



Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data

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ABSTRACT

Pollen analysis of Miocene and Pliocene sediments from the Iberian Peninsula shows a progressive reduction in plant diversity through time caused by the disappearance of thermophilous and high-water requirement plants. In addition, an increase in warm-temperate (mesothermic), seasonal-adapted “Mediterranean” taxa, high-elevation conifers and herbs (mainly *Artemisia*) occurred during the Middle and Late Miocene and Pliocene. This has mainly been interpreted as a response of the vegetation to global and regional processes, including climate cooling related to the development of the East Antarctic Ice Sheet and then the onset of the Arctic Ice Sheet, uplift of regional mountains related to the Alpine uplift and the progressive movement of Eurasia towards northern latitudes as a result of the northwards subduction of Africa. The development of steppe-like vegetation in southern Iberia is ancient and probably started during the Oligocene. The onset of a contrasted seasonality in temperature during the Mid-Pliocene superimposed on the pre-existing seasonality in precipitation, the annual length of which increased southward. The Mediterranean climatic rhythm (summer drought) began about 3.4 Ma and caused the individualization of modern Mediterranean ecosystems. Quaternary-type Mediterranean climatic fluctuations started at 2.6 Ma (Gelasian) resulting in repeated steppe vs. forest alternations. A latitudinal climatic gradient between the southern and the northern parts of the Iberian Peninsula existed since the Middle Miocene.

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1. Introduction

The Miocene and Pliocene, from 23.03 to 2.558 Ma, is a crucial time-interval, as the climate of the mid-latitude regions evolved from warm conditions during the Miocene to a cooler Pleistocene, i.e. from a greenhouse to an icehouse world. The geographical position of the Iberian Peninsula, between Africa and Eurasia and between Mediterranean and temperate climates, makes this region of great interest for paleobotanic and paleobiogeographic studies. Mainly because of their southern geographical situation, these areas served as a refuge for mostly thermophilous plants that otherwise would have vanished from Eurasia during the Pleistocene glaciations, and today the southern part of the Iberian Peninsula contains Miocene, Pliocene and Pleistocene relics in their present-day flora (Quézel and Médail, 2003; Thompson, 2005). Alpine tectonics was active during the Neogene, producing uplift of the Pyrenees and Betics and the closure of the Betic and Rifian corridors during the Tortonian and Messinian, respectively, which caused the desiccation of the Mediterranean Sea (Messinian Salinity Crisis). Then, important paleogeographical changes also occurred (see below; Rögl, 1998; Meulenkamp and Sissingh, 2003) that may have contributed to the pattern of the modern vegetation.

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In the last 30 years an intensive effort has been done in order to reconstruct the vegetation and climate of the Iberian Peninsula during the Miocene and Pliocene and extensive pollen studies, using a botanical approach, contributed to achieve this target (Bessedik, 1984; Diniz, 1984a,b; Suc, 1984; Bessedik, 1985; Suc et al., 1992, 1995a,b; Fauquette et al., 1998a, 1999; Jiménez-Moreno, 2005; Fauquette et al., 2006; Agustí et al., 2006; Fauquette et al., 2007; Jiménez-Moreno and Suc, 2007; Jiménez-Moreno et al., 2007a,b).

In this paper, we present a synthesis of pollen data, allowing the vegetation reconstruction and the calculation of climatic parameters for the Iberian Peninsula during the Miocene and Pliocene (Figs. 1 and 2). The deduced temporal climatic variations will be discussed within the frame of latitudinal gradients during the Miocene and Pliocene.

2. Methods for vegetation and climate reconstruction

Pollen identification was accomplished at the finest possible taxonomic level by comparing the Neogene pollen grains with their present-day relatives using modern pollen collections, (un)published pollen atlases and pollen databases. Percentages of pollen taxa were calculated on the total sum of the pollen grains, standard synthetic diagrams (Suc, 1984) were constructed (Fig. 2). In these pollen diagrams, taxa have been arranged into 12 different groups based on



Fig. 1. Geographic position of the considered pollen localities. (1) Rio Maior F16; (2) Carmona; (3) Andalucía G1; (4) Alborán A1; (5) Andalucía A1; (6) Gor; (7) Rubielos de Mora; (8) Tarragona E2; (9) Orera; (10) Zaratán; (11) Garraf 1; (12) Sant Pau d'Ordal; (13) La Rierussa; (14) Sanabastre and Sampsor; (15) Can Vilella and (16) Caranceja.

ecological requirements (mainly the thermic ones such as mean annual temperature) of their living nearest representatives (most often at the genus level), with respect to the Nix's (1982) classification: megathermic plants (living in areas with a tropical climate); mega-mesothermic plants (living in areas with a subtropical climate); *Cathaya*, an altitudinal conifer living today in the subtropical zone of China; mesothermic plants (living in areas with a warm-temperate climate); meso-microthermic plants (living in areas with a cool-temperate climate); microthermic plants (living in areas with a cold climate); non-significant elements; Cupressaceae, which may inhabit most of these climatic zones, the pollen of which is impossible to be identified at the genus level; Mediterranean xerophytes (living in areas with a summer drought); herbs and shrubs where plants of various significance are grouped. Such synthetic pollen diagrams provide a macro-visualization of the main changes in the vegetation (see Fig. 2) and allow an easier comparison with reference oxygen isotope curves. This method has been proven to be a very efficient tool for high-resolution land climate reconstructions; for example, characterizing warm-cool alternations related to Milankovitch cycles for both the Miocene (Jiménez-Moreno et al., 2005, 2007b) and the Pliocene (Popescu, 2001, 2006; Popescu et al., 2006a,b).

The climate was quantified using the 'Climatic Amplitude Method' developed by Fauquette et al. (1998a,b), which is able to reconstruct the climate of periods for that no analogue exists in the modern pollen floras. This transfer function was applied to all the selected pollen sequences in order to produce comparable and homogenous climate results (Figs. 3–5). Southern European Neogene pollen floras contain a mixture of temperate, warm-temperate and subtropical plants (even some tropical plants during the Miocene), which live today in different and distant parts of the world.

The past climate is estimated by transposing the climatic requirements of the maximum number of modern taxa to the fossil data. This approach relies on the relationship between the relative

pollen abundance of each individual taxon and the corresponding present-day climate. Presence/absence limits, as well as abundance thresholds, have been defined for 60 taxa from modern pollen floras and the literature. This method takes into account not only the presence/absence criterion but also pollen percentages to provide more reliable reconstruction. Low abundances of some megathermic and mega-mesothermic taxa (e.g. *Microtropis fallax*, *Avicennia*) are meaningful and should be taken into account, as pollen grains of these plants are generally under-represented because they suffer some disadvantage in the transport. Conversely, low abundances of wind-pollinated taxa (e.g. *Quercus*, *Alnus*, *Corylus*) might reflect long-distance transport of these high pollen producers by air and then water. In this case, very low pollen percentages could have a weak significance. With this method, the most probable climate for a past pollen assemblage is estimated as the climatic interval in which the highest number of taxa can exist.

The climatic estimate is presented as an interval and as a 'most-likely value', which corresponds to a mean that is weighted according to the size of the climatic intervals of all taxa exceeding their presence/absence and/or abundance thresholds. As the precision of the information obtained from a taxon's climatic interval is inversely related to the breadth of this interval, the weights are greater for taxa with smaller intervals. In this paper, we present reconstructions of two climatic parameters estimated from the pollen data: mean annual temperature (T_a) and mean annual precipitation (P_a). High-latitude/altitude trees were excluded from the reconstruction process. Selection of the trees to be classified as high-latitude/altitude and then exclusion of the quantification process results from numerous pollen studies (e.g. Suc et al., 1995a,b, 1999; Jiménez-Moreno, 2005) that show the Neogene vegetation zonation to follow a similar latitudinal and altitudinal zonation to that observed in present-day Southeastern China (Wang, 1961), where most of the thermophilous taxa that disappeared from Europe during the Neogene are found today. The estimates obtained,

