Floristic changes in the Iberian Peninsula and Balearic Islands (south-west Europe) during the Cenozoic

José M. Postigo Mijarra , Eduardo Barrón , Fernando Gómez Manzaneque and Carlos Morla

Unidad de Botánica, Escuela Técnica Superior de Ingenieros de Montes, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, Madrid, Spain and Instituto Geológico y Minero de España, Ríos Rosas, Madrid, Spain

ABSTRACT

Aim The aim of this work was to identify the main changes in the flora and vegetation of the Iberian Peninsula over the Cenozoic Era, to record the disappearance of taxa associated with these changes and to determine the influence of climate and human activity on these events.

Location The Iberian Peninsula and Balearic Islands.

Methods A critical review was made of the palaeobotanical literature with the aims of detecting patterns of floristic change and extracting information on the disappearance of different taxa over the Cenozoic. These data are viewed alongside the most recent data for the climate of this period. A critical analysis is made of the role of Palaeotropical and Arctotertiary taxa in the forest communities of the Iberian Peninsula throughout the Cenozoic.

Results Although the Eocene–Oligocene transition was a time when many taxa disappeared, the most outstanding events occurred between the end of the Oligocene and throughout the Miocene. Substantial floristic changes took place over this period, including the disappearance of 177 Palaeotropical taxa. This was probably related to acute cooling and aridification; no evidence exists that the Messinian Salinity Crisis had any important effect in the Iberian Peninsula. The last great disappearance of Palaeotropical taxa (36 in total) ended in the Middle–Late Piacenzian; Arctotertiary taxa were most affected during the Pleistocene. The Lower–Middle Pleistocene transition, best represented by marine isotopic stages (MIS) 36–34 and 20–18 and characterized by a change in glacial cyclicity, was the time of the last notable disappearance of taxa.

Main conclusions This work provides the first chronogram of extinctions for the Iberian flora, and records the disappearance of 277 taxa during the Cenozoic. A clear relationship was detected between the main climatic events and the latest appearances of the different taxa.

Keywords
Balearic Islands, Cenozoic, floristic change, historical biogeography, Iberian Peninsula, palaeobotany, palaeoclimate, palaeoecology, plant geography, Quaternary.

Correspondence: José María Postigo Mijarra, Universidad Politécnica de Madrid, ETSI Montes, Unidad de Botánica, Ciudad Universitaria s/n, 28040 Madrid, Spain. E-mail: jm.postigo@upm.es

INTRODUCTION

The palaeobotanical data provided by outcrops from around the Iberian Peninsula (Figs 1–3) suggest its Cenozoic flora to have been highly diverse and composed of taxa very different from those of today. The modern flora of the Iberian Peninsula is thus the product of the appearance and disappearance of taxa during the Cenozoic. Climate, geology and ecology must all have had a direct impact on the survival of the different elements. Many studies on changes in the Cenozoic climate have been published in recent years, and the main trends have been established at a global level (Zachos *et al.*, 2001; Lisiecki & Raymo, 2005; Mosbrugger *et al.*, 2005). Determining the influence of these past
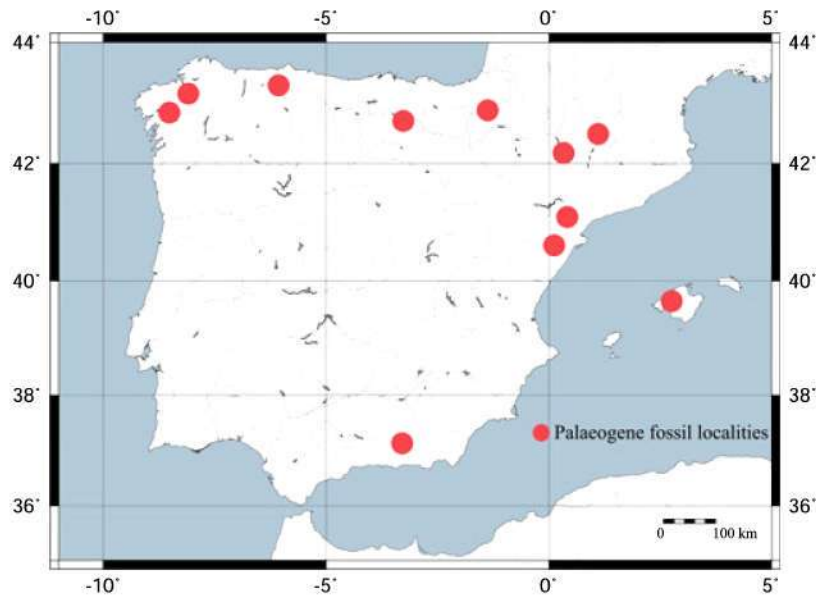
Figure 1 Palaeogene sites of the Iberian Peninsula and Balearic Islands. The inner lines mark the main rivers and channels in the Iberian Peninsula. The Palaeogene is represented by a small number of fossil localities. Several of these fossil sites are placed in northern Iberia.
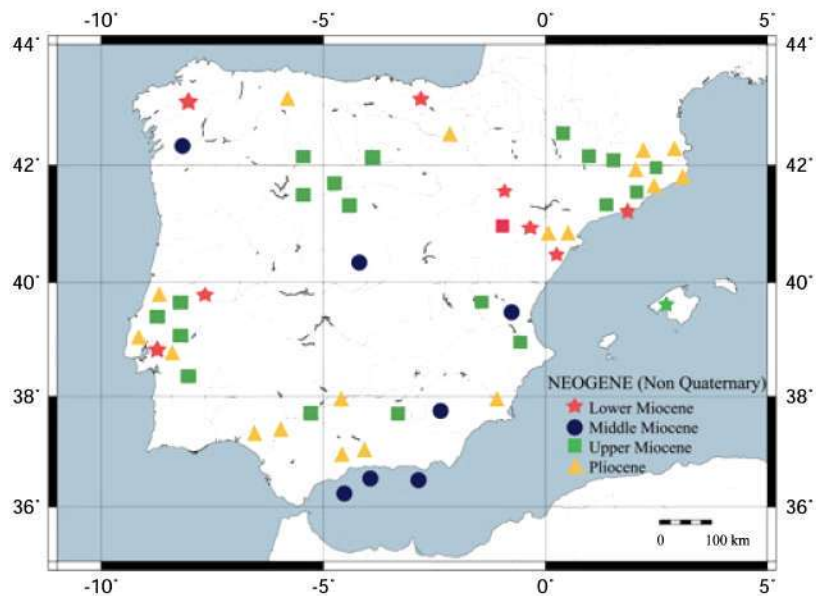

Figure 2 Miocene and Pliocene sites of the Iberian Peninsula and Balearic Islands. Note the high number of fossil localities in north-east and south-west Iberia and the general lack of fossil localities in the interior of the Iberian Peninsula.

episodes of change on the then existent flora, however, is a more complex matter.

Numerous studies on the palaeobiogeographical features of the Cenozoic flora of Europe – mainly of the Neogene – have been undertaken (Mai, 1989, 1991, 1995; Suc, 1989; Suc *et al.*, 1992), although the characteristics of the palaeofloras of western Eurasia remain largely unknown (Utescher *et al.*, 2007). Several different vegetation units have been described in Europe for these periods. Engler (1879–1882) was the first to use the terms 'Palaeotropical' and 'Arctotertiary' flora,

although it was Mai (1989, 1991) who proposed that these terms be used to describe ecological units (or geofloras). According to Mai, a 'Palaeotropical geoflora' was present in Europe from the Late Cretaceous to the Late Miocene, consisting of paratropical rain forests, subtropical rain and laurel forests, temperate laurel forests and laurel–conifer forests (the latter constrained by edaphic factors). At the same time, an 'Arctotertiary geoflora' existed, represented by warm temperate rain forests, lowland and swamp forests – the ancestors of mixed mesophytic forests. Later, for the
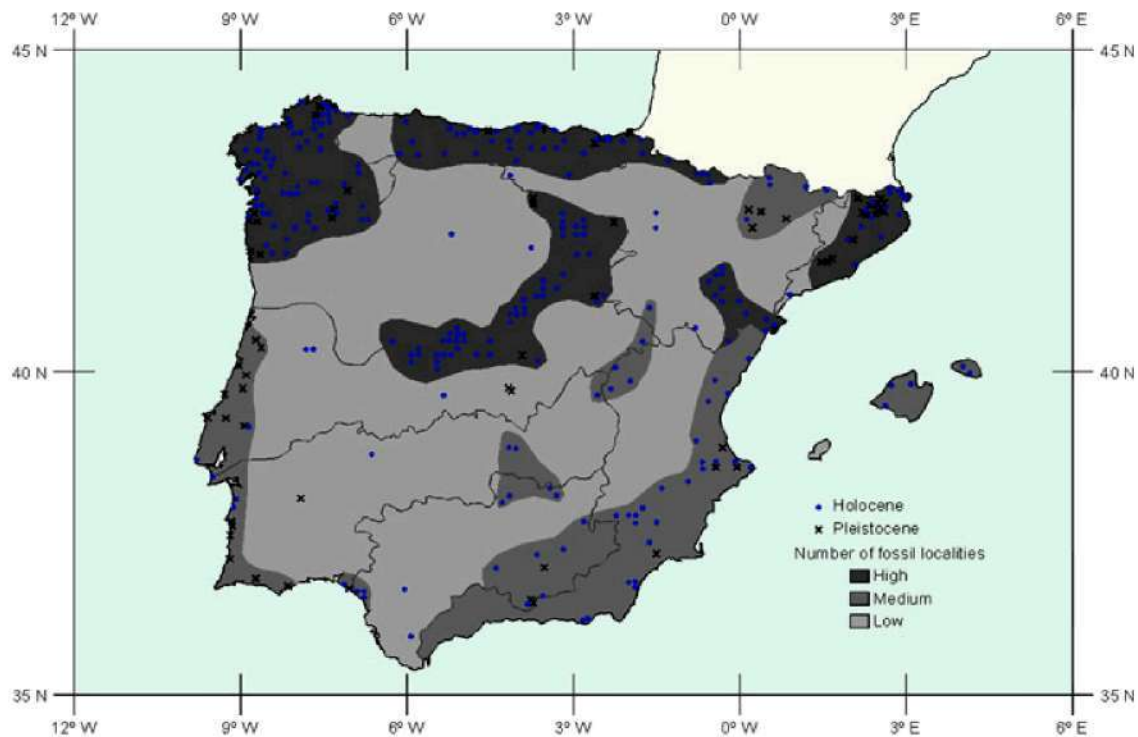
Figure 3 Quaternary sites of the Iberian Peninsula and Balearic Islands. Dark grey indicates areas with a high number of fossil localities; these are mainly in northern Iberia and the centre of the peninsula (Spanish Central Range). There is a notable lack of fossil records in the inner basins.

Palaeogene, Collinson & Hooker (2003) proposed: a polar, broad-leaved deciduous forest for the Palaeocene–Eocene; broad-leaved, paratropical to subtropical evergreen rain forests for the Late Palaeocene to the Eocene; and a broad-leaved, mixed deciduous and evergreen forest plus vegetation with sclerophyllous elements for the Late Eocene and Oligocene. Finally, Utescher & Mosbrugger (2007) and Utescher *et al.* (2007) describe, through the use of plant functional types, a large number of phytosociological classes for both the Palaeogene and Neogene.

Different floristic elements coexisted in the Iberian Peninsula for long periods of time, leading to complex mosaics of vegetation (Mai, 1989, 1991; Palamarev, 1989; Costa *et al.*, 2005). Indeed, the Iberian Peninsula's fossil record is witness to this mixing of plant types. This is further corroborated by the modern-day existence of a significant group of species of Palaeotropical origin, the distribution of which is very localized and restricted to Iberia (Castroviejo *et al.*, 1986; Costa *et al.*, 2005).

The aims of the present work were to describe the main floral changes of the Iberian Peninsula registered in the Cenozoic, in the context of the available palaeoclimatic data, and to determine the origin of the peninsula's modern-day flora.

MATERIALS AND METHODS

Palaeobotanical data for the Cenozoic of other regions of the Northern Hemisphere are much more abundant than for the Iberian Peninsula (Hably, 1987; Wolfe, 1992). Neither in Spain nor in Portugal have Cenozoic plant fossils enjoyed the traditional interest they have attracted in other European countries; the majority of Iberia's Tertiary floras are therefore only incompletely known (Barrón *et al.*, 1996). Nonetheless, those studies that have been published are of great palaeogeographical interest and provide very valuable data on the flora of south-western Europe and its evolution.

