STEPPES, SAVANNAHS, FORESTS AND PHYTODIVERSITY RESERVOIRS DURING THE PLEISTOCENE IN THE IBERIAN PENINSULA

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Abstract

A palaeobotanical analysis of the Pleistocene floras and vegetation in the Iberian Peninsula shows the existence of patched landscapes with *Pinus* woodlands, deciduous and mixed forests, parklands (savannah-like), shrublands, steppes and grasslands. Extinctions of Arctotertiary woody taxa are recorded during the Early and Middle Pleistocene, but glacial refugia facilitated the survival of a number of temperate, Mediterranean and Ibero-North African woody angiosperms. The responses of Iberian vegetation to climatic changes during the Pleistocene have been spatially and temporarily complex, including rapid changes of vegetation in parallel to orbital and suborbital variability, and situations of multi-centennial resilience or accommodation to climatic changes. Regional characteristics emerged as soon as for the Middle Pleistocene, if not earlier: Ericaceae in the Atlantic coast indicating wetter climate, thermo-mediterranean elements in the south as currently, and broad-leaf trees in the northeastern. Overall, steppe landscapes and open *Pinus* woodlands prevailed over many continental regions during the cold spells of the Late Pleistocene. The maintenance of a high phytodiversity during the glacials was linked to several refuge zones in the coastal shelves of the Mediterranean and intramountainous valleys. Northern Iberia, especially on coastal areas, was also patched with populations of tree species, and this is not only documented by palaeobotanical data (pollen, charcoal) but also postulated by phylogeographical models.

Key words: Pleistocene, Palynology, Anthracology, Iberian Peninsula, Vegetation Refugia

1.- Introduction

Published material dealing with vegetational landscapes of the Iberian Pleistocene have considerably increased over the last few decades. This involves more studied sites, a broader time span, new long continuous sequences, the filling up of crucial geographic gaps, and a visible effort of bio-correlation. However, our knowledge of the Pleistocene vegetation is still incomplete, and a review of these gaps, together with a summary of the major developments is needed. The goal of this paper is therefore to critically revisite and synthetise the available palaeobotanical information, mainly in the form of pollen and charcoal records, but also plant megafossils and seeds (Fig. 1, Table 1). This information will be presented by periods (Early, Middle and Late Pleistocene) with the aim of illustrating the broad spectrum of vegetation changes in various parts of the Iberian Peninsula, characterised by different climatic influences, as well as the location and composition of glacial refugia for temperate and Mediterranean woody species.

A limitation to produce contending models of vegetation dynamics for the study period is the very small number of long, continuous palaeobotanical sequences available for the Iberian Peninsula. We are still dependent on the information derived from few sites such as Padul (Florschütz et al., 1971, Pons and Reille, 1988), Carihuela (Carrión et al., 1999, Fernández et al., 2007), and the marine ODP 976 site in the south (Combourieu-Nebout et al., 1999), and Area Longa in the north (Gómez-Orellana et al., 2007). To correlate these data with the number of fragmentary pollen sequences is challenging. At a first sight, regardless of the patchiness of the physical context, the general patterns of the Pleistocene European vegetation history are shared in the Iberian scene. However, there are peculiarities, especially related with the floristic composition and the spatial pathway of permanence of thermophilous floras during cold-arid periods. These patterns will be a topic of particular attention in this paper.

2.- Present-day mosaics of climate and vegetation

Strong climatic and geographic gradients and topographic contrasts have contributed to a marked physiographic heterogeneity in the Iberian Peninsula and Balearic Islands (Fig. 1). Owing to its relatively low latitude, this is one of the European regions that persisted mostly free of glaciated areas during the Pleistocene. Iberia is also one of the Mediterranean peninsulas with the highest floristic diversity and endemism (Castroviejo, 2002, Sainz-Ollero and Moreno, 2002). Many factors have contributed to this richness, but tectonic history including the existence of islands and episodic bridges with North Africa during the Late Tertiary, appear most relevant (Rodríguez-Sánchez et al., 2008).

The orography of the Iberian Peninsula is characterized by mountain chains, which are aligned East-West and which determine a varied types of climates (Capel Molina, 1981) and habitat (Fig. 1). Current, and plausibly past vegetation distributions, were deeply marked by these transversal biological barriers that impeded a fluid latitudinal taxa migration in response to climatic oscillations. In the north, the Pyrenees, the Cantabrian Cordillera and the Galaico-Leoneses Mountains underline the most important limit between the Atlantic and the Mediterranean Iberia. These Atlantic regions are characterized by an important oceanic influence with high precipitation (more than 1000 mm/yr and without summer drought) and cool-milder annual temperatures (13º to 15ºC). The centre of the peninsula is also crossed by mountain ranges, mainly the Central System (Ayllón, Guadarrama, Gredos and Serra da Estrela), which divides the two plateaux (northern and southern “mesetas”) that correspond to the Duero and Tajo river basins, respectively. Another important mountain chain is the Iberian System that runs from the North-West to the South-East and marks the limit between river basins that flow to the Atlantic Ocean or to the Mediterranean Sea. A strong continentality is derived from this orography. Central Iberia shows the typical summer drought of Mediterranean climates with strong thermic contrasts (lower than 6º C in winter and more than 26º C in summer), and including some semi-arid areas such as the North-East Ebro Basin, with 300 mm of annual precipitation. The southernmost Betic and Penibetic Mountain Systems have permitted an altitudinal scenario for species migrations during the Pleistocene (Carrión, 2002a). Coastal eastern and southern lowlands exhibit mild climates with severe summer drought and annual temperatures higher than 18ºC.

The geological map is puzzling (Vera, 2004), but overall, the Iberian Peninsula can be divided into a western, siliceous and an eastern, calcareous zone, with some material intrusions in between. Logically, this partitioning is critical for the vegetation distribution, and added to climate, they determines the biogeographical provinces within the Eurosiberian and Mediterranean regions (Rivas Martínez, 2007). The Eurosiberian Region comprises a narrow band from the eastern Pyrenees to Galicia and to the north-western slopes of Portugal, with a climate characterized by high annual precipitation without summer drought and a vegetation dominated by mesic forests with *Quercus, Fagus, Tilia, Ulmus, Acer,* and *Fraxinus*, sometimes mixed with *Pinus sylvestris, Pinus uncinata* and *Abies alba* at altitude. The Mediterranean Region occupies the rest of the Peninsula and the Balearic Islands and enjoys a generally warmer and drier climate characterized by summer drought (Capel Molina, 1981). The great extension of Mediterranean Iberia implies an important spatial variation related not only to the geology, but also to coastal (Atlantic or Mediterranean) or continental influences, and to altitudinal gradients, which condition the eventual occurrence/dominance of semi-deciduous or evergreen *Quercus, Pinus* and *Juniperus* formations (Fig. 1). Higher average temperatures allow the existence of a thermomediterranean belt in eastern and southern coastal areas with sclerophyllous forest-scrub that includes *Quercus coccifera*, *Pistacia lentiscus*, *Ceratonia siliqua*, *Chamaerops humilis*, *Pinus halepensis,* and *P. pinea* among other species. The mesomediterranean belt is often characterized by *Quercus ilex* and *Quercus suber* formations, and, at the supramediterranean belt, by semi-deciduous formations of *Quercus faginea* and *Quercus pyrenaica,* and coniferous forests with *Pinus sylvestris*, *Pinus nigra, Pinus pinaster,* and sporadically *Juniperus thurifera* are developed. Coniferous open woodlands can reach and be widespread along the highest elevation, the oromediterranean belt.

The aforementioned arid lands in the northeastern and southeastern of Iberia are characterized by steppe formations with xerophytic Poaceae (such as *Stipa* and *Lygeum*), Asteraceae, Chenopodiaceae (such as *Salsola* and *Suaeda*) and even interesting biogeographical disjunctions such as *Krascheninnikovia ceratoides,* which testify to a larger distribution, fragmented after the desiccation of the Mediterranean Sea during the Messinian crisis (Pérez-Collazos and Catalán, 2007). The semi-arid southeastern is also characterized by Ibero-Maghrebian, xerothermic elements such as *Periploca angustifolia, Withania frutescens, Maytenus senegalensis, Osyris quadripartita*, and *Tetraclinis articulata*, among others (Carrión et al., 2009b). Finally, in the south-western, it is worth mentioning the presence of palaeotropical species like *Prunus lusitanica*, *Rhododendron ponticum*, *Laurus nobilis*, *Davalia canariensis* and *Psilotum nudum,* among others, which may have persisted since the Tertiary or before, and contribute significantly to the floristic particularity of the region (Costa Tenorio et al., 1990, Blanco-Castro et al., 1997, García-Antón et al., 2002, Calleja et al., 2009).

3.- Stratigraphy and main climatic trends

The first glacial periods with open vegetation in Europe (Suc and Popescu, 2005) started at 2.589 Ma (pre-cyclostratigraphy: 2.4 Ma) at the Gauss-Matuyama transition across the marine isotopic stages (MIS) 100, 98, and 96 (Shackleton et al., 1995) (Fig. 2). This will be taken as the base of the Quaternary and the Pleistocene (Leigh Mascarielli, 2009). The preparation of these cold MIS is already seen in the earlier MIS 104 and 102. Two stages subdivide the Early Pleistocene: i) the Gelasian Stage, which starts at MIS 103, 20 ka after the Gauss/Matuyama boundary, with an astrochronological age of 2.589 Ma, and which has been ratified in 1996 (Rio et al., 1998); and ii) the Calabrian Stage at MIS 65 (only 25 ka before the top of the Olduvai Chron, with an astrochronological age of 1.795 Ma) up to the top of Jaramillo sub-chron at MIS 25 (at about 0.99 Ma).