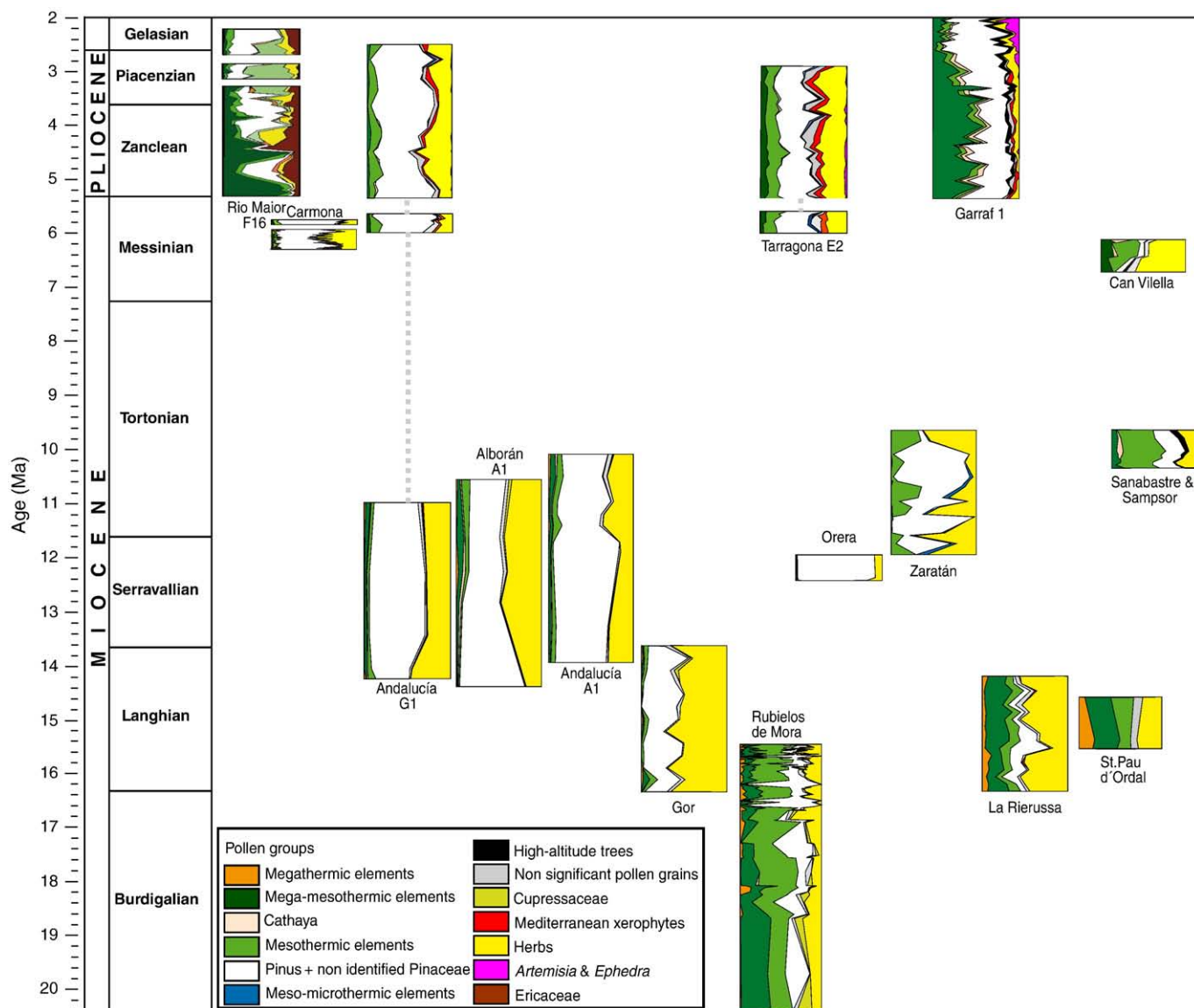


Fig. 2. Synthetic pollen diagrams of selected sections. Taxa have been grouped according to their ecological significance as follows: (1) Megathermic (i.e. tropical) elements (*Avicennia*, *Amanoa*, *Alchornea*, *Fothergilla*, *Exbucklandia*, Euphorbiaceae, Sapindaceae, Loranthaceae, Arecaceae, Acanthaceae, Passifloraceae, Rutaceae, *Mussaenda* type, *Acacia*, *Sindora*, *Croton*, *Bombax*, *Buxus bahamensis* type, *Mappianthus*, Rubiaceae, *Phyllanthus* type, Melastomataceae, Simarubaceae). (2) Mega-mesothermic (i.e. subtropical) elements (*Taxodiaceae*, *Engelhardia*, *Platycarya*, Sapotaceae, *Microtropis fallax*, *Symplocos*, *Rhoiptelea*, *Distylium*, *Embolanthera*, *Hamamelis*, *Rhodoleia*, *Corylopsis*, Hamamelidaceae, Loranthaceae, Celastraceae, *Leea*, *Aesculus*, *Cyrillaceae–Clethraceae*, Araliaceae, *Nyssa* and *Liriodendron*). (3) *Cathaya*, an altitudinal conifer living today in Southern China. (4) Mesothermic (i.e. warm-temperate) elements (deciduous *Quercus*, *Carya*, *Pterocarya*, *Carpinus*, *Juglans*, *Celtis*, *Zelkova*, *Ulmus*, *Tilia*, *Acer*, *Parrotia* cf. *persica*, *Liquidambar*, *Alnus*, *Salix*, *Populus*, *Fraxinus*, *Buxus sempervirens* type, *Betula*, *Fagus*, *Ostrya*, *Hedera*, *Lonicera*, *Elaeagnus*, *Ilex*, *Tilia*, *Parrotiopsis jacquemontiana*, *Restionaceae* and *Castanea–Castanopsis*). (5) *Pinus* and poorly preserved Pinaceae pollen grains. (6) Meso-microthermic (i.e. mid-altitude) trees (*Tsuga*, *Cedrus* and *Sciadopitys*). (7) Microthermic (i.e. high-altitude) trees (*Abies*, *Picea*). (8) Non-significant pollen grains (undetermined, poorly preserved pollen grains and some cosmopolitan or widely distributed elements such as Rosaceae and Ranunculaceae). (9) Cupressaceae. (10) Mediterranean xerophytes (*Quercus ilex-coccifera* type, *Olea*, *Phillyrea*, *Pistacia*, *Ceratonia*, *Nerium*, *Ziziphus* and *Cistus*). (11) Herbs and shrubs (Poaceae, *Erodium*, *Geranium*, *Convolvulus*, Asteraceae Asteroideae, Asteraceae Cichorioideae, Lamiaceae, *Plantago*, *Euphorbia*, Brassicaceae, Apiaceae, *Knautia*, *Helianthemum*, *Rumex*, *Polygonum*, *Asphodelus*, Campanulaceae, Ericaceae, Amaranthaceae–Chenopodiaceae, Caryophyllaceae, Plumbaginaceae, Cyperaceae, Potamogeton, *Sparganium–Typha* and Nymphaeaceae) including some subdesertic elements (*Lygeum*, *Neurada*, *Nitraria*, *Calligonum*, *Prosopis*, Agavaceae). (12) Steppe elements (*Artemisia* and *Ephedra*).

therefore, correspond to the climate at low- to middle-low-altitude (Fauquette et al., 1998a). *Pinus* and non-identified Pinaceae (due to poor preservation of these bisaccate pollen grains) have been excluded from the pollen sum of the fossil pollen spectra (Fauquette et al., 1998a, 1999). Pollen grains of these taxa are often over-represented in the sediments because of their high-production and/or overabundance in air and (fluvial and marine) water transport (Heusser, 1988; Cambon et al., 1997; Beaudouin et al., 2007).

The sedimentary sequences have been dated using foraminifera, calcareous nannoplankton, magnetostratigraphy or mammals (Table 1). Although none of the pollen successions covers the entire Miocene–Pliocene time-interval (Fig. 2), they provide a discontinuous

but reliable record of vegetation and climate changes in time and space in the Iberian Peninsula.

3. Neogene flora and vegetation

3.1. Plant diversity

Even if some parts of the Iberian Peninsula are characterized today by a very diverse flora and are main refuge areas of thermophilous plants (Quézel and Médail, 2003), a richer and more diverse flora (at the family and genus level) has been identified for the Miocene and Pliocene that consisted of plants today growing in different

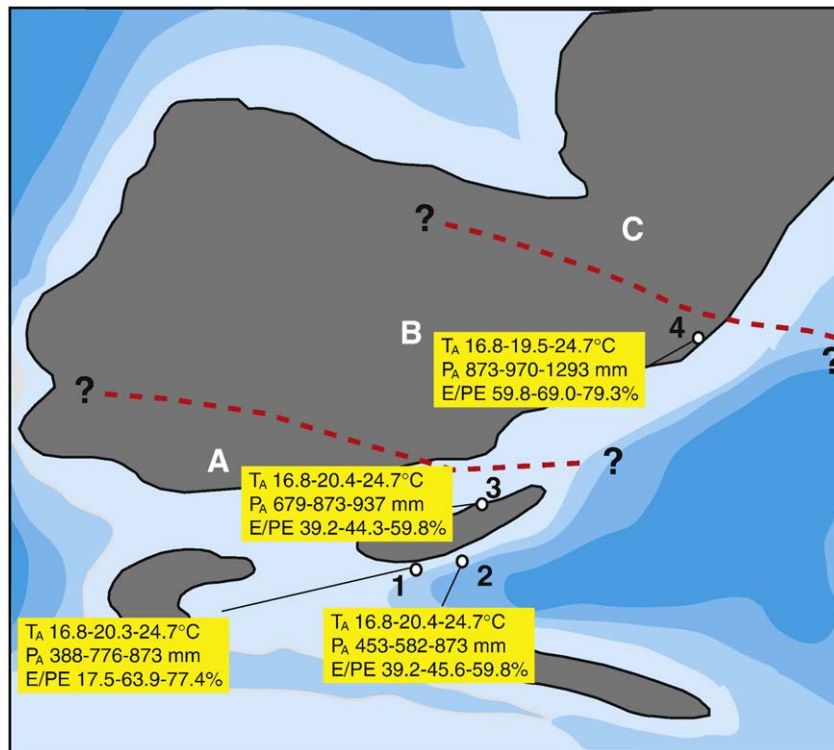


Fig. 3. Location of selected studied sites covering the Middle Miocene in the Iberian Peninsula and their climatic estimates in the palaeogeographical framework of the early Serravallian (from Rögl, 1998). Pollen localities (Jiménez-Moreno, 2005): (1) Andalucía G1; (2) Alborán A1; (3) Gor and (4) La Rierussa. Two rough vegetational domains can be recognized in the Iberian Peninsula at that time (A and B). Modified from Jiménez-Moreno and Suc (2007). Note that today's mean annual temperature (T_A) for Málaga (next to Andalucía G1 and Alborán A1) is 17.5 °C; for Gor is ca. 14 °C and for La Rierussa ca. 16 °C. Mean annual precipitation (P_A) for Málaga is ca. 600 mm; for Gor ca. 450 mm and for La Rierussa ca. 550 mm.

geographic areas (the most significant of them are pointed out in bold characters):

- (1) Tropical and subtropical Africa, America and Asia (*Avicennia*, *Bombax*, Caesalpiniaceae, Euphorbiaceae, *Engelhardia*, *Platycarya*, Rubiaceae, Rutaceae, *Symplocos*, Taxodiaceae, Hamamelidaceae, *Myrica*, Sapotaceae and Vitaceae);
- (2) Warm-temperate latitudes of the Northern Hemisphere (*Acer*, *Alnus*, *Betula*, Cupressaceae, *Fagus*, *Populus*, deciduous *Quercus* and *Salix*);
- (3) Mediterranean region (*Olea*, *Phillyrea*, *Ceratonia*, evergreen *Quercus*).

