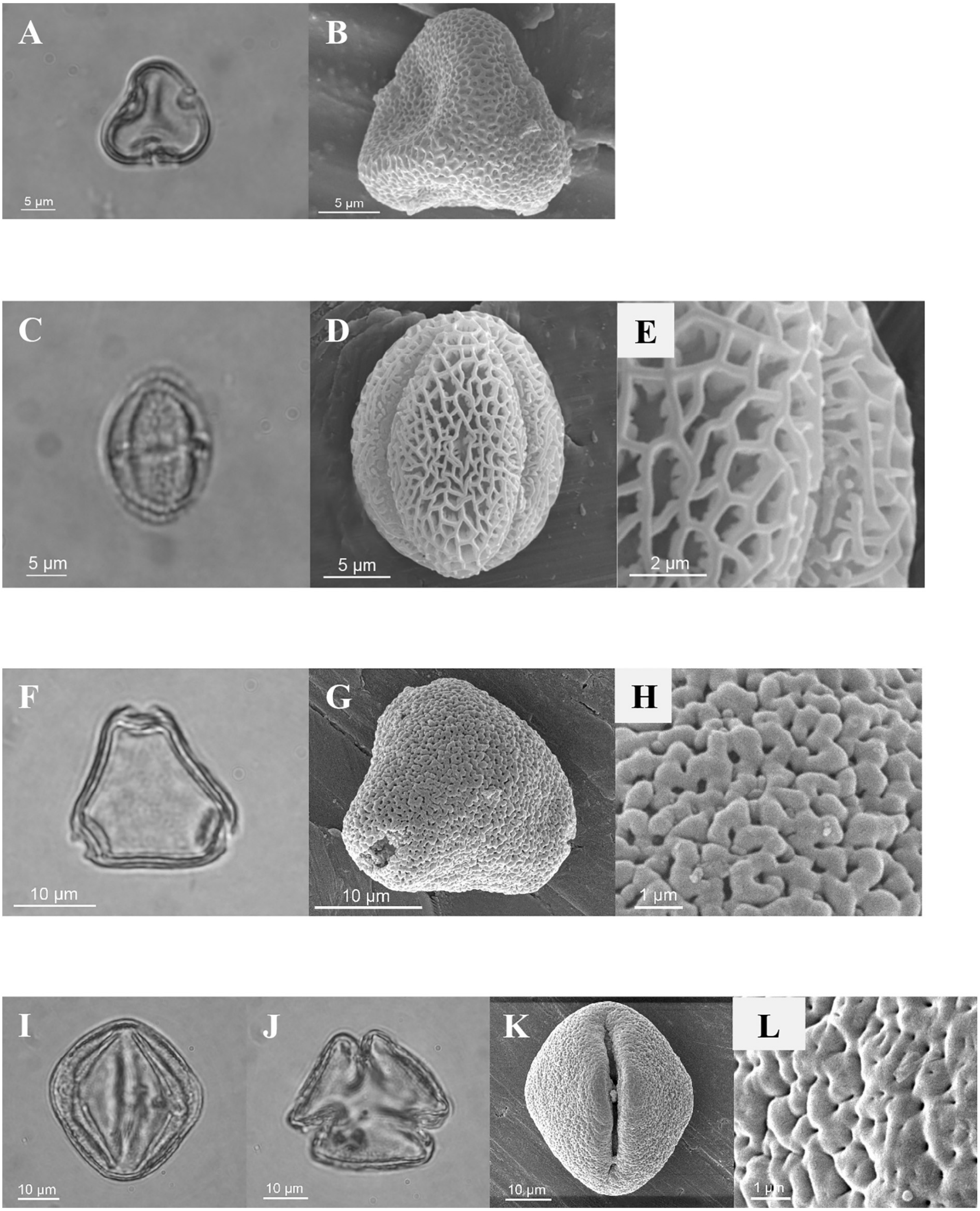


Fig. 4. Plate with selected taxa. *Craigia* pollen: A, polar view in LM; B, polar view in SEM. *Zanthoxylum* pollen: C, equatorial view in LM; D, equatorial view in SEM; E, detail of the exine surface. *Symplocos* pollen: F, LM polar view; G, SEM polar view; H, detail of the exine surface. *Diplopanax* pollen: I, equatorial view in LM; J, polar view in LM; K, equatorial view in SEM; L detail of the exine surface.

existence approach utilises the modern climatic distribution from a fossil taxon's nearest living relative's realised niche to reconstruct palaeoclimates (Mosbrugger and Utescher, 1997; Utescher et al., 2014). By comparing the climatic ranges of all fossil taxa in a pollen assemblage it is possible to produce a range within which all plants could coexist (Mosbrugger and Utescher, 1997; Utescher et al., 2014). As such climate reconstructions using the co-existence approach should be considered as ranges, not mid-values with error margins or “most-likely” values (Mosbrugger and Utescher, 1997; Utescher et al., 2014). As each value in a co-existence approach range is of equal probability, presenting co-existence approach data in any format other than a range, is to present it incorrectly (Utescher et al., 2014; Pound and Salzmann, 2017). When applying the co-existence approach to the Neogene the influence of modern relict taxa can introduce uncertainty into the reconstructions; so the relic taxa *Cathaya* and *Craigia* were excluded from the analysis in this manuscript (Utescher et al., 2014).

The Integrated Plant Record (IPR) technique was applied to the Rio Maior pollen assemblages in an attempt to reconstruct the zonal vegetation (vegetation biome) (Kovar-Eder and Kvaček, 2007; Kovar-Eder et al., 2008; Teodoridis et al., 2011). Following the classification scheme presented by Kovar-Eder et al. (2008) and updated by Teodoridis et al. (2011), each pollen taxon was classified into one of the 13 IPR types (Fig. 6). These were then presented as percentages of the assemblage to show the development of biome-scale (zonal) and local-scale (azonal) vegetation on the west Atlantic margin of the Iberian Peninsula.

More recently, Martinetto et al. (2017) identified a series of plant taxa that were extirpated in Europe during the Pliocene and Pleistocene, but still survive in the humid regions of east Asia today. These were termed HUTEAs (Humid Thermophilous plant taxa of East Asian Affinity) and were shown to be particularly sensitive to the cooling climate of the Pliocene and Pleistocene (Martinetto et al., 2017). To understand how HUTEA taxa responded on the west Atlantic Margin of the Iberian Peninsula, we used the classification scheme presented by Martinetto et al. (2017) and determined the number of HUTEA, CTEA (Cool-Tolerant extinct European taxa of East Asian affinity) and TEWA (Thermophilous European, West Asian and/or African elements) that were present in each pollen assemblage of Rio Maior (supplementary Table 2). To determine if the loss of HUTEA taxa led to a decrease in pollen taxa diversity, or if these taxa were replaced by others, the Shannon-Wiener Diversity Index (H′) was calculated (Shannon, 1948; Smith and Wilson, 1996). The Shannon-Wiener Diversity Index (H′) is presented in a standardised format (distance from the mean of the dataset, using the number of standard deviations from the mean as a measure of distance).

3. Results

The detailed study of 56 samples (RM.116 – RM.7) from core F98 allowed identification of 127 different taxa from a total of 22,850 pollen and spore grains counted (Supplementary Table 1). Almost all the samples revealed an extremely rich and diverse palynomorph assemblage. Although, the diversity decreased towards the top of the core, which may in part be due to unfavourable sediments for preservation. Many elements were recorded for the first time in Piacenzian sediments for this latitude (Figs. 3, 4). Supplementary Table 2 summarises the pollen and spores identified along with the assigned nearest-living relative that was used for the co-existence approach (Fig. 5), the IPR classifications used in an attempt to reconstruct biome scale vegetation (Fig. 6) and HUTEA, CTEA & TEWA classifications used to evaluate when these taxa were extirpated on the west Atlantic margin of the Iberian Peninsula (Fig. 7).

3.1. Pollen zones

3.1.1. Pollen zone RM1

Pollen Samples RM.116 – RM.105 (125.7–119 m core depth). This lowermost zone was characterised by the dominance of *Pinus* in the pollen count (20–50%). All the other gymnosperms (*Cathaya*, *Picea*, *Taxodium* type and *Tsuga*) occurred in rare numbers (Fig. 3). Pteridaceae were the most abundant spores in the samples. The dominant arboreal angiosperms were *Quercus* (10–15%), *Engelhardia* (4–11%) and *Myrica/Morella* (6–10%). Also present in lower percents were *Carya*, *Liquidambar*, Oleaceae and *Ulmus* (Fig. 3). *Cercidiphyllum* and *Craigia* were identified in the basal two samples of Pollen Zone RM1. Low counts of *Symplocos* and *Nyssa* occurred throughout this interval. Ericaceae pollen were also present in every sample comprising an average of 20% of the pollen percent. Herbaceous plants occurred in low abundance with Amaranthaceae, Asteraceae, Cistaceae and Poaceae. Sample RM.108 at 119.5 m contained a peak of *Typha* together with high quantities of *Botryococcus* supporting the presence of a freshwater (probably lacustrine) environment.

In Pollen Zone RM1, there was a decrease in MAT from 16.8–18.2 °C at 121.5 m to 15.7–16.6 °C at 120.5 m, a possible decrease in CMMT from 3.8–12.2 °C to 2.9–3.8 °C, an increase in MPwet from 178 to 204 mm to 216–225 mm and an increase in MPwarm from 116 to 120 mm to 173–177 mm (Fig. 5).

3.1.2. Pollen zone RM2

Pollen Samples RM.103 – RM.101 (117.0–115.2 m). This zone was defined by increase percentages of *Myrica/Morella* (12–27%), *Symplocos* (16–28%) and *Engelhardia* (8–15%); with *Corylus* (4%) and *Salix* (6%) had their highest abundances in this zone (Fig. 3). Cistaceae, Ericaceae and *Quercus* pollen percents decreased when compared with Pollen Zone RM1. Pollen of Sapotaceae was present in frequent numbers. *Carya*, Gymnosperms, *Nyssa*, Rutaceae, *Taxodium* type and *Trigonobalanopsis* were only present in rare occurrences (Fig. 3) The herbaceous pollen and fern spore counts were low. Many of the indeterminate pollen grains in this zone may have been previously identified as Cyrillaceae-Clethraceae by Diniz (1984). However, using a SEM it was not possible to confidently confirm that the exine surface matched the description for the Cyrillaceae-Clethraceae group.