In 1996, the INQUA and International Commission of Stratigraphy (ICS) jointly proposed that the Early-Middle boundary of the Pleistocene should be at the Brunhes-Matuyama magnetic reversal boundary, at 0.781 ka (Fig. 2). However, this has not yet been ratified (Gibbard and van Kolfschoten, 2005). Head and Gibbard (2005) recommend the MIS 19 for this boundary, in which the Matuyama-Brunhes boundary occurs, even though this stage is not an exceptionally significant palaeoenvironmental event. The period covered by the Gelasian-Calabrian Stages (GCS) is delimited by the two shifts in astronomical forcing: from precession to obliquity at the Gauss-Matuyama (at 2.6 Ma), and from obliquity to eccentricity at the top of Jaramillo (at 0.9 Ma) (Fig. 2). The difference between the end of the Early Pleistocene and the end of the Calabrian covers a 200 ka-long period of transition between obliquity and eccentricity forcing. It is generally accepted that a first opening of the landscape would correlate to the Piacenzian-Gelasian transition and a second one to the final Calabrian / onset of the Middle Pleistocene. The Gelasian-Calabrian transition is not believed to correspond with any major environmental change (Cita et al., 2008).

The rest of the Pleistocene chronology is not so controversial, but it must be kept in mind that most of the more recent boundaries are actually not officially defined. In general, the Middle to Late Pleistocene limit is associated with the base of the Eemian period during the Marine Isotope Stage 5 (MIS 5).

In summary, the most significant change seems to be caused by the replacement of low-amplitude 41 ka obliquity forced climate cycles of the Early Pleistocene to, progressively, a high-amplitude 100 ka rhythm of eccentricity-dominated cycles during the Middle and Late Pleistocene (Raymo et al., 2004, Clark et al., 2006, Lisiecki and Raymo, 2007). This change relates to a substantial increase of global ice volume and parallels a transition to a strongly non-linearly forced climate system, with a profound effect on the vegetation landscape of the northern hemisphere (Head and Gibbard, 2005). Interestingly, this may have a connection with the regional extinction of cold-intolerant vascular plants (Svenning, 2003, Postigo et al., 2009).

4.- Iberian floras and vegetation during the Pleistocene

Early to Middle Pleistocene records are scarce while Late Pleistocene sequences are more abundant. Josefa Menéndez-Amor (Madrid, Spain) and Frans Florschütz (Leiden, the Netherlands) conducted pioneer palynological work in many sites of Spain (e.g. Menéndez-Amor and Florschütz, 1959), whereas Villalta and Vicente (1972) produced the first publications on the analysis of fossil leaves. Since that time, palaeobotanical studies and scientists became more numerous. In Portugal, the first Quaternary palaeobotanical works (palynology included) were carried out by Teixeira (1943), followed by Andrade (1944). Their research was later compiled by Zbyszewski (1953). Quaternary palaeobotanical work became more frequent since the 1970s (e.g. Diniz, 1972) and a first data collection was produced by Mateus and Queiroz (1993). Pleistocene anthracological research is relatively recent (Figueiral, 1990, for NW Portugal, Ros Mora, 1987, for Catalonia, Badal, 1991, and Grau, 1990, for the Valencia region in the Levant, Rodríguez-Ariza, 1996, for Andalusia, Uzquiano, 1992a, for the Cantabrian region) but currently, charcoal analysis is a common method for palaeoecological reconstruction (Allué, 2002, Carrión-Marco, 2005, Badal et al., 2008, Uzquiano, 2008).

4.1.- The Early Pleistocene (2.6-0.8 Ma)

Eight palaeobotanical Iberian sites of an Early Pleistocene age are discussed (Table 2). They have been selected either because of their extension in time or because they provide exceptional taxonomic resolution. The present level of information remains very patchy and involves some biases. Six of these sites are concentrated in north-eastern Spain (Garraf 1, Incarcal Crespià, Tres Pins, Bòbila Ordis, Molí Vell and Cal Guardiola; sites 104, 62, 72, 55, 66 and 56, respectively, in Fig. 1), and only one comes from the south (marine core ODP site 976, site 112 in Fig. 1). The remaining site comes from the central peninsula (Atapuerca, site 38 in Fig. 1). Another bias is in favour of low altitude sites, with the exception of Atapuerca (Table 2).

It is worth emphasizing that pollen records for this period have no analogs in the present vegetation both at the species composition and assembling levels (Fauquette et al., 1998a). Rather, similar, although not identical assemblages can be found in Asia and North America (Suc, 1980, Leroy, 1990, Roiron, 1992). The picture could also be somewhat inherited from the Pliocene, during which Fauquette et al. (1998a, 1998b) have suggested that temperature and precipitation were higher than currently in the interglacials and similar to the present in the glacial periods.

The Garraf 1 borehole record, offshore Barcelona (site 104 in Fig. 1), extends from the Late Miocene to the Early Pleistocene (Suc and Cravatte, 1982). The nineteen Pleistocene samples at the top of the core are largely dominated by conifers and *Artemisia* (Fig. 3). Other important arboreal taxa are Taxodiaceae and *Quercus*. In the underlying pollen zone, a coastal forest has been reconstructed, whose extent in the Early Pleistocene is reduced by the first glacial periods. These spectra have been correlated to MIS 108-98 (Suc and Popescu, 2005). Trends towards both cooling and aridification have been suggested (Fauquette et al., 1998a, 1998b). The northeastern site of Crespià (site 62 in Fig. 1), renowned for its rich mammal fauna, provides crucial palaeobotanical information through well-preserved leaf imprints (Villalta and Vicente, 1972). Four hundred specimens formed the basis for a new study of the two levels rich in leaves by Roiron (1983, 1992). Interglacial forests have been depicted with *Quercus cerris, Carpinus suborientalis, Carya minor, Acer integerrimum, Zelkova crenata, Parrotia persica* and *Carpinus orientalis*. This is largely a deciduous forest, but the assemblages include subxerophytic species (*Carpinus orientalis*, *Quercus cerris* and *Acer monspessulanum*). Following Roiron (1983, 1992), species identified are consistent with a Mediterranean type of climate.

Two pollen sequences at Tres Pins (site 72 in Fig. 1), south of Crespià, although non-dated, illustrate a glacial period dominated by *Pinus*, Asteraceae and Poaceae followed by an interglacial phase with *Carpinus betulus*-t., deciduous *Quercus*, *Carya* and *Ulmus-Zelkova* (Leroy, 1987, 1997). The top of the core is affected by shallowing of the lake as indicated by the development of *Cladium mariscus* and *Thelypteris palustris*, and by soil formation with non-polleniferous levels. The site of Bòbila Ordis (Fig. 4) is made of a succession of at least three lakes nested in each other and separated by faults and karstic collapses (Leroy, 2008). This site (site 55 in Fig. 1), has been studied by several generations of palynologists and yielded more than 250 samples (Elhaï, 1966, Geurts, 1977, Julià and Suc, 1980, Leroy, 2008). Lake 1, the oldest, is dated by palaeomagnetism (Løvlie and Leroy, 1995) and by micromammals (Leroy, 2008). It embraces at least one glacial-interglacial cycle. Lake 2 produced pollen assemblages typical of a glacial period: *Pinus*, Poaceae and Asteraceae (Leroy, 1988). In the sediment of Lake 3, large mammals bones have been found. Based on this and on the glacial and interglacial periods reconstructed by palynology, the Bòbila Ordis sequences have been correlated to MIS 36 to 33 (Elhaï, 1966, Geurts, 1977, Julià and Suc, 1980, Leroy, 1987). During the interglacials, a deciduous forest occurred, with deciduous *Quercus*, *Ulmus, Pinus*, *Carpinus betulus, Carya* and the *Parrotia persica*. The conifers such as hemlock or fir only developed at the end of the interglacials. The glacial periods are weakly developed, but the landscape opened up with the expansion of *Pinus*, Asteraceae, Poaceae, and eventually *Artemisia*. It has been suggested that Tres Pins is slightly older than Bòbila Ordis, on the basis of the occurrence of the ulteriorly extinct *Pterocarya, Carya* and *Parrotia persica*.

The site of Molí Vell (site 66 in Fig. 1), north of Rio Fluvià near Dosquers, was studied in outcrop, and twenty samples showed: i) a first phase of open landscape with *Pinus* and deciduous trees such as *Quercus, Tilia, Ulmus, Carya* and *Corylus*; ii) a second phase with increasingly forested landscape and development of deciduous forests especially with *Quercus, Carya* and *Ostrya*; and finally, iii) a slight re-opening of the vegetation, probably under cooler and wetter conditions, as suggested by decreasing *Quercus* and increasing *Carya-Abies* assemblages (Geurts, 1977, 1979, De Deckker et al., 1979). Geurts also published a very detailed analysis on the sublaminae of a varved unit from Molí Vell (De Deckker et al., 1979). Subannual pollen samples were analysed and showed the seasonal signal of successive plant blooming: *Quercus* in the beige layers which have been attributed to spring and *Tilia* and *Pinus* in grey layers linked to early summer.