3.2. Vegetation organization

The vegetation was characterized by a complex mosaic due to its dependency on several factors (water availability, characteristics of the soils, orientation of relief slopes, etc.) that were superimposed to a latitudinal–altitudinal organization. The most important factor, as of today, was the latitude, controlling both temperature and precipitation. In addition, the vegetation was organized in altitudinal belts, and if we compare the Neogene vegetation reconstructed in this area with the one growing today in subtropical to temperate Southeastern China (Wang, 1961), the most reliable present-day model (Suc, 1984; Axelrod et al., 1996; Jiménez-Moreno, 2005; Jiménez-Moreno et al., 2005; Jiménez-Moreno, 2006; Jiménez-Moreno et al., 2007a,b), the following plant environments can be distinguished:

- (1) a coastal marine environment, characterized by the presence of an impoverished mangrove composed of *Avicennia* and halophytes (such as Amaranthaceae–Chenopodiaceae, *Armeria* and *Tamarix*);
- (2) An open vegetation with subdesertic plants such as *Nitraria*, *Neurada*, *Ephedra*, *Convolvulus*, *Lygeum*, *Prosopis*, Caesalpinia-

- ceae and *Acacia*, which are representative of a steppe or a wood–shrub vegetation at low altitude. Similar modern assemblages are present on the Red Sea coasts, on the shorelines of the Arabian Peninsula, and in North Africa (Quézel, 1965; Quézel and Médail, 2003);
- (3) a broad-leaved evergreen forest, from the coastal plains to about 700 m in altitude, mainly made up of *Taxodium* or *Glyptostrobus*, *Myrica*, *Rhus*, Theaceae, Cyrillaceae–Clethraceae, *Bombax*, Euphorbiaceae, *Distylium*, *Castanopsis*, Sapotaceae, Rutaceae, Rubiaceae, *Mussaenda*, *Ilex*, *Hedera*, *Ligustrum*, *Jasminum*, Hamamelidaceae, *Engelhardia* and *Rhoiptelea*;
- (4) an evergreen and deciduous mixed forest, above 700 m altitude, characterized by deciduous *Quercus*, *Engelhardia*, *Platycarya*, *Carya*, *Pterocarya*, *Fagus*, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis*, *Acer*, etc. Within this vegetation belt, a riparian vegetation has been identified, composed of *Salix*, *Alnus*, *Carya*, *Zelkova*, *Ulmus*, *Liquidambar*, etc. The shrub level was dominated by Ericaceae, *Ilex*, Caprifoliaceae, etc.;
- (5) above 1000 m, a mid-altitude deciduous and coniferous mixed forest with *Betula*, *Fagus*, *Cathaya*, *Cedrus* and *Tsuga*;
- (6) above 1800 m in altitude, a coniferous forest with *Abies* and *Picea*.

3.3. What is the origin of the modern southern Iberian steppes?

Pollen data from southern Iberia point out that an open vegetation inhabited the region since the earliest Miocene: indeed, southward the region of Tarragona, herbs represent at least 70–80% of the pollen flora (*Pinus* excluded) in all the studied localities (Fig. 2) illustrating a steppe-like vegetation context, except for Rubielos de Mora, which displays a local riparian forest isolated within the regional steppic feature (Fig. 2). Reliability of such an open palaeovegetation landscape is also supported by the recently demonstrated under-representation of herbs with respect to trees in the pollen floras (Favre et al., 2008).

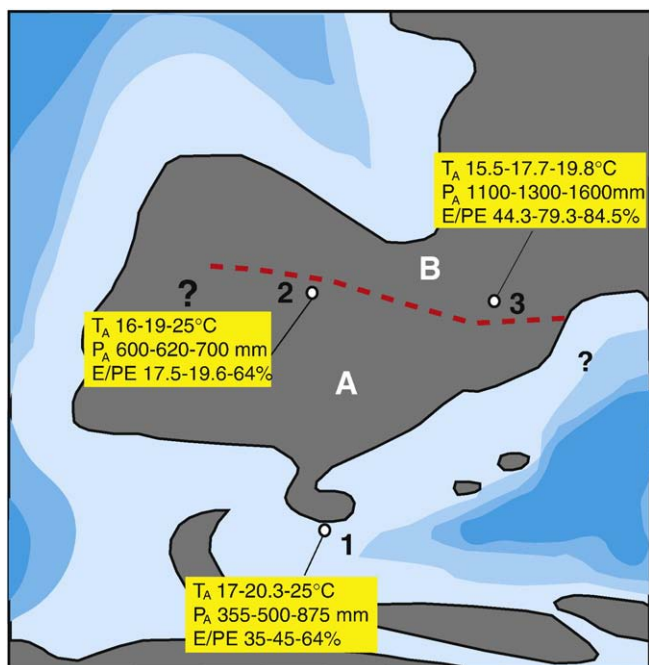


Fig. 4. Location of selected studied sites covering the Tortonian around 10 Ma in the Iberian Peninsula and their climatic estimates in the palaeogeographical framework of the Late Tortonian (Paramonova et al., 2004). Pollen localities: (1) Andalucía A1, (2) Zaratán (Rivas-Carballo et al., 1994), (3) Sanabastre and Sampsor sites in Cerdanya (Bessedik, 1985). Note that today's mean annual temperature (T_A) for Roquetas de Mar (next to Andalucía A1) is 18 °C; for Valladolid (next to Zaratán) is ca. 13 °C and for Cerdanya ca. 9 °C. Mean annual precipitation (P_A) for Roquetas de Mar is ca. 250 mm; for Valladolid ca. 450 mm and for Cerdanya ca. 700 mm.

An aspect of this organization of the vegetation needs some comments. The present-day southern Iberia steppe vegetation has been often considered to have an anthropic origin, i.e. to be very recent. The evidence of the ancient status of this open vegetation structure, introduced some interrogation within the phytogeographic conviction about this modern steppe (see Quézel and Médail, 2003: p. 95): which part is to be allocated to primitive steppes and to the recent anthropozoogenic activities, respectively? Our results, documenting a large development of “warm steppes” in southeastern Iberia, already in the earliest Miocene, are a serious argument (considering also their continuity throughout the Pliocene) supporting the importance of the primitive steppes with respect to their modern distribution. An open vegetation structure composed of herbs and shrubs adapted to dry and warm conditions existed in the southernmost Europe and Northern Africa during the earliest Miocene and probably during the Oligocene, probably being an indicator of the onset of the development of the Sahara Desert (Swezey, 2009). The plants that contributed to such open vegetation changed through time up to its present-day constitution, being still dominated by the subdesertic taxa.

4. Vegetation dynamics

4.1. Burdigalian–Langhian

The regular occurrence and abundance of thermophilous species typical of the lowest altitudinal belts described above and the relative scarcity of altitudinal elements (Fig. 2) characterized the vegetation in the Iberian Peninsula at this time.

The southern part of the Iberian Peninsula (localities: Andalucía G1, Alborán A1, Andalucía A1, Gor; Figs. 2 and 3) was characterized by vegetation dominated by herbs (mostly Poaceae) and shrubs, which were probably under-represented in the pollen records (Favre et al., 2008). A mangrove with *Avicennia* and saline bearing elements such

as Amaranthaceae–Chenopodiaceae, *Ephedra*, Plumbaginaceae, Caryophyllaceae, *Plantago* and *Tamarix*, inhabited coastal environments. Today, this kind of impoverished mangrove represents the northernmost limit of mangroves and occurs under arid or semi-arid conditions as in the Red Sea and Persian Gulf (White, 1983; Audru et al., 1987). Pollen spectra are also characterized by the abundance of subdesertic elements, such as *Nitraria*, *Lygeum*, *Prosopis*, *Neurada*, and *Calligonum* indicating very dry and warm conditions, as these taxa are found today in North Africa under hyper-arid conditions (Saharan elements, with *Neurada* and *Calligonum* indicating dunes). Thermophilous (i.e. megathermic and mega-mesothermic) plants such as *Taxodium*-type, *Engelhardia*, Sapotaceae, *Myrica*, *Alchornea*, *Mussaenda* type, Melastomataceae, Rutaceae, *Avicennia* and *Sindora*; and mesothermic plants, such as *Quercus* deciduous-type, *Carya* and *Zelkova*, also contribute to such a pollen assemblage. *Cathaya*, a gymnosperm today restricted to some subtropical mid-altitude forests of Southeastern China, is also present but generally in very low percentages. Mid-altitude (*Cedrus*, *Tsuga*) and high-altitude (*Abies*, *Picea*) conifers appear only occasionally. The vegetation, according to the high percentage of herbs in the pollen spectra, was typical of an open environment. Percentages of the remaining groups are very low. The mesothermic trees were probably restricted to mid- or high-altitude environments.