Between Pollen Zones RM1 and RM2 there was an increase in reconstructed MAT (15.7–16.6 °C to 17.2–23.9 °C) and CMMT (2.9–3.8 °C to 4.3–16.7 °C) (Fig. 5). There was an interval of fluctuating WMMT between Pollen Zones RM2 and RM3 with decreasing MAP: from 1217 to 1355 mm yr^{-1} at 115.2 m to 1037-1090 mm yr^{-1} at 111.25 m (Fig. 5).

3.1.3. Pollen zone RM3

Pollen Samples RM.97 – RM.85 (111.25–104.6 m). In this zone, *Pinus* and Ericaceae pollen were the most abundant pollen (20–35%), *Quercus* and *Myrica/Morella* had average percentages of 12% and *Engelhardia* comprised 5% of the total count. *Symplocos* pollen values dropped from 16 to 28% in Pollen Zone RM2 to < 1% in this zone (Fig. 3). Additional arboreal taxa were represented by frequent occurrences of Betulaceae, Carya, *Castanea*, *Ilex*, *Juglans* and *Tsuga*. Whilst, *Cathaya*, *Diplopanax Liquidambar*, Oleaceae, Taxodiaceae and *Ulmus* were present consistently through this zone (Fig. 3). There was an increase in herbaceous plants represented by pollen of Amaranthaceae, Apiaceae, Asteraceae, Cistaceae, Euphorbiaceae and Poaceae. Samples RM.87, RM.89 and RM.90 yielded abundant *Botryococcus* (outside the pollen count). *Keteleeria* and *Sequoia* pollen had their last occurrences at this zone (Fig. 3).

A further decrease in MAP is reconstructed in Pollen Zone RM3 to 823–932 mm yr^{-1} at 110 m was accompanied by a decrease in MPwarm from 115 to 120 mm at 111.25 m to 61–79 mm at 110 m (Fig. 5). Following the MAP minimum at 110 m was an increase in MAP to 1037–1217 mm yr^{-1} and a possible increase in MPdry (Fig. 5). An increase in MPwarm and MAP occurred by 107 m when compared to 110 m (Fig. 5). At the end of Pollen Zone RM3 (104.6 m), there was a probable decrease in CMMT from 3.8–12.2 °C to 2.9–3.8 °C and an increase in WMMT from 23.6–23.8 °C to 25.2–26.5 °C. MAP dropped from 1037 to 1090 mm yr^{-1} at 104.6 m to 823–932 mm yr^{-1}, MPwarm also decreased from 115 to 120 mm to 61–79 mm (Fig. 5).

3.1.4. Pollen zone RM4

Pollen Samples RM.84 – RM.73 (103.8–90.1 m). This pollen zone was characterised by the marked reduction of *Pinus* and *Quercus* pollen to lower percentages than in Pollen Zone RM3 (Fig. 3). Arboreal taxa were dominated by *Myrica/Morella* pollen (20%, decreasing towards the top of the zone) and *Engelhardia* (4–8%). *Osmunda* spores increased in occurrence (12–24%), particularly in the interval from 103.8 to96.1 m (Fig. 3). Towards the top of this zone (92.5–90.1 m) there was a marked influx of *Symplocos* (20%) and *Nyssa* (15%). The non-arboreal taxa were present in low counts, although Fabaceae pollen appears to

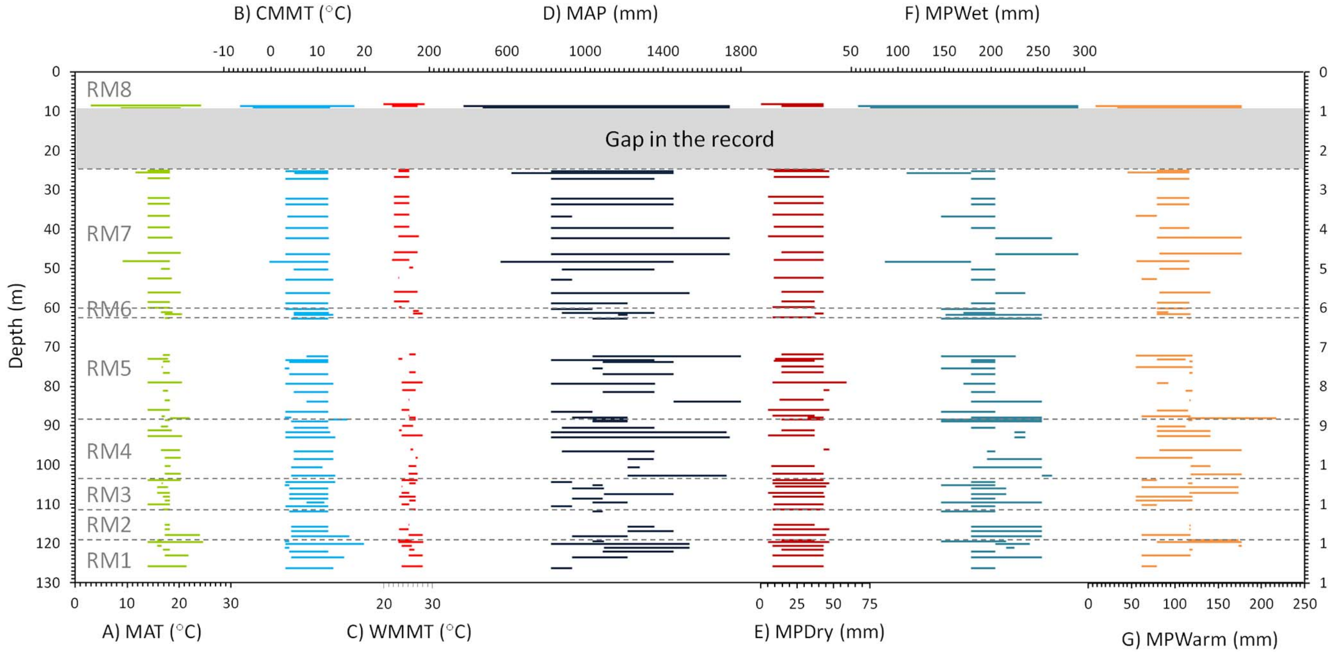


Fig. 5. Reconstructed temperature and precipitation parameters reconstructed from the Rio Maior pollen assemblages, plotted against depth in the core and the Pollen Zones (grey horizontal dashed lines). Horizontal bars represent the full range reconstructed by the co-existence approach (Utescher et al., 2014). A. Mean Annual Temperature (MAT); B. Cold Month Mean Temperature (CMMT); C. Warm Month Mean Temperature (WMMT). D. Mean Annual Precipitation (MAP) in mm yr-1; E. Mean Precipitation of the dry month (MPdry) in mm; F. Mean Precipitation of the wet month (MPwet) in mm; G. Mean Precipitation of the warm month (MPwarm) in mm.

be better represented in this pollen zone, particularly the genus *Ornithopus* which is not recorded above this zone (Fig. 3).

In Pollen Zone RM4, at 102.2 m, there were increases in MAP (823–932 mm yr^{-1} to 1217–1724 mm yr^{-1}), MPwet (178–204 mm to 254–265 mm) and MPwarm (61–79 mm to 118–177 mm) (Fig. 5). CMMT had also increased by 102.2 m to 4.3–13.6 °C (Fig. 5). At 98.1–96.1 m, MPdry increased from 7 to 37 mm to 43–47 mm, whilst WMMT decreased at 96.1 m core depth from 26.5–26.9 °C to 25.4–26.0 °C (Fig. 5). MPdry then decreased at 92.5 m to 5–37 mm, whereas MPwet increased from 195 to 204 mm to 225–236 mm (Fig. 5). At 90.1 m MPwet decreased to 178–204 mm, MPdry increased to 43 mm and WMMT increased to 23.8–26.0 °C (Fig. 5).

3.1.5. Pollen zone RM5

Pollen Samples RM.71 – RM.51 (88.5–62.5 m). The abundance of *Pinus* (25%) and (10–15%) *Quercus* increased through this zone, whilst *Myrica/Morella* and *Engelhardia* maintained similar counts with smaller fluctuations between samples (Fig. 3). There was a peak in abundance of *Engelhardia*, *Myrica/Morella* and *Zanthoxylum* in sample RM.55 at 73.5 m (Fig.3). In contrast to the previous zone, *Nyssa* and *Symplocos* numbers decreased (< 1%). There was a more consistent presence of many pollen types in this zone, in particular: *Buxus*, *Carya*, *Castanea*, *Ilex*, *Juglans*, Oleaceae, Rosaceae and Taxodiaceae (Fig. 3). *Osmunda* spores were relatively low in abundance in the basal part of the zone but increased towards the top; with a peak (35%) at 79 m (RM.59). Other spores of Gleicheniaceae and Pteridaceae showed a sporadic increase though this zone (Fig. 3). The last recorded occurences of *Cercidiphyllum*, *Diplopanax*, and *Mortoniodendron* were in this pollen zone (Fig. 3).

Pollen Zone RM5 (88.5–62.5 m) contains the warmest interval of the entire record at 88 m with MAT reconstructed at 18.2–22.0 °C and CMMT as 12.2–16.3 °C (Fig. 5). This was immediately followed by cooler temperatures at 87.5 m (MAT = 16.6–17.2 °C and CMMT = 2.9–4.3 °C) (Fig. 5). By 64 m CMMT had increased to 7.5–12.2 °C and there were increases in MAP (823–1037 m yr^{-1} to 1451–1809 mm yr^{-1}) and MPwarm (79–112 mm to 115–118 mm) (Fig. 5). A probable increase in MPdry from 13 to 43 mm at 83.5 m to 43–47 mm at 81 m was accompanied by a decrease in MAP to 1090–1355 mm yr^{-1} (Fig. 5). MPwarm decreased from 112 to 120 mm at 81 m to 79–92 mm at 79 m, before increasing to 116–120 mm at 76.5 m (Fig. 5). A possible cooling in MAT (16.8–18.2 °C to 16.6–16.8 °C), CMMT (3.8–12.2 °C to 2.9–3.8 °C) and a probable decrease in MAP (1090–1451 mm yr^{-1} to 1037–1090 mm yr^{-1}) occurred at 75 m (Fig. 5). These changes reversed at 73.5 m: MAT returned to 16.8–18.2 °C, CMMT returned to 3.8–12.2 °C and MAP returned to 1090–1451 mm yr^{-1} (Fig. 5). Also at 73.5 m WMMT decreased from 25.7 °C to 25.2 °C, this cooling continued to 73 m (23.0–23.8 °C) and was accompanied by a decrease in MPwarm from 116 to 120 mm to 79–112 mm (Fig. 5). WMMT increased to 25.2–26.5 °C at 72 m (Fig. 5).