The present work involved an exhaustive review of the palaeobotanical studies of the Cenozoic in the Iberian Peninsula and the Balearic Islands (for convenience these will be referred to collectively here as the Iberian Peninsula or Iberia) (Figs 1–3), with the aim of describing the floristic changes that occurred during this time. A chronogram was constructed to reflect these data (Fig. 4). This included all the taxa recorded in the different Cenozoic outcrops so far examined. These taxa were mainly identified from their pollen, spores and leaf and wood remains; carpological studies of the Iberian Cenozoic are scarce (Álvarez Ramis, 1975; Menéndez Amor, 1975; Gregor & Günther, 1985; Cabrera *et al.*, 1994; Barrón, 1996; Barrón & Diéguez, 2001; Martín-Closas *et al.*, 2006), except for those performed on Holocene materials associated with archaeological remains (Ruiz *et al.*, 1997). Similarly, very few studies containing data on flowers or inflorescences have been published (Barrón, 1996; Barrón & Diéguez, 2001; Postigo Mijarra *et al.*, 2003).
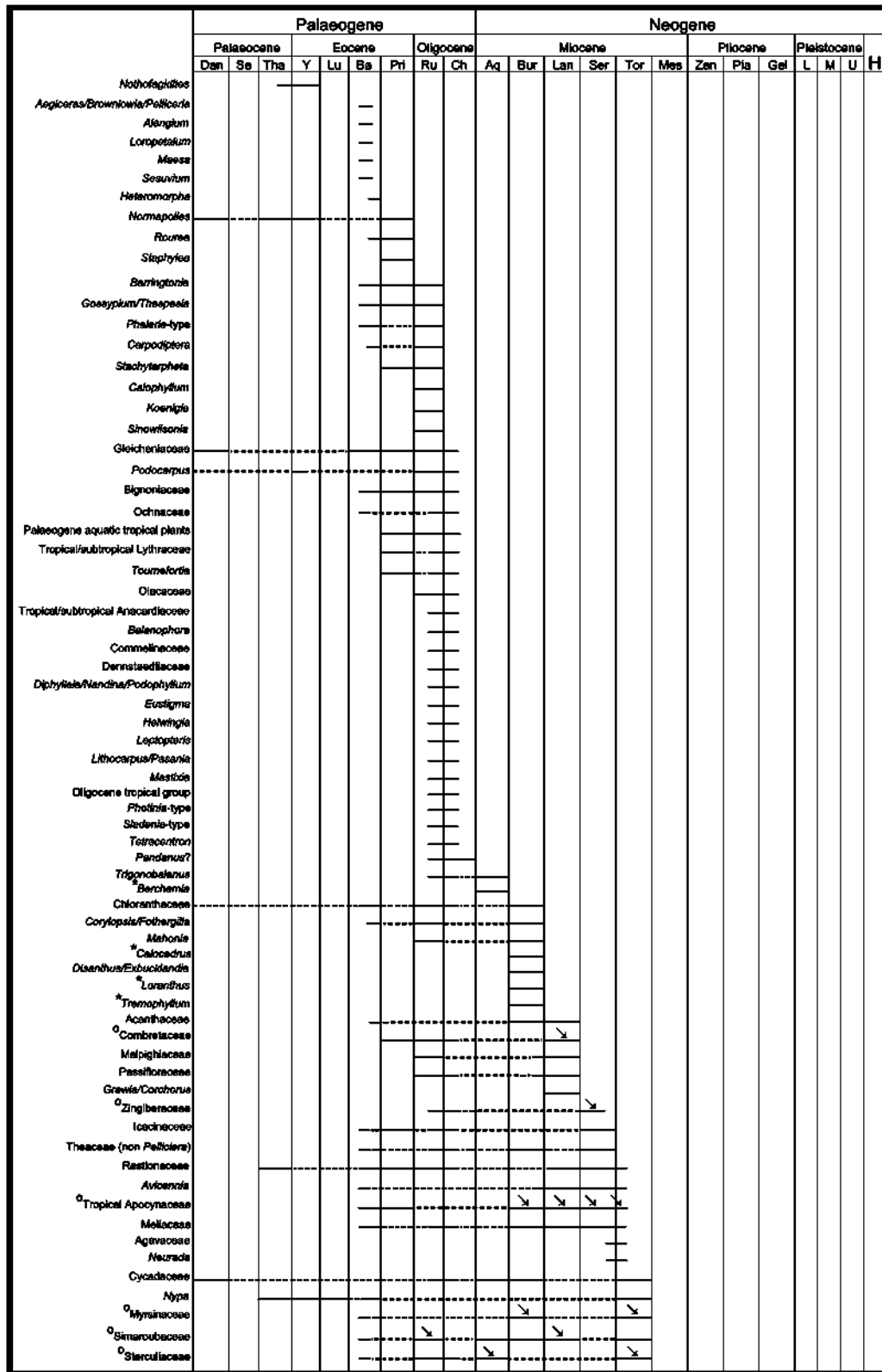
Figure 4 Disappearance chronogram for the main plant taxa of the Iberian Peninsula and Balearic Islands during the Cenozoic. Symbols: *, taxa exclusively identified from megaremains; °, taxa identified from both pollen and megaremains (taxa without a symbol are identified only from palynomorphs); ↘, age at which a particular taxon was documented from megaremains; dotted line, time interval for which a given taxon has not yet been identified. Abbreviations: Dan, Danian; Se, Selandian; Tha, Thanetian; Y, Ypresian; Lu, Lutetian; Ba, Bartonian; Pri, Priabonian; Ru, Rupelian; Ch, Chattian; Aq, Aquitanian; Bur, Burdigalian; Lan, Langhian; Ser, Serravalian; Tor, Tortonian; Mes, Messinian; Zan, Zanclean; Pia, Piacenzian; Gel, Gelasian; L, Lower Pleistocene; M, Middle Pleistocene; U, Upper Pleistocene; H, Holocene.

Palaeogene / Neogene chronostratigraphic chart

	Palaeogene								Neogene												
	Palaeocene			Eocene				Oligocene		Miocene						Pliocene			Pleistocene		
	Dan	Se	Tha	Y	Lu	Ba	Pri	Ru	Ch	Aq	Bur	Lan	Ser	Tor	Mes	Zan	Pia	Gel	L	M	U	H

Taxa listed (top to bottom): °Tropical/subtropical Rutaceae, Bombacaceae, Nyctaginaceae, Colporate *Buxus*, *Robinia, *Gleditsia, *Annonaceae, Calpurnia/Sophora, Cercidiphyllum, *Ficus (non F. carica), Nelumbo, *Torreya, Tropical Euphorbiaceae, Tropical/subtropical Rubiaceae, Melastomataceae, Clethraceae-Cyrillaceae, Cyatheaceae, Ginkgo?, °Andromeda/Leucothoe, °Palmae (non Chamaerops and Nypa), °Ebenaceae, °Magnoliaceae, Platycarya, Schizaeaceae, °Caesalpiniaceae (non Ceratonia and Gleditsia), Menispermaceae, *Celastrus, Hamamelis, °Pittosporum, °Sapindaceae, Distylium, Microtropis, *Notholaea, *Lauraceae (non Laurus), °Rhus, Parrotiopsis, Rhoiptelea, Embothrium, *Rhizophora, °Sapotaceae, °Zelkova, *Cupressus, Vigna, °Engelhardia, Nyssa, Sciadopitys, °Taxodiaceae, Symplocos, °Araliaceae (non Hedera), Cathaya, Vitaceae (non Vitis), °Liquidambar, °Tsuga, Elaeagnaceae, Eucommiaceae, °Pterocarya, °Parrotia, Keteleeria, *Aesculus, °Carya, °Mimosaceae, °Ostrya, Pinus type haploxylon, °Picea, Syringa, °Platanus, Cedrus

Figure 4 Continued

All taxa identified from the earliest to the latest reports were considered (Heer, 1880, 1881; Bellot & Vieitez Cortizo, 1945). With the exception of a few cases mentioned in the text, the ages and diagnoses attributed by the different authors consulted were respected. Notwithstanding, some interpretations are our own since botanical systematics and

Table 1 Genera that disappeared from the Iberian Peninsula and Balearic Islands during the Cenozoic grouped by their time of disappearance and listed within their respective families (as represented in Fig. 4).

EOCENE

Acanthaceae: *Ruellia*

Apocynaceae: *Alstonia*-type and *Parsonsia*

Araliaceae: *Tupidanthus-Schefleropsis*

Caesalpiniaceae: *Daniellia* and *Julbernardia*-type

Euphorbiaceae: *Amanoa, Austrobuxus-Dissilaria, Centroplacus, Croton* and *Drypetes*

Icacinaceae: *Gonocaryum*-type

Menispermaceae: *Pachygone*

Ochnaceae: *Schurmansia*

Palmae: *Daemonorops* and *Sclerosperma*

Rubiaceae: *Hedyotis, Oldendandia* and *Paedicalyx*

Rutaceae: *Evodia*-type

OLIGOCENE

Araliaceae: *Acanthopanax, Brassaiopsis, Gilbertia, Heteropanax, Panax, Polyscias, Schefflera, Scheffleropsis* and *Tetrapanax*

Caesalpiniaceae: *Crudia* and *Tamarindus*

Cupressaceae: *Chamaecyparis?*

Ebenaceae: *Euclea*

Euphorbiaceae: *Antidesma, Claoxylon, Homalanthus, Macaranga, Mallotus, Spondianthus* and *Phyllantus*

Icacinaceae: *Desmostachys*

Lauraceae: *Lindera, Litsea, Nectandra* and *Phoebe*

Meliaceae: *Aglaia*-type

Menispermaceae: *Arcangelisia*-type, *Cocculus, Tiliacora*-type and *Tinomiscium*-type

Nyctaginaceae: *Pisonia*

Ochnaceae: *Ochna*

Olacaceae: *Olax*

Palmae: *Areca, Arenga?, Borassus, Calamus, Caryota*-type, *Flagellaria, Lepidocaryum*-type, *Oncosperma* and *Trachycarpus*

Rubiaceae: *Psychotria*

Rutaceae: *Clausena, Fagara, Orixa*-type and *Ptelea*

Sapindaceae: *Litchi*-type

Sapotaceae: *Chrysophyllum*

Schizaeaceae: *Anemia/Mohria*

Sterculiaceae: *Sterculia*

Taxodiaceae: *Metasequoia?* and *Sequoiadendron*

Theaceae: *Gordonia*-type

Vitaceae: *Ampelopsis* and *Cayratia*

MIOCENE

Apocynaceae: *Echitonium*

Araliaceae: *Aralia*

Caesalpiniaceae: *Caesalpinia* and *Cassia*

Combretaceae: *Terminalia*

Cycadaceae: *Zamia*

Euphorbiaceae: *Alchornea, Jathropa, Mussaenda* and *Ricinus*

Fabaceae: *Dalbergia*

Lauraceae: *Neolitsea*

Malpighiaceae: *Hiraea*

Myrsinaceae: *Ardisia* and *Myrsine*

Palmae: *Sabal*

Rubiaceae: *Cephalanthus*

Rutaceae: *Toddalia* and *Zanthoxylon*

Salviniaceae: *Salvinia*

Sapotaceae: *Mimusops*

Table 1 Continued

Schizaeaceae: *Lygodium*

Simaroubaceae: *Ailanthus* and *Picrasma*

Sterculiaceae: *Byttneriophyllum* and *Reevesia*

Taxodiaceae: *Cryptomeria*

Vitaceae: *Cissus* and *Leea*

the study methods used in palaeobotany have substantially changed since the 19th century (Jones & Rowe, 1999). Hence, the true presence of certain taxa cited for the Iberian fossil record is questioned, and these dubious taxa have not been included in the figures or tables showing taxa that have disappeared. For example, some fossils taken to indicate a taxon show ambiguous morphology; such is the case for the remains of one Oligocene leaf from Mallorca attributed to the genus *Cercis* (Colom, 1983), which, based on its venation pattern, could be assigned to a member of the genus *Daphnogene* (Lauraceae). Further, the requirements of some cited taxa make their presence in Iberia in the associated geological period unthinkable; e.g. *Larix*, an Arctotertiary genus currently with a boreal or Alpine distribution, is cited by Cavagnetto (2002) for the Oligocene in the As Pontes Basin, but at that time the region had a tropical/subtropical climate. Finally, certain typical Gondwanan genera (*Banksia, Protea, Dryandroides* and *Conospermum*) represented by large numbers of fossils have long been attributed to the family Proteaceae (Heer, 1855–1859; de Saporta, 1863). However, morphological and anatomical studies would seem to relate these finds to the family Myricaceae (Ferguson, 1971) or to certain members of the Juglandaceae (Menéndez Amor, 1955; Jungwirth, 2004). Further, no pollen grains that could be related to this family have yet been found in the Iberian Peninsula.