Cal Guardiola (site 56 in Fig. 1), north of Barcelona, yielded a rich flora that came all from one chaotic debris flow, level D2, representing a snapshot of time somewhere between 1.2 and 0.8 Ma (Postigo et al., 2007). A hundred pieces of wood were identified, including *Acer* aff. *pseudoplatanus*, deciduous *Quercus*, *Aesculus hippocastanum, Ulmus, Acer campestre* and *Fraxinus angustifolia*. Twenty-five pollen samples and two coprolites provided a palynoflora suggestive of a mixed forest with significant amounts of evergreen *Quercus* with *Pinus* and Cupressaceae. The mesocratic group is represented by deciduous *Quercus*, *Viburnum opulus, Carya, Castanea* and *Juglans.* Small but significant amounts of Mediterranean taxa are also recorded: *Phillyrea*, *Pistacia*, *Cistus*, Thymelaeaceae and *Chamaerops*-type.

Only a small part of the Atapuerca sequence (province of Burgos, site 38 in Fig. 1), below horizon TD8, reaches the Early Pleistocene. Hominid remains have been found in the underlying horizon TD6 and have been dated by luminescence and palaeomagnetism (Berger et al., 2008, Parès and Pérez-González, 1999). A first study of TD6, TD5 and TD4 (although only five, two and one samples were studied, respectively; Cattani et al., 1994, García-Antón, 1995, 1998) and first data of new TD6 (Burjachs, 2001) reveal similar results: an open Mediterranean woodland (evergreen and deciduous *Quercus* with *Olea*) with herbaceous taxa (Poaceae and

Chenopodiaceae). *Celtis*, *Castanea, Ceratonia, Carpinus* t. *betulus* and Taxodiaceae are present in TD6. A more complete study is ongoing (Burjachs, pers. comm.).

The ODP site 976 in the Alboran Sea (site 112 in Fig. 1) yielded a 366 m long composite core (Combourieu-Nebout et al., 1999). A detailed analysis of the obliquity–forced MIS31 to 23 has become available recently (Joannin, 2007). Some difficulties for precise palaeoenvironmental reconstruction of Iberia are inherent to this marine sequence: 1) pollen sources are believed to be from both southern Spain and northern Africa; and 2) *Pinus* might be over-represented, as in all marine sequences. Several vegetation shifts are noticed, varying from prevailing mesothermic (such as *Quercus* and Ericaceae) to steppic phases (*Artemisia* and *Ephedra*). A mountain belt with *Cedrus, Tsuga, Abies* and *Picea* is also detected at altitude at the end of the interglacials. Cupressaceae is more abundant at the beginnings of interglacials. Asteraceae (especially liguliflorae), Caryophyllaceae and Poaceae are also well represented.

Some of the most famous failures to extract pollen from lake sequences should also be cited (Carrión et al., 2009): Baza-Orce, where at least five palynologists unsuccessfully worked with diverse lithological materials (Agustí and Julià, 1990, Gibert et al., 1988). From Mas Miquel quarry in Catalonia (site 65 in Fig. 1), dated by Early Pleistocene mammals, two attempts to analyse the pollen in twelve samples in lacustrine sediment failed as the results indicated poorly preserved pollen and pollution (Geurts, 1977, 1979, Leroy, 1990). The Incarcal quarry at Crespià (site 62 in Fig. 1), with its leaves and mammals bones, has also delivered only unsatisfactory results (Geurts, 1977, 1979, Suc, 1980, Leroy, 1990). Moreover, it is not uncommon that Early Pleistocene sites are poorly dated. Some longer sequences in Iberia with steps of vegetation changes have been correlated to the Piacenzian-Gelasian transition or to the Calabrian-Ionian transition with the danger of the "suck in" phenomenon (Baillie, 1991). The first phase of landscape opening was clearly shown in the Garraf 1 core (site 104 in Fig. 1; Suc and Cravatte, 1982), and the second step (in the transitional period between the end of the Calabrian and the beginning of the Middle Pleistocene) is perhaps recorded in the ODP 976 marine core (site 112 in Fig. 1) with the pronounced decrease of *Abies* in the coniferous forests (Combourieu-Nebout et al., 1999).

In conclusion, vegetational landscapes during the Late Pliocene-Early Pleistocene, were characteristically diverse. *Pinus* was quite an abundant and persistent element. In areas such as northeastern Catalonia, dense forests developed during the interglacials. Glacial periods are brief but the landscape opened up with the development of *Pinus*, Poaceae and Asteraceae liguliflorae (especially) and some tubuliflorae (but not so much *Artemisia*).

4.2.- The Middle Pleistocene (800-125 ka)

The scarcity of palaeobotanical data attributed to the Middle Pleistocene in Iberia, in respect to other Mediterranean regions from southern Europe such as Greece, Italy or France (which reveal even longer sedimentary records), is worth mentioning. The available information corresponds to fragmentary sequences, with a very low number of studied samples, which are geographically and chronologically discontinuous coverage (Table 1). In addition, most of the sites are not well dated and assigned only generally to glacial (Riss) or interglacial (Mindel-Riss) conditions. Exceptions include Atapuerca (site 38 in Fig. 1) in northern Spain (García-Antón and Sainz-Ollero, 1991, Cattani et al., 1994, García-Antón, 1995, 1998, Burjachs, 2001), and Morgandinho (site 35 in Fig. 1) in the Portuguese Algarve (Antunes et al., 1986), which show palaeoflora data for the end of the Early Pleistocene and the beginning of the Middle Pleistocene.

During the last few years several palynological studies have been made in marine cores from the Atlantic coast (Desprat et al., 2005, 2006, Roucoux et al., 2006, 2007) and the Mediterranean Sea (Combourieu-Nebout et al., 1999); but the correlation between marine and continental data is rather difficult due to the differences in source areas of pollen rain and the uncertainties of chronological models. The Morgandinho site (site 35 in Fig. 1) spans the end of the Early Pleistocene to the beginning of the Middle Pleistocene (Antunes et al., 1986). Only two samples show a landscape dominated by conifers, mainly *Pinus* that reaches 70%, but also *Picea* (3%) and *Keteeleria* (8%), as a signal of its persistence in the region during this period. The interpretation of the flora allowed the authors to locate the record at the limit between the Early and the Middle Pleistocene, perhaps between MIS 20 and 17. In the rest of the Portuguese sites (Table 1) attributed imprecisely to the Mindel-Riss interglacial or the Riss glaciations (Andrade, 1944, Teixeira, 1943, Zbyzewski, 1958), the presence of *Pinus*, *Quercus*, *Betula* and Ericaceae is noticeable.

In northeastern Iberia, further palaeoenvironmental data are recorded around Olot (Girona). Geurts (1979) studied five samples from a Middle Pleistocene sequence in Mas Grill (site 64 in Fig. 1) showing a climatically mild, forested environment dominated by *Pinus*, *Quercus* and *Alnus*. The presence of *Fagus*, *Ostrya*, *Juglans* and *Carya* was also noticed. At Val d'en Bas (site 73 in Fig. 1), below a volcanic crust dated at 250 ka ago (Cross et al., 1986), a *Pinus* forest with *Abies* and other mesophytes such as *Carpinus* and *Juglans* is recorded, linked with the warmest period of an interglacial. In the upper part of this sequence, colder and arid conditions are revealed by the dominance of *Pinus*. *Abies* and *Pinus* are also the main tree taxa of the nearby Plà de les Presses (site 68 in Fig. 1; Pérez-Obiol et al., 1986), at the same time. The base of Plà de l'Estany (site 67 in Fig. 1; Burjachs, 1990, 1994) recorded a later colder phase with steppe expansion (*Pinus,* Poaceae and Asteraceae), dated by the author as MIS 6, before the last interglacial. Pollen and charcoal studies from the Cuesta de la Bajada palaeontological site, in Teruel (site 58 in Fig. 1; Santonja et al., 2000, Uzquiano unpublished data, respectively) show *Juniperus thurifera* remains (>80%) with a slight presence of *Pinus sylvestris*-type (7.5%) at an estimated age of **>**300 ka (**>**MIS 9: Santonja, pers. comm.), associated to fauna and Mousterian lithic remains. Pollen analyses show that during MIS 6 an open landscape dominated by grasses and scattered *Pinus*, with some steppe elements (Santonja et al., 2000).

The Acheulean-Mousterian, Lezetxiki archaeological sequence in Guipúzcoa (site 17 in Fig. 1), northern Spain, attributed to the end of the Middle Pleistocene, shows *Pinus* forests with *Quercus, Castanea, Carpinus* and *Juglans* (Sánchez-Goñi, 1988, Isturitz and Sánchez-Goñi, 1990, Sánchez-Goñi, 1992). Nearby, at the open-air Palaeolithic settlement of Irikaitz (site 10 in Fig. 1; Arrizabalaga et al., 2003, Ruiz-Alonso, 2004) the floristic assemblage is attributed to an interglacial period (Eemian or Holsteinian) or, at least for the lowest levels, to the Cromerian (Arrizabalaga and Iriarte, 2005). Charcoal remains commonly include deciduous *Quercus* (between 50-70%), *Alnus* (6-17%), *Corylus* (6-15%) and *Fagus*, *Salix*, Rosaceae, *Fraxinus* and *Acer*. Sporadic evidences of *Carpinus, Ulmus, Frangula alnus, Populus* and Fabaceae are also noticed.