3.1.6. Pollen zone RM6

Pollen Samples RM.49 – RM.48 (61.5–61.0 m). This short interval in the core marks a distinct change from Pollen Zone RM5 (Fig. 3). There was an increase of Pteridaceae spores, as well as pollen of *Cathaya* and *Nyssa*, with the former reaching a peak abundance (27%) at 61 m (RM.48). This zone also contained high counts of *Leitneria*, a sub-tropical plant that today is found in the southeast of the USA. *Engelhardia* had higher counts then *Quercus*, although this is this the last zone where *Engelhardia* pollen has a noticeable presence (Fig. 3). *Zanthoxylum* represents 2% of this pollen zone (Fig. 3). Rare pollen of *Craigia*, Palmae and *Trigonobalanopsis*, had their last occurences in this zone (Fig. 3). A possible increase in MPdry occurred from Pollen Zone RM5 into Pollen Zone RM6: from 8 to 37 mm at 62.5 m to 37–43 mm at 61.5 m and was accompanied by an increase in WMMT to 26.0–27.9 °C (Fig. 5).

3.1.7. Pollen zone RM7

Pollen Samples RM.47 – RM.13 (60.0–25.0 m). This pollen zone was characterised by a reduction in pollen and spore diversity - most of the remaining paratropical and warm-temperate taxa had their last occurrences in this zone (Fig. 3). Pollen of Sapotaceae and *Zanthoxylum* disappeared at the base of this zone, followed by the last occurrences of *Leitneria*, *Nyssa*, Rutaceae and *Symplocos* pollen (Fig. 3). *Cathaya*, *Engelhardia*, *Taxodium* typeand *Tsuga* occurred throughout this zone in low percentages and disappeared at the top of the zone (Fig. 3). *Pinus*

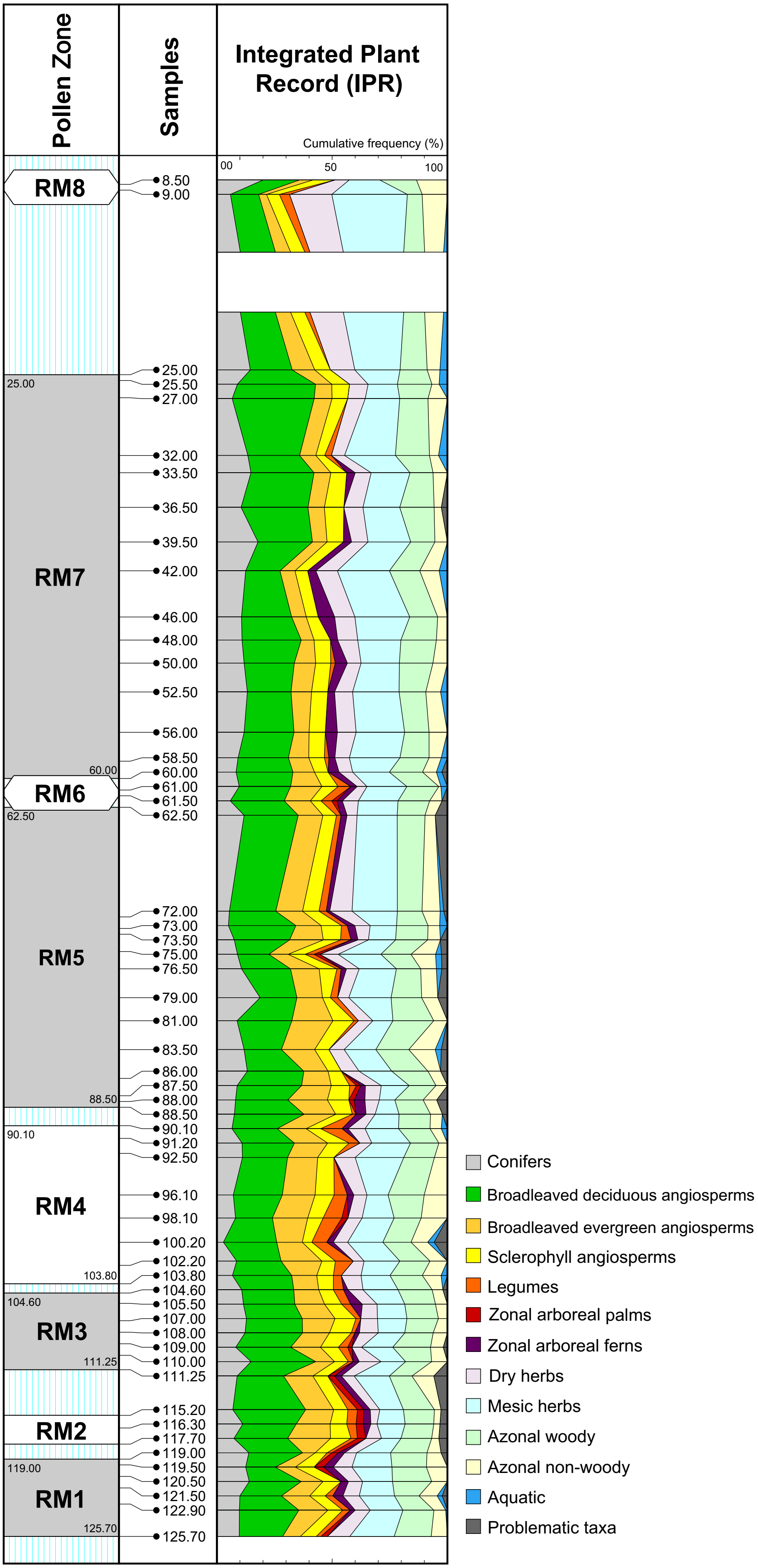


Fig. 6. The proportion of each of the IPR vegetation classifications (following Kovar-Eder et al., 2008; Teodoridis et al., 2011) plotted against core depth and the pollen zones defined in Fig. 3. The classification scheme divides each taxon into either zonal vegetation (biome scale) or azonal vegetation (local-scale). The classification of taxa is available in Supplementary information 2.

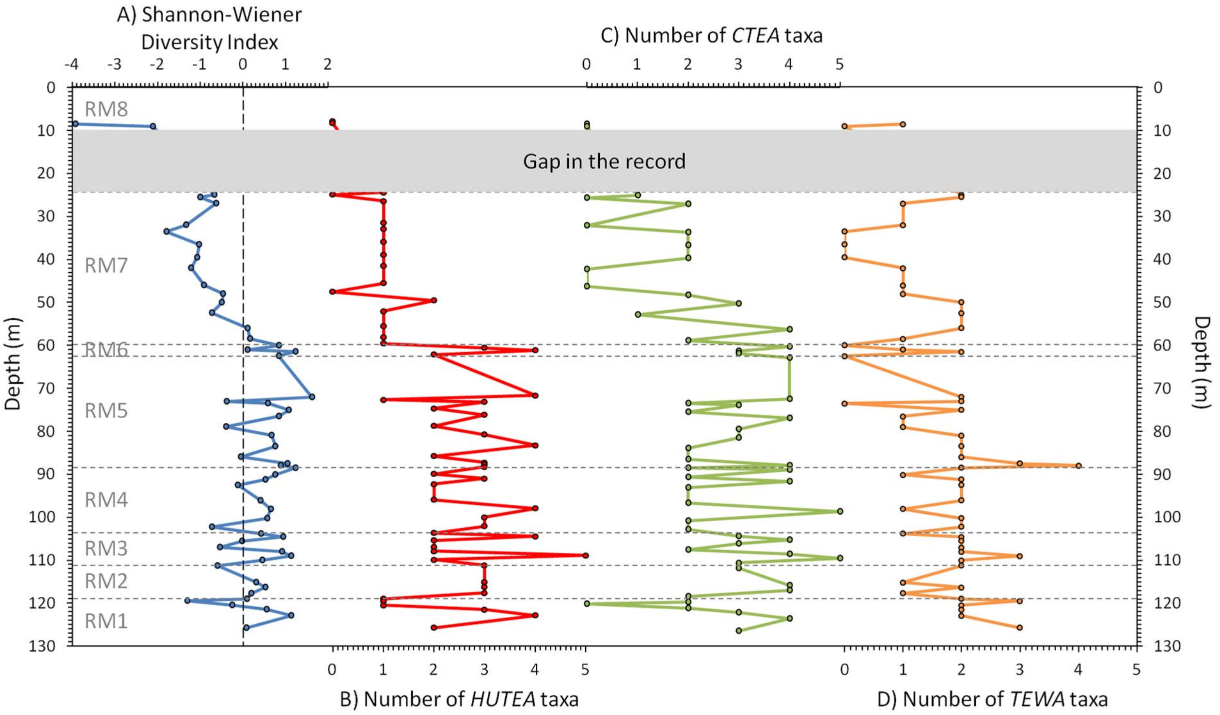


Fig. 7. Changes in the H′ Shannon-Wiener Diversity Index (A) and the number of climate sensitive taxa (B, C & D) plotted against depth in the core and the Rio Maior Pollen Zones (grey horizontal dashed lines). A. Standardised (number of standard deviations from the mean) H′ diversity Index of the Rio Maior pollen assemblages. The vertical dashed line from 0 represents the mean H′ diversity Index for the entire record. B. Number of HUTEA (Humid thermophilous plant taxa of East Asian affinity) taxa. C. Number of CTEA (Cool-Tolerant extinct European taxa of East Asian affinity) taxa. D. Number of TEWA (Thermophilous European, West Asian and/or African elements) pollen taxa in the Rio Maior assemblages. HUTEA, CTEA and TEWA were classified using the classification schemes in Martinetto et al. (2017) and can be found in supplementary information 2.

became the dominant taxon in the pollen spectrum (approx. 40%) together with a marked increase in Ericaceae, *Myrica/Morella* and *Quercus* (Fig. 3). Pollen of *Alnus* Asteraceae and Cupressaceae, became more frequent in this pollen zone (Fig. 3). The percentage of fern spores and herbaceous pollen appeared in similar quantities to previous pollen zones, but with lower taxonomic diversity (Fig. 3).