Vegetation in the northeastern part of the Iberian Peninsula (Rubieler de Mora, La Rierussa and Sant Pau d'Ordal sections; Figs. 2 and 3) was also characterized by the high-abundance of herbs and shrubs, with Poaceae, Asteraceae, and halophytes such as Amaranthaceae–Chenopodiaceae and Plumbaginaceae (Jiménez-Moreno, 2005). Thermophilous elements (mostly *Taxodium*-type and *Engelhardia*) were abundant and *Avicennia* mangrove also populated the coastal area. However, many of the subdesertic elements identified in the southern part of the Iberian Peninsula were not present here and Caesalpiniaceae and *Acacia* are recorded in lower percentages. The rest of the assemblage is characterized by temperate elements

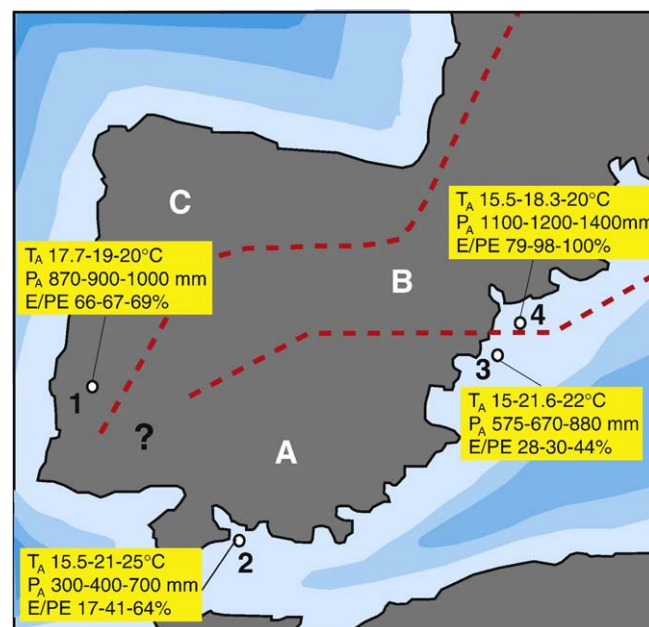


Fig. 5. Location of selected studied sites covering the Early Pliocene around 5.3–5 Ma in the Iberian Peninsula and their climatic estimates in their palaeogeographical framework (Clauzon et al., 1995; Clauzon, 1996; Jolivet et al., 2006). Pollen localities: (1) Rio Maior F16 (Diniz, 1984a,b), (2) Andalucía G1 (Suc et al., 1995a), (3) Tarragona E2 (Bessais and Cravatte, 1988) and (4) Garraf 1 (Suc and Cravatte, 1982). Note that today's mean annual temperature (T_A) for Rio Maior is ca. 16 °C; for Tarragona is ca. 15 °C and for Garraf is ca. 15 °C. Mean annual precipitation (P_A) for Rio Maior is ca. 950 mm and for Tarragona and Garraf is ca. 600 mm.

Table 1
Age control of the 16 considered pollen localities indicating the authors of the pollen analyses.

#	Section	Datation	Age	Pollen analysis by
1	Rio Maior F16	Fauquette et al. (1999)	Pliocene	Diniz (1984a)
2	Carmona	F.J. Sierro and W. Krijgsman (personal communications)	Messinian	J.-P. Suc, N. Feddi and J. Ferrier, unpublished
3	Andalucía G1	ELF (1984)	Langhian- Pliocene	Jiménez-Moreno, 2005; Jiménez-Moreno and Suc, 2007; Bessais (unpublished); Suc et al. (1995b)
4	Alborán A1	Chevron (1986)	Late Langhian–Early Tortonian	Jiménez-Moreno, 2005; Jiménez-Moreno and Suc, 2007
5	Andalucía A1	ELF, 1984; Rodríguez-Fernández et al., 1999	Late Langhian–Early Tortonian	Jiménez-Moreno, 2005; Jiménez-Moreno and Suc, 2007
6	Gor	Martín Pérez and Viseras (1994)	Langhian	Jiménez-Moreno, 2005; Jiménez-Moreno and Suc, 2007
7	Rubielos de Mora	Crusafont-Pairó et al., 1966; Bessais and Cravatte, 1988, 1974; Montoya et al., 1996; Jiménez-Moreno et al., 2007b	Option 1 of Jiménez-Moreno et al. (2007b) Aquitanian–Burdigalian	Jiménez-Moreno, 2005; Jiménez-Moreno et al., 2007a,b
8	Tarragona E2	Bessais and Cravatte (1988)	Late Messinian–Pliocene	Bessais and Cravatte (1988)
9	Orera	Abdul Aziz (2001, 1988)	Serravallian	Jiménez-Moreno (2005)
10	Zaratán	Rivas-Carballo et al. (1994)	Serravallian–Tortonian	Rivas-Carballo et al. (1994)
11	Garraf 1	Suc and Cravatte, 1982; Matias i Sendra, 1990; Suc and Zagwijn, 1983	Pliocene	Suc and Cravatte (1982)
12	La Rierussa	Magné (1978); C. Müller in Bessedik (1985)	Langhian	Bessedik, 1985; Jiménez-Moreno, 2005; Jiménez-Moreno and Suc, 2007
13	Sant Pau d' Ordal	Bessedik (1985)	Langhian	Bessedik (1985)
14	Can Vilella	Agustí et al. (2006)	Messinian	M.-J. Pérez Villa in Agustí et al. (2006)
15	Sanabastre and Sampsor	Agustí and Roca (1987)	Tortonian	Bessedik (1985)
16	Caranceja	Alcalde Olivares et al. (2004)	Late Pliocene	Alcalde Olivares et al. (2004)

(mainly *Carya*, *Zelkova* and *Buxus sempervirens* type). Mid- and high-altitude conifers are very scarce in these samples. This is in agreement with the pollen data of Bessedik (1985) for the same area (La Rierussa and Sant Pau d'Ordal sections). Such pollen spectra suggest scattered forests developing at low altitude along humid environments (rivers, lakes) or at mid-altitude, but in general, not as open as in southern Spain.

Pollen assemblages from the Iberian Peninsula denote the juxtaposition of greatly contrasted environments in the lowlands: a broad-leaved evergreen forest and a steppe or a wood–shrub vegetation. The presence of subdesertic taxa (*Nitraria*, *Lygeum*, *Prosopis*, *Neurada*, *Calligonum* and *Caesalpinaceae*), which grow conditioned by a long dry season, together with others showing very high water requirements (like *Engelhardia*, *Platycarya*, *Rubiaceae*, *Hamelidaceae*, *Taxodium*-type, *Nyssa*, *Sapotaceae* and *Myrica*), needing constant water, has two possible explanations. This could be due to the structure of the vegetation in altitudinal belts and the effect of humid cloud masses, which cling to the mountains at an altitude of ca. 400–500 m (Bessedik, 1984), similar to the Canary Islands today (Rivas-Martínez, 1987). Secondly, there may have been significant availability of water sources along rivers or around lakes, as has been interpreted as the cause of such a floral assemblage in the Rubielos de Mora lacustrine Basin (Jiménez-Moreno, 2005; Jiménez-Moreno et al., 2007a,b) and which frequently occurs in subtropical and tropical Africa, for instance around Lake Tanganyika. In both situations water availability clearly controls the vegetation and would compensate for the lack of precipitations in the summer time. Swamp forests were also well developed during this time period as *Taxodium* or *Glyptostrobus*, *Nyssa* and *Myrica* show comparatively high values in the pollen spectra as well as ecologically related riparian forests, with *Platanus*, *Liquidambar*, *Zelkova*, *Carya*, *Pterocarya* and *Salix*.

Areas at higher altitude were characterized by an evergreen and deciduous mixed forest mainly composed of mesothermic elements such as *Quercus*, *Carya*, *Pterocarya*, *Fagus*, *Ericaceae*, *Ilex*, *Caprifoliaceae*, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis*, *Acer*, and also *Engelhardia* and *Platycarya*. It should also be mentioned that conifer pollen, mainly *Pinus* and indeterminate *Pinaceae*, can be particularly abundant in marine sediments, presumably because of the capacity of bisaccate pollen for long-distance transport (Heusser, 1988; Suc and Drivaliari, 1991; Cambon et al., 1997; Beaudouin, 2003). *Cathaya*, a gymnosperm today restricted to some subtropical mid-altitude forests of South-eastern China, was also present but generally in very low percentages.

Other mid-altitude (*Cedrus* and *Tsuga*) and high-altitude (*Abies* and *Picea*) conifers were very scarce.