The taxa cited in palynological studies may sometimes appear controversial. Few reports actually contain photographs or other graphical representations of palynomorphs (for example Suc, 1980; Pais, 1981; Van Campo, 1989; Rivas Carballo *et al.*, 1994; Barrón, 1996; Barrón & de Santisteban, 1999; Cavagnetto, 2002; Barrón *et al.*, 2006a). In addition, in most of these studies (i.e. except for those of Pais, 1981; Van Campo, 1989; Barrón, 1996), identifications have been based on traditional light microscopy (LM) observations; this is a problem since some taxa are only distinguishable by scanning electron microscopy (SEM). This is true of some Hamamelidaceae species belonging to the genera *Corylopsis, Distylium* and *Hamamelis*, the pollen grains of which are of similar morphology in LM (see the pollen databases of the Florida Institute of Technology and the University of Arizona: http://research.fit.edu/paleolab/pollen.php and http://www.geo.arizona.edu/palynology/polonweb.html, respectively). These Hamamelidaceae identifications, plus those referring to Taxodiaceae, have, nevertheless, been included (Suc, 1980; Diniz, 1984; Bessedik,

1985; Cavagnetto & Anadón, 1996; Jiménez Moreno & Suc, 2007; Jiménez Moreno et al., 2007). All these identifications, however, require confirmation by SEM studies, since the modern species of these genera do show some exclusive pollen characteristics.

Table 1 shows the genera belonging to the families represented in Fig. 4. With the aim of summarizing as many data as possible in this figure, certain sets of taxa with clear ecological affinities were grouped together (e.g. as 'Palaeogene aquatic plants' or within the 'Oligocene tropical group'). The genera included in these groups are shown in Tables 1 and 2. On other occasions groups were formed following taxonomic criteria, e.g. Aegiceras/Brownlowia/Pelliceria, Gossypium/Thespesia, Disanthus/Exbucklandia, Lithocarpus/Pasania, Diphylleia/Nandina/Podophyllum and Corylopsis/Fothergilla. The studies in which these taxa are cited are recorded in Appendix S1 in Supporting Information. In general, the text refers to genera and families according to the traditional botanical taxonomic criteria of Cronquist (1981). For the construction of the chronogram, the scales proposed by Calvo et al. (1993) and Gradstein et al. (2004) were used. The beginning of the Quaternary was considered to be 2.58 Ma, the current boundary of the Gelasian Stage (Gradstein et al., 2004; Pillans, 2004; Clague, 2006). The change of the Quaternary limit from 1.8 to 2.58 Ma allows the inclusion of areas considered to be of Tiglian or Plio-Pleistocene age within the early Quaternary (Pillans, 2004; Clague, 2006). Phytochorological criteria were used to define the two large biogeographical units of the Iberian Peninsula, following, as much as possible, the proposed nomenclature of Ebach et al. (2008).

Table 2 Genera and families of taxa that disappeared from the Iberian Peninsula and Balearic Islands during the Cenozoic based on the taxon groups shown in Fig. 4.

Palaeogene aquatic tropical plants	Aponogeton (Aponogetonaceae), Halogaris (Halogaraceae) and Hydrocleys (Limnocharitaceae)
Oligocene tropical group	Acrostichum (Pteridaceae), Albizia (Mimosaceae), Canna (Cannaceae), Castanopsis (Fagaceae), Diervilla (Caprifoliaceae), Eugenia (Myrtaceae), Fothergilla (Hamamelidaceae), Fragaea (Potaliaceae), Glehnia (Umbelliferae), Gynandriris (Iridaceae), Hemsleya (Cucurbitaceae), Heritiera (Malvaceae), Hydrocotile (Umbelliferae), Rhyticarpus (Umbelliferae) and Siphonodon (Celastraceae)
Tropical/subtropical Anacardiaceae	Lannea, Mangifera and Spondias
Bignoniaceae	Adenocalymna, Spathodea, Stereospermum and Tecomaria
Tropical/subtropical Lythraceae	Decodon, Lawsonia-type, Pemphis, Rotala and Woodfordia

RESULTS AND DISCUSSION

The Palaeocene–Late Eocene interval and the Eocene–Oligocene transition

Few palaeobotanical studies are available for the Eocene and Oligocene periods, and nearly all are palynological in nature and mostly restricted to materials from the Ebro Basin and the Betic and Pyrenean mountain ranges (Fig. 1). During the Upper Cretaceous the territories that today form part of the Iberian Peninsula were populated by Palaeotropical forests of high floral diversity (de Porta et al., 1985; Mai, 1991; Vicente i Castells, 2002). Of particular importance in their composition were plants producing Normapolles pollen grains, possibly assignable to primitive Fagales (Schönenberger et al., 2001; Friis et al., 2006).

According to sedimentological and faunal evidence and the presence of ferralitic crusts and bauxitization processes, the climate that developed during this period was tropical, probably with seasonal rainfall (López-Martínez, 1989). During this period progressive substitutions of different types of Normapolles are observed, which must be related to the general evolution of this group in Europe. The Normapolles group last appeared in the Upper Eocene at Sosís (Lérida) (de Sitter, 1961).

Although the Palaeobotanical record for the Iberian Eocene is rather sketchy, it appears to indicate the disappearance of Normapolles as well as 31 Palaeotropical genera (Fig. 4, Tables 1 and 2) that now inhabit tropical and subtropical regions, mostly in eastern Asia. These include typical mangrove taxa such as Aegiceras, Brownlowia and Pelliceria (for which the only record known in Iberia is restricted to the Bartonian), Julbernardia-type taxa and Daniellia (members of the family Caesalpinaceae today restricted to savanna environments) and genera such as Alangium that show a continuous record throughout the Palaeogene and Neogene in other parts of Europe (Nagy, 1985; Gastaldo et al., 1998; Knobloch & Konzalová, 1998; Kovar-Eder et al., 1998; Mai, 1998). Their disappearance from the fossil record may be related to the notable climatic changes that took place during the second half of the Eocene and which culminated in the Eocene–Oligocene transition (EOT).

The growing trend towards aridity in the Late Eocene, manifested mainly in coastal areas, was probably caused by oceanic regression that generated a continentalization of the Eurasian climate along with a global fall in temperature (López-Martínez, 1989; Mai, 1989). From the Early Eocene climatic optimum (50–52 Ma) until the start of the Oligocene (34 Ma) there was a progressive fall in temperature that lasted 17 Myr before culminating in the EOT (about 34 Ma) and a long glaciation (lasting 400 kyr) – the Oi-1 glaciation – that coincided with the appearance of an ice cap in the Antarctic (Miller et al., 1991; Zachos et al., 2001; Mosbrugger et al., 2005).

The palynological record of the Ebro Basin allows the identification of the first signs of floristic change associated

with the EOT in the Bartonian–Priabonian. Mangroves disappeared during this period, and plants associated with dry climates and open country, such as *Ephedra* and Caesalpiniaceae, increased. *Barringtonia*, Boraginaceae, Chenopodiaceae, *Combretum*, *Linum*, Plumbaginaceae and Thymelaeaceae also appeared (Cavagnetto & Anadón, 1996). The Early Oligocene ecosystems of the Ebro Basin detected in Unit T3 also show an important reduction in mega-mesothermal and megathermal taxa. The appearance of the genus *Acacia* and the abundance of Cupressaceae pollen suggest a new phase of the dry period started in the Priabonian (Cavagnetto & Guinet, 1994; Cavagnetto & Anadón, 1996).

## Stepwise changes in the Late Oligocene–Late Miocene

From the Late Eocene onwards the terrestrial climate became colder and drier, leading to important changes in the flora of Central Europe and North America (Wolfe, 1978, 1992; Collinson, 1992; Knobloch *et al.*, 1993). Both the marine and terrestrial isotope records of Central Europe reveal a marked fall in mean annual temperatures during the Oligocene compared with the Eocene (Fig. 5) (Zachos *et al.*, 2001; Mosbrugger *et al.*, 2005). This cooling was maintained until the end of the Oligocene when a new warming began (the Late Oligocene Warming), although this was followed by a brief but strong glacial maximum (lasting 200 kyr) at the Oligocene–Miocene boundary (23 Ma) known as Mi-1. This was followed

by a series of less intense, intermittent glaciations (Miller *et al.*, 1991; Paul *et al.*, 2000; Zachos *et al.*, 2001; Billups *et al.*, 2004). According to Mosbrugger *et al.* (2005), this cooling was especially noticeable during winter, with marked thermal seasonality apparent at certain times during the Oligocene and Miocene.

Palaeontological and sedimentological evidence indicates the Miocene climatic optimum (MCO) to have lasted between 13.5–14.0 and 18 Ma in Central Europe (Böhme, 2003). At the end of the Burdigalian there was a time of high rainfall, although later, during the Langhian, there were droughts lasting up to 6 months. The MCO finished abruptly in the Middle Miocene (Langhian–Serravalian) between 13.5 and 14 Ma, when there was a significant fall in the mean annual temperature of at least 7°C. Analyses for Europe show that the fall in temperature and rainfall from the Middle to Late Miocene also provoked a seasonal and latitudinal climatic gradient across the continent (Bruch *et al.*, 2007). At the end of the Miocene the process of aridification intensified, extending the area occupied by open ecosystems, encouraging the appearance or expansion of several families of plants adapted to such environments (Singh, 1988).

The Oligocene

In general, the Iberian Oligocene fossil record reflects a broad-leaved, paratropical to subtropical evergreen rain forest
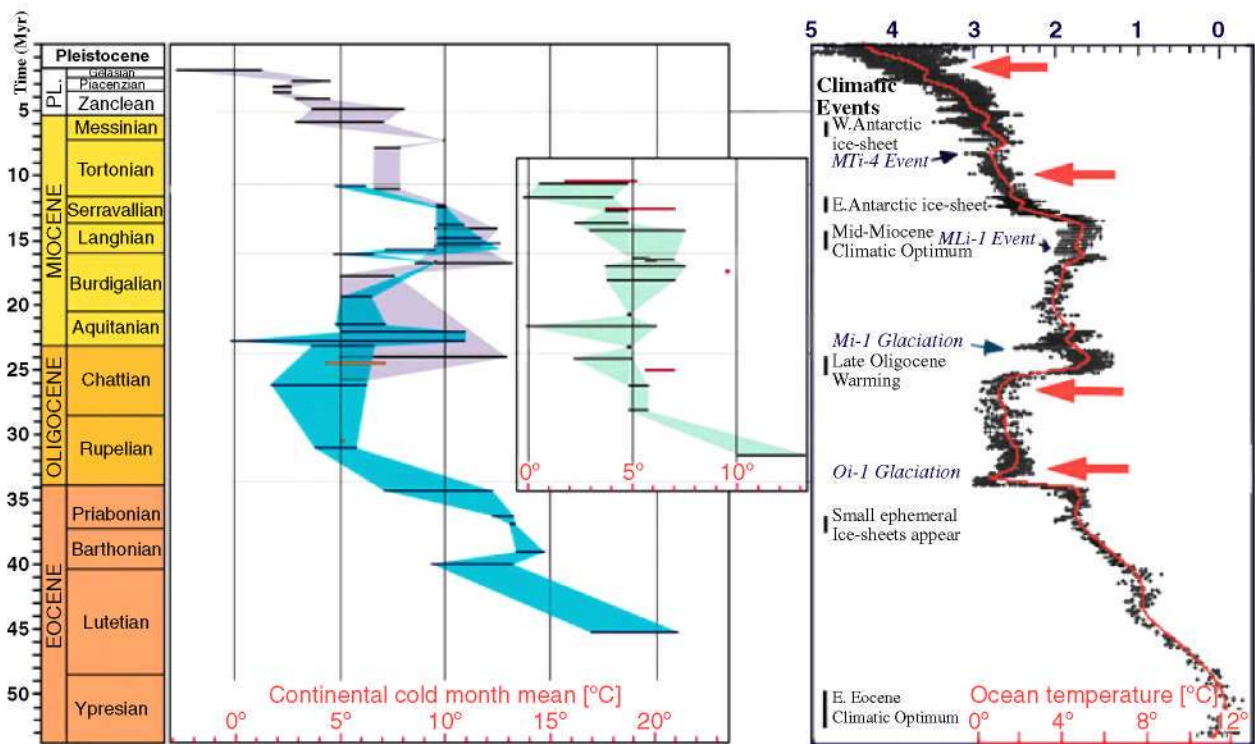
Figure 5 Continental temperature curves for Central Europe over the last 45 Myr in comparison with the global marine oxygen isotope record of Zachos *et al.* (2001), adapted from Mosbrugger *et al.* (2005) (© 2005 National Academy of Sciences, USA). The arrows show the time of the main floristic changes of the Iberian Peninsula and Balearic Islands in the Cenozoic. The inset highlights the data for the Molasse Basin (Central Europe) as provided in the original figure.