A decrease in WMMT (to 23.1–23.6 °C) and MPdry (to 8–37 mm) is reconstructed at the start of Pollen Zone RM7 (60 m) (Fig. 5). At 50 m WMMT increased to 25.2–26.0 °C, MPwarm increased to 82–116 mm and there was a possible increase in MPdry to 43 mm (Fig. 5). WMMT then probably decreased at 48 m to 21.6–25.2 °C and MPwet possibly decreased to 86–178 mm (Fig. 5). At 46 m core depth MPwet increased to 204–293 mm before it probably decreased at 39.5 m to 178–204 mm (Fig. 5). There was a final decrease in MPwarm from 82 to 116 mm at 39.5 m to 54–79 mm at 36.5 m, this then probably increased at 33.5 m to 79–116 mm (Fig. 5). A final fluctuation in MPwet occurred at 14–13 m core depth with first a probable decrease to 109–178 mm and a final increase to 178–204 mm (Fig. 5).

3.1.8. Pollen zone RM8

Pollen Samples RM.8 – RM.7 (9.0–8.5 m). This pollen zone comprises the only two productive samples in the uppermost 25 m of the core. The top sample was dominated by *Pinus* (64%), whereas at 9 m, Ericaceae (44%) and Asteraceae (23%) were the most abundant taxa. Pollen of *Alnus* increased through this zone, whilst pollen of *Castanea*, Cistaceae, *Myrica/Morella* and Poaceae were rare (Fig. 3). Pollen of herbaceous plants increased in proportion (20%) through this pollen zone (Fig. 3). Fern spores only represent 2% of total. This zone has the lowest diversity of the whole record (Fig. 3). All climate reconstructions in Pollen Zone RM8 (8.5–9 m) have wide ranges due to the relatively low number of taxa preserved (Fig. 5).

3.2. Integrated plant record, diversity and climate sensitive taxa

Using the IPR the pollen assemblages were classified into biome (zonal) and local (azonal) vegetation types (Fig. 6). In the Rio Maior F98 core, biome vegetation types were more abundant than local scale vegetation types. Within the biome-scale types, broadleaved deciduous trees and mesic herbs were the dominant classifications for the entire length of the core (Fig. 6). Broadleaved evergreen trees remain a constant element of the assemblage until the start of Pollen Zone RM7, from where the proportions of broadleaved evergreen trees gradually decrease (Fig. 6). Pollen Zone RM6 contains the last occurrence of zonal palms, which were present in isolated peaks of one or two samples in every pollen zone below RM6 (Fig. 6). Zonal arboreal ferns were present in the record until 32 m (Pollen Zone RM7) and typically show an increase in abundance when zonal palms were present (Fig. 6). Sclerophyll and dry environment herbs remain relatively constant through the record until they increase in Pollen Zone RM8. Legume elements are sporadically absent, but present in all pollen zones (Fig. 6).

The standardised H′ shows levels of pollen diversity fluctuating around the mean value for the entire core until the end of Pollen Zone RM6 (Fig. 7a). At the beginning of Pollen Zone RM7, H′ falls below the mean value for the core and continues to decline until the end of the record (Fig. 7a). A significant drop in H′ is also present towards the end of Pollen Zone RM1, at the boundary between Pollen Zone RM2 and RM3, in the middle of RM3, at the start of RM4 and twice in the middle of RM5 (Fig. 7a). The H′ record is mirrored by the number of HUTEA taxa present in the pollen assemblages, which shows a decrease to a single taxon at the end of Pollen Zone RM1, in the middle of Pollen Zone RM5 and in Pollen Zones RM7 and RM8 (Fig. 7b). The number of CTEA taxa also show a decrease at the end of Pollen Zone RM1 and during Pollen Zone RM7 (Fig. 7c). Conversely, TEWA taxa show an increase at the end of Pollen Zone RM1 and their largest abundance on the boundary between Pollen Zones RM4 and RM5 (Fig. 7d).

4. Discussion

4.1. Palaeoenvironment and palaeoclimate of Rio Maior

The Rio Maior F98 core pollen record shows an overall trend of decreasing diversity in tree and shrub taxa and a proportional increase in herbaceous taxa during the latest Piacenzian into the early Gelasian (Figs. 3, 6 & 7). Pollen Zones RM1 to RM6 are dominated by a diverse mixed evergreen and deciduous forest with a warm-temperate and humid climate, except in Pollen Zone RM5. In Pollen Zone RM5, the co-existence approach reconstructs CMMT > 6 °C and therefore this could classify as subtropical; if coldest winter temperature is used to define the subtropics (Corlett, 2013). Pollen Zone RM7 represents a gradual transition from the warm-temperate mixed forests of the earlier Piacenzian to the less diverse open woodlands of the Gelasian (Figs. 3, 6 & 7). Using the IPR calculations on zonal vegetation types to reconstruct biome-scale vegetation, would reconstruct the entire record as sub-humid sclerophyll woodland, open xeric woodland and xeric steppe (Kovar-Eder and Kvaček, 2007; Kovar-Eder et al., 2008; Teodoridis et al., 2011). The difference in the IPR based reconstruction and the qualitative reconstruction of the Rio Maior vegetation is based on the biasing influence of a diverse herbaceous component (Teodoridis et al., 2011). In the IPR calculations, if the taxonomic list contains > 30% herbaceous taxa then the vegetation is reconstructed as open woodland or if it is > 40% it is classified as a steppe (Kovar-Eder et al., 2008). However, it has been shown that modern deciduous and mixed forests can contain up to 70% herbaceous taxa (Teodoridis et al., 2011). The application of SEM to document the full taxonomic diversity of the Rio Maior pollen assemblages likely means that more of the herbaceous component from the diverse Piacenzian warm-temperate forests has been recorded (Figs. 3, 4 & 7a).

The pollen assemblage likely reflects different habitats and variations in the forest associated with climate fluctuations during the Piacenzian in a lacustrine setting, as can be seen in the relatively high proportion of azonal (local-scale) vegetation types (Fig. 6) (Pound et al., 2015; Panitz et al., 2016). In the immediate swamp and riparian areas surrounding the lake, trees such as *Alnus*, *Craigia*, *Engelhardia*, *Liquidambar*, *Nyssa*, Sapotaceae, *Taxodium* type, and *Zanthoxylum* were found (Fig. 8a) as attested in some other Pliocene sites of the central Mediterranean area (e.g. Bertini, 2010). In areas with better drainage, the forest composition comprised *Acer*, *Carya*, *Cathaya*, *Juglans*, *Myrica/Morella*, *Quercus*, *Trigonobalanopsis* and *Ulmus* with abundant Ericaceae species (Fig. 8a); similar assemblages though with Ericaceae in lower abundances have been pointed out in northern and central Italian sites (Bertini and Martinetto, 2008; Bertini, 2010). Shrubs and lianas included *Hedera*, *Lonicera*, Rosaceae and Vitaceae. Herbaceous plants, include pollen of the Asteraceae, Apiaceae, Campanulaceae, Fabaceae (*Astragalus*, *Ornithopus*, *Genista*), Euphorbiaceae (*Euphorbia*, *Mercurialis*) Poaceae (Vieira, 2009). Pollen of parasitic plants such as *Arceuthobium*, *Loranthus* and *Viscum* are present. Possible indicators of altitude include *Betula*, and *Picea* (Bertini, 2010; 2001). Abundant spores of *Osmunda* and Pteridaceae attest to intervals of high precipitation in Pollen Zones RM1, RM3, RM4 and RM5 (Figs. 3; 5). Previously, this vegetation record has been assumed to represent the entire Pliocene based on the original age determinations of Diniz (1984) and has been correlated with other early Pliocene records to generate syntheses of Iberian or western European vegetation and climate (e.g. Fauquette et al., 1999, 2007; Jiménez-Moreno et al., 2010), which multiple lines of evidence show is no longer the case (Cachão, 1990; Silva, 2001; Ramos and Cunha, 2004; Vieira, 2009). Pollen Zones RM1 to RM7 belong to the Piacenzian, whilst Pollen Zone RM8 is assigned to the Gelasian (Figs. 3 & 6).

Pollen Zone RM1 contains an interval (120.5–119 cm) of reduced H′ diversity, less HUTEA taxa, less CTEA taxa and a reconstructed drop in MAT and CMMT (Figs. 5 & 7). As Pollen Zone RM1 is part of the Piacenzian, it is likely that this interval may correspond to Marine Isotope Stage (MIS) M2 – the first strongly positive oxygen isotope excursion of NN16 and the Piacenzian (Haywood et al., 2013a). This glaciation event has been linked to 20–60 m sea level fall and a reduction in Sea Surface Temperature (SST) of 3–4 °C at the same latitude as the Rio Maior record (Naafs et al., 2010; Tan et al., 2017). Climate model simulations of this glaciation indicate that MAP would have increased over the western Iberian Peninsula (Tan et al., 2017). This is not seen in the co-existence approach reconstructions from Rio Maior, but an increase in the wettest and warmest months precipitation is reconstructed (Fig. 5). *Typha* forms a significant proportion of the pollen assemblage at the top of Pollen Zone RM1 and is accompanied by pollen of *Nuphar* indicating a marsh ecosystem bordering the Tagus Basin Piacenzian lake (Fig. 8a) (Willard et al., 2004). Aquatic taxa are present throughout the Rio Maior core, but in relatively small amounts after Pollen Zone RM1, this expansion of local swamps during the MIS M2 glaciation might be the result of global shifts in precipitation that are predicted by modelling (Tan et al., 2017).