4.2. Serravallian

Important changes in the vegetation occurred gradually during this period of time: several megathermic elements (*Buxus bahamensis* group, *Bombax*, *Dodonaea*, *Croton* and *Meliaceae*), most of them typical from a broad-leaved evergreen forest, became rare and most of them disappeared from the Iberian Peninsula (Bessedik, 1985; Jiménez-Moreno, 2005). The evergreen–deciduous mixed forest suffered a great transformation due to the loss and decrease in the abundance of several thermophilous evergreen plants and the increase in deciduous mesothermic plants, such as deciduous *Quercus*, *Fagus*, *Alnus*, *Acer*, *Betula*, *Alnus*, *Carpinus*, *Ulmus*, *Zelkova* and *Tilia*. Thus, the vegetation showed a tendency towards increasing proportions of mesothermic deciduous elements coming from higher altitudes/latitudes. Even if the thermophilous elements decreased during this period, the swamp forest continued to be well developed. This palaeofloristic change occurred slowly and gradually without major fluctuations. A similar vegetation change is observed during the same time-interval in pollen records from other areas of Europe (e.g., southern France, Switzerland, Austria and Hungary: Bessedik, 1985; Jiménez-Moreno, 2005; Jiménez-Moreno et al., 2005; Jiménez-Moreno, 2006; Jiménez-Moreno et al., 2008).

Open vegetation seems to generally characterize the lowlands of the Iberian Peninsula at that time. However, the south (Andalucía G1, Alborán A1 and Andalucía A1 sections) featured higher amounts of subdesertic plants than the north, and the north (Orera section) featured higher amounts of montane indicators such as *Pinus*, *Cathaya*, *Tsuga* and *Sciadopitys*, indicating the proximity of a mountain range.

4.3. Tortonian

A reduction in thermophilous plants, and in plant diversity, continued in the Iberian Peninsula during the Tortonian. For example, *Avicennia*, which previously populated the coastal areas, also vanished, with a last appearance in Tortonian sediments from the southernmost part of Spain (cores Andalucía A1 and Alborán A1). At the same time, conifers from mid- (*Cathaya*, *Tsuga* and *Cedrus*) and high-altitude (*Picea* and *Abies*) belts strengthened.

The vegetation in the southern part of the Iberian Peninsula (localities: Andalucía G1, Alborán A1, Andalucía A1; Fig. 2 and 4) was

characterized by an open vegetation dominated by herbs and shrubs, with Poaceae as the most representative, but also saline bearing elements such as Amaranthaceae–Chenopodiaceae, *Ephedra*, Plumbaginaceae, Caryophyllaceae, *Plantago* and *Tamarix*. Subdesertic plants, such as *Nitraria*, *Lygeum*, *Prosopis*, *Neurada*, and *Calligonum* were also present in this area. However, pollen data also indicate the presence of forests on the surrounding uplands.

Forested environments characterized the northeastern part of the Iberian Peninsula (Sanabastre/Sampso sites in La Cerdanya; Bessedik, 1985), where arboreal pollen dominates with low values of herbaceous taxa. The pollen flora is characterized by the dominance of *Quercus*, *Fagus*, *Alnus* and conifers (*Cathaya*, *Pinus*, Taxodiaceae), reflecting the presence of mixed deciduous forests and swamp environments. *Abies*, a high-altitude conifer is also recorded. Only a few megathermic plants are present with low values. However, the presence, in the Cerdanya Basin, of plants such as evergreen *Quercus* (in the microflora) or even *Cassia*, *Mahonia*, *Cinnamomum*, *Banksia* and *Combretaceae* (in the macroflora; Menéndez Amor, 1955) indicates a warmer climate than today. At Zaratán, the pollen assemblages were similar to those found today in the southwestern Mediterranean region with sclerophyllous woods of *Quercus* and pines associated with species characteristic of open vegetation as Cistaceae, Cupressaceae, Ericaceae, Geraniaceae and *Plantago*. The presence of deciduous taxa indicates a warm–temperate climate in this region (Rivas-Carballo et al., 1994).

4.4. Messinian

Vegetation data from the Atlantic side of the Iberian Peninsula only comes from the Carmona area in the Guadalquivir Basin (southern Spain; Figs. 1 and 2). Pollen data from Carmona come from two sections and the pollen flora (analyses by J.-P. Suc, N. Feddi and J. Ferrier, unpublished) was dominated by herbs (alternating Poaceae and Asteraceae mainly) including rare subdesertic elements such as *Lygeum* and *Neurada*. *Pinus* was abundant and showed several fluctuations. Tree frequencies were low and were mostly constituted by deciduous *Quercus*.

The Andalucía G1 core showed open environments for the southern part of the Iberian Peninsula (Fig. 2), with vegetation rich in herbs, mainly Asteraceae, Poaceae, *Nitraria*, *Neurada* and *Calligonum*. *Lygeum* and other Mediterranean xerophytes were present. Arboreal taxa were frequent, dominated by deciduous *Quercus*, Taxodiaceae, *Myrica* and *Alnus*, indicating the existence of more humid places in the hinterland or moister conditions at higher altitudes. *Pinus* continued to show important percentages.

In southern Catalonia (core Tarragona E2; Bessais and Cravatte, 1988) vegetation was characterized by the predominance of herbs (mainly Asteraceae and Poaceae, *Lygeum*, *Nitraria* and *Calligonum*), indicating dry to very dry environments. Mediterranean xerophytes were very frequent, making pollen assemblages very close to the modern thermo-Mediterranean association (Bessais and Cravatte, 1988). The presence of pollen grains of arboreal taxa (mainly deciduous *Quercus*, Taxodiaceae, *Alnus*, *Carya*) indicates more humid places in the hinterland and along the rivers. *Pinus* was moderately abundant. As for Andalucía G1, pollen data did not show any distinct variation in the vegetation between the Messinian and Pliocene parts of the section.

Pollen data from the Can Vilella section in Cerdanya (NE Iberian Peninsula) revealed a riparian forest environment (Taxodiaceae, *Alnus*, *Myrica*, Cyrillaceae–Clethraceae, *Engelhardia*, *Cephalanthus*, *Pterocarya*, *Populus*, *Nyssa* and *Salix*) with many associated herbs (Cyperaceae, Poaceae and *Typha*; Agustí et al., 2006). *Pinus* was very scarce.

4.5. Pliocene

The same vegetation dynamics, marked by the disappearance of thermophilous plants and the increase in mesothermic and meso-

microthermic plants, continued. A mosaic of different plant associations inherited from the Miocene also characterized the vegetation at that time.

Vegetation data from the Atlantic side of the Iberian Peninsula comes from the Rio Maior F16 core (Portugal; Figs. 1 and 2). Vegetation in this area differs from the rest of the Iberian Peninsula by the high representation of Ericaceae, which still characterizes the Atlantic coast environments today (Oldfield, 1959). The pollen diagram of Rio Maior (Diniz, 1984a,b) shows the dominance of mega-mesothermic trees (mainly *Cathaya*, *Engelhardia*, *Sequoia*, *Myrica* and *Taxodium*). Mediterranean xerophytes such as *Olea*, *Phillyrea*, *Cistus*, Rhamnaceae and *Quercus ilex*-type were also significantly represented. In this pollen diagram, altitude indicators such as *Abies*, *Tsuga*, *Sciadopitys* were weakly represented, thus indicating that relief was far away or else was not very significant. The pollen study of Caranceja (Alcalde Olivares et al., 2004), located in Cantabria (northern Spain) and dated as Late Pliocene, also shows abundant percentages of Ericaceae. This probably indicates an Atlantic climatic influence that reaches as far as this locality (Fig. 1) in northern Spain.

The region of Catalonia (northeastern Spain) can be split into the Northwest and the Southwest Mediterranean (Suc, 1989), each represented by one site: Garraf 1 (Suc and Cravatte, 1982) in the Northwest Mediterranean zone and Tarragona E2 in the Southwest Mediterranean (Bessais and Cravatte, 1988; Suc et al., 1995b). At Garraf, mega-mesothermic trees were dominant, among them *Taxodium*-type indicating swamp conditions, *Engelhardia*, and *Symplocos*. The end of the pollen sequence was marked by the decrease of arboreal taxa to the advantage of herbaceous taxa (notably *Artemisia*, Asteraceae), indicating the beginning of the first glacial–interglacial cycles (Suc and Cravatte, 1982). Conversely, Tarragona was characterized by a predominance of herbs (mainly Asteraceae and Poaceae). Some herbaceous taxa such as *Lygeum*, *Nitraria* and *Calligonum* were also found, indicating very dry and warm conditions. Today these taxa can be found in North Africa under subdesertic conditions (Fauquette et al., 1998a). There are decreased values of arboreal pollen grains compared to the Northwest Mediterranean zone, predominantly Taxodiaceae, *Engelhardia* and deciduous *Quercus*, as before. Mediterranean xerophytes were regularly represented in this pollen diagram. In fact, the pollen assemblages resemble the modern thermo-Mediterranean formation (Bessais and Cravatte, 1988).

In southern Spain (Andalucía G1 core), the composition of the pollen spectra is more or less similar to that of Tarragona, i.e. large quantities of herbs, including subdesertic herbs. Trees were well represented most likely due to the presence of nearby relief. Climatic fluctuations are recorded throughout the sequence of Andalucía G1 (Fauquette et al., 2007). During the Pliocene, this region was characterized by a more or less similar vegetation type as today, i.e. an open subdesertic landscape (Suc et al., 1995b) but with more thermophilous taxa, found today in North Africa.

The mixed deciduous forest (mainly made up of conifers like *Pinus*, and several deciduous trees such as *Quercus*, *Acer*, *Carpinus*, *Carya*, *Pterocarya*, *Liquidambar*, *Platanus*, *Tilia*, *Ulmus* and *Zelkova*), situated at higher altitude, as well as the trees belonging to the highest altitudinal belts (*Cathaya*, *Cedrus*, *Tsuga*, *Picea* and *Abies*), became more abundant during this period. Another important fact that makes a difference between Pliocene and Miocene vegetation is the strong development of the steppe with *Artemisia* in the Iberian Peninsula since the Early Pliocene (see Garraf 1 pollen diagram; Fig. 2).