(Collinson & Hooker, 2003) well adapted to periods of seasonal drought – appropriate for a hot climate with no large seasonal variations. Sclerophylls were well represented in these Oligocene communities (Hably & Fernández Marrón, 1998) and laurel forests were common, although many were confined to riparian environments – areas where the microclimate and soil conditions were adequate (Sanz de Siria, 1992; Barrón & Peyrot, 2006). The number of taxa that disappeared from the Iberian fossil record over the Oligocene is very high. To date the loss of 117 taxa has been recorded (as revealed by palynological evidence), all of which were Palaeotropical except for several genera of the families Cupressaceae and Taxodiaceae (Cavagnetto & Anadón, 1996; Cavagnetto, 2002) (Fig. 4, Tables 1 and 2). With the exception of the latter conifers, the rest of the taxa that disappeared at this time (e.g. *Acanthopanax, Areca, Brassaiopsis, Caryota, Clausena, Diphylleia, Eustigma, Fragaea, Glehnia, Hemsleya, Heteropanax, Helwingia, Lithocarpus, Mangifera, Mastixia, Nandina, Oncosperma, Pasania, Podophyllum, Poliscyas, Sinowilsonia, Siphonodon, Sladenia, Trachycarpus, Tetracentron* and *Tetrapanax*) now largely inhabit the tropical or subtropical regions of Asia and the Indo-Pacific. *Diphylleia, Glehnia* and *Lithocarpus* are also represented in North America. *Adenocalymma, Canna, Carpodiptera, Decodon, Diervilla, Hydrocleys* and *Fothergilla* also disappeared from the Iberian Peninsula and are now found only in North America, as did *Spathodea, Tecomaria* and *Tamarindus*, which now live in Africa. The reduction in the number of genera suffered by the families Araliaceae, Euphorbiaceae, Menispermaceae and Palmae is also remarkable (Table 1) and indicative of significant changes occurring in Iberian plant landscapes.

During the Lower Oligocene, temperate deciduous vegetation and high-latitude mixed deciduous forest (Utescher & Mosbrugger, 2007) progressively extended across Europe. According to Knobloch (1992) and Knobloch *et al.* (1993), and unlike in Central Europe which had been home to a large number of Arctotertiary taxa since the Oligocene (Knobloch, 1986; Prothero, 1994), the Iberian Peninsula experienced a progressive increase in the number of Arctotertiary taxa starting in the Lower Miocene. Until this time paratropical and subtropical evergreen forests (Collinson & Hooker, 2003) were dominant. Thus, there was a clear diachrony in Europe with respect to the replacement of Palaeotropical taxa by Arctotertiary forms.

The Miocene

The Miocene is represented in nearly all the sedimentary basins of the Iberian Peninsula (Alonso-Zarza *et al.*, 2002; Civis, 2004) (Fig. 2). During the Lower and Middle Miocene, Iberia saw the expansion of Arctotertiary taxa, which eventually dominated the Atlantic face of the peninsula as well as certain mountain ranges (Pais, 1981, 1986; Alcalá *et al.*, 1996; Roiron *et al.*, 1999; Barrón & Diéguez, 2001; Barrón *et al.*, 2006a). In contrast, the abrupt climate changes of this period led to the disappearance from the peninsula's fossil record of 65 Palaeotropical taxa (Fig. 4, Table 1). The latter are nowadays found in tropical and subtropical areas around the world, except for *Corylopsis, Disanthus, Exbucklandia, Nypa* and *Reevesia*, which are found only in Asia. Paratropical and subtropical evergreen taxa characterized areas close to the sea where they developed xerophytic formations with conifers, Mimosacae, Caesalpiniaceae and Fabaceae; members of the Lauraceae continued to form part of the riparian vegetation (Fernández Marrón, 1979; Bessedik, 1984, 1985; Sanz de Siria, 1985; Barrón, 1999; Barrón *et al.*, 2006b). In fact, the eastern face of the Iberian Peninsula remained home to mangroves characterized by *Avicennia* during the Burdigalian–Langhian (Bessedik, 1981, 1985).

During the Iberian Upper Miocene a series of very arid phases occurred. Around 8.5 Ma there was an extremely dry phase during which rain was almost absent in the centre of the Iberian Peninsula. The first signs of these conditions appear in the Middle Miocene record, but they became generalized in the Duero Basin during the Vallesian (Lower Tortonian) (Valle & Salvador de Luna, 1985a,b; Rivas Carballo & Valle, 1987; Rivas Carballo, 1991a,b; Rivas Carballo *et al.*, 1994; Valle *et al.*, 2006). These dry phases were almost certainly the cause of the disappearance during the Tortonian of Palaeotropical families such as Cycadaceae, Meliaceae, Myrsinaceae, Restionaceae, Simaroubaceae, Sterculiaceae, Bombacaceae and Nyctaginaceae from Iberian ecosystems, as well as of aquatic plants such as *Nelumbo*. Although some of these taxa were well adapted to seasonal drought they probably could not stand the acute falls in temperature associated with the 18 glacial/interglacial cycles detected for the end of the Tortonian (Hodell *et al.*, 2001).

There are very few data available on the Messinian vegetation of the Iberian Peninsula, and no outstanding floristic changes can be determined with respect to the Upper Tortonian and the Zanclian (Solé de Porta & de Porta, 1977; Suc & Cravatte, 1982; Valle & Peñalba, 1987; Bessais & Cravatte, 1988; Van Campo, 1989; Valle & Rivas Carballo, 1990; Barrón, 1996; Rivas Carballo & Valle, 2005; Agustí *et al.*, 2006; Fauquette *et al.*, 2006). The only tropical genera to show their last records during the Messinian were members of the family Melastomataceae, Euphorbiaceae (*Ricinus*) and Rubiaceae (*Cephalanthus*).

The Pliocene: the Middle–Late Piacenzian extinction

Generally, the subtropical climate that developed in the Zanclian became drier with more intense summer droughts during the Piacenzian, accompanied by a slight drop in temperature owing to the installation of a Mediterranean climate rhythm (Suc & Cravatte, 1982; Sanz de Siria, 1987). This led to a transformation of the plant cover, including the spread of xerophytes such as *Olea, Pistacia* and *Artemisia*, and the progressive disappearance of taxa such as *Ginkgo, Andromeda*, Pittosporaceae, Menispermaceae, nearly all the Palmae and a fair number of tropical-type Hamamelidaceae (Suc, 1980; Suc & Cravatte, 1982; Valle, 1982, 1983; Sanz de Siria,

1987, 1994; Suc et al., 1995). The palaeobotanical data agree with those provided by the marine isotope record. The cooling that occurred over the Zanclian, approximately during MIS TG5–MIS GI1, was progressive, leading to periodic variations of temperature (Lisiecki & Raymo, 2005). Later, during the Mammoth subchron (MIS M2), a significant change in the isotope record can be seen, marking a brusque cooling about 3.3 Ma. This might be related to the climatic changes already mentioned for the Piacenzian. Finally, the interval between the isotope stages MIS M2 and MIS 104 – about 2.7–3.3 Ma – reflects an acute cooling over a relatively short period of time compared to the cooling periods of the Zanclian and early Piacenzian (Lisiecki & Raymo, 2005, 2007). A progressive reduction in summer rainfall and the development of a dry season coinciding with the warmest period of the year occurred around 3.1–3.2 Ma, thus initiating Mediterranean seasonality (Suc & Cravatte, 1982). This led to the expansion of the palaeomediterranean-type xerophytic plants installed in the area since the Oligocene (Palamarev, 1989). During the Piacenzian (Fig. 4), evergreen laurel forests disappeared almost completely from the Iberian Peninsula – a clear indication of long periods of summer drought accompanied by a fall in temperature. Seven genera of the family Lauraceae disappeared during this period: *Apollonias*, *Cinnamomum*, *Daphnogene*, *Lindera*, *Ocotea*, *Persea* and *Sassafras*. However, although it suffered considerably, the family Lauraceae was not completely lost, as indicated by the persistence until modern times of *Laurus nobilis*. Nonetheless, it must have suffered great difficulty during periods of extreme cold during the last third of the Quaternary (Rodríguez-Sánchez & Arroyo, 2008). Its persistence, along with that of other (non-Lauraceae) lauroid plants, was possible because it was able to settle in places of high humidity where it is easier to survive the cold (Postigo Mijarra et al., 2008).

The final appearance of arborescent ferns such as Cyatheaceae, and of the genus *Gingko* (Valle & Civis, 1978; Suc, 1980), is also notable. Although the family Taxodiaceae survived until the start of the Middle Pleistocene in the Iberian Peninsula, it suffered a notable reduction in its diversity, last appearing as pollen grains (Suc, 1980; Diniz, 1984) and wood specimens attributable to the genus *Sequoia* (Alcalde Olivares et al., 2004). Mangroves with *Rhizophora* also made their last appearance in the western Mediterranean at this time (Sendra et al., 2000). Until the Piacenzian, genera such as *Dodonaea*, *Pittosporum* and *Notolaea* – currently of some importance in Australia – arrived in the Iberian Peninsula. Finally, *Distylium*, *Diospyros*, *Embolanthera*, *Liriodendron*, *Magnolia*, *Microtropix*, *Parrotiopsis*, *Platycarya*, *Rhoiptelea* and *Sapindus* all disappeared; many of these are currently restricted partially or totally to Southeast Asia. A significant group of 36 taxa disappeared in this period.

The species that seemed to disappear from the Iberian Peninsula during the Zanclian may have persisted during at least some of the Piacenzian. Given the available data it may be more appropriate to speak of intense Piacenzian floristic change, an event that reached its high point at the end of this period between 2.7 and 3.3 Ma. As a whole, the Middle–Final Piacenzian plant disappearance episode is one of the best characterized events of the Iberian Cenozoic, and was probably the last great change in Iberian plant landscapes.

The Pliocene–Pleistocene transition

At the end of the Piacenzian and throughout the Gelasian, between 1.8 and 2.58 Ma, thermal contrasts became ever greater and the progressive cooling that was under way became more acute (Lisiecki & Raymo, 2005). Only three sites with fossils from the time are known in the Iberian Peninsula, Crespià (de Villalta & Vicente, 1972; Suc, 1980; Roiron, 1983, 1992), Tres Pins (Leroy, 1987, 1997) and Caranceja (Alonso et al., 1999; Alcalde Olivares et al., 2004). These outcrops provide the last references to the genera *Cupressus*, *Zelkova* and *Bumelia* (Sapotaceae) for the Iberian Peninsula. Leaf remains resembling those of *Zelkova carpinifolia* have been found at Crespià (Roiron, 1983); no younger macroremains have been found. However, this may not mean that this genus became extinct in Iberia; the palynological record may contain evidence of its existence but this could be masked by the similarity of its pollen to that of *Ulmus*.

The Middle Pleistocene transition

The large number of data available for the Quaternary (although the total for the Pleistocene is much smaller than for the Holocene; Fig. 3) allow for an in-depth picture of the evolution of this period's floras to be drawn. The last great floristic change in the Iberian Peninsula took place in the Lower Pleistocene, culminating in the Middle Pleistocene transition (MPT). The first significant change in the climate of this period came about 1.4 Ma during the so-called Early Pleistocene transition, when there was an abrupt reduction in the amplitude of the 41-kyr cycle associated with a much shorter duration of glacial periods (Lisiecki & Raymo, 2007). The MPT started about 1250 ka and ended about 700 ka, and was characterized by an increase in the severity of glaciations and the emergence of 100-kyr cycles (with the widest temperature fluctuations about 0.7 Ma) (Fig. 6) (Raymo et al., 2004; Clark et al., 2006). The increased continental aridity was surely another notable effect of the MPT on the flora of the Iberian Quaternary. Such an effect has been detected in Africa and Asia (Tiedemann et al., 1994; Clemens et al., 1996; Williams et al., 1997). A notable fall in temperature along with marked dryness would have been decisive in the total disappearance of many species. However, this alone does not explain all the changes in flora during the MPT. The emergence of a 100-kyr cycle and much shorter interglacial periods must have had a determining influence on the recovery of some populations after periods of retreat and restriction to certain areas. Unfortunately, it is difficult to quantify the relative importance of these factors with respect to the taxa that became extinct in Iberia during this period. Tolerance of the cold probably had a very important effect on survival (Svenning, 2003). However, resistance to recurrent seasonal
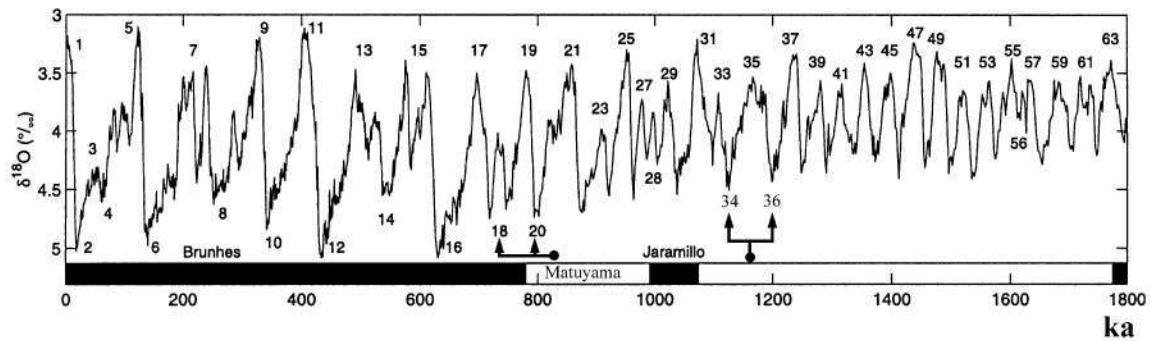
Figure 6 The LR04 benthic δ^{18} stack from 0 to 1800 thousand years ago (ka). Adapted from Lisiecki & Raymo (2005). Arrows show the times of the last significant disappearances of taxa in the Iberian Peninsula and Balearic Islands over the Pleistocene. The numbers on the figure indicate the marine isotopic stages.

drought or fire (as seen in the modern Mediterranean) and the inherent mechanisms of each species' reproductive biology may also have been important. This interval of the Quaternary is represented by an important group of Waalian (end of the Lower Pleistocene or the Lower–Middle Pleistocene transition, 1.4–0.8 Ma) sites in the Iberian Peninsula (Elhaï, 1966; Geurts, 1977, 1979; Julià & Suc, 1980; Antunes et al., 1986; Leroy, 1987, 1988, 2008; Postigo Mijarra et al., 2007).