Several Middle Pleistocene palaeontological sites and fluvial terrace deposits have been studied in central Iberia. The longest is from The Galería, in the Atapuerca area, Burgos (site 38 in Fig. 1), which reaches 3 m depth (García-Antón and Sainz-Ollero, 1991), and is dated to 256 ka at the bottom and 200 ka at the top of the deposit (Berger et al., 2008). Being the only relatively continuous sequence of the site, it displays hiatuses and sections with poor pollen preservation (García-Antón and Sainz-Ollero, 1991, Cattani et al., 1994, García-Antón, 1995, 1998, Burjachs, 2001). Galería´s pollen record from Atapuerca is dominated by deciduous and evergreen *Quercus* and, occasionally, high frequencies of *Pinus* and *Cupressaceae*. Palynological diversity is high and includes Mediterranean (*Olea, Pistacia, Phillyrea, Myrtus, Vitis, Celtis* and *Ceratonia*) and temperate woody taxa (*Betula, Corylus, Carpinus, Alnus, Fagus, Acer, Juglans, Castanea, Platanus* and *Salix*) (Fig. 5) that fluctuate suggesting shifts in a mosaic landscape through time. The oldest phase is milder, as suggested by *Fagus* and Ericaceae. Afterwards, Mediterranean landscapes with *Olea* preceded a parkland steppe with *Pinus*, Poaceae and Asteraceae. Finally, a temperate Mediterranean forest developed (Fig. 5).

In the vicinity, the palaeontological sites of Torralba and Ambrona (Soria, sites 36 and 49 in Fig. 1, respectively, and around 150 m a.s.l. higher than Atapuerca), show open vegetation with *Pinus* parkland. In the first published study from Torralba (Menéndez-Amor and Florschütz, 1963), a steppe extension of Poaceae, Chenopodiaceae and *Pinus* was dated as from the Mindel-Riss period using faunal remains. More recent papers for Ambrona (Howell et al. 1995) and for both sites (Ruiz-Zapata et al., 2003b) also show the dominance of *Pinus*, but in alternation with *Juniperus* and phases of Poaceae, *Artemisia* and other composites. Other tree taxa such as *Quercus*, *Castanea, Fagus, Alnus, Betula, Juglans, Salix, Ulmus* and *Olea* are also present (Ruiz-Zapata et al., 2003b). Macro-remains of *Pinus sylvestris* have been identified in Torralba by Postigo (2003). Both Middle Pleistocene sites are not synchronous. In fact, Ambrona seems to have been occupied prior to Torralba (Pérez-González et al., 1997).

The pollen analyses of hyaena coprolites from Villacastín in Segovia (site 51 in Fig. 1; Carrión et al., 2007), attributed to MIS 6, also show a mosaic of open and wooded habitats with abundant *Pinus* and *Juniperus*, steppe-grassland areas and patches of mixed *Quercus* forest. In the same region, Menéndez-Amor and Florschütz (1963) published the sequence of Villaverde in Madrid (site 52 in Fig. 1) noticing a a similar steppe landscape of Poaceae, Chenopodiaceae and *Pinus*. The Formación Pinedo on the Tagus terraces (site 41 in Fig. 1; Martín-Arroyo et al., 1995, 1996a, Martín-Arroyo, 1998, Ruiz-Zapata et al., 2004) reveals a shifting mosaic of *Pinus* and *Quercus*, with continuous occurrences of *Olea, Juniperus,* Cistaceae and minor evidences of *Betula, Castanea, Ulmus, Juglans, Alnus, Fraxinus* and *Salix*. The authors attribute this alternation to different periods within the Riss glaciation (probably corresponding to MIS 9, 8, 7 and 6).

The peatbog of Padul in Granada (site 93 in Fig. 1) provides the longest pollen sequence from southern Spain. According to Florschütz et al. (1971) (but see controversy in Pons and Reille, 1988), the base of the sequence would include the Mindel-Riss interglacial and the Riss period. Pollen records depict an alternation of cold-steppe landscapes of *Pinus, Artemisia,* Chenopodiaceae and *Ephedra* with more temperate phases such as: i) the Granada interglacial (Mindel-Riss, Holstein) with significant forest development (arboreal pollen, AP, 60-70%) of *Abies, Tsuga, Fagus, Quercus, Ilex, Juglans* and *Vitis*; or ii) the Padul interstadial (during the Riss glaciation), where increases of *Quercus, Fagus, Ilex* and *Abies* are evident. Finally, the River Aguas sequence in Almería, dated as MIS 6, is characterized by low arboreal pollen percentages (*Pinus,* evergreen *Quercus* and *Olea*) while steppe taxa (*Artemisia,* Chenopodiaceae, *Ephedra, Lygeum* and Asteraceae) and shrubs dominate (Thymelaeaceae, *Myrtus* and Cistaceae) suggesting dry climate conditions (Schulte et al., 2008).

The *Homo heidelbergensis-neanderthalensis* site of Cueva Negra del Estrecho del Río Quípar in inland Murcia, southeastern Spain (site 82 in Fig. 1), provided palynological results (Carrión et al., 2003) with considerable diversity of trees and shrubs, including mesophytic conifers (*Pinus pinaster, Taxus*), broad-leaf (*Quercus, Corylus, Acer, Arbutus, Ulmus* and *Salix*) and warm-loving taxa (*Olea, Pistacia, Phillyrea* and *Cistus*). Based on Walker et al. (1998)´s chronostratigraphical inferences, these spectra were contextualized by Carrión et al. (2003) within the Late Pleistocene. Ulterior dating combined with palaeontological findings suggest an age older than 0.5 Ma (Walker et al., 2006, Scott and Gibert 2009), but the correspondence with the climatostratigraphy of the Middle Pleistocene is still to be elucidated.

Marine pollen sequences embracing the Middle Pleistocene: ODP 976 (site 112 in Fig. 1; Combourieu-Nebout et al., 1999), MD95-2042 (site 109 in Fig. 1; Sánchez-Goñi et al., 1999) (Fig. 6), MD01-2443 (site 105 in Fig. 1; Roucoux et al., 2006) and MD01-2447 (site 106 in Fig. 1; Desprat et al., 2006, 2007), show similar general patterns than continental records. Thus, steppe stages are characterized by *Ephedra, Artemisia* and Chenopodiaceae, occasionally with *Juniperus*, while temperate phases are featured by deciduous *Quercus, Corylus, Betula, Carpinus,* and Mediterranean elements. *Olea* and evergreen *Quercus* maxima represent thermic stages both in marine (MD01-2443: site 105 in Fig. 1; Roucoux et al., 2006) and inland pollen records (*i.e.* Atapuerca: site 38 in Fig. 1; García-Antón and Sainz-Ollero, 1991, or Formación Pinedo: site 41 in Fig. 1; Martín-Arroyo et al., 1995). *Pinus* pollen, generally over-represented in marine sediments, is difficult to interpret in terms of woodland cover. In any case, continental records with high values for *Pinus* pollen during the Middle Pleistocene correlate with marine records, thus indicating that pinewoods were widespread.

Finally, the Middle Pleistocene history of vegetation traces a modern flora with the relictual presence of *Keteeleria, Platanus, Carya, Ostrya,* and *Cedrus,* among others. *Juglans* and *Castanea,* formerly considered as reintroduced, never became extinct during this period (Sánchez-Goñi, 1988, García-Antón et al., 1990, Carrión and Sánchez-Gómez, 1992, Postigo et al., 2007, 2009).

4.3.- The Late Pleistocene (125-11.5 ka)

More data with a generally better chronological control are available for Late Pleistocene Iberian sites, but too many geographical and temporal discontinuities persist (Table 1, Fig. 7). The scarcity of Eemian records and of long sequences is noteworthy. Thereafter, we provide a regional description of palynological and macrobotanical records.

4.3.1.- North / Northwestern Iberia

Most of the available information is from 80 ka BP onwards (Table 1, Fig. 7), with the exception of Area Longa´s pollen record (site 2 in Fig. 1), which spans from MIS 5c to MIS 3 (Gómez-Orellana et al., 2007). The base of Area Longa (MIS 5c) is dominated by deciduous woodland (*Alnus*, *Quercus robur* type, *Corylus*, *Betula* and *Carpinus*) with relatively high contributions of *Fagus*. During the Lower Pleniglacial (MIS 4), high percentages of *Erica*, *Calluna* and Poaceae indicate heath and temperate grassland as predominant vegetation types with low prevalence of conifers and persistence of broad-leaf trees such as *Quercus robur* type, *Corylus*, *Fagus*, *Carpinus*, *Ulmus* and *Ilex* (Fig. 8). The possibility of long-distance pollen transport and sedimentary reworking has been shown to be negligible (Gómez-Orellana et al., 2007). In two Cantabrian caves (Covalejos and El Castillo, sites 4 and 6 in Fig. 1, respectively), charcoal remains assigned to the MIS 4 (Uzquiano, 1992b, 2007, in press) testify the presence of *Pinus sylvestris*-type and *Betula*. At El Castillo cave, above the Level 22, dated at <89 ka BP (U-Th date), an alternation of these taxa and the occurrence of *Fagus*, are noticed (Uzquiano, 1992a, 2007).