Pollen Zone RM2 contains an increase in broadleaved evergreen trees, arboreal palms and arboreal ferns, along with an increase in H′ diversity showing a return to warmer moder diverse forests following the MIS M2 glaciation (Figs. 6 & 7). This interval likely represents an early part of the warm PRISM interval (Haywood et al., 2013a). As the climate, H′ diversity and IPR vegetation type proportions remain relatively constant until the end of Pollen Zone RM6, these likely contain the entire PRISM interval to the next major positive oxygen isotope excursion (MIS G10) at around 2.8 Ma (Lisiecki and Raymo, 2005). During Pollen Zone RM2, pollen of *Symplocos* reaches its first of two peaks (Fig. 3). Today *Symplocos* (Fig. 4) is a genus of around 300 species of trees and shrubs that inhabit subtropical to tropical humid environments (Wang et al., 2004). This environmental preference is consistent with the rest of the pollen assemblages from Pollen Zone RM2 and the reconstructed palaeoclimate, which indicates a MAP of 1217–1451 mm and MPwarm of 116–118 mm (Fig. 4). The second peak in *Symplocos* pollen comes towards the end of Pollen Zone RM4 and is accompanied by a peak in *Nyssa* pollen and high WMMT (23.8–26.0 °C) and MPdry (43 mm) (Figs. 3; 4). Modern species of *Nyssa* inhabit temperate to tropical climates; many have a preference for humid environments and have adaptations to survive seasonal flooding (Eyde, 1997). *Nyssa* pollination is predominantly entomophilous (though limited anemophilous pollination does occur in some species) and thus any significant accumulation of its pollen in the fossil record is normally autochthonous - indicating a wetland environment (Eyde, 1997; Sun et al., 2009; Rich et al., 2015). A second peak in *Nyssa* pollen is found in Pollen Zone RM6, together with a significant amount of *Leitneria* pollen (Fig. 3). Today the genus *Leitneria* is monospecific and only found in swampy environments of the southern USA (Sharma et al., 2008). Pollen Zone RM6 also reconstructs the warmest WMMT (26.0–27.9 °C) and one of the intervals of highest MPdry (37–43 mm) (Fig. 4). The high summer temperature, the higher precipitation and the last occurrence of diverse HUTEA taxa means that RM6 may well correspond to the last major warm interval of the Piacenzian, which has been dated in the high-latitudes of the North Atlantic to 3.29–3.18 Ma (Panitz et al., 2016). Alternatively, forests and warm conditions prevailed at Lake El'gygytgyn (North-eastern Russian) until 3.06 Ma, which is also the modelled interval for peak warmth in the Iberian Peninsula (Andreev et al., 2014; Prescott et al., 2014).

In Pollen Zone RM7, at the top of the Piacenzian, the general floral content changes with less HUTEA taxa, declining H′ diversity and a gradual reduction in the number of CTEA taxa (Figs. 3; 7). The co-existence approach reconstructs a drop in WMMT by at least 2.4 °C from the last sample in Pollen Zone RM6 to the first sample in Pollen Zone RM7 (Fig. 5). From the start of Pollen Zone RM7 *Quercus* pollen becomes permanently more frequent than *Engelhardia* (Fig. 3). Overall, Pollen Zone RM7 contains the highest loss of pollen types with around 40 taxa disappearing from the Rio Maior record before the end of this zone (Figs. 3 & 7). Not all of these losses are taxa associated with warm

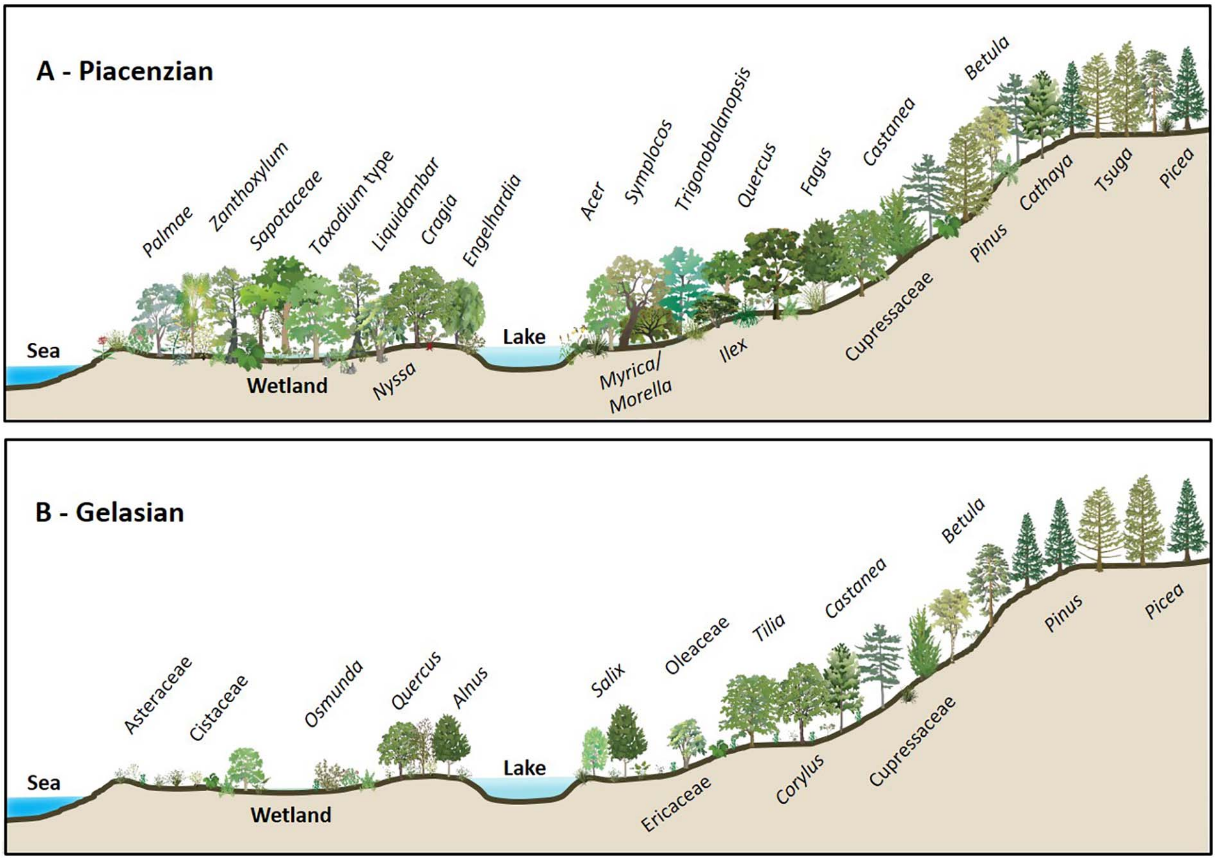


Fig. 8. Pollen-based vegetation reconstruction of the Rio Maior sub-basin during the Piacenzian (3.6–2.8 Ma) (A) and Gelasian (2.58 Ma) (B).

and humid climates: *Cistus* and *Ephedra* for example are more typical of open sclerophyllous or xerophytic environments (Fauquette et al., 2007). Pollen of herbaceous plants forms a higher proportion of Pollen Zone RM7 than the preceding six zones, but they are still subsidiary to the pollen of broadleaved deciduous trees (Fig. 6). This increase of herbaceous plants indicates a change from the dense subtropical/warm-temperate mixed forest of pollen zones RM1 – RM6 to a less diverse and probably more open environment. The palaeoclimate reconstructions indicate a decline in precipitation of the wettest month (MPwet) and a decrease in WMMT, when compared to Pollen Zone RM6 (Fig. 5). Pollen Zone RM7 corresponds to the final portion of the Piacenzian and the loss of diversity and climate sensitive taxa likely reflects the global cooling and aridification that followed the last interval of sustained Piacenzian warmth before the onset of major northern hemisphere glaciations in the Gelasian (Andreev et al., 2014; Panitz et al., 2016; Martinetto et al., 2017; Boyd et al., 2018).

The lower part of pollen zone RM7 can be correlated with Diniz (1984) assemblage G and the macrofossil bearing outcrop in Abum area (Pais, 1987). The reported presence of leaves representing palm species (*Chamaerops humilis* and *Sabal* cf. *haeringiana*) *and* Lauraceae (*Cinnamomum polymorphum and Oreodaphne heeri*) from this outcrop (Teixeira, 1942, 1954; Teixeira and Pais, 1976) reveals that some groups of plants are not preserved in the Rio Maior pollen and spore record (Figs. 3 & 6). In particular, genera of the Lauraceae produce non-resistant pollen and, thus, are rarely or never encountered in fossil palynomorph assemblages (e.g. Bertini and Roiron, 1997).

The final Pollen Zone RM8 (Gelasian) yielded less diverse assemblages when compared with the rest of the core (Figs. 3 & 7). This decline in diversity and absence of climate sensitive HUTEA and CTEA taxa is comparable to the records from central Italy (Martinetto et al., 2017). There is an increase of herbaceous plants (mainly Asteraceae) and a reduction of all tree and shrub taxa except *Alnus*, *Pinus* and Ericaceae (Figs. 3 & 6). Ericaceae pollen is only present in the first sample of Pollen Zone RM8 and may indicate a wetter Pleistocene environment (González-Sampériz et al., 2010). The second sample contained mostly *Pinus* pollen with *Alnus* and Asteraceae, which probably represents an open pine woodland (Fig. 8B) (González-Sampériz et al., 2010). *Artemisia* pollen wasn't identified in Pollen Zone RM8 (Vieira, 2009). The absence of *Artemisia* indicates that, contrary to the rest of the Iberian Peninsula, there was no development of a steppe environment on the Western Atlantic coast (Fig. 8B) (Fauquette et al., 2007; Barrón et al., 2010; Jiménez-Moreno et al., 2010).