A significant number of taxa seem to disappear for ever from the Iberian fossil record at the start of the MPT (c. 1.2 Ma; MIS 36), including Cathaya, Elaeagnus, Engelhardia, Eucommia, Keteleeria, Liquidambar, Nyssa, Parrotia, Parthenocissus, Pterocarya, Sciadopitys, Symplocos and Tsuga. Others lasted through to the Lower–Middle Pleistocene (c. 800 ka; MIS 20–18). Such is the case for Aesculus and the family Taxodiaceae, probably making the Iberian fossil record for these taxa one of the last in Europe (Postigo Mijarra et al., 2007, 2008). It would appear that MIS 36–34 and 20–18 were key points of inflection for the floristic groups of the Iberian Peninsula (Fig. 6). On the one hand there was the change from 41-kyr to 100-kyr cyclicity, and on the other hand the cooling that took place about 900 ka which led to the first long glaciation of the Pleistocene (80 ka) (Lisiecki & Raymo, 2005). Things were not much different in other areas of southern Europe, although Arctotertiary taxa have been found at numerous sites in the Italian Peninsula representing the first stages of the Lower Pleistocene, e.g. Fornace Tini (Urban et al., 1983), Rio Ferraio, Piedrafitta, Stirone (Lona & Bertoldi, 1972) and the Leffe Basin (Ravazzi & Rossignol, 1995). These sites date from before MIS 36–34. With the 41- to 100-kyr cycle change, a significant number of taxa disappeared from Tenaghi Philippon in Greece, the most significant changes occurring in MIS 22–16 (Tzedakis et al., 2006). Compared with sequences for northern Europe, the much earlier disappearance of taxa such as Aesculus, Engelhardia, Liquidambar, Nyssa, Symplocos and Zelkova during the Pliocene–Pleistocene transition (Zagwin, 1960) is a notable difference.

After the MPT the records of Carya and Ostrya are quite imprecise, although they probably became extinct in Iberia in the Middle Pleistocene (Geurts, 1977, 1979). It seems unlikely that they could have withstood the hard climatic conditions reigning between 0.43 Ma (MIS 12) and 0.87 Ma (MIS 22) – a time of extreme Pleistocene cold (Becquey & Gersonde, 2002). However, pollen grains belonging to Mimosaceae have been found for the Middle Pleistocene (Geurts, 1979) – which is quite hard to interpret; further studies will be needed before any conclusions can be drawn. It does not seem likely that the aforementioned taxa would have withstood the second notable climate change of the Pleistocene – the Middle Brunhes Event (MBE) – which took place c. 430 ka (MIS 12/11) (Jansen et al., 1986; EPICA Community Members, 2004). This event occurred on a global scale that marked the start of greater variability in the length of glacial and interglacial periods.

Extinctions during the Upper Pleistocene and Holocene: natural or due to human activities, or both?

One of the genera that disappeared at the end of the Quaternary was Cedrus. Its presence in the Iberian fossil record is almost constant from the Eocene to the Upper Pleistocene (Fig. 4), but its citation within the last glacial–interglacial cycle may be due to pollen grains coming from trees in North Africa (Magri & Parra, 2002). Further studies are needed to determine whether this is the case.

Picea is another taxon well represented during the Tertiary in the Iberian Peninsula but which disappeared at the end of the Upper Pleistocene. In Europe, the Quaternary history of this taxon is well documented (Collignon & Fabre, 2000; Ravazzi, 2002; Ravazzi et al., 2006). In the interior of the peninsula it was continuously present from the Oligocene until the Upper Pleistocene (Fig. 4); wood, cones and pollen remains have all been collected (Menéndez Amor & Florschütz, 1959; Uzquiano, 1995; Alonso et al., 1999; Barrón & Diéguez, 2001; Alcalde Olivares et al., 2004; Desprat et al., 2005; Gómez-Orellana et al., 2007). Pollen is also known from the Holocene (Pantaleón-Cano et al., 2003). The disappearance of Picea during the Würm glaciation as a consequence of low temperatures is difficult to understand. Its microthermal nature could have allowed it to become established at the foot of Iberian mountain ranges during the coldest parts of the

Quaternary without much difficulty. In fact, it persisted throughout most of the cold phases of the Middle Pleistocene. However, the lack of water during these cold times and the influence of the Mediterranean climate (with its dry summers) must have taken their toll. Changes in water availability have been proposed to have had a critical impact on the survival of *Picea* in other parts of Europe (Ravazzi *et al.*, 2006), although in the Iberian Peninsula competition with conifers such as *Abies* (that produce shady forests) also needs to be taken into account. There is no evidence of any anthropogenic influence in its final demise. New studies will be needed to determine the role of this taxon in the Quaternary landscapes of the Iberian Peninsula. Finally, *Pinus haploxylon* is another conifer that is well represented during the Quaternary. Pollen records are found in Plio-Pleistocene and Lower Pleistocene sequences in the north-east of the peninsula (Julià & Suc, 1980; Leroy, 1987, 1997). Burjachs (2006) cites this taxon for the Abric Romaní site, but also records its disappearance in MIS 3 and cites no Middle Pleistocene reference.

Among the angiosperms, *Platanus* has a long palaeontological history, its first Iberian records dating from the Aquitanian (Fig. 4). Although the fossil record is patchy, it is known to have persisted until the Holocene (García Antón *et al.*, 1990). The cold periods of the Quaternary are thought to have left it isolated in a few areas of the Iberian Peninsula providing refugia for flora of Arctotertiary origin. The case of *Syringa*, however, is quite different. The representation of this taxon in south-western Europe is reduced to a single record for the Upper Pleistocene in Catalonia (40–70 ka) (Burjachs & Julià, 1994). Currently its distribution is restricted to the eastern Mediterranean. The aforementioned single Iberian reference shows that this genus did not form an important part of the Iberian plant cover, but confirms Catalonia to have offered refuge to Arctotertiary flora during the cold phases of the Quaternary.

A number of other taxa with more or less ample Cenozoic records, and with representation in the Iberian Pleistocene and Holocene, can still be found growing naturally in the Iberian Peninsula today. Such is the case of *Juglans*, *Castanea*, *Vitis*, *Ceratonia*, *Carpinus* and *Fagus* (Aizpuru & Catalán, 1984; Stevenson & Moore, 1988; García Antón *et al.*, 1990; Carrión & Sánchez-Gómez, 1992; Martínez Atienza & Morla, 1992; Hewitt, 1999; Grau Almero *et al.*, 2004; Krebs *et al.*, 2004; Costa *et al.*, 2005; Magri *et al.*, 2006; Postigo Mijarra *et al.*, 2008). Their Iberian fossil records contrast strongly with the final disappearance of these taxa in Central and northern Europe (Zagwin, 1960; Van der Hammen *et al.*, 1971; Postigo Mijarra *et al.*, 2008).

CONCLUSIONS

The great climatic events that led to substantial changes in temperature, water availability and rainfall patterns over the Cenozoic were probably the main reason behind the main changes in the flora of the Iberian Peninsula recorded in its fossil record. In total, 277 taxa became extinct in Iberia during the Cenozoic. Such changes can be seen in the Palaeocene as substitutions of the different genera of *Normapolles*. Over the Eocene–Piacenzian, Palaeotropical elements found today in the different tropical and subtropical regions of the world successively disappeared (Fig. 5). The patent floristic change of the Priabonian–Chatian interval was related to the aridification that began in the Late Eocene.

Palaeotropical taxa survived longer in the Iberian Peninsula than in other areas of Europe, probably as a consequence of its palaeolatitude and its varied orography (including large mountain systems and sedimentary basins), which allowed for altitudinal displacements and stable microclimate conditions. Moreover, the Tethys and Atlantic oceans may have played a key role by attenuating temperatures and providing constant humidity across several peninsular areas. From the Oligocene and during the Miocene, many Iberian regions must have had floras of a mixed Palaeotropical/Arctotertiary nature. However, little by little, Arctotertiary taxa gained ground over their Palaeotropical counterparts as seasonality, the trend towards lower temperatures and reductions in rainfall, became more pronounced. Palaeotropical plants became ever more scarce, victims of new climates (especially from the MCO onwards) and of direct competition with new species arriving from Europe.

During the Miocene, Palaeotropical elements continued to disappear – a gradual disappearance due to the fall in mean annual temperature and recurrent drought. At the same time Arctotertiary taxa arrived to substitute them. However, some of these Arctotertiary genera, such as *Calocedrus*, *Torreya*, *Cercidiphyllum*, *Robinia* and *Gleditsia*, also found themselves unable to resist the climate changes of the Iberian Miocene. In total, 177 taxa became extinct in Iberia during the Oligocene and Miocene.

During the Middle–Late Piacenzian (2.7–3.3 Ma), Palaeotropical elements made their last appearance; 36 taxa are known to have been lost due to the notable cold and the onset of Mediterranean seasonality. During the MPT, and probably related to the change in glacial cyclicity, a notable disappearance of 14 Arctotertiary elements occurred. These losses, along with those among the remaining Palaeotropical flora (notably *Engelhardia* and members of the family Araliaceae that today live in tropical areas) were related to the increased severity of the glaciations, a reduction in the length of the interglacial periods, a change in cyclicity from 41 to 100 kyr, and the increased dryness of the coldest times. MIS 36–34 and 20–18 stand out as the key moments in the Quaternary disappearance of taxa from the Iberian Peninsula.

It is difficult to think of human activity as the cause of the complete or near-complete disappearance of some taxa. Certain genera, such as *Platanus* and *Syringa*, seem to have disappeared due to natural causes, although the non-persistence of *Picea* might be related to climate change, competition with other taxa and the activity of humans.

The disappearance chronogram for Cenozoic flora proposed in this work differs from the model established for Central and

northern Europe: the Palaeotropical flora of the latter areas disappeared much sooner than in Iberia. The mixing and coexistence of Palaeotropical and Arctotertiary floras over much of the Iberian Miocene and the first part of the Pliocene, along with the appearance of Mediterranean-type taxa from the Middle Pliocene, represent further differences with respect to Central and northern Europe. In addition, the disappearance of many mainly Arctotertiary taxa of ample Cenozoic presence occurred later in Iberia (at the Early–Middle Pleistocene boundary) than in Central Europe, confirming that the Iberian Peninsula had offered refugia to these taxa since pre-Quaternary times.

ACKNOWLEDGEMENTS

REFERENCES

Agustí, J., Oms, O., Furió, M., Pérez-Vila, M.J. & Roca, E. (2006) The Messinian terrestrial record in the Pyrenees: the case of Can Vilella (Cerdanya Basin). *Palaeogeography, Palaeoclimatology, Palaeoecology,* **238,** 179–189.

Aizpuru, I. & Catalán, P. (1984) Presencia del carpe en la Península Ibérica. *Anales del Jardín Botánico de Madrid,* **41,** 143–146.

Alcalá, B., Benda, L. & Ivanovic Calzaga, Y. (1996) Erste palynologische Untersuchungen zur Altersstellung des Neogen-Beckens von Xinzo de Limia (Prov. Orense, Spanien). *Newsletter on Stratigraphy,* **34,** 31–38.

Alcalde Olivares, C., García Antón, M., Gómez Manzaneque, F. & Morla Juaristi, C. (2004) Palaeoenvironmental interpretation of the Neogene locality Caranceja (Reocín, Cantabria, N Spain) from comparative studies of wood, charcoal, and pollen. *Review of Palaeobotany and Palynology,* **132,** 133–157.

Alonso, A., García Amorena, I., Garzón, G., Gómez Manzaneque, F., González Díez, A., Morla Juaristi, C., Remondo, J. & Roig, S. (1999) Estudio preliminar del yacimiento de macrorrestos vegetales de Caranceja (Reocín, Cantabria, España). *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica),* **94,** 23–40.

Alonso-Zarza, A.M., Armenteros, I., Braga, J.C., Muñoz, A., Pujalte, V. & Ramos, E. (2002) Tertiary. *The geology of Spain* (ed. by W. Gibbons and T. Moreno), pp. 293–334. The Geological Society of London, London.