During the MIS 3, three phases of deciduous woodland expansion are observed in Area Longa (site 2 in Fig. 1): i) before 42 ^{14}C uncal. ka BP with dominance of deciduous *Quercus*; ii) a *Betula* phase between 42-35 uncal. ka BP and iii) a new predominance of deciduous *Quercus* around 33 uncal. ka BP (Gómez-Orellana et al., 2007). These cycles, along with smaller-scale fluctuations, correlate well with the ice-core record, including a vegetation response to Heinrich events and Dansgaard-Oeschger cycles. In addition, intermittent pollen occurrences of meso-thermophytes suggest nearby refugial areas. The oscillations observed in Area Longa during MIS 3 parallel those at Oia and Moucide (sites 20 and 19 in Fig. 1, respectively; Gómez-Orellana, 2002, Gomez-Orellana et al., 2007), Lagoa de Lucenza (site 14 in Fig. 1; Muñoz-Sobrino et al., 2001), Laguna Sanguijuela (site 32 in Fig. 1; Muñoz-Sobrino et al., 2004), Lleguna (site 34 in Fig. 1; Muñoz-Sobrino et al., 2004), and Lagoa de Marinho (site 31 in Fig. 1; Ramil-Rego et al., 1993a) pollen records.

Anthracological work in Asturian and Cantabrian caves confirms this mosaic of vegetation (Uzquiano, 2008) (Fig. 9). At El Esquilleu cave (site 8 in Fig. 1), the charcoal flora from the upper levels (39-36.5 uncal. ka BP) is diverse. *Pinus sylvestris*-type decrease (from 60% to <10%) in favour of a varied group of taxa such as *Betula, Juniperus, Corylus, Fraxinus, Salix, Sorbus aria, Prunus avium, Laurus nobilis, Rhamnus alaternus, Arbutus unedo*, Fabaceae, and Ericaceae, amongst others (Uzquiano 2008). At El Castillo and Covalejos caves (sites 6 and 4 in Fig. 1, respectively), *Betula* is also dominant during the interval 42-37 uncal. ka BP with an outstanding presence of *Sorbus,* and small amounts of *Pinus sylvestris*-type, *Corylus avellana, Hippophae rhamnoides, Laurus nobilis, Rhamnus alaternus,* Ericaceae and Fabaceae (Uzquiano, 2008). El Conde cave (site 7 in Fig. 1) reveals *Pinus sylvestris*-type dominance in association with *Betula*, *Sorbus* and the presence of deciduous *Quercus*. In addition, the earliest evidence of *Quercus ilex* charcoal in the Cantabrian region is recorded (>38 and around 31-29 uncal. ka BP) (Uzquiano et al., 2008), in correspondence with the last phase of the Area Longa MIS 3 sequence (site 2 in Fig. 1). In Cobrante cave (site 3 in Fig. 1), *Betula* is dominant (>90%) around 30 uncal. ka BP and, in Sopeña rockshelter (site 22 in Fig. 1), *Juniperus* is the main taxon (53%) alternating with heathland shrubs (26%), some *Pinus sylvestris*-type evidences and *Betula, Salix* and Fabaceae (Uzquiano, unpublished data) showing the climatic deterioration prior to MIS 2.

Pollen spectra and charcoal remains assigned to MIS 2 reveal open landscapes from 21,000 to 17 cal. ka BP (Lago de Ajo site 12 in Fig. 1; Lagoa de Lucenza, site 14 in Fig. 1; Laguna Sanguijuela, site 32 in Fig. 1; La Roya, site 29 in Fig. 1; Altamira cave, site1 in Fig. 1; Cobrante cave, site 3 in Fig. 1), indicating cold and dry conditions with *Artemisia* and *Pinus-Juniperus* woods as dominant at a regional scale, but with deciduous trees in all localities (McKeever, 1984, Uzquiano, 1992a, Allen et al., 1996, Muñoz-Sobrino et al., 2004, 2007). *Salix* and *Juniperus* were the main taxa exploited by Cantabrian prehistoric humans in those times (Uzquiano, 1992a, 1992b, in press). During the Lateglacial, pollen sequences show the expansion of *Pinus* and *Juniperus*, as well as increasing frequencies of deciduous taxa, mainly *Betula* and *Quercus* were obtained (Lago de Ajo, site 12 in Fig. 1: Mckeever, 1984, Allen et al., 1996; Lagoa de As Lamas, site 30 in Fig. 1: Maldonado, 1994; La Roya, site 29 in Fig. 1: Allen et al., 1996; Pozo de Carballal, site 21 in Fig. 1: Muñoz-Sobrino et al., 1997; Lagoa de Marinho, site 31 in Fig. 1: Ramil-Rego et al., 1993a, Muñoz-Sobrino et al., 2007). Similar results are shown by charcoal analyses from cave sites, with deciduous and evergreen *Quercus, Corylus, Castanea, Fagus, Acer* and *Betula* (Uzquiano 1992a, 1998), associated with the dominant taxa *Juniperus*, *Salix,* Fabaceae and *Pinus* (*i.e.* Los Azules and Las Caldas in Asturias, sites 18 and 16 in Fig. 1, and Altamira, Cobrante, El Linar, Cualventi, La Pila and Las Aguas in Cantabria, sites 1, 3, 9, 5, 11 and 15 in Fig. 1, respectively) (Uzquiano, 1992a, in press). Both pollen and charcoal depict steppe expansions as particularly significant from 12,600 to 11,700 cal. yr BP (Uzquiano, 1998, Muñoz-Sobrino et al., 2007).

In Charca da Candiera (site 26 in Fig. 1), at the Serra da Estrela (Portugal), *Quercus* forest developed early between 14,060-12,850 cal. yr BP, followed by a rapid contraction and a new steppe development (van der Knaap and van Leeuwen, 1997). At the Guadiana estuary (site 28 in Fig. 1), the core CM5 (Beliche, Portugal) also recorded an evergreen and semi-deciduous *Quercus* forest without the sclerophyllous taxa that define the Holocene in the area (*Olea, Phillyrea* and *Pistacia*) at 13,000-12,840 cal. yr BP (Fletcher et al., 2007). The arrival of the Younger Dryas is characterized by the increase of *Pinus*, low *Quercus* percentages and the expansion of *Juniperus, Ephedra distachya* type, *Artemisia* and *Centaurea* (Fletcher et al., 2007).

In the Portuguese Estremadura, most information has been obtained from the study of archaeological charcoal (Aubry et al., 2001, Figueiral, 1993, 1995, Figueiral and Terral, 2002, Zilhão et al., 1995) recovered from one open-air site (Cabeço de Porto Marinho, site 25 in Fig. 1), and four caves (Lapa do Anecrial, Buraca Escura, Buraca Grande and Gruta do Caldeirão, sites 33, 23, 24 and 27 in Fig. 1). In the lowlands, the earliest data assigned to the MIS 3 were obtained in the Aurignacian (33,000 uncal. yr BP) and Gravettian (23,500 uncal. yr BP) levels from Cabeço de Porto Marinho (site 25 in Fig. 1). In this site, the assemblage (*Pinus sylvestris*-type, *Pinus pinaster-pinea*, Fabaceae and *Erica*) seems to show open steppe-like communities, although evergreen *Quercus* are also present. During the MIS 2, plant species usually associated with open mountain-type habitats, are identified by charcoal at Lapa do Anecrial (site 33 in Fig.

1), Buraca Escura (21,820±200 uncal. yr BP; site 23 in Fig. 1), Buraca Grande (23,920± 300 and 17,850± 200 uncal. yr BP; site 24 in Fig. 1) and Gruta do Caldeirão (Solutrean levels; site 27 in Fig. 1). The plant assemblage identified includes *Pinus sylvestris*-type, Fabaceae (in all sites), *Erica* (Lapa do Anecrial) and *Buxus sempervirens* (Buraca Escura, Buraca Grande, Gruta do Caldeirão). However, at Buraca Grande (site 24 in Fig. 1) and Gruta do Caldeirão (site 27 in Fig. 1), more thermophilous elements such as *Olea,* evergreen *Quercus*, *Rhamnus* and *Phillyrea* were identified, indicating that these plants could have survived in sunlit slopes of protected areas. Western Iberia could thus be also considered as a refuge area for thermophilous taxa during the colder periods of the Pleistocene. This would explain the early Holocene development of species such as *Olea* (Figueiral, 1998). Additional charcoal data for the late MIS 2 are available from Cabeço de Porto Marinho (site 25 in Fig. 1), where Magdalenian levels testify the remarkable spread of Mediterranean *Pinus* (*pinaster* - *pinea*) and the gradual disappearance of *Pinus sylvestris*-type. The charcoal assemblages are here dominated by evergreen species and only two deciduous elements are recorded (*Quercus* and *Fraxinus*) (Figueiral, 1993, Zilhao et al., 1995). At that time, *Pinus* woodland appeared to replace more open plant communities in western Iberia.