4.2. Regional vegetation and climate during the Piacenzian

Current PRISM4 vegetation reconstructions for the Piacenzian show the presence of warm-temperate mixed forest on the Atlantic margin of western Europe and temperate xerophytic shrubland on the Mediterranean coast of the Iberian Peninsula (Salzmann et al., 2008; Salzmann et al., 2013; Dowsett et al., 2016). The presence of a warm and humid forest environment is confirmed from this study for Pollen Zones RM1-RM6 (Fig. 6). It was proposed that during cooler and drier intervals of the Piacenzian that xerophytic shrubland might have been present on the Atlantic coast of the Iberian Peninsula (Salzmann et al., 2013) This cold-dry scenario, proposed to get around the different temporal scales of climate modelling (typically hundreds of years) and proxy based syntheses (typically on greater than 10s of thousands of years), is not supported by the new results from Rio Maior (Figs. 3, 5 & 6). Instead the Atlantic coast of Iberia appears to have maintained a warm and humid climate throughout the Piacenzian, with intervals of forests with reduced diversity likely coinciding with glaciation intervals such as MIS M2 (Fig. 7a). The first sample of Pollen Zone RM4 contains a pollen assemblage from which the co-existence approach reconstructs the lowest MAP of the warm-interval of the record (presumed to be older than 2.8 Ma) of 823–932 mm (Fig. 5). This likely corresponds to one of the other major positive oxygen isotope excursions before 2.8 Ma (e.g. KM2 or G20), but without greater sample resolution and precision dating it is not possible to determine which (Lisiecki and Raymo, 2005; Haywood et al., 2013a).

The relatively high precipitation reconstructed for the majority of the Rio Maior palynology record is substantially different from Piacenzian reconstructions on the Mediterranean side of the Iberian Peninsula, where values were potentially as low as 600 mm yr^{-1} (Fig. 5; Fauquette et al., 2007). Alkenone reconstructed SST from around the Iberian Peninsula show that both the Mediterranean and the Atlantic had SST of 25–27 °C (Khélifi et al., 2009, 2014; Tzanova and Herbert, 2015; Furota et al., 2016). However, it has been proposed that the progressive closure of the Indonesian throughflow would have reduced precipitation from the African Monsoon and the delivery of moisture to the Mediterranean (Sarnthein et al., 2017). Climate modelling struggles to reconstruct increased precipitation across the western side of the Iberian Peninsula (Haywood et al., 2013b; Rosenbloom et al., 2013; Tindall and Haywood, 2015; Chandan and Peltier, 2017). It has been shown that the presence of a lake can support a more humid local vegetation in a wider environment characterised by lower precipitation (Pound et al., 2014). Whilst the Tagus Basin did contain a lake that could have modulated a more arid environment to support the vegetation present in the new pollen record, it would not account for the comparable flora recovered from S. Pedro da Torre in northern Portugal (Vieira et al., 2011). Instead it would appear that the diverse warm-temperate mixed forests of the Atlantic margin of Iberia were sustained until at least 2.8 Ma by a source of precipitation that at present cannot be reproduced in climate modelling experiments (Haywood et al., 2013b; Chandan and Peltier, 2017). Closure of the Central American Seaway has previously been demonstrated as a means to increase precipitation across the northern hemisphere (Lunt et al., 2008), but more recent work shows reductions in precipitation in the northern hemisphere when this oceanic gateway is closed (Brierley and Fedorov, 2016; Tan et al., 2017).

5. Conclusions

The Rio Maior fossil pollen and spores recovered from borehole F98 clearly demonstrate the presence of a high-diversity warm and humid forest in Pollen Zones RM1-RM6. Using the revised chronology of the Tagus Basin, it is inferred that Pollen Zones RM1-RM6 represent 3.6–2.8 Ma and that the Pollen Zones RM2-RM6 represent the PRISM “mid-Pliocene Warm Period”. Pollen Zone RM1 is inferred to end with the MIS M2 glaciation and shows a significant drop in H′ diversity, climate sensitive taxa, MAP and CMMT. It is only in the latest Piacenzian (Pollen Zone RM7) that a trend for cooler and more open vegetation begins. Pollen Zone RM7 starts with a reconstructed decrease in WMMT and contains decreasing H′ diversity exemplified by the loss of climate sensitive taxa. The Gelasian (Pollen Zone RM8) is characterised by a low diversity pollen assemblage dominated by Ericaceae and *Pinus* pollen representing and open pine woodland. Whilst Pollen Zone RM8 contains only two productive samples and might be biased by taphonomy, it is consistent with other records from the Pleistocene of the Iberian Peninsula. Previously, some of these pollen zones were incorrectly correlated with records of Zanclean age of the eastern Iberian Peninsula and southern Europe, but this is no longer supported by the revised chronology of the Tagus Basin.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.01.018.

Acknowledgments

This paper honours the memory of Professor João Pais, Portuguese palaeobotanist and palynologist who was the lead author's PhD supervisor and sadly passed away in 2016.

A special thank you goes to Reinhard Zetter from Vienna University for his kind support with the SEM method and analyses. This research work was part of the PhD project supported by the Portuguese Foundation for Science and Technology (Ref. SFRH/BD/18754/2004). The work of Diamantino I. Pereira was partially co-funded by the European Union through the European Regional Development Fund, based on COMPETE 2020 (Programa Operacional da Competitividade e Internacionalização), project ICT (UID/GEO/04683/2013) with reference POCI-01-0145-FEDER-007690 and national funds provided by Fundação para a Ciência e Tecnologia. We thank Adele Bertini, Harry Dowsett and Edoardo Martinetto for their insightful and constructive reviews that greatly improved the final manuscript.

References

Andrade, M.M., 1944. Estudo polínico de algumas formações turfo-lignitosas Portuguesas. In: Publicações do Museu e Laboratório Mineralógico e Geológico da Faculdade de Ciencias do Porto XXXVII (2° sér.), pp. 5–11.

Andreev, A.A., Tarasov, P.E., Wennrich, V., Raschke, E., Herzschuh, U., Nowaczyk, N.R., Brigham-Grette, J., Melles, M., 2014. Late Pliocene and Early Pleistocene vegetation history of northeastern Russian Arctic inferred from the Lake El'gygytgyn pollen record. Clim. Past 10, 1017–1039. http://dx.doi.org/10.5194/cp-10-1017-2014.

Barrón, E., Rivas-Carballo, R., Postigo-Mijarra, J.M., Alcalde-Olivares, C., Vieira, M., Castro, L., Pais, J., Valle-Hernández, M., 2010. The Cenozoic vegetation of the Iberian Peninsula: a synthesis. Rev. Palaeobot. Palynol. 162, 382–402.

Bertini, A., 2001. Pliocene climatic cycles and altitudinal forest development from 2.7 Ma in the Northern Apennines (Italy): evidence from the pollen record of the Stirone section (5.1 to 2.2 Ma). Geobios 34, 253–265.

Bertini, A., 2010. Pliocene to Pleistocene palynoflora and vegetation in Italy: state of the art. Quat. Int. 225, 5–24.

Bertini, A., Martinetto, E., 2008. Messinian to Zanclean vegetation and climate of Northern and Central Italy. Boll. Soc. Paleontol. Ital. 47 (2), 105–121.

Bertini, A., Roiron, P., 1997. Evolution de la végétation et du climat pendant le Pliocène moyen en Italie centrale: apport de la palynologie et de la macroflore à l'étude du bassin du Valdarno supérieur, (coupe de Santa Barbara). CR Acad. Sci. Paris 324, 763–771 Séries 2a.

Boyd, J.L., Riding, J.B., Pound, M.J., De Schepper, S., Ivanovic, R.F., Haywood, A.M., Wood, S.E.L., 2018. The relationship between Neogene dinoflagellate cysts and global climate dynamics. Earth Sci. Rev. 177, 366–385.

Brierley, C.M., Fedorov, A.V., 2016. Comparing the impacts of Miocene–Pliocene changes in inter-ocean gateways on climate: central American seaway, Bering Strait, and Indonesia. Earth Planet. Sci. Lett. 444, 116–130.

Cachão, M., 1990. Posicionamento biostratigráfico da jazida pliocénica de Carnide (Pombal). Gaia 2, 11–16.

Chandan, D., Peltier, W.R., 2017. Regional and global climate for the mid-Pliocene using the University of Toronto version of CCSM4 and PlioMIP2 boundary conditions. Clim. Past 13, 919–942.

Corlett, R.T., 2013. Where are the subtropics? Biotropica 45, 273–275.

Cunha, P., 1992. Estratigrafia e Sedimentologia Dos depósitos Do Cretácico Superior e Terceário de Portugal Central, a Leste de Coimbra. Tese de doutoramento. Centro de Geociências da Universidade de Coimbra (262p).

Cunha, P.M., Barbosa, B.P., Reis, R., 1993. Synthesis of the Piacenzian onshore record, between the Aveiro and Setúbal parallels (Western Portuguese margin). Ciênc. Terra 12, 35–43.

Diniz, F., 1984. Apports de la palynologie à la connaissance du Pliocène portugais. Rio Maior: un basin de référence pour l'histoire de la flore, de la végétation et du climat de la façade atlantique de l'Europe meridionale. Dissertação de Doutoramento. Université des Sciences et Techniques de Languedoc, Montpellier (230 p).

Diniz, F., 2001. Aspects of the Plio-quaternary transition in Rio Maior: pollen records, vegetation and climate. In: Actas V Reunião do Quaternário Ibérico – I Congresso do Quaternário de Países de Línguas Ibéricas, pp. 109–112.

Diniz, F., 2003. Os depósitos detrítico-diatomíticos de Abum (Rio Maior). Novos aspectos paleoflorísticos e implicações paleoclimáticas. Ciênc. Terra V, 7 CDRom A49-A52.

Diniz, F., Mörner, N.-A., 1995. The Reuverian/Pretiglian transition in Rio Maior, Portugal. In: XIV International Congress INQUA, Schriften der Alfred-Wegner-Stiftung 2/95, pp. 64.

Dowsett, H.J., Poore, R.Z., 1991. Pliocene sea surface temperatures of the North Atlantic Ocean at 3.0 Ma. Quat. Sci. Rev. 10, 189–204.

Dowsett, H., Thompson, R., Barron, J., Cronin, T., Fleming, F., Ishman, S., Poore, R., Willard, D., Holtz, T., 1994. Joint investigations of the Middle Pliocene climate I: PRISM paleoenvironmental reconstructions. Glob. Planet. Chang. 9, 169–195.