Álvarez Ramis, C. (1975) Quelques considérations écologiques sur le gisement vallésien de Can Llobateres (Barcelone, Espagne). *Actes 100ème Congrés National des Sociétés Savantes, Paris,* fasc. 2, 11–16.

Antunes, M.T., Mein, P., Nascimento, A. & Pais, J. (1986) Le gisement pleistocène de Morgadinho, en Algarve. *Ciencias da Terra (UNL),* **8,** 9–22.

Barrón, E. (1996) *Estudio tafonómico y análisis paleoecológico de la macro y microflora miocena de la cuenca de la Cerdaña.* PhD Thesis, Universidad Complutense de Madrid, Madrid.

Barrón, E. (1999) Estudio macroflorístico del afloramiento mioceno de concreciones carbonáticas de Izarra (Álava, España). Aspectos tafonómicos, paleoecológicos y bioestratigráficos. *Revista Española de Paleontología,* **14,** 123–145.

Barrón, E. & de Santisteban, C. (1999) Estudio palinológico de la cuenca miocena de Rubielos de Mora (Teruel, España). Aspectos paleoecológicos y paleobiogeográficos. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica),* **95,** 67–82.

Barrón, E. & Diéguez, C. (2001) Estudio macroflorístico del Mioceno Inferior lacustre de la Cuenca de Rubielos de Mora (Teruel, España). *Boletín Geológico y Minero,* **112,** 13–56.

Barrón, E. & Peyrot, D. (2006) La vegetación forestal en el Terciario. *Paleoambientes y cambio climático* (ed. by J.S. Carrión, S. Fernández and N. Fuentes), pp. 55–76. Fundación Séneca, Agencia Ciencia y Tecnología, Murcia.

Barrón, E., Rivas-Carballo, M.R. & Valle, M.F. (1996) Síntesis bibliográfica de la vegetación y clima de la Península Ibérica durante el Neógeno. *Revista Española de Paleontología,* Número Extraordinario, 225–236.

Barrón, E., Lassaletta, L. & Alcalde Olivares, C. (2006a) Changes in the Early Miocene palynoflora and vegetation in the east of the Rubielos de Mora Basin (SE Iberian Ranges, Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen,* **242,** 171–204.

Barrón, E., Hernández, J.M., López-Horgue, M.A. & Alcalde Olivares, C. (2006b) Palaeoecology, biostratigraphy and palaeoclimatology of the lacustrine fossiliferous beds of the Izarra Formation (Lower Miocene, Basque-Cantabrian basin, Álava province, Spain) based on palynological analysis. *Revista Española de Micropaleontología,* **38,** 321–338.

Becquey, S. & Gersonde, R. (2002) Past hydrographic and climatic changes in the subantarctic zone of the South Atlantic – the Pleistocene record from ODP Site 1090. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **182,** 221–239.

Bellot, F. & Vieitez Cortizo, E. (1945) Primeros análisis polínicos en las turberas galaicas. *Anales del Instituto de Edafología, Ecología y Fisiología Vegetal,* **4,** 281–307.

Bessais, E. & Cravatte, J. (1988) Les écosystèmes végétaux pliocènes de Catalogne méridionale. Variations latitudinales dans le domaine nord-ouest méditerraneen. *Geobios,* **21,** 49–63.

Bessedik, M. (1981) Un mangrove à *Avicennia* L. en Méditerranée occidentale au Miocène Inférieur et Moyen. Implications paléogéographiques. *Comptes Rendus de l'Academie des Sciences, Paris,* **293,** 469–472.

Bessedik, M. (1984) The early Aquitanian and upper Langhian–lower Serravallian environments in the northwestern Mediterranean Region. *Paléobiologie Continentale,* **14,** 153–179.

Bessedik, M. (1985) *Reconstitution des environments Miocènes des régions nordouest mediterraneennes a partir de la palynologie.* PhD Thesis, Université de Montpellier II, France.

Billups, K., Pälike, H., Channell, J.E.T., Zachos, J.C. & Shackleton, N.J. (2004) Astronomic calibration of the late Oligocene through early Miocene geomagnetic polarity time scale. *Earth and Planetary Science Letters*, **224**, 33–44.

Böhme, M. (2003) The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 389–401.

Bruch, A., Uhl, D. & Mosbrugger, V. (2007) Miocene climate in Europe – patterns and evolution. A first synthesis of NECLIME. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **253**, 1–7.

Burjachs, F. (2006) Palinología y restitución paleoecológica. *Ecosistemas*, **15**, 7–16.

Burjachs, F. & Julià, R. (1994) Abrupt climatic changes during the last glaciation based on pollen analysis of the Abric Romaní, Catalonia, Spain. *Quaternary Research*, **42**, 308–315.

Cabrera, L., Jung, W., Kirchner, M., Sáez, A. & Schleich, H.H. (1994) Crocodilian and palaeobotanical findings from the Tertiary lignites of the As Pontes Basin (Galicia, NW-Spain) (Crocodylia, Plantae). *Courier Forschungsinstitut Senckenberg*, **173**, 153–165.

Calvo, J.P., Daams, R., Morales, J., López-Martínez, N., Agustí, J., Anadón, P., Armenteros, I., Cabrera, L., Civis, J., Corrochano, A., Díaz-Molina, M., Elizaga, E., Hoyos, M., Martín-Suárez, E., Martínez, J., Moissenet, E., Muñoz, A., Pérez-García, A., Pérez-González, A., Portero, J.M., Robles, F., de Santisteban, C., Torres, T., Van der Meulen, A.J., Vera, J.A. & Mein, P. (1993) Up-to-date Spanish continental Neogene synthesis and paleoclimatic interpretation. *Revista de la Sociedad Geológica de España*, **6**, 29–40.

Carrión, J.S. & Sánchez-Gómez, P. (1992) Palynological data in support of the survival of walnut (*Juglans regia* L.) in the western Mediterranean area during last glacial times. *Journal of Biogeography*, **19**, 623–630.

Castroviejo, S., Laínz, M., López González, G., Montserrat, P., Muñoz Garmendia, F., Paiva, J. & Villar, L. (eds) (1986) *Flora Ibérica. Plantas vasculares de la Península Ibérica e Islas Baleares.* Vol. I. *Lycopodiaceae–Papaveraceae.* Real Jardín Botánico, CSIC, Madrid.

Cavagnetto, C. (2002) Palynoflora from the As Pontes Basin in Galicia, Spain at the transition Rupelian–Chattian (Oligocene). *Palaeontographica Abteilung B*, **263**, 161–204.

Cavagnetto, C. & Anadón, P. (1996) Preliminary palynological data on floristic and climatic changes during the Middle Eocene–Early Oligocene of the eastern Ebro basin, northeast Spain. *Review of Palaeobotany and Palynology*, **92**, 281–305.

Cavagnetto, C. & Guinet, P. (1994) Pollen fossile de Leguminosae–Mimosoideae dans l'Oligocène inférieur de l'Ebre (Espagne) – implications paléoclimatiques et paléogeographiques. *Review of Palaeobotany and Palynology*, **81**, 327–335.

Civis, J. (2004) Cuencas Cenozoicas. Rasgos generales: estructuración. *Geología de España* (ed. by J.A. Vera), pp. 531–533. Instituto Geológico y Minero de España, Madrid.

Clague, J. (2006) Open letter by INQUA, Executive Committee. *Quaternary Perspectives*, **16**, 158–159.

Clark, P.U., Archer, D., Pollard, D., Blum, J.D., Rial, J.A., Brovkin, V., Mix, A.C., Pisias, N.G. & Roy, M. (2006) The middle Pleistocene transition: characteristics, mechanisms, and implications for long-term changes in atmospheric pCO_2. *Quaternary Science Reviews*, **25**, 3150–3184.

Clemens, S.C., Murray, D.W. & Prell, W.L. (1996) Nonstationary phase of the Plio-Pleistocene Asian monsoon. *Science*, **274**, 943–948.

Collignon, A.M. & Fabre, J.M. (2000) Contribution to the postglacial history at western margin of *Picea abies*' natural area using RAPD markers. *Annals of Botany*, **85**, 713–722.

Collinson, M.E. (1992) Vegetational and floristic changes around the Eocene/Oligocene boundary in western and central Europe. *Eocene–Oligocene climatic and biotic evolution* (ed. by D.R. Prothero and W.A. Berggren), pp. 437–450. Princeton University Press, Princeton.

Collinson, M.E. & Hooker, J.J. (2003) Palaeogene vegetation of Eurasia: framework for mammalian faunas. *Deinsea*, **10**, 41–83.

Colom, G. (1983) *Los lagos del Oligoceno de Mallorca.* Gràfiques Miramar S.A., Palma de Mallorca.

Costa, M., Morla Juaristi, C. & Sainz Ollero, H. (eds) (2005) *Los bosques ibéricos: una interpretación geobotánica*, 4th edn. Editorial Planeta, Barcelona.

Cronquist, A. (1981) *An integrated system of classification of flowering plants.* Columbia University Press, New York.

Desprat, S., Sánchez Goñi, M.F., Turon, J.L., McManus, J.F., Loutre, M.F., Duprat, J., Malaizé, B., Peyron, O. & Peypouquet, J.P. (2005) Is vegetation responsible for glacial inception during periods of muted insolation changes? *Quaternary Science Reviews*, **24**, 1361–1374.

Diniz, F. (1984) *Apports de la palynologie à la connaissance du Pliocène Portugais Rio Maior: un bassin de reference pour l'histoire de la flore, de la végétation et du climat de la façade atlantique de l'Europe Meridionale.* PhD Thesis, Université Montpellier 2, France.

Ebach, M.C., Morrone, J.J., Parenti, L.R. & Viloria, A.L. (2008) International Code of Area Nomenclature. *Journal of Biogeography*, **35**, 1153–1157.

Elhaï, H. (1966) Deux gisements du Quaternaire moyen. *Bulletin de l'Association Française pour l'Étude du Quaternaire*, **6**, 69–78.

Engler, A. (1879–1882) *Versuch einer Entwicklungsgeschichte der Pflanzenwelt seit der Tertiärperiode*, Vols 1–2. Engelmann, Leizpig.

EPICA Community Members (2004) Eight glacial cycles from an Antarctic ice core. *Nature*, **429**, 623–628.

Fauquette, S., Suc, J.-P., Bertini, A., Popescu, S.-M., Warny, S., Bachiri Taouiq, N., Perez Villa, M., Chikhi, H., Subally, D., Feddi, N., Clauzon, G. & Ferrier, J. (2006) How much did

climate force the Messinian salinity crisis? Quantified climatic conditions from pollen records in the Mediterranean region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **238**, 281–301.

Ferguson, D.K. (1971) The Miocene flora of Kreuzau, Western Germany. 1. The leaf-remains. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, AFD Natuurkunde Tweede Reeks*, **60**, 1–297.

Fernández Marrón, M.T. (1979) Essai de résolution de problemes stratigraphiques de la limite Paleogène–Neogène par les études de macroflore. *Annales Geologiques des Pays Helleniques, hors-série*, **1**, 403–412.

Friis, E.M., Pedersen, K.R. & Schönenberger, J. (2006) Normapolles plants: a prominent component of the Cretaceous rosid diversification. *Plant Systematics and Evolution*, **260**, 107–140.

García Antón, M., Morla Juaristi, C. & Sainz Ollero, H. (1990) Consideraciones sobre la presencia de algunos vegetales relictos terciarios durante el Cuaternario en la Península Ibérica. *Boletín Real Sociedad Española de Historia Natural (Sección Biológica)*, **86**, 95–105.

Gastaldo, R.A., Riegel, W., Püttmann, W., Linnemann, U.G. & Zetter, R. (1998) A multidisciplinary approach to reconstruct the Late Oligocene vegetation in central Europe. *Review of Palaeobotany and Palynology*, **101**, 71–94.

Geurts, M.A. (1977) Approche palynostratigraphique des depots calcareux Quaternaires en Catalogne. *Acta Geológica Hispánica*, **12**, 86–89.

Geurts, M.A. (1979) Approche palynostratigraphique des depots calcareux quaternaires dans la region de Banyoles-Besalc (Catalogne). *Actas de la IV Reunión del grupo de trabajo del Cuaternario* (ed. by R. Julià, M.A. Marqués, A. Mir, D. Serrat and F. Gallart), pp. 106–115. Banyoles, Girona.

Gómez-Orellana, L., Ramil-Rego, P. & Muñoz Sobrino, C. (2007) The Würm in NW Iberia, a pollen record from Area Longa (Galicia). *Quaternary Research*, **67**, 438–452.

Gradstein, F.M., Ogg, J.G., Smith, A.G., Agterberg, F.P., Bleeker, W., Cooper, R.A., Davydov, V., Gibbard, P., Hinnov, L.A., House, M.R., Lourens, L., Luterbacher, H.-P., McArthur, J., Melchin, M.J., Robb, L.J., Shergold, J., Villeneuve, M., Wardlaw, B.R., Ali, J., Brinkhuis, H., Hilgen, F.J., Hooker, J., Howarth, R.J., Knoll, A.H., Laskar, J., Monechi, S., Powell, J., Plumb, K.A., Raffi, I., Röhl, U., Sanfilippo, A., Schmitz, B., Shackleton, N.J., Shields, G.A., Strauss, H., Van Dam, J., Veizer, J., van Kolfschoten, Th. & Wilson, D. (2004) *A geologic time scale 2004*. Cambridge University Press, Cambridge.