5. Climate change

The high presence of thermophilous elements during the Early (Burdigalian) and the early Middle Miocene (Langhian) suggests the existence of a warm, subtropical climate. The floral assemblages during that time clearly reflect the Miocene Climatic Optimum (MCO: Zachos et al., 2001; Shevenell et al., 2004). This is supported by the

estimated temperature values, based on the “Climatic Amplitude Method”, that shows most likely values of mean annual temperatures (Ta) between 17 and 21 °C at Rubielos de Mora and La Rierussa (Fig. 3) and even higher values for southern Spain, between 17 and 25 °C (Andalucía G1, Alborán A1 and Gor sections). The presence of several xerophytes in the pollen spectra (*Acacia*, *Prosopis*, *Calligonum*, *Lygeum*, *Neurada*, *Nitraria*, Caesalpiniaceae, *Ephedra* and Convolvulaceae), particularly in southern Spain, and in the macrofloras of the Iberian Peninsula (presence of Proteaceae, Mimosaceae and Caesalpiniaceae) (Sanz de Siria Catalan, 1993), suggests that the overall climate was very dry and characterized by a strong seasonality with periods without any precipitation for 7–9 months (Sanz de Siria Catalan, 1993; this study). A dry subtropical climate is also in accordance with the previous climatic interpretations for the Early Miocene based on fossil mammals (Calvo et al., 1993). Precipitation estimates for the Iberian Peninsula at that time of about 743 mm for southern Spain, 900–1700 mm for the Rubielos de Mora area, and 900–1300 mm for La Rierussa in northeastern Spain (Jiménez-Moreno, 2005) are not in accordance with values of less than 500 mm mean annual precipitation suggested by the pollen record of subdesertic plants (*Lygeum*: 150–400 mm; *Neurada*: 20–200 mm; *Nitraria*: 50–150 mm; *Calligonum*: 40–100 mm; Fauquette et al., 1998a,b) identified in this study. Those values seem to be over-estimated, notably for southern Spain, due to the mixture of taxa of different vegetation types, subtropical trees with high-humidity requirements and subdesertic herbs, biasing the estimation of the precipitation. These results reflect in fact local humid conditions under a generalized dry climate that could be due to either the effect of humid cloud masses, which cling to the mountains at an altitude of ca. 400–500 m (Bessedik, 1984), or to significant availability of water sources along rivers or around lakes.

A tendency towards cooler conditions occurred in the late Mid-Miocene (Serravallian) and Late Miocene (Tortonian) as many thermophilous plants disappeared reducing plant diversity from the Iberian Peninsula (Bessedik, 1985; Jiménez-Moreno, 2005). On the other hand, mesothermic plants (mainly deciduous *Quercus*, *Alnus*, etc.) and high-elevation conifers increased. This climatic change is related to a gradual decrease in temperature after the MCO that has been well-documented on a worldwide scale and has been correlated with the general decrease in temperature observed by several authors as a gradual increase in the isotopic $\delta^{18}\text{O}$ values of foraminifera from deep-sea sediments [DSDP Sites 608: Miller et al. (1991) and 588: Zachos et al. (2001)] during this period and related to an increase in the size of the East Antarctic Ice Sheet (EAIS; Zachos et al., 2001). Estimated temperatures point to slightly colder temperatures than previous times in northern Spain during the Serravallian and Tortonian, with mean annual temperature estimates around 18.8 °C (Orera section), 19 °C (Zaratán) and 18 °C (La Cerdanya) (Fig. 4). This temperature drop has also been observed in several palaeobotanical studies in Central Europe, with decreases in temperatures of about 1.5 °C in the Forecarpathian Basin (Ivanov et al., 2002), 2–3 °C in Hungary (Jiménez-Moreno et al., 2005), about 2 °C in the Pannonian Basin (Erdei et al., 2007), 2–3 °C in Serbia (Utescher et al., 2007) and Germany (Mosbrugger et al., 2005) and 2 °C in Austria (Jiménez-Moreno et al., 2008). Precipitation estimates seem to be higher than today in northern Spain during this period, with values around 1200 mm in Orera for the Serravallian and 600 mm and 1300 mm for Zaratán and La Cerdanya respectively.

Pollen data from the Messinian in the Iberian Peninsula show a similar climate before, during and after the Messinian Salinity Crisis (Fauquette et al., 2006). Therefore the main factor leading to this event seems to be the successive closures of the Betic and Rifian corridors, isolating the Mediterranean Sea from the Atlantic Ocean. Climate reconstructions for the Iberian Peninsula before the Messinian Salinity Crisis show a warm and dry climate for southwestern Spain (Carmona area), with most-likely Ta estimates around 20.5–

22.5 °C. Mean annual precipitation is very low in this area, with most-likely values around 400–500 mm. At Can Vilella, in La Cerdanya region, the climate was warm and humid. Ta was around 15 to 19.8 °C with a most likely value of 17 °C. Mean annual precipitation was high, ranging between 1000 and 1350 mm with a most likely value of 1150 mm (Fauquette et al., 2006). The climate during the first desiccation (i.e. marginal) phase of the Messinian Salinity Crisis in the Mediterranean region is documented for the Iberian Peninsula at Carmona, Tarragona E1 and Andalucía G1 (Fauquette et al., 2006). Climate during the marginal desiccation phase was warm and dry, with the same climatic amplitudes as before the crisis. The site of Tarragona, located more to the north, shows slightly higher values of mean annual precipitation (between 700 and 900 mm with a MLV around 800 mm). The climate after the Messinian Salinity Crisis, during the Early Pliocene, seems to have been very similar to that of the previous times and in the Iberian Peninsula, it was warm and dry (Fauquette et al., 1999).

Pliocene climate in the southern Iberian Peninsula is recorded in the Andalucía G1 core (Fauquette et al., 1999). A cooling event, which occurred at around 4.5 Ma in other pollen sequences (Suc and Zagwijn, 1983) is recorded in the pollen data (Suc et al., 1995b) and is also evident in the mean annual temperature reconstruction (Fauquette et al., 1999; Fig. 5). Other less important oscillations follow this event and, finally, a decrease in temperature that corresponds to the cooling that took place at 3.4 Ma (Zagwijn, 1960; Suc and Zagwijn, 1983; Suc, 1984). At this site, mean annual temperatures were equivalent to 6 °C higher than today (17 °C). Few changes are recorded for Pa, with values in between 400 and 600 mm.

Pliocene climate data from the Atlantic side of the Iberian Peninsula comes from the Rio Maior F16 core (Portugal; Fig. 5; Fauquette et al., 1999). The mixture of Mediterranean xerophytes and mega-mesothermic taxa shows a complex vegetation structure, which makes climate reconstructions difficult. Mediterranean xerophytes may have been either an integral part of the forest associations or already adapted to drier conditions, allowing colonization of some areas, e.g. calcareous areas (Diniz, 1984a). This mixture of ecological types resulted in high climatic variability in the climate reconstruction, particularly for mean annual precipitation. In general, temperatures and precipitation were similar or higher than today with a Ta between 15 and 20 °C and Pa around 1300 mm. However, precipitation may have been lower than today, during phases characterized by high frequencies of Mediterranean taxa.

The Pliocene climatic reconstruction made from the sequence of Tarragona E2 (Fauquette et al., 1999), covering the period from 5.32 to 3 Ma, shows temperatures higher than today, between 17 and 25 °C, and precipitation similar or higher than today, between 600 and 1200 mm (Fig. 5). At Tarragona, the mixture of taxa of different vegetation types, mega-mesothermic trees and subdesertic herbs gives important variations in the climatic estimations from one spectrum to the next, particularly for annual precipitation. Even with these variations, the amount of precipitation is lower than at sites in the northwestern domain (in particular Garraf 1; Fauquette et al., 1998b), indicating the transition to a different climate regime.

The Garraf 1 pollen diagram (Suc and Cravatte, 1982) is particularly important because it is a continuous well-dated long record that provides a palaeoclimatic record from the lowermost Zanclean (5.32 Ma) to the latest Gelasian (about 1.8 Ma). In this area, the Early Pliocene was warm and humid, with a trend toward progressively cooler and drier conditions through time, from the beginning to the end of the sequence. At around 4.5 Ma, a cooling is seen in the pollen data, marked by a decrease in thermophilous trees and an increase in herbs. Our quantitative reconstruction does not indicate changes through this period (Fauquette et al., 1998b). In fact, the decrease in subtropical plants was not very important and even though their pollen percentages decreased, they still exceeded the thresholds and we conclude that the climate did not change

significantly during this interval. This cooling was followed by a warm period during which the temperatures were higher than today. Annual precipitation was also very high, falling between 1100 and 1600 mm (vs. 610 mm today). Another cooling event occurred at around 3.4 Ma, immediately after the Zanclean–Piacenzian boundary (Suc and Zagwijn, 1983; Suc, 1984). This event was characterized at Garraf 1 by a strong decrease in the pollen of mega-mesothermic trees and by an increase in herb pollen. This event is evident in the palaeoclimatic reconstruction, even though the decrease of the annual temperatures was not very pronounced. The inferred changes in temperature and moisture were probably responsible for the reduction in the cover of Taxodiaceae swamps, the increase in open vegetation, and other changes in vegetation structure (Suc and Cravatte, 1982). Mega-mesothermic taxa progressively diminished between ca. 3.4 and 2.6 Ma, although there were a few oscillations. The last warming period within this interval occurred at around 3.1–3.0 Ma, as illustrated by the occurrence of the final significant percentages of subtropical pollen taxa. This climatic event is not really obvious in the climatic reconstruction by Fauquette et al. (1998b). At this time temperature of the warmest month increased (26 to 28 °C), although neither the annual temperatures nor the coldest month changed. From about 2.6 Ma to the end of the sequence, the pollen diagram is characterized by rapid alternations between steppe and forest linked to glacial–interglacial fluctuations (Suc and Zagwijn, 1983). These alternations are well marked in the climatic reconstruction: during glacial phases annual temperatures decreased to values similar to those of the present time; during interglacial phases temperatures again increased. Variations in annual precipitation were seemingly rapid through this period and reached very low values during this interval (equivalent to modern ones). During the Pliocene, before the first high-amplitude glacial–interglacial cycles, our method suggests that annual temperatures were 1 to 5 °C warmer, and annual precipitation was 400 to 1000 mm higher than Present. This interpretation is in agreement with the climates inferred from pollen data by Willard (1994) for a mid-latitude site (36°N) in southeastern Virginia (USA) where annual temperatures were 2.5 °C higher than today.