Dowsett, H., Barron, J., Poore, R., 1996. Middle Pliocene sea surface temperatures: a global reconstruction. Mar. Micropaleontol. 27, 13–25.

Dowsett, H., Robinson, M., Haywood, A.M., Salzmann, U., Hill, D., Sohl, L.E., Chandler, M., Williams, M., Foley, K., Stoll, D.K., 2010. The PRISM3D paleoenvironmental reconstruction. Stratigraphy 7, 123–139.

Dowsett, H., Dolan, A., Rowley, D., Moucha, R., Forte, A.M., Mitrovica, J.X., Pound, M., Salzmann, U., Robinson, M., Chandler, M., Foley, K., Haywood, A., 2016. The PRISM4 (mid-Piacenzian) paleoenvironmental reconstruction. Clim. Past 12, 1519–1538.

Erdtman, G., 1971. Pollen Morphology and Plant Taxonomy. Angiosperms. Hafner

Publishing Company, New York (553p).

Eyde, R.H., 1997. Fossil record and ecology of *Nyssa* (Cornaceae). Bot. Rev. 63, 97–123.

Fauquette, S., Suc, J.P., Guiot, J., Diniz, F., Feddi, N., Zheng, Z., Bessais, E., Drivaliari, A., 1999. Climate and biomes in the West Mediterranean area during the Pliocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 152, 15–36.

Fauquette, S., Suc, J.-P., Jiménez-Moreno, G., Micheels, A., Jost, A., Favre, E., Bachiri Taoufiq, N., Bertini, A., Clet-Pellerin, M., Diniz, F., Farjanel, G., Feddi, N., Zheng, Z., 2007. Latitudinal climatic gradients in the Western European and Mediterranean regions from the Mid-Miocene (c. 15 Ma) to the Mid-Pliocene (c. 3.5 Ma) as quantified from pollen data. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.), Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies. The Geological Society, London, pp. 481–502.

Furota, S., Nakamura, H., Sawada, K., 2016. Long-chain alkenones and related distinctive compounds in the late Miocene and Pliocene sediments from the Gulf of Cadiz, eastern North Atlantic. Org. Geochem. 101, 166–175.

González-Sampériz, P., Leroy, S.A.G., Carrión, J.S., Fernández, S., García-Antón, M., Gil-García, M.J., Uzquiano, P., Valero-Garcés, B., Figueiral, I., 2010. Steppes, savannahs, forests and phytodiversity reservoirs during the Pleistocene in the Iberian peninsula. Rev. Palaeobot. Palynol. 162, 427–457.

Haywood, A.M., Ridgwell, A., Lunt, D.J., Hill, D.J., Pound, M.J., Dowsett, H.J., Dolan, A.M., Francis, J.E., Williams, M., 2011. Are there pre-quaternary geological analogues for a future greenhouse warming? Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. 369, 933–956.

Haywood, A.M., Dolan, A.M., Pickering, S.J., Dowsett, H.J., McClymont, E.L., Prescott, C.L., Salzmann, U., Hill, D.J., Hunter, S.J., Lunt, D.J., Pope, J.O., Valdes, P.J., 2013a. On the identification of a Pliocene time slice for data–model comparison. Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. 371.

Haywood, A.M., Hill, D.J., Dolan, A.M., Otto-Bliesner, B.L., Bragg, F., Chan, W.-L., Chandler, M.A., Contoux, C., Dowsett, H.J., Jost, A., Kamae, Y., Lohmann, G., Lunt, D.J., Abe-Ouchi, A., Pickering, S.J., Ramstein, G., Rosenbloom, N.A., Salzmann, U., Sohl, L., Stepanek, C., Ueda, H., Yan, Q., Zhang, Z., 2013b. Large-scale features of Pliocene climate: results from the Pliocene model Intercomparison project. Clim. Past 9, 191–209.

Haywood, A.M., Dowsett, H.J., Dolan, A.M., Rowley, D., Abe-Ouchi, A., Otto-Bliesner, B., Chandler, M.A., Hunter, S.J., Lunt, D.J., Pound, M., Salzmann, U., 2016. Pliocene Model Intercomparison (PlioMIP) Phase 2: scientific objectives and experimental design. Clim. Past 12, 663–675. http://dx.doi.org/10.5194/cp-12-663-2016.

IPCC, 2013. Climate change 2013: the physical science basis. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA (1535 pp).

Jiménez-Moreno, G., Fauquette, S., Suc, J.P., 2010. Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. Rev. Palaeobot. Palynol. 162, 403–415.

Kapp, R.O., Davis, O.K., King, J.E., 2000. Pollen and Spores, second edition. American Association of Stratigraphic Palynologists Foundation Publication (279 pp).

Khélifi, N., Sarnthein, M., Andersen, N., Blanz, T., Frank, M., Garbe-Schönberg, D., Haley, B.A., Stumpf, R., Weinelt, M., 2009. A major and long-term Pliocene intensification of the Mediterranean outflow, 3.5–3.3 Ma ago. Geology 37, 811–814.

Khélifi, N., Sarnthein, M., Frank, M., Andersen, N., Garbe-Schönberg, D., 2014. Late Pliocene variations of the Mediterranean outflow. Mar. Geol. 357, 182–194.

Kovar-Eder, J., Kvaček, Z., 2007. The integrated plant record (IPR) to reconstruct Neogene vegetation: the IPR-vegetation analysis. Acta Palaeobot. 47, 391–418.

Kovar-Eder, J., Jechorek, H., Kvacek, Z., Parashiv, V., 2008. The integrated plant record: an essential tool for reconstructing neogene zonal vegetation in Europe. PALAIOS 23, 97–111.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ^{18}O records. Paleoceanography 20, PA1003. http://dx.doi.org/10.1029/2004PA001071.

Liu, L., Maiorano, P., Zhao, X., 1996. Pliocene – Pleistocene calcareous Nannofossils from the Iberia abyssal plain. Proc. Ocean Drill. Program Sci. Results 149, 147–164.

Louwye, S., Head, M.J., Schepper, S., 2004. Dinoflagellate cyst stratigraphy and palaeoecology of the Pliocene in northern Belgium, southern North Sea Basin. Geol. Mag. 141, 353–378.

Lunt, D.J., Ridgwell, A., Valdes, P.J., Seale, A., 2008. “Sunshade World”: a fully coupled GCM evaluation of the climatic impacts of geoengineering. Geophys. Res. Lett. 35, L12710. http://dx.doi.org/10.1029/2008GL033674.

Martinetto, E., Momohara, A., Bizzarri, R., Baldanza, A., Delfino, M., Esu, D., Sardella, R., 2017. Late persistence and deterministic extinction of “humid thermophilous plant taxa of East Asian affinity” (HUTEA) in southern Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 467, 211–231.

Martini, E., 1971. Standard tertiary and quaternary calcareous nannoplankton zonation. In: Proceedings of the 2nd Planktonic Conference, Roma. 1970. pp. 739–785.

Mosbrugger, V., Utescher, T., 1997. The coexistence approach — a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 134, 61–86.

Naafs, B.D.A., Stein, R., Hefter, J., Khélifi, N., De Schepper, S., Haug, G.H., 2010. Late Pliocene changes in the North Atlantic Current. Earth Planet. Sci. Lett. 298, 434–442.

Okada, H., Bukry, D., 1980. Supplementary modification and introduction of code numbers of the low -latitude coccolith biostratigraphic zonation (Bukry 1973, 1975). Mar. Micropaleontol. 5, 321–325.

Otero, M.P.S., Suárez-Cervera, M., Gracia, R.V., 1996. Atlas de Polen de Galicia I. Deputación de Ourense. (358pp).

Pais, J., 1987. Macrorrestos de gimnospérmicas dos diatomitos de Rio Maior (Portugal). Vol. Hom. O. Veiga Ferreira. Ed. Delta. pp. 51–66.

Panitz, S., Salzmann, U., Risebrobakken, B., De Schepper, S., Pound, M.J., 2016. Climate variability and long-term expansion of peatlands in Arctic Norway during the late Pliocene (ODP Site 642, Norwegian Sea). Clim. Past 12, 1043–1060.

Pena dos Reis, R., Proença Cunha, P., Barbosa, B., Antunes, M.T., Pais, J., 1992. Excursion B - mainly continental Miocene and Pliocene deposits from Lower Tagus and Mondego Tertiary basins. Ciênc. Terra 37–56 (UNL), n° esp. II.

Pound, M.J., Salzmann, U., 2017. Heterogeneity in global vegetation and terrestrial climate change during the late Eocene to early Oligocene transition. Sci. Rep. 7, 43386.

Pound, M.J., Tindall, J., Pickering, S.J., Haywood, A.M., Dowsett, H.J., Salzmann, U., 2014. Late Pliocene lakes and soils: a data - model comparison for the analysis of climate feedbacks in a warmer world. Clim. Past 10, 167–180.

Pound, M.J., Lowther, R.I., Peakall, J., Chapman, R.J., Salzmann, U., 2015. Palynological evidence for a warmer boreal climate in the Late Pliocene of the Yukon Territory, Canada. Palynology 39, 91–102.

Prescott, C.L., Haywood, A.M., Dolan, A.M., Hunter, S.J., Pope, J.O., Pickering, S.J., 2014. Assessing orbitally-forced interglacial climate variability during the mid-Pliocene Warm Period. Earth Planet. Sci. Lett. 400, 261–271.

Ramos, A., Cunha, P.P., 2004. Facies associations and palaeogeography of the Zanclean piacenzian marine incursion in the Mondego cape-Nazaré area (onshore of Central Portugal). In: Abstracts book of the 23rd International Meeting of IAS, (227p).

Reille, M., 1999. Pollen et Spores d'Europe et d'Afrique du nord, seconde édition. Laboratoire de Botanique Historique et Palynologie (535pp).

Rich, F.J., Vance, R.K., Rucker, C.R., 2015. The palynology of upper Pleistocene and Holocene sediments from the eastern shoreline and central depression of St. Catherines Island, Georgia, USA. Palynology 39, 234–247.