Grau Almero, E., Duque Espino, D.M. & Cuenca García, C. (2004) Paleoambiente y paisaje en La Serena. *El edificio protohistórico de 'La Mata' (Campanario, Badajoz) y su estudio territorial* (ed. by A. Rodríguez Díaz), pp. 29–74. Universidad de Extremadura, Cáceres.

Gregor, H.-J. & Günther, T. (1985) Neue Pflanzenfunde aus dem Vallesium (jüngeres Neogen) von Libros (Becken von Teruel, Spanien). *Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz NF*, **13**, 297–309.

Hably, L. (1987) A comprehensive study of the Hungarian Neogene floras. *Annales. Instituti Geologici Publici Hungarici*, **70**, 497–501.

Hably, L. & Fernández Marrón, M.T. (1998) A comparison of the Oligocene floras of the Tethyan and Central-Paratethyan areas on the basis of Spanish and Hungarian macroflora. *Tertiary Research*, **18**, 67–76.

Heer, O. (1855–1859) *Flora Tertiaria Helveticae. Die Tertiäre flora der Schweiz*. J. Wurster and Company, Winterthur, Switzerland.

Heer, O. (1880) Apperçu sur la flore tertiaire du Portugal. *Comptes Rendus de la 9ème Session du Congress International d'Anthropologie, Archéologie et Préhistoire* (ed. by l'Académie Royale des Sciences), pp. 119–128. Académie Royal des Sciences, Lisbonne.

Heer, O. (1881) *Contributions à la flore fossile du Portugal*. Section de Travaux Géologiques du Portugal, Académie Royal des Sciences, Lisbon.

Hewitt, G.M. (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, **68**, 87–112.

Hodell, D.A., Curtis, J.H., Sierro, F.J. & Raymo, M.E. (2001) Correlation of late Miocene to early Pliocene sequences between the Mediterranean and North Atlantic. *Paleoceanography*, **16**, 164–178.

Jansen, J.H.F., Kuijpers, A. & Troelstra, S.R. (1986) A mid-Brunhes climatic event: long-term changes in global atmosphere and ocean circulation. *Science*, **232**, 619–622.

Jiménez Moreno, G. & Suc, J.P. (2007) Middle Miocene latitudinal climatic gradient in Western Europe: evidence from pollen records. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **253**, 208–225.

Jiménez Moreno, G., Fauquette, S., Suc, J.P. & Aziz, H.A. (2007) Early Miocene repetitive vegetation and climatic changes in the lacustrine deposits of the Rubielos de Mora Basin (Teruel, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **250**, 101–113.

Jones, T.P. & Rowe, N.P. (eds) (1999) *Fossil plants and spores: modern techniques*. The Geological Society, London.

Julià, R. & Suc, J.P. (1980) Analyse pollinique des dépôts lacustres du Pléistocène Inférieur de Banyoles (Bañolas, site de la Bòbila Ordis-Espagne: un élément nouveau dans la reconstitution de l'histoire paléoclimatique des régions méditerranéennes d'Europe occidentale). *Geobios*, **13**, 5–19.

Jungwirth, E. (2004) The determination and taxonomic problems of Palaeogene fossil macroflora from Slovenia and Croatia. *Natura Croatica*, **13**, 187–196.

Knobloch, E. (1986) Palaeofloristic and palaeoclimatic changes in the Cretaceous and Tertiary periods (facts, problems and tasks). *Lecture Notes in Earth Sciences*, **8**, 371–373.

Knobloch, E. (1992) Comparisons between the Cretaceous and Tertiary floras of central and southwest Europe: a commentary. *Revista Española de Paleontología*, **7**, 161–165.

Knobloch, E. & Konzalová, M. (1998) Comparison of the Eocene plant assemblages of Bohemia (Czech Republic) and Saxony (Germany). *Review of Palaeobotany and Palynology*, **101**, 29–41.

Knobloch, E., Kvaček, Z., Bužek, C., Mai, D.H. & Batten, J.D. (1993) Evolutionary significance of floristic changes in the Northern Hemisphere during the Late Cretaceous and Palaeogene, with particular reference to Central Europe. *Review of Palaeobotany and Palynology*, **78**, 41–54.

Kovar-Eder, J.K., Meller, B. & Zetter, R. (1998) Comparative investigations on the basal fossiliferous layer at the opencast mine Oberdorf (Köflach-Voitsberg lignite deposit, Styria, Austria; Early Miocene). *Review of Palaeobotany and Palynology*, **101**, 125–145.

Krebs, P., Conedera, M., Pradella, M., Torriani, D., Felber, M. & Tinner, W. (2004) Quaternary refugia of the sweet chestnut (*Castanea sativa* Mill.): an extended palynological approach. *Vegetation, History and Archaeobotany*, **13**, 145–160.

Leroy, S. (1987) *Analyse palynologique de deux nouvelles sections du Pleistocene Inferieur de Banyoles (Catalogne)* (ed. by J. Civis Llovera and M.F. Valle Hernández), pp. 307–313. Actas del VI Simposio de Palinología, APLF, Salamanca, Spain.

Leroy, S. (1988) Image pollinique d'une steppe du Pliocène supérieur à Bobila Ordis, Banyoles (Catalogne). *Institut Français de Pondichéry, Travaux Scientifiques et Techniques. Actes Deuxieme Symposium APLF, Bordeaux*, **25**, 197–207.

Leroy, S. (1997) Climatic and non-climatic lake-level changes inferred from a Plio-Pleistocene lacustrine complex of Catalonia (Spain): palynology of the Tres Pins sequences. *Journal of Paleolimnology*, **17**, 347–367.

Leroy, S. (2008) Vegetation cycles in a disturbed sequence around the Cobb-Mountain subchron in Catalonia (Spain). *Journal of Palaeolimnology*, **40**, 851–868.

Lisiecki, L.E. & Raymo, M.E. (2005) A Pliocene–Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanography*, **20**, PA1003, doi:10.1029/2004PA001071.

Lisiecki, L.E. & Raymo, M.E. (2007) Plio-Pleistocene climate evolution: trends and transitions in glacial cycle dynamics. *Quaternary Science Reviews*, **26**, 56–69.

Lona, F. & Bertoldi, R. (1972) La storia del Plio-Pleistocene Italiano in alcune sequenze vegetazionali lacustri e marine. *Memorie della Accademia Nazionale dei Lincei*, **11**, 1–47.

López-Martínez, N. (1989) Tendencias en paleobiogeografía. El futuro de la biogeografía del pasado. *Paleontología: nuevas tendencias* (ed. by E. Aguirre), pp. 271–296. Consejo Superior de Investigaciones Científicas (CSIC), Madrid.

Magri, D. & Parra, I. (2002) Late Quaternary western Mediterranean pollen records and African winds. *Earth and Planetary Science Letters*, **200**, 401–408.

Magri, D., Vendramin, G., Comps, B., Dupanloup, I., Geburek, Th., Gömöry, D., Latalowa, M., Litt, Th., Paule, L., Roure, J.M., Tantau, I., van der Knaap, W.O., Petit, R.J. & de Beaulieu, J.-L. (2006) A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist*, **171**, 199–221.

Mai, D.H. (1989) Development and regional differentiation of the European vegetation during the Tertiary. *Plant Systematics and Evolution*, **162**, 79–91.

Mai, D.H. (1991) Palaeofloristic changes in Europe and the confirmation of the Arctotertiary–Palaeotropical geofloral concept. *Review of Palaeobotany and Palynology*, **68**, 29–36.

Mai, D.H. (1995) *Tertiäre Vegetationsgeschichte Europas.* Fischer, Jena.

Mai, D.H. (1998) Contribution to the flora of the middle Oligocene Calau Beds in Brandenburg, Germany. *Review of Palaeobotany and Palynology*, **101**, 43–70.

Martín-Closas, C., Wójcicki, J.J. & Fonollá, L. (2006) Fossil charophytes and hydrophytic angiosperms as indicators of lacustrine trophic change. A case study in the Miocene of Catalonia (Spain). *Cryptogamie Algologie*, **27**, 357–379.

Martínez Atienza, F. & Morla, C. (1992) Aproximación a la paleocorología holocena de *Fagus* en la Península Ibérica a través de datos paleopolínicos. *Investigaciones Agrarias (Fuera de Serie)*, **1**, 135–145.

Menéndez Amor, J. (1955) La Depresión Ceretana Española y sus vegetales fósiles. Característica fitopaleontológica del Neógeno de la Cerdaña Española. *Memorias Real Academia de Ciencias Exactas, Físicas y Naturales de Madrid, Serie Ciencias Naturales*, **28**, 1–344.

Menéndez Amor, J. (1975) Análisis paleobotánico de algunas muestras de lignitos procedentes de Puentes de García Rodríguez (La Coruña). *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)*, **73**, 121–124.

Menéndez Amor, J. & Florschütz, F. (1959) Algunas noticias sobre el ambiente en el que vivió el hombre durante el gran interglaciar en dos zonas de ambas Castillas. *Estudios Geológicos*, **15**, 277–283.

Miller, K.G., Wright, J.D. & Fairbanks, R.G. (1991) Unlocking the ice house: Oligocene–Miocene oxygen isotopes, eustasy, and margin erosion. *Journal of Geophysical Research*, **96B4**, 6829–6848.

Mosbrugger, V., Utescher, T. & Dilcher, D. (2005) Cenozoic continental climatic evolution of Central Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 14964–14969.

Nagy, E. (1985) Sporomorphs of the Neogene in Hungary. *Geologica Hungarica, Series Palaeontologica*, **47**, 1–234.

Pais, J. (1981) *Contribuição para o conhecimento da vegetação Miocénica da parte ocidental da Bacia do Tejo.* PhD Thesis, Universidade Nova de Lisboa, Lisbon.

Pais, J. (1986) Évolution de la végétation et du climat pendant le Miocène au Portugal. *Ciências da Terra (UNL)*, **8**, 179–191.

Palamarev, E. (1989) Paleobotanical evidences of the Tertiary history and origin of the Mediterranean sclerophyll dendroflora. *Plant Systematics and Evolution*, **162**, 93–107.

Pantaleón-Cano, J., Yll, E.I., Pérez Obiol, R. & Roure, J.M. (2003) Palynological evidence for vegetational history in semi-arid areas of the western Mediterranean (Almería, Spain). *The Holocene*, **13**, 109–119.

Paul, H.A., Zachos, J.C., Flower, B.P. & Tripati, A. (2000) Orbitally induced climate and geochemical variability across the Oligocene/Miocene boundary. *Paleoceanography*, **15**, 471–485.

Pillans, B. (2004) Proposal to redefine the Quaternary. *Episodes*, **27**, 127.

de Porta, J., Kedves, M., Solé de Porta, N. & Civis, J. (1985) Palinología del Maastrichtiense del Barranco de la Posa (Lérida, España). Problemática regional. *Revista d'Investigacions Geologiques*, **40**, 5–28.

Postigo Mijarra, J.M., Barrón, E. & Morla, C. (2003) Inflorescences of the subclass Commelinidae (Liliatae, Magnoliophyta) in the Neogene of the Iberian Peninsula. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **4**, 229–243.

Postigo Mijarra, J.M., Burjachs, F., Gómez Manzaneque, F. & Morla Juaristi, C. (2007) A palaeoecological interpretation of the lower–middle Pleistocene Cal Guardiola site (Terrassa, Barcelona, NE Spain) from the comparative study of wood and pollen samples. *Review of Palaeobotany and Palynology*, **146**, 247–264.

Postigo Mijarra, J.M., Gómez Manzaneque, F. & Morla Juaristi, C. (2008) Survival and long-term maintenance of Tertiary trees in the Iberian Peninsula during the Pleistocene: first record of *Aesculus* L. (Hippocastanaceae) in Spain. *Vegetation, History and Archaeobotany*, **17**, 351–364.

Prothero, D.R. (1994) The late Eocene–Oligocene extinctions. *Annual Review of Earth and Planetary Sciences*, **22**, 145–165.

Ravazzi, C. (2002) Late Quaternary history of spruce in southern Europe. *Review of Palaeobotany and Palynology*, **120**, 131–171.

Ravazzi, C. & Rossignol, M. (1995) Vegetation change in a climatic cycle of Early Pleistocene age in the Leffe Basin (northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **117**, 105–122.

Ravazzi, C., Donegana, M., Vescovi, E., Arpenti, E., Caccianiga, M., Kaltenrieder, P., Londeix, L., Marabini, S., Mariani, S., Pini, R., Battista, G. & Wick, L. (2006) A new Late-glacial site with *Picea abies* in the northern Apennine foothills: an exception to the model of glacial refugia of trees. *Vegetation, History and Archaeobotany*, **15**, 357–371.

Raymo, M.E., Oppo, D.W., Flower, B.P., Hodell, D.A., McManus, J.F., Venz, K.A., Kleiven, K.F. & McIntyre, K. (2004) Stability of North Atlantic water masses in face of pronounced climate variability during the Pleistocene. *Paleoceanography*, **19**, PA2008, doi:10.1029/2003PA000921.

Rivas Carballo, M.R. (1991a) The development of vegetation and climate during the Miocene in the southeastern sector of the Duero Basin (Spain). *Review of Palaeobotany and Palynology*, **67**, 341–351.

Rivas Carballo, M.R. (1991b) La vegetación y el clima durante el Mioceno (Aragoniense superior-Vallesiense) en el sector suroriental de la depresión del Duero (España). *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)*, **86**, 53–64.

Rivas Carballo, M.R. & Valle, M.F. (1987) Palinología de la cuenca del Duero Peñafiel (Valladolid). *Actas de Palinología (Actas del VI Simposio de Palinología, A.P.L.E.)* (ed. by J. Civis Llovera and M.F. Valle Hernández), pp. 345–350. Universidad de Salamanca, Salamanca.

Rivas Carballo, M.R. & Valle, M.F. (2005) Polen y dinoflagelados del límite Tortoniense/Messiniense del sondeo de testigo continuo 'Huelva' (Cuenca el Guadalquivir, España). Interpretación paleoambiental. *Revista de la Sociedad Geológica de España*, **18**, 233–239.

Rivas Carballo, M.R., Alonso Gavilán, G., Valle, M.F. & Civis, J. (1994) Miocene palynology of the central sector of the Duero Basin in relation to palaeogeography and palaeoenvironment. *Review of Palaeobotany and Palynology*, **82**, 251–264.

Rodríguez-Sánchez, F. & Arroyo, J. (2008) Reconstructing the demise of Tethyan plants: climate-driven range dynamics of *Laurus* since the Pliocene. *Global Ecology and Biogeography*, **17**, 685–695.

Roiron, P. (1983) Nouvelle étude de la macroflore Plio-Pleistocène de Crespià (Catalogne, Espagne). *Geobios*, **16**, 687–715.

Roiron, P. (1992) *Flores, végétation et climats du Neogène Mediterranéen: apports de macroflores du Sud de la France et du Nord-Est de l'Espagne*. PhD Thesis, Université de Montpellier II, Montpellier.

Roiron, P., Ferrer, J., Lihan, E., Rubio, C., Bienvenido Díez, J., Popescu, S. & Suc, J.P. (1999) Les flores du bassin lacustre de Rubielos de Mora. Nouvelles donnés sur les conditions climatiques au Miocène Inferiéur dans le région de Teruel (Espagne). *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes*, **329**, 897–904.

Ruiz, B., Andrade, A., Dorado, M., Gil, M.J., Franco, F., López, P., Arnanz, A.M., López-Sáez, J.A., Macías, R. & Uzquiano, P. (1997) Paleobotánica: concepto y métodos. *El paisaje vegetal de la Comunidad de Madrid durante el Holoceno final* (ed. by P. López), pp. 61–93. Consejería de Eduacación y Cultura, Comunidad de Madrid, Madrid.

Sanz de Siria, A. (1985) Datos para el conocimiento de las floras Miocénicas de Cataluña. *Paleontología i Evolució*, **19**, 167–177.

Sanz de Siria, A. (1987) Datos para el conocimiento de las floras Pliocénicas de Cataluña. *Paleontología i Evolució*, **21**, 295–303.

Sanz de Siria, A. (1992) Estudio de la microflora Oligocena de las cercanías de Cervera (Colección Martí Madern del Museo de Geología de Barcelona). *Treballs del Museu de Geología de Barcelona*, **2**, 269–379.

Sanz de Siria, A. (1994) La evolución de las paleofloras en las cuencas Cenozoicas Catalanas. *Acta Geológica Hispánica*, **29**, 169–189.

de Saporta, G. (1863) Études sur la végétation du sud-est de la France à l'époque Tertiaire. *Annales des Sciences Naturelles, Partie Botanique*, Pt 1 Ser. 4, **19**, 5–124.

Schönenberger, J., Pedersen, K.R. & Friis, E.M. (2001) Normapolles flowers of fagalean affinities from the late Cretaceous of Portugal. *Plant Systematics and Evolution*, **226**, 205–230.

Sendra, J., De Renzi, M. & Fortea, F.A. (2000) La flora vascular marina del konservat fossil-lagerstätte del Plioceno Superior de Cuevas del Almanzora (Almería, España). *I Congreso Ibérico de Paleontología/XVI Jornadas de la Sociedad Española de Paleontología* (ed. by J.B. Díez and A.C. Balbino), pp. 142–144. Universidade de Evora, Portugal.

Singh, G. (1988) History of arid land vegetation and climate – a global perspective. *Biological Review*, **63**, 159–195.

de Sitter, L.U. (1961) La phase tectogénétique pyrénéenne dans les Pyrénées Meridionales. *Comptes Rendus de la Société Géologique de France*, **8**, 224–225.

Solé de Porta, N. & de Porta, J. (1977) Primeros datos palinológicos del Messiniense (= Turoliense) de Arenas del Rey (Provincia de Granada). *Stvdia Geologica Salmanticensia*, **13**, 67–88.

Stevenson, A.C. & Moore, P.D. (1988) Studies in the vegetational history of SW Spain IV. Palynological investigations of a valley mire at the El Acebrón, Huelva. *Journal of Biogeography*, **15**, 339–361.

Suc, J.P. (1980) *Contribution a la connaissance du Pliocène et du Pleistocène inferieur des régions mediterranéennes d'Europe occidentale par l'analyse palynologique des dêpots du Languedoc-Roussillon (Sud de la France) et de la Catalogne (nord-est de l'Espagne)*. PhD Thesis, Université de Montpellier II, Montpellier.

Suc, J.-P. (1989) Distribution latitudinale et étagement des associations végétales au Cénozoïque supérieur dans l'aire ouest-méditerranéenne. *Bulletin de la Société Géologique de France*, **8**, t.v 3, 541–550.

Suc, J.-P. & Cravatte, J. (1982) Etude palynologique du Pliocène de Catalogne (nord-est de l'Espagne). *Paléobiologie Continentale*, **13**, 1–31.

Suc, J.-P., Clauzon, G., Bessedik, M., Leroy, S., Zheng, Z., Drivaliari, A., Roiron, P., Ambert, P., Martinell, J., Domenech, R., Matías, I., Julià, R. & Anglada, R. (1992) Neogene and Lower Pleistocene in southern France and northeastern Spain, Mediterranean environments and climate. *Cahiers de Micropaléontologie*, **7**, 165–186.

Suc, J.-P., Diniz, F., Leroy, S., Poumot, Cl., Bertini, A., Dupont, L., Clet, M., Bessais, E., Zheng, Z., Fauquette, S. & Ferrier, J. (1995) Zanclean (~Brunssumian) to early Piacenzian (~early–middle Reuverian) climate from 4° to 54° north latitude (West Africa, West Europe and West Europe and West Mediterranean areas). *Mededelingen Rijks Geologische Dienst*, **52**, 43–56.

Svenning, J.C. (2003) Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters*, **6**, 646–653.

Tiedemann, R., Sarnthein, M. & Shackleton, N.J. (1994) Astronomic timescale for the Pliocene Atlantic $\delta^{18}O$ and dust flux records of Ocean Drilling Program Site 659. *Paleoceanography*, **9**, 619–638.

Tzedakis, P.C., Hooghiemstra, H. & Pälike, H. (2006) The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. *Quaternary Science Reviews*, **25**, 3416–3430.

Urban, B., Arias, C., Bigazzi, G. & Bonadona, F.P. (1983) Early Pleistocene palynostratigraphy of Fornace Tini, Valle Ricca (central Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **41**, 153–164.

Utescher, T. & Mosbrugger, V. (2007) Eocene vegetation patterns reconstructed from plant diversity – a global perspective. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **247**, 243–271.

Utescher, T., Erdei, B., François, L. & Mosbrugger, V. (2007) Tree diversity in the Miocene forests of western Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **253**, 226–250.

Uzquiano, P. (1995) La disparition de *Picea* à la fin du Pléistocéne supérieur en región cantabrique d'aprés l'anthracoanalyse: déterminisme climatique et anthropique. *Comptes Rendus de l'Academie des Sciences de Paris*, **321**, 545–551.

Valle, M.F. (1982) *Estudio palinológico del Plioceno del NE de España*. PhD Thesis, Universidad de Salamanca, Salamanca.

Valle, M.F. (1983) Nuevas aportaciones palinológicas al Plioceno de Can Albareda (Barcelona). *Stvdia Geologica Salmanticensia*, **19**, 151–159.

Valle, M.F. & Civis, J. (1978) Investigaciones palinológicas en el Plioceno inferior de Can Albareda (Barcelona). *Palinología, número extraordinario*, **1**, 463–468.

Valle, M.F. & Peñalba, C. (1987) Aspectos palinológicos en el Neógeno del Suroeste de España. *Paleontología del Neógeno de Huelva (W. Cuenca del Guadalquivir)* (ed. by Departamento de Paleontología de la Universidad de Salamanca)pp. 153–158. Universidad de Salamanca, Salamanca.

Valle, M.F. & Rivas Carballo, M.R. (1990) Palinología del tránsito Tortoniense/Messiniense en las facies neógenas del borde norte de la Cuenca del Guadalquivir (E. de Sevilla). *Polen, esporas y sus aplicacio* (ed. by G. Blanca, C. Díaz de la Guardia, M.C. Fernández, M.I. Rodríguez-García and A.T. Romero García), pp. 453–457. APLE Universidad de Granada, Granada.

Valle, M.F. & Salvador de Luna, J.V. (1985a) Resultados palinológicos en el borde sur-occidental de la Cuenca del Duero. Abezames (Zamora). *Estudios Geológicos*, **41**, 69–75.

Valle, M.F. & Salvador de Luna, J.V. (1985b) Palinología del Neógeno de la Cuenca del Duero. Castrillo del Val (Burgos). *Estudios Geológicos*, **41**, 237–241.

Valle, M.F., Rivas Carballo, M.R. & Alonso Gavilán, G. (2006) Síntesis de la vegetación y clima durante el Mioceno en la Cuenca del Duero. *Geo-Temas*, **9**, 213–217.

Van Campo, E. (1989) Flore pollinique du Miocene Supérieur de Venta del Moro (Espagne). *Acta Palynologica*, **1**, 9–32.

Van der Hammen, T., Wijmstra, T.A. & Zagwijn, W.H. (1971) The floral record of the late Cenozoic of Europe. *The Late Cenozoic glacial ages* (ed. by K.K. Turekian), pp. 392–424. Yale University Press, New Haven.

Vicente i Castells, J. (2002) Estudi morfològic de la flora Cretàcica d'Isona (Pallars Jussá). *Institut d'Estudis de la*

Natura del Barcelonès Nord, Societat d'Història Natural, Sèrie monogràfica, núm. **2**, 1–223.

de Villalta, J.F. & Vicente, J. (1972) Una flora del Cuaternario antiguo en las cercanías de Crespià. *Acta Geológica Hispánica*, **7**, 120–128.

Williams, D.F., Peck, J., Karabanov, E.B., Prokopenko, A.A., Kravchinska, V., King, J. & Kuzmin, M.I. (1997) Lake Baikal record of continental climate response to orbital insolation during the past 5 million years. *Science*, **278**, 1114–1117.

Wolfe, J.A. (1978) A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist*, **66**, 694–703.

Wolfe, J.A. (1992) Climatic, floristic and vegetational changes near the Eocene/Oligocene boundary in North America. *Eocene–Oligocene climatic and biotic evolution* (ed. by D.R. Prothero and W.A. Berggren), pp. 421–436. Princeton University Press, Princeton.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science*, **292**, 686–693.

Zagwin, W.H. (1960) Aspects of the Pliocene and Early Pleistocene vegetation in the Netherlands. *Mededelingen van de Geologische Stichting, Ser. C,* **III**, 1–78.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Taxa included in Figure 4 and documents in which they are recorded.

BIOSKETCHES

José M. Postigo Mijarra has research interests in Neogene vegetation dynamics and environmental change. He has a particular interest in the Quaternary dynamics of species distributions. His current work focuses on the flora and vegetation of Pleistocene landscapes in the Iberian Peninsula.

Eduardo Barrón is a palaeobotanist and is interested in systematics, palaeoecology, palaeobiogeography and biostratigraphy.

Fernando Gómez Manzaneque is a lecturer in botany and geobotany whose research interests include Cenozoic palaeoecology, forest biogeography and Iberian flora.

Carlos Morla Juaristi is a lecturer in botany and geobotany whose research interests include the biogeography of the Iberian Peninsula, palaeobotany and the palaeoecology of the Late Quaternary of the western Mediterranean.