4.3.2.- Central Iberia

In Central Iberia, no long palaeobotanical sequences are available for the Late Pleistocene. The oldest data from MIS 5 (110-80 ka BP) have no temporal continuity due to the existence of hiatuses and/or the short timespan recorded (Formación Pinedo, in Toledo, site 41 in Fig. 1: Martín-Arroyo et al., 1999). Pollen data from Formación Pinedo resemble those obtained for the rest of the Iberian Peninsula. *Pinus* is accompanied by relatively dense Mediterranean scrub with *Olea*, *Juniperus* and evergreen *Quercus*, along with some riparian elements such as *Salix*. The development of the Mediterranean vegetation is in agreement with the current bioclimatic characteristics of these areas of Central Spain (Blanco-Castro et al., 1997) and the typical Eemian vegetation formations from Mediterranean areas, where *Olea* dominates (Tzedakis, 1994, Carrión et al., 1998, Sánchez-Goñi et al., 1999, Klotz et al., 2003). The study of Carrión et al. (2007) at Villacastín in Segovia, and Torrejones in Guadalajara (sites 51 and 50 in Fig. 1, respectively), explored vegetation change during the period 80,000-60,000 years ago (MIS 4). The pollen assemblages indicate the existence of woody taxa (*Quercus*, *Taxus*, *Betula*, *Castanea*, *Prunus*, Ericaceae and *Juniperus*) in a steppe landscape dominated by grasses, with abundant *Artemisia* and other composites, and the occasional presence of *Ephedra nebrodensis* and Caryophyllaceae. Unpublished data from anthracological analysis in Camino rockshelter (site 40 in Fig. 1) and Buena Pinta cave (site 39 in Fig. 1), both in Madrid, reveal poor charcoal remains preservation, *Pinus sylvestris*-type being the most relevant taxon while *Quercus*, *Fraxinus, Sorbus/Crataegus,* Pomoideae*, Salix* and *Populus* are also present (Uzquiano, pers. comm.).

The palaeoenvironmental reconstruction available for MIS 3 and 2 is only based on three sequences from Ciudad Real: Tablas de Daimiel-TD (site 48 in Fig. 1), in the National Park of Tablas de Daimiel (Valdeolmillos, 2005, Valdeolmillos et al., 2003), Fuentillejo *maar* lake (site 42 in Fig. 1; Vegas et al., 2008), in the central Spanish volcanic Field of Calatrava, and Arenales de San Gregorio-TASG-1 (site 37 in Fig. 1; Ruiz-Zapata et al., 2000) in the NW of Ciudad Real. The sequence TD (site 48 in Fig. 1) presents frequent sterile levels but some inferences can be made (Valdeolmillos et al., 2003). *Betula* formations are firstly replaced by *Pinus* and *Juniperus* later, culminating with the development of an open landscape where Poaceae and Chenopodiaceae dominate. These spectra reflect cold and arid conditions and they are associated to Heinrich events: H4 at about 36,000 uncal. ^{14}C years (between 11. 2 and 10.8 m depth of the TD sequence) and H3 at about 28,000 uncal. ^{14}C years and located between 7.8 and 7.4 m depth (Valdeolmillos et al., 2003). Similar conditions are detected in the Fuentillejo sequence (FUENT-

1, site 42 in Fig. 1) by Vegas et al. (2008) during the MIS 2, with possible temperature fluctuations during arid phases. The sequence Arenales de San Gregorio (site 37 in Fig. 1) corresponds to a clay dune dated by OSL/TL to the Last Glacial Maximum (LGM): 23-22 ka (Ruiz-Zapata et al., 2000). At that time, the strong seasonal variation and the scarcity of woody vegetation would facilitate the existence of aeolian processes and dune formations as Arenales de San Gregorio-TASG-1. Pollen analysis reveals the existence of steppe vegetation adding to low occurrences of *Pinus, Juniperus*, *Quercus*, *Betula*, *Corylus* and *Castanea*. Finally, a short pollen record was carried out at Mesa de Ocaña-MO in Toledo (site 46 in Fig. 1), by Ruiz-Zapata et al. (2000). This study was done on a sandy loess formation, dated as Younger Dryas (11 ka BP) using IRSL. Along 2.70 m depth, a progressive loss of the arboreal vegetation, mainly constituted by *Pinus*, takes place. Then, *Pinus* is replaced by *Juniperus* and finally, by steppe formations. Scattered occurrences of *Quercus*, *Betula*, *Corylus* and *Alnus* are also recorded.

Ruiz-Zapata et al. (2003a) studied a pollen core from Laguna Grande (site 45 in Fig. 1), at Sierra de Neila in the Iberian System, which covers the cold events H2 (c. 21 cal. ^{14}C ka BP) and H1 (c. 14 cal. ka ^{14}C BP). The pollen assemblages are typical of cold and arid conditions (*Artemisia* and Chenopodiaceae dominance), but *Betula, Fagus*, *Corylus*, *Ilex* and evergreen and deciduous *Quercus* developed after both Heinrich events indicating the abrupt climatic oscillations that characterized the Lateglacial period. More data from this period are shown in Hoyos de Iregua (site 43 in Fig. 1; Gil-García et al., 2002), Laguna del Hornillo (site 44 in Fig. 1; Gómez-Lobo, 1993) and Quintanar de la Sierra sequence (site 47 in Fig. 1; Peñalba et al., 1997). All these sites reveal an herbaceous vegetation with isolated *Pinus* and *Betula,* shaping a savannah-like landscape. The presence of meso-thermophilous taxa such as deciduous *Quercus*, *Corylus* and evergreen *Quercus* is not negligible. During the Younger Dryas event, an important tree reduction is observed.

4.3.3.- Northeastern Iberia

The overall picture is not different from the former, and includes *Pinus* forests with or without *Juniperus*, *Juniperus*-dominated formations, mixed *Pinus-Quercus* forests, patches of mesophilous trees, savannah-like vegetation, grasslands and steppes, which fluctuate in response to stadial/interstadial shifts. Pollen data concerning MIS 5 lack chronological control, although the study of a new long pollen sequence covering all the Late Pleistocene and Holocene is currently in progress (El Cañizar de Villarquemado, in Teruel, site 59 in Fig. 1: González-Sampériz, in preparation).

The Pla de l'Estany pollen record (site 67 in Fig. 1; Burjachs, 1990) shows in its zone B an important tree component dominated by *Abies, Fagus,* deciduous *Quercus*, *Carpinus* and other mesophytes, pointing to the Eemian s.s. (5e) during MIS 5. Concerning MIS 4, only Abric Romaní (Fig. 7 and Fig. 10), near Barcelona (site 53 in Fig. 1), shows a well-dated palaeobotanical information during 70-40 ka BP, with tree pollen percentages of 40-60%, dominated by *Pinus* but with continuous presence of *Juniperus, Rhamnus, Quercus, Olea-Phillyrea, Betula, Fagus, Pistacia* and other woody taxa (Burjachs and Julià, 1994). Similar data are provided at Pla de l'Estany (site 67 in Fig. 1; Burjachs, 1990) and, during the MIS 3, at l'Arbreda cave (site 63 in Fig. 1; Ros Mora, 1987, Burjachs, 1993) and Banyoles (site 54 in Fig. 1; Pérez-Obiol and Julià, 1994); the hyena coprolites from Gabasa cave (site 61 in Fig. 1; González-Sampériz et al., 2003) and El Portalet (site 60 in Fig. 1; González-Sampériz et al., 2006) in Huesca; and San Juan de Mozarrifar in Zaragoza (site 70 in Fig. 1; González-Sampériz et al., 2005), show a tree component dominated by *Pinus* and *Juniperus* with the presence of evergreen and deciduous *Quercus* and other woods such as *Betula, Corylus, Alnus, Tilia, Buxus* and even *Olea-Phillyrea*. The xerophytic component is composed of Poaceae, Asteraceae, Chenopodiaceae, *Ephedra fragilis* and *distachya* types and/or *Artemisia* in the whole sequences. Both pollen and charcoal reveal a mosaic-like landscape dominated by conifers (*Pinus sylvestris*-

type followed by *Juniperus*), associated with evergreen and deciduous *Quercus, Corylus, Buxus sempervirens, Acer opalus* and *A. monspessulanum, Sorbus domestica, Rhamnus cathartica, R. alaternus, Prunus amygdalus*, and even *Fagus sylvatica,* as shown at Cova 120 (site 57 in Fig. 1) and l'Arbreda cave (site 63 in Fig. 1) by anthracological analyses (Agustí et al., 1987, Ros Mora, 1987, Burjachs and Allué, 2003).

The MIS 2 in north-eastern Spain is served by more substantial information. Both Banyoles (site 54 in Fig. 1) and l'Arbreda cave (site 63 in Fig. 1) show savannahs of *Pinus* with *Juniperus,* along with the presence of *Betula, Acer, Corylus,* deciduous and evergreen *Quercus, Tilia, Alnus, Ulmus, Salix* and *Olea* among others, indicating the location of regional refugial areas in a patched landscape still dominated by steppes of Poaceae and *Artemisia* (Pérez-Obiol and Julià, 1994). In the Central Pyrenees a relative abundance of palynological data occurs in the Gállego valley, with Tramacastilla (site 71 in Fig. 1; Montserrat, 1992) and El Portalet sequences (González-Sampériz et al., 2006), amongst others (González-Sampériz et al., 2005). At El Portalet peat bog (site 60 in Fig. 1), a sedimentary hiatus coeval to the LGM and associated to a glacier readvance, is observed between 22-18 cal. ka BP. After that, with the beginning of the Lateglacial period, some mesophytes (mainly *Betula*) as well as *Pinus* and *Juniperus* develop, behaving like pioneer trees during the Bølling and Allerød warm phases. Lowland records of this area, as Salada de Mediana (site 69 in Fig. 1; Valero-Garcés et al., 2000a, 2000b, González-Sampériz et al., 2003) provide further, circumstantial evidence for the existence of regional and/or local populations of *Juniperus*, evergreen and deciduous *Quercus, Corylus, Betula, Salix, Alnus, Juglans, Pistacia, Myrtus, Rhamnus,* and *Olea*. The high frequencies of *Corylus* pollen at this sequence can be interpreted as the local existence of a refugial area under a regionally savannah-steppe dominance. Another striking feature of the Salada de Mediana pollen diagram is its relatively high AP values by comparison with present-day xeromorphic vegetation (evergreen *Quercus*: 10-20%, *Corylus*: 10-40%, *Pinus*: 30-60% and *Juniperus*: 10-25%).

4.3.4.- South-Southeastern Iberia

The Levant and south-southeastern areas show a particularly high diversity of landscapes during the Late Pleistocene, including mountain grasslands and lowland steppes, coniferous savannahs and forests in mid-altitudes, and refugial populations of trees and shrubs in coastal shelves and intramontane valleys during the coldest stages (Carrión et al., 2008). The most frequent tree genera included *Pinus, Quercus, Juniperus, Abies, Corylus, Betula, Alnus, Ulmus, Salix, Castanea, Fraxinus, Juglans, Acer, Sorbus, Taxus, Olea, Pistacia, Phillyrea, Arbutus* and *Myrtus*.

The most significant palaeobotanical records are the nearby Padul and Carihuela sequences (sites 93 and 78 in Fig. 1, respectively), in Granada (Florschütz et al., 1971, Pons and Reille, 1988, Carrión, 1992a, Carrión et al., 1998, 1999, Fernández et al., 2007), covering the majority of the Late Pleistocene (MIS 5, 4, 3 and 2) (Fig. 7). No other data are referenced in the Levant in respect to MIS 5 and 4, except an assignment of "pollen zone A" from Laguna de Villena (site 87 in Fig. 1), in Alicante (Yll et al., 2003), dated as older than 47,450 uncal. ^{14}C BP and attributed by the authors to the Early Würmian Pleniglacial (around MIS 4) based on the high percentages of steppe taxa (40% of *Artemisia* and abundance of *Ephedra*). It is noticeable that at the same level of Laguna de Villena, AP also reaches high values and it is composed mainly by *Pinus* followed by *Juniperus*, evergreen *Quercus* and the presence of deciduous *Quercus, Corylus, Betula, Alnus, Ulmus, Tilia* and *Olea*. These spectra are especially relevant to demonstrate the continuous presence of arboreal populations in the region, as well as during the MIS 3 in Navarrés (site 91 in Fig. 1; Carrión and van Geel, 1999), Laguna de San Benito (site 86 in Fig. 1; Dupré et al., 1996) and Malladetes cave (site 90 in Fig. 1; Dupré, 1988) in Valencia, Cova Beneito in Alicante (site 79 in Fig. 1; Carrión and Munuera, 1997) and Perneras cave in Murcia (site 94 in Fig. 1; Carrión et al., 1995). All these sequences show an important Mediterranean component with evergreen *Quercus, Olea*, *Pistacia* and *Myrtus*, despite the existence of steppe formations, and next to coniferous woodlands with mesophytes. In addition, a significant presence of hyper-thermophilous scrub can be observed in the Mousterian sites of Perneras cave (site 94 in Fig. 1) and Sima de las Palomas (site 99 in Fig. 1) in the Murcian coast (*i.e.*, *Periploca, Osyris, Withania, Maytenus,* and *Myrtus*) (Carrión et al., 1995, 2003).

The Lateglacial period is also characterized in this area by a great biodiversity of vegetation landscapes, which include *Pinus* forests with or without *Juniperus*, Mediterranean formations with thermophytes, deciduous trees, grasslands and steppes (see the pollen diagrams of Túnel dels Sumidors in Valencia (site 101 in Fig. 1; Dupré, 1988), Salines in Alicante (site 95 in Fig. 1; Giralt et al., 1999) or Algarrobo cave (site 74 in Fig. 1; Munuera and Carrión, 1991, Carrión et al., 2003), besides the previously mentioned sites for MIS 3.

In respect to charcoal remains (Fig. 9), only six archaeological sites (caves and rockshelters) with anthracological analyses are available from southeastern Iberia: Cova Beneito, Tossal de la Roca, Cova de Les Cendres, La Ratlla del Bubo, Cova Bolumini and Santa Maira (sites 79, 100, 81, 85, 80 and 97 in Fig. 1 and Table 1, respectively). MIS 3 conditions are shown by data from Cova Beneito (site 79 in Fig. 1), with mainly *Pinus sylvestris*-type and scant *Juniperus phoenicea* (Uzquiano unpublished data). During the Lateglacial, *Pinus nigra* dominated an assemblage also formed by *Juniperus*, Fabaceae, *Buxus sempervirens, Pistacia terebinthus* and *P. lentiscus, Olea europaea* var. *sylvestris*, *Ephedra*, *Rhamnus, Crataegus, Fraxinus oxyphylla, Ficus* and *Cistus*. *Quercus faginea* and *Q. ilex-coccifera* increased when the Holocene approaches (Badal, 1991). At Tossal de la Roca (site 100 in Fig. 1), for example, *Quercus faginea* type had its first appearance around 15 uncal. ^{14}C ka BP, developing a continuous presence from 12.4 uncal. ^{14}C ka BP on, and became dominant in the Early Holocene (Uzquiano, 1988, Cacho et al., 1995) while in Santa Maira (site 97 in Fig. 1), both in Alicante, *Pinus halepensis, P. pinea-pinaster, Rosmarinus* and *Hedera* were present along with evergreen *Quercus* (increasing frequencies) and deciduous *Quercus* (which decreased in the upper part of the Lateglacial, Magdalenian occupations), marking the transition to the Holocene (Aura et al., 2005).

As mentioned earlier, the Late Pleistocene floras of southern Iberia are mainly known due to two long records (Fig. 11): Padul peat bog (site 93 in Fig. 1; Florschütz et al., 1971, Pons and Reille, 1988) and Carihuela cave (site 78 in Fig. 1; Carrión et al., 1998, 1999, Fernández et al., 2007), which add to some short pollen sequences (see Table 1) and the hyena coprolites pollen records from Las Ventanas and Gorham's caves (sites 88 and 83 in Fig. 1; Carrión et al., 2001 and 2008, respectively). The main features of this period are:

- a MIS 5 (Eemian period, last Interglacial) dominated by *Olea* and *Quercus* formations with a great diversity of conifers, deciduous and evergreen, mesothermophilous woods: *Pinus, Abies, Cedrus, Taxus, Juniperus, Alnus, Betula, Acer, Corylus, Ulmus, Fraxinus, Buxus* and *Vitis* in Padul (site 93 in Fig. 1; Pons and Reille, 1988) and *Pinus, Juniperus, Alnus, Betula, Corylus, Ulmus, Fraxinus, Juglans, Salix, Castanea, Pistacia, Myrtus, Buxus,* Ericaceae and *Phillyrea* in Carihuela (site 78 in Fig. 1; Carrión et al., 1998);

- During the MIS 4- MIS 3 an alternation of i) *Artemisia,* Poaceae, Asteraceae, Chenopodiaceae and *Ephedra distachya* steppes and, ii) forest taxa development that includes mainly *Pinus* and some *Quercus*, Oleaceae and other trees. Apart from Padul and Carihuela, this pattern is seen at Boquete de Zafarraya and Bajondillo caves in Málaga (sites 77 and 76 in Fig. 1; Lebreton et al., 2006 and López-Sáez et al., 2007, respectively); and Gorham's cave in Gibraltar (site 83 in Fig. 1; Carrión et al., 2008). Charcoal remains indicate *Pinus* as dominant taxum with *Pinus nigra* (Nerja cave in Málaga, site 92 in Fig. 1: Badal, 1991; Aura et al., 2002) and *Pinus pinea-pinaster* (Gorham's cave in Gibraltar, site 83 in Fig. 1: Carrión et al., 2008), followed by Fabaceae, *Juniperus, Cistus, Rhamnus-Phillyrea, Olea, Prunus, Sorbus-Crataegus, Erica* and *Quercus* sp.

- a Lateglacial *Quercus* colonisation suggesting the proximity of glacial refugia for woody taxa. The mid-elevation Siles lake record in Jaén (site 98 in Fig. 1) is especially relevant here, because its pollen diagram shows a continuous presence of arboreal populations, a "tree reservoir", in the Andalusian mountain ranges at middle altitudes (Carrión, 2002a). A littoral pollen sequence from San Rafael, Almería (site 96 in Fig. 1; Pantaleón-Cano et al., 2003) also shows continuous curves for evergreen and deciduous *Quercus*, as well as for *Olea,* during the LGM and the Lateglacial. Charcoal data from Hoyo de la Mina in Málaga (site 84 in Fig. 1; Uzquiano, unpublished data) and Gorham's cave (site 83 in Fig. 1; Carrión et al., 2008) reflect, at 18 cal. ^{14}C ka BP, a dominant *Quercus ilex – Olea - Pinus pinaster-pinea* complex followed by Fabaceae, deciduous *Quercus*, *Pistacia lentiscus*, *Phillyrea, Juniperus, Fraxinus, Salix-Populus, Quercus suber* type, *Crataegus, Sambucus, Arbutus, Rhamnus alaternus* and *lycioides, Prunus* sp., *Cistus* sp., *Rosmarinus, Lonicera, Smilax* or *Viscum*, while Ambrosio cave, in Almería (site 75 in Fig. 1), shows at around 16.5 cal. ^{14}C ka BP (Rodríguez-Ariza, 2005), a charcoal content dominated by *Juniperus* sp., followed by *Pinus sylvestris*-type, *Prunus* and the presence of *Quercus faginea, Quercus ilex-coccifera, Cistus, Rosmarinus* and Fabaceae. Similar data were obtained at Nerja cave (site 92 in Fig. 1) and La Ratlla del Bubo rockshelter (site 85 in Fig. 1; Badal, 1991).