Open herbaceous formations in the Iberian Peninsula and Morocco are then known since the Burdigalian (Suc et al., 1995a,b; Bachiri Taoufiq et al., 2001; Jiménez-Moreno, 2005; Jiménez-Moreno and Suc, 2007). They developed significantly during the Zanclean in other regions of the Mediterranean area (Suc et al., 1999) but were relatively poor in *Artemisia*, except in Anatolia (Popescu, 2006). It is at the end of the Pliocene, as the climate got cooler and glacial–interglacial cycles appeared in the Northern Hemisphere, when the steppes with *Artemisia* (probably of Anatolian origin; Popescu, 2006) became of significant importance in the Iberian Peninsula as everywhere along the northern Mediterranean coastlines (Suc et al., 1995b) during the glacial periods (Suc and Cravatte, 1982; Combourieu Nevout and Vergnaud Grazzini, 1991; Beaudouin, 2003) and even during interglacials (Subally et al., 1999) because of the ambivalent significance of *Artemisia* from the temperature viewpoint (cold vs. warm species: Subally and Quézel, 2002) and some influence of the monsoon (Joannin et al., 2007).

The decrease in thermophilous plants and, on the contrary, the noticeable increase in mesothermic plants and altitudinal trees during the Miocene and Pliocene, can be interpreted as a result of the above-mentioned climatic cooling, or from the uplift of the surrounding mountains in this area, which was very intense during the studied time period, or the progressive movement of Eurasia (and the Iberian Peninsula) towards northern latitudes as a result of the northwards collision of Africa. In all the cases, altitudinal elements would increase. However, the estimated climate, using only taxa growing at low to middle–low altitude, seems to confirm a decrease in mean annual temperatures, which was most likely insufficient to explain the development of an *Abies–Picea* forest. All the phenomena coexisted

and it is quite difficult to separate one process from the other (global climatic forcing vs. regional tectonics and relief uplift), due to the tectonic situation of the studied area and the fact that all of them may have interfered. What is clear is that even if the uplift of the surrounding mountains may have influenced the regional climate and the increase in conifers observed in the pollen spectra, the evolution of the vegetation during the Miocene was very dependent on the global climatic signal as shown in previous studies (Jiménez-Moreno, 2005; Jiménez-Moreno et al., 2005; Mosbrugger et al., 2005; Jiménez-Moreno, 2006; Böhme et al., 2007; Utescher et al., 2007).

6. Climatic latitudinal gradient

A latitudinal climatic gradient between southern and northern Iberian Peninsula has been observed in the pollen data and the climate reconstructions since the Middle Miocene (Jiménez-Moreno and Suc, 2007; Fauquette et al., 2007). Both pollen and climatic estimations show a decrease in temperature and a reduction in dryness from South to North.

6.1. Middle Miocene

Jiménez-Moreno and Suc (2007) showed that during the Middle Miocene the vegetation in southern Spain (Fig. 2) was characterized by the predominance of herbs and shrubs, with abundant subdesertic elements, such as *Nitraria*, *Lygeum*, *Prosopis*, *Neurada* and *Calligonum*. They characterized this vegetation as typical of an open environment. On the other hand, in Northeastern Spain and even though the vegetation was also rich in herbs and shrubs, subdesertic indicators such as Caesalpiniaceae and *Acacia*, only occurred at very low percentages. Jiménez-Moreno and Suc (2007) described two main vegetation domains (zones A and B; Fig. 3) in the Iberian Peninsula during the Middle Miocene, with a clear latitudinal zonation in the vegetation. The presence, all along this transect, of plants characterized by high thermic requirements such as *Engelhardia*, *Myrica*, *Taxodium*-type, *Mussaenda*-type and *Avicennia*, indicates that the latitudinal temperature gradient was lower than today. This is consistent with the presence of abundant thermophilous taxa in other Middle Miocene pollen data from Central and Northern Europe (Jiménez-Moreno, 2005; Jiménez-Moreno and Suc, 2007). Liu and Leopold (1994) also observed the occurrence of thermophilous plants at higher latitudes in North America. These authors estimated a thermic gradient of 0.3 °C per degree of latitude for North America (between 35°N and 65°N) during the Middle Miocene.

Mean annual temperatures reconstructed from our pollen data (Fig. 3) do not show many significant changes looking at the intervals. However, the Most Likely Values (MLVs) from south to north show decreasing annual temperatures. Moreover, the thermic gradient is weaker than the modern one as the differences between the Miocene and the modern temperatures are between ca. 2 °C in southern Spain and ca. 4 °C in northern Spain. The MLV is less robust than the entire interval (as a single value can not reflect the life–optimum of a plant assemblage) but, as it is weighted according to the size of the climatic intervals of each plant exceeding its presence/absence and/or abundance thresholds, variations of the MLV may be considered as real temperature changes.

The precipitation reconstruction shows increasing values from south to north, as today, with even higher amounts than today in northern Spain but almost equivalent amounts of precipitation than today in southern Spain.

The MLVs reconstructed from pollen data between 36.4°N and 47°N (Fauquette et al., 2007) indicate that during the Middle Miocene the thermic gradient in Western Europe was around 0.48 °C per degree in latitude whereas it is around 0.6 °C today (Ozenda, 1989). This result is in agreement with the climatic estimations obtained by

Bruch et al. (2004) using European fossil floras, also finding a lower latitudinal temperature gradient than today.

6.2. Late Miocene

This climatic latitudinal gradient is also evident in the pollen and climatic reconstructions for the Late Miocene (Tortonian: Fauquette et al., 2007; Fig. 4; Messinian: Fauquette et al., 2006; Favre et al., 2007) in the Iberian Peninsula. Although less pollen data exist for this period, a clear latitudinal gradient is observed for both temperature and precipitation. During the Tortonian, forested environments are indicated in the northern Iberian Peninsula (Sanabastre/Sampson sites in Cerdanya, Bessedik, 1985), where arboreal pollen dominates with low values of herbaceous taxa. At Zaratan, the pollen assemblages are more similar to those found today in the southwestern Mediterranean region with sclerophyllous woods of *Quercus* and pines associated with species characteristic of open vegetation as Cistaceae, Cupressaceae, Ericaceae, Geraniaceae and *Plantago* (Rivas-Carballo et al., 1994). Finally, in the southern part of the Iberian Peninsula, the pollen spectra are largely dominated by herbaceous taxa, indicating dry open environments with the presence of subdesertic herbs. The climatic reconstructions based on these pollen sequences show that climate was warm and humid in northern Iberian Peninsula (most-likely values ca. 4 to 9 °C and annual precipitation rainfall 100 to 600 mm higher than today), and warm and dry in the south Mediterranean region (most-likely values of 3 to 4 °C higher and less than 200 mm higher than today). The climatic estimates show that the north–south climatic gradient that existed during the Tortonian was similar to today, with increasing temperature and decreasing precipitation, but with higher temperatures (Fig. 4). This persistence is also supported by mammals (see Casanovas-Vilar and Agustí, 2007). Fauquette et al. (2007), taking into account other available pollen records from Western Europe, calculated a thermal gradient of around 0.6 °C per degree in latitude. The climatic latitudinal gradient is also very clear for the Messinian (Fauquette et al., 2006). To the south, herb assemblages are dominated by Poaceae, Asteraceae, *Plantago*, *Erodium* and subdesertic plants like *Lygeum*, which today characterizes the southern Mediterranean region under a thermo-Mediterranean climate (from semi-arid to arid conditions, with mean annual precipitation from around 500 to 100 mm, and under high annual temperatures from around 16 to 26 °C; Fauquette et al., 1998b). On the other hand, the north is characterized by more humid and colder conditions with temperature estimations around 15–22 °C and precipitations around 680–870 mm in Tarragona E1 and 1070–1300 mm in Can Vilella (Fauquette et al., 2006).

A crucial environmental change probably occurred during the Tortonian, which led to the disappearance of hominoids from Europe (Andrews and Bernor, 1999) causing the lack of food (mostly fruits) throughout a significant part of the year, a hypothesis expressed by Andrews (1992). This assumption is supported by pollen data from Southwestern Europe (Suc et al., 1999) and plant macrofossils from Northeastern Iberia (Agustí et al., 2003), which indeed show that during the Tortonian, trees producing fruits throughout the year were predominantly replaced by those displaying only a seasonal production of fruits.