Rosenbloom, N.A., Otto-Bliesner, B.L., Brady, E.C., Lawrence, P.J., 2013. Simulating the mid-Pliocene warm period with the CCSM4 model. Geosci. Model Dev. 6, 549–561.

Salzmann, U., Haywood, A.M., Lunt, D.J., Valdes, P.J., Hill, D.J., 2008. A new global biome reconstruction and data-model comparison for the Middle Pliocene. Glob. Ecol. Biogeogr. 17, 432–447.

Salzmann, U., Dolan, A.M., Haywood, A.M., Chan, W.-L., Voss, J., Hill, D.J., Abe-Ouchi, A., Otto-Bliesner, B., Bragg, F.J., Chandler, M.A., Contoux, C., Dowsett, H.J., Jost, A., Kamae, Y., Lohmann, G., Lunt, D.J., Pickering, S.J., Pound, M.J., Ramstein, G., Rosenbloom, N.A., Sohl, L., Stepanek, C., Ueda, H., Zhang, Z., 2013. Challenges in quantifying Pliocene terrestrial warming revealed by data-model discord. Nat. Clim. Chang. 3, 969–974.

Sarnthein, M., Grunert, P., Khélifi, N., Frank, M., Nürnberg, D., 2017. Interhemispheric teleconnections: late Pliocene change in Mediterranean outflow water linked to changes in Indonesian through-flow and Atlantic meridional overturning circulation, a review and update. Int. J. Earth Sci. http://dx.doi.org/10.1007/s00531-017-1505-6.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423.

Sharma, J., Schrader, J.A., Graves, W.R., 2008. Ecology and phenotypic variation of *Leitneria floridana* (Leitneriaceae) in Disjunct native habitats. Castanea 73, 94–105.

Silva, C.M., 2001. Gastrópodes pliocénicos Marinhos de Portugal. Sistemática, paleobiologia, paleoecologia e paleobiogeografia. PhD, Fac. Ciências. Univ. Lisboa, pp. 661–675.

Sivak, J., 1975. Les caractères de diagnose des grains de pollen à ballonnets. Pollen Spores 17, 349–421.

Smith, B., Wilson, J.B., 1996. A consumer's guide to eveness indices. Oikos 76, 70–82.

Stuchlik, L., Ziembińska-Tworzydło, M., Kohlman-Adamka, A., Grabowska, I., Ważyńska, H., Sadowska, A., 2001. Atlas of Pollen and Spores of the Polish Neogene, Volume 1-Spores. L. Stuchlik. (158pp).

Stuchlik, L., Ziembińska-Tworzydło, M., Kohlman-Adamka, A., Grabowska, I., Ważyńska, H., Sadowska, A., 2002. Atlas of Pollen and Spores of the Polish Neogene. Vol. 2 - Gymnosperms. L. Stuchlik. (237pp).

Suc, J.P., 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. Nature 307, 429–432.

Suc, J.P., Zagwijn, W.H., 1983. Plio-Pleistocene correlations between the northwestern Mediterranean region and northwestern Europe according to recent biostratigraphic and palaeoclimatic data. Boreas 12 (153), 166.

Suc, J.P., Diniz, F., Leroy, S., Poumot, C., Bertini, A., Clet, M., Bessais, E., Ferrier, J., 1995a. Zanclean (~Brussumian) to early Piacenzian (~early-middle Reuverian) climate from 4° to 54° north latitude (West Africa, West Europe and West Mediterranean). Med. Rijks Geol. Dienst. Netherlands 52, 43–56.

Suc, J.P., Bertini, A., Combourieu-Nebout, N., Diniz, F., Leroy, S., Russo-Ermolli, E., Zheng, Z., Bessais, E., Ferrier, J., 1995b. Structure of West Mediterranean vegetation and climate since 5.3 Ma. Acta Zool. Cracov. 38, 3–16.

Suc, J.-P., Fauquette, S., Bessedik, M., Bertini, A., Zheng, Z., Clauzon, G., Suballyova, D., Diniz, F., Quezel, P., Feddi, N., Clet, M., Bessais, E., Bachiri, Taoufiq N., Méon, H., Combourieu-Nebout, N., 1999. Neogene vegetation changes in West European and West circum-mediterranean areas. In: Agusti, J., Rook, L., Andrews, P. (Eds.), Hominoid Evolution and Climatic Change in Europe. 1. Cambridge Univ. Press, pp. 378–388.

Sun, B.-L., Zhang, C.-Q., Lowry, P.P., Wen, J., 2009. Cryptic dioecy in *Nyssa yunnanensis* (Nyssaceae), a critically endangered species from tropical eastern Asia. Ann. Mo. Bot. Gard. 96, 672–684.

Tan, N., Ramstein, G., Dumas, C., Contoux, C., Ladant, J.-B., Sepulchre, P., Zhang, Z., De Schepper, S., 2017. Exploring the MIS M2 glaciation occurring during a warm and high atmospheric CO_2 Pliocene background climate. Earth Planet. Sci. Lett. 472, 266–276.

Teixeira, C., 1942. Sobre a existência de Palmeiras do género *Sabal* no Pliocénico português. Bol. Soc. Port. Ci. Nat. 14 (28), 135–138.

Teixeira, C., 1944a. Pinheiro fóssil do Pliocénico de Rio Maior. Bol. Soc. Broteriana 19 (2ª série), 201–209.

Teixeira, C., 1944b. Sequóia fóssil Do Cenozóico português. Publicações do Museu e Laboratório Mineralógico e Geológico da Faculdade de Ciências do Porto 2ª série 33. pp. 1–8.

Teixeira, C., 1954. A palmeira anã - Chamaerops humilis L. - no Pliocénico Português. Boletín de la Real Sociedad Española de Historia Natural, Volumen homenaje a F. Hernandez Pacheco. pp. 659–662.

Teixeira, C., 1973–74. Sur la présence de *Pittosporum* dans le Pliocène du Portugal. Rev. Fac. Ciênc. Lisboa 11 (2), 599–601 2ª série, C.

Teixeira, C., Pais, J., 1976. Introdução à paleobotânica. As grandes fases da evolução dos vegetais. Ed. autores. (210 p).

Teixeira, C., Zbyszewski, G., 1951. Note sur le Pliocène de la Région à l'Ouest de Pombal. Comun. Serv. Geol. Portugal XXXII (Parte 1), 295–302.

Teodoridis, V., Kovar-Eder, J., Mazouch, P., 2011. The IPR-vegetation analysis applied to modern vegetation in SE China and Japan. PALAIOS 26, 623–638.

Tindall, J.C., Haywood, A.M., 2015. Modeling oxygen isotopes in the Pliocene: large-scale features over the land and ocean. Paleoceanography 30, 1183–1201.

Tzanova, A., Herbert, T.D., 2015. Regional and global significance of Pliocene sea surface temperatures from the Gulf of Cadiz (Site U1387) and the Mediterranean. Glob. Planet. Chang. 133, 371–377.

Utescher, T., Bruch, A.A., Erdei, B., François, L., Ivanov, D., Jacques, F.M.B., Kern, A.K., Liu, Y.S., Mosbrugger, V., Spicer, R.A., 2014. The coexistence approach—theoretical background and practical considerations of using plant fossils for climate quantification. Palaeogeogr. Palaeoclimatol. Palaeoecol. 410, 58–73.

Valdes, B., Diez, M.J., Fernandez, I., 1987. Atlas Polinico de Andalucia Occidental. Instituto de desarrollo regional n°43, Universidad de Sevilla. Excma. Diputacion de Cadiz (450pp).

Vieira, M., 2009. Palinologia do Pliocénico da Orla Ocidental Norte e Centro de Portugal: Contributo para a compreensão da cronostratigrafia e da evolução paleoambiental. Ph.D. thesis. Universidade do Minho, Braga, Portugal (389 p).

Vieira, M., Sousa, L., Pais, J., Pereira, D., 2006. Palynological study of Vale do Freixo Pliocene (Pombal, Mondego Basin, Portugal). In: Abstract book 7th European Palaeobotany-Palynology Conference, (151p).

Vieira, M., Zetter, R., Castro, L., Pais, J., Pereira, D., 2009. Método combinado de observação em microscópia óptica e electrónica de varrimento para estudo de palinomorfos (Combinated LM-SEM method for palynomorphs study). Comun. Geol. 96, 123–128.

Vieira, M., Poças, E., Pais, J., Pereira, D., 2011. Pliocene flora from S. Pedro da Torre deposits (Minho, NW Portugal). Geodiversitas 33, 71–85.

Wang, Y., Fritsch, P.W., Shi, S., Almeda, F., Cruz, B.C., Kelly, L.M., 2004. Phylogeny and infrageneric classification of Symplocos (Symplocaceae) inferred from DNA sequence data. Am. J. Bot. 91, 1901–1914.

Willard, D.A., Bernhardt, C.E., Weimer, L., Cooper, S.R., Gamez, D., Jensen, J., 2004. Atlas of pollen and spores of the Florida Everglades. Palynology 28, 175–227.

Zagwijn, W.H., 1960. Aspects of the Pliocene and Early Pleistocene Vegetation in the Netherlands. Mededelingen van de Geologische Stichting Serie C. 3 (5) 78p.

Zbyszewski, G., 1943. Une reconnaissance géologique dans la region de Rio Maior: l'âge dês lignites du gisement de Espadanal. Comun. Serv. Geol. Portugal 24, 3–21.

Zbyszewski, G., 1949. Contribution à la conaissance du Pliocène Portugais. Comun. Serv. Geol. Portugal 30, 59–79.

Zbyszewski, G., 1967. Estudo geológico da bacia dos lignitos de Rio Maior. Estudos Notas e Trabalhos do Serviço Fomento Mineiro. 17. pp. 5–105.

Zbyszewski, G., Almeida, F.M., 1959. Carta Geológica de Portugal na escala 1/50000. Folha 26D Caldas da Rainha. Serviços Geológicos de Portugal, Lisboa.

Zetter, R., 1989. Methodik und Bedeutung einer routinemäßig kombinierten lichtmikroskopischen und rasterelektronenmikroskopischen Untersuchung fossiler Mikrofloren. Cour. Forschungsinst. Senck. 109, 41–50.