4.3.5.- Marine records

Nine Iberian margin marine sequences have yielded pollen analyses for the Late Pleistocene period (timespan and coordinates are included in Table 1). They are, from N-NW to SW-S-SE: MD03-2697 (site 107 in Fig. 1; Naughton et al., 2007, Sánchez-Goñi et al., 2008), MD99-2331 (site 111 in Fig. 1; Sánchez-Goñi et al., 2005, Naughton et al., 2007), MD95-2039 (site 108 in Fig. 1; Roucoux et al., 2001, 2005), SO75-6KL (site 113 in Fig. 1; Boessenkool et al., 2001), MD95-2042 (site 109 in Fig. 1; Sánchez-Goñi et al., 1999, 2008), SU 8113 (site 114 in Fig. 1; Parra, 1994, Carrión et al., 2000, Magri and Parra, 2002), 8057B (site 102 in Fig. 1;

Hooghiemstra et al., 1992), ODP 976 (site 112 in Fig. 1; Combourieu-Nebout et al., 1999, 2002, 2009) and MD95-2043 (site 110 in Fig. 1; Sánchez-Goñi et al., 2002, Fletcher and Sánchez-Goñi, 2008). Overall, the same vegetation trends and main dominant taxa (excepting *Pinus* and, evidently, *Cedrus* inputs from northern Africa) are shown in respect to continental records. Fletcher and Sánchez-Goñi (2008) suggest a strong similarity between the MD95-2043 Alborán record (site 110 in Fig. 1) and the Padul sequence (site 93 in Fig. 1; Pons and Reille, 1988), at a regional point of view. In both records, *Quercus ilex, Q. suber* and deciduous *Quercus* type's have a continuous presence and develop during interstadials, in opposition to steppe taxa fluctuations. In addition, Sánchez-Goñi et al. (1999, 2008) record in the Portuguese margin (site 109 in Fig. 1), at the MD95-2042 (Fig. 12), a *Quercus* forest development associated to the last interglacial, with the typical presence of *Carpinus* and *Olea* (with low values) that characterize the Eemian Mediterranean period in continental sequences (Tzedakis, 1994, Carrión et al., 1998, Klotz et al., 2003).

4.4.- Summary remarks

Vegetation changes recorded in Iberia during the Pleistocene match regional and global climatic changes, in spite of local particularities observed in continental records that respond to the varied mosaic and patched vegetation landscape formed by coeval steppes, savannahs and forests. Regional characteristics emerged as soon as for the Middle Pleistocene, if not earlier: Ericaceae in the Atlantic coast, thermo-mediterranean elements in the south, and broad-leaf trees in the northeastern. Unfortunately, no data are available from each region. The Early Pleistocene already shows glacial periods with very open vegetation, often characterised by a steppe with abundant Asteraceae liguliflorae. Few Middle Pleistocene records exist so far; they show that there are still some plant extinctions (Arctotertiary woody taxa) but their precise timing is still unknown. Glacial steppes seems to be still dominated by Asteraceae other than *Artemisia* in the

N-E, while *Artemisia* spread in the inland and the southeast sequences, showing possible moisture differences across the Iberian Peninsula. The Late Pleistocene record is rather well covered, but the Eemian (MIS 5e) still remains very poorly documented. For glacial steppes, both herbaceous assemblages were recorded but *Artemisia* dominates, excepting in the Cantabrian region. Again, more data are necessary to take into account the dominance of *Artemisia* in glacial steppes across Iberia as a response to increasing xericity.

The climatic influences are obvious since both pollen and charcoal data allow us to mark a thermic and moisture availability gradient, as in present times, between N-NW regions (with more cool-cold steppes and higher moisture conditions translated to mesophytes expansion during improved climatic conditions) and Mediterranean areas of Iberia (where thermophytes survived during glacial times, and the steppe components imply very dry conditions). Nevertheless, the most significant and common nexus amongst all the Iberian territory during the Pleistocene (particularly during the Late Pleistocene) was the set of evidences recorded in terms of refugial areas for mesothermophilous taxa, as we shall discuss later.

5.- Discussion

5.1.- Controls of vegetation changes during the Pleistocene: Milankovitch cyclicity, suborbital forcing and amplitude of changes

Pleistocene floras of Iberia are strongly dependent on their geographical location and on contrasting topography. Climate forcing on vegetation change has been of crucial importance as well (Tzedakis et al., 2003, Tzedakis, 2007, Claussen, 2008, Claussen et al., 2008, Berger et al., 2008, Fletcher and Sánchez-Goñi, 2008). The most significant changes appear to have occurred in pace with orbital forcing, especially with the replacement of 41 ka obliquity climate cycles by 100 ka rhythm of eccentricity dominated cycles (Raymo et al., 2004, Clark et al., 2006, Lisiecki and Raymo, 2007). These climate changes imply increases of severity and duration of cold stages, and have had a strong effect in physical landscape (Head and Gibbard, 2005), including vegetation. Not in vain, they may have been a "coup de grâce" to the disappearance of tree genera like *Aesculus, Parrotia* and *Zelkova* (Postigo et al., 2007, 2009).

It is well known that, in orbital frequencies, there is a general correspondence between tree population size and composition, and ice volume extension, marking strong variations between glacial and interglacial periods (Tzedakis et al., 2003). In the Early and Middle Pleistocene successions, Milankovitch cycles have been so far observed in only a few sequences because few go beyond one climatic cycle (*i.e.* Bòbila Ordis, Atapuerca, Padul and ODP 976). In Bòbila Ordis, glacials and interglacials have been correlated to MIS 36-33 owing to the presence of the Cobb Mountain subchron. Rapid and frequent changes in vegetation are linked to obliquity forcing, but the glacial minima and the interglacial maxima are less extreme than after the end of the Early Pleistocene (Leroy, 2007). The diagrams of Bòbila Ordis, Tres Pins, Padul, Val d'en Bas, Pla de l'Estany, Atapuerca and ODP 976 (see Table 1 for references) show periods of drastic deforestation with < 20 % of mesic pollen component in glacial phase. Some fairly large fluctuations between levels can be also observed in Early-Middle Pleistocene records (Andrade, 1944, Teixeira, 1943, Zbyzewsky, 1958, Suc and Cravatte, 1982, Suc and Popescu, 2005), although each glacial-interglacial cycle of shorter sequences is probably represented only by 1 or 2 samples.

Even though the lengths of pre- and post-temperate phases of the different interglacial floristic compositions have varied through time, the duration of these temperate parts has remained relatively constant (first two thirds of an obliquity cycle and after 1 Ma ago half a precession cycle) throughout at least the last 5 Ma (Leroy and Seret, 1992, Leroy, 2007, Tzedakis, 2007). So, Mediterranean forest expansion during interglacial successions reflect, at the same time, the influence of precessional changes and maximum summer radiation (Tzedakis, 2007). In the ODP 976 core (Combourieu-Nebout et al., 1999, 2009) the obliquity influence is superimposed by precession cycles of 21 ka: the usual dynamic is seen as mesothermics replaced by altitude elements and ended with halo-xerophytes. Fletcher and Sánchez-Goñi (2008) remarked on the influence of precession on the amplitude and composition of forest development in MD95-2043.

Suborbital frequencies have been a pervasive feature since, at least, the last 500 ka (Tzedakis et al., 2003). In this sense, peaks of steppe vegetation have been related to North Atlantic influences (mainly Heinrich and Dansgaard-Oeschger events) in pollen diagrams from Iberian marine records (*i.e.* Roucoux et al., 2001, 2005, Sánchez-Goñi et al., 2005, 2008), but it is not easy to observe the same correlation in the continental domain. Only a few sites such as El Portalet in the Pyrenees (González-Sampériz et al., 2006) show a clear-cut response to abrupt cold events ever since 33 cal. ka BP, including Heinrich event 3 (HE 3), HE 2, Late Glacial Maximum (LGM), HE 1, Oldest Dryas, Older Dryas, Intra Allerød Cold Period (IACP), Younger Dryas and 8.2 ka event. The chronological framework and resolution analyses could be the cause for these marine-continental data differences because suborbital forcings imply abrupt changes that require very high-resolution data while orbital influences are more progressive. Nevertheless, a closer examination of the Mediterranean data reveals significant and specific regional patterns in vegetation succession, reflecting local intrinsic properties. Therefore, local particularities and the resilience of Iberian Mediterranean vegetation must also be taken into account to explain some apparent contradictions (Carrión, 2001, Carrión et al., 2010, this issue).

It can be summarized that Pleistocene palaeobotanical data for