6.3. Pliocene

The abundant and widely distributed Pliocene pollen data make the latitudinal differences in vegetation easily identifiable (Suc, 1989; Suc et al., 1995a). Three main vegetation domains (Fig. 5) were described by Suc (1989), Suc et al. (1995a) and Fauquette et al. (2007) in the Iberian Peninsula during the Pliocene, with a clear latitudinal zonation in the vegetation. The site on the Atlantic coast of the Iberian Peninsula (Fig. 5, zone C, Rio Maior) shows forested vegetation

dominated by Taxodiaceae, Ericaceae and mesothermic deciduous trees. In the northernmost part of the Iberian Peninsula (Garraf 1; Fig. 5, zone B), the forests were dominated by Taxodiaceae, accompanied by mega-mesothermic plants such as *Engelhardia*, *Symplocos* and *Platycarya*. At that time, the region of Tarragona belonged from the vegetation point of view to the southern Iberian ecosystems as the transition zone with the northern Mediterranean vegetation was identified between Barcelona and Tarragona (Suc et al., 1999), exactly as it is today for the transition between the meso-Mediterranean vegetation belt and the thermo-Mediterranean one (Rivas-Martínez, 1987; Quézel and Médail, 2003). Indeed, in areas south of Tarragona (Tarragona E2; Fig. 5, zone A) the vegetation was characterized by Mediterranean xerophytic ecosystems ('matorral' composed by *Olea*, *Phillyrea*, *Pistacia*, *Ceratonia*, evergreen *Quercus*, *Nerium*, *Cistus*) and, more to the south (Andalucía G1), by open environments dominated by subdesertic plants like *Lygeum*, *Neurada*, *Nitraria*, *Calligonum*, Geraniaceae and Agavaceae. Since the Zanclean, a thermal threshold existed between Barcelona and Tarragona, as it does today, separating thermo-Mediterranean from meso-Mediterranean formations (Suc et al., 1995a). Since the Mid-Pliocene, another thermal and/or xeric threshold existed between the northern and southern edge of the Eastern Pyrenees, which could be related to the onset or strengthening of northern "cold" winds (Suc et al., 1999).

A north–south climatic gradient existed during the Pliocene, with, as of today, increasing temperatures and decreasing precipitation (Fig. 5). The thermal gradient calculated on the 'most-likely values' of mean annual temperatures during the Pliocene in Western Europe is very similar to that observed today, i.e. around 0.6 °C per degree in latitude (Fauquette et al., 2007).

7. Paleoclimatology

Located between the mid-latitude temperate zone and the Sahara Desert and also influenced by the Atlantic Ocean, the Iberian Peninsula experiences a warm and dry climate in the southern part and a warm and wetter climate in its northern part since almost the Middle Miocene. Like today, a latitudinal gradient in temperature and precipitation was a very important feature in the Mediterranean region, with drier areas along the African coast and significantly wetter areas north of the Mediterranean Sea. Today, the moisture flux in the Mediterranean region comes mostly from the Atlantic Ocean (Mariotti et al., 2002).

During the Mid-Miocene, the different temperature gradient compared to today may be due to a different oceanic circulation that forces atmospheric changes and thus climate changes. Indeed, the continental configuration of the world during the Miocene was similar to the present. However, plate tectonics led to intense palaeogeographical changes around the world, especially during the Early and Middle Miocene. These changes, in particular the opening of some sea gateways (Drake passage, Bering Strait) and the closure of others (the Atlantic–Pacific passage across Panama, the passage between the Indian Ocean and the Tethys) (Pagani et al., 2000; Hall et al., 2003; Schmidt, 2006; Pfuhl and McCave, 2006), together with some others like modifications in atmospheric CO₂, orbital forcing and ice–climate feedbacks (DeConto and Pollard, 2003a,b), contributed to fluctuations in the Neogene climate. Changes in oceanic circulation at that time led to the establishment of the modern ocean circulation pattern (e.g. the Antarctic Circumpolar Current) that in turn, affected the global climate. In addition, many atmospheric general circulation model simulations have shown the influence of the uplift of mountain ranges and plateaus (Rocky mountains, Andean, Himalayas, Alps, Tibetan Plateau) on global climate through changes in the atmospheric circulation (e.g. Ruddiman and Kutzbach, 1989; Ramstein et al., 1997; Fluteau et al., 1999; Kutzbach and Behling, 2004). However, in spite of these global modifications, the climate pattern in the Iberian

Peninsula was the same as today: a warm and dry climate in the south and a warm and wetter climate in the North.

From the Late Miocene (Tortonian) to the Mid-Pliocene, the vegetation and climatic latitudinal gradients (in particular the thermal one) differ from those of the Middle Miocene. Temperatures were higher than today, as during the Middle Miocene, but the difference between the North and South was greater than during the Mid-Miocene resulting in a similar gradient in temperature and vegetation to today. For what concerns the Late Miocene, simulations with the AGCM ECHAM4 coupled to a slab ocean model have been made in order to study the climate response during the Tortonian to a generally low palaeogeography, a weaker-than-present palaeoceanic heat transport and a changed palaeovegetation (Steppuhn et al., 2006; Micheels et al., 2007). Although the simulations tend to be too cool at higher latitudes and show an overall reduction of the meridional temperature gradient compared to the present (Steppuhn et al., 2006; Micheels et al., 2007), our data from Europe agree with the model simulations. For example, in the Mediterranean region, the simulated climate is slightly warmer and drier than today, which agrees with our data from southwestern Europe (Sicily, Central Spain). In Northern Africa and southern Spain, the Tortonian model simulates warmer and less arid conditions than today. Our evidence for subdesertic herbs indicating arid conditions and forest elements in Morocco and southern Spain does not completely support the climate modelling results. However, it should be noted that these two groups of plants certainly developed at different altitudes that may not be adequately resolved by the climatic model (Fauquette et al., 2006).

During the Pliocene, the thermal gradient was similar to the modern one. However, the precipitation gradient was more accentuated, with a larger difference between the Pliocene and today in the North than in the South. This pattern is confirmed for the Pliocene by climate model simulations realized by Haywood et al. (2000a,b) using the HadAM3 version of the U.K. Meteorological Office's (UKMO) general circulation model. Haywood et al.'s simulations (2000b) show annual zonal average precipitation similar to modern values between around 30 and 42°N and higher than today between 42 and 51°N, that is in agreement with proxy-data. The authors have explained this pattern by an increased arrival of southwestern air masses. During the Mid-Pliocene, the enhancement of the Icelandic low- and Azores high-pressure systems and the stronger pressure gradient in the North Atlantic caused an intensification of annual westerly wind strength. Combined with warmer sea surface temperatures, the atmospheric transport of heat and moisture over Europe and the Mediterranean region was increased (Haywood et al., 2000a). This pattern is in agreement with the development of Ericaceae moors along the European Atlantic coast that suggest an enhanced westerly wind pattern (Suc et al. 1995a,b) and with the development of open environments dominated by subdesertic plants along the Southeastern coast of the Iberian Peninsula which is submitted to enhanced wind coming from the South (Haywood et al., 2000a).

8. Conclusions

A synthesis of pollen data, interpreted vegetation and palaeoclimatic estimates from Miocene and Pliocene sediments from the Iberian Peninsula has permitted us to observe temporal climatic variations and to notice clear spatial climatic gradients.

The abundance of thermophilous elements and high temperature estimates during the Early Miocene (Burdigalian) and the early Middle Miocene (Langhian) suggest the existence of a warm, subtropical climate. The floral assemblages during that time clearly document the Miocene Climatic Optimum.

A tendency towards cooler conditions occurred since the late Mid-Miocene and persisted during the Pliocene as many thermophilous plants disappeared reducing plant diversity from the Iberian Peninsula. On the other hand, mesothermic plants, high-elevation conifers

and Mediterranean xerophytes increased. The beginning of the glacial-interglacial fluctuations and the expansion of *Artemisia* mark the Early Pleistocene in this area.

The vegetation in the Iberian Peninsula reflects a clear climatic latitudinal gradient since the Middle Miocene. In all of the considered periods, the quantitatively reconstructed climate shows, in comparison to today, higher mean annual temperatures along the gradient and increases in mean annual precipitation in the northernmost part of the Iberian Peninsula, but similar precipitation to today in the southern part of it. The results also show a clear latitudinal gradient of temperature and precipitation, increasing for temperatures but decreasing for precipitation from north to south. The results show that the thermal gradient has evolved in time. During the Middle Miocene, the presence of mega-mesothermic taxa in pollen spectra at all sites shows that the thermal latitudinal gradient was weaker than the modern one. Based on the climate reconstructed from pollen data, the thermal gradient was around 0.48 °C per degree of latitude whereas it is today around 0.6 °C degree in Western Europe. Since the Tortonian, the vegetation distribution and the climate reconstruction show a thermal latitudinal gradient similar to the modern one. The transition from the weak thermal latitudinal gradient of the Mid-Miocene to the modern-like gradient of the Pliocene and Pleistocene appears to take place during the Middle-Late Miocene, before or during the Tortonian. The precipitation gradient was more accentuated than today from the Mid-Miocene to the Mid-Pliocene: the precipitation anomalies between the Neogene and today are larger in the North than in the South. The transition from this pattern to the modern latitudinal gradient took place after the Mid-Pliocene, at the time of the first glacial-interglacial cycles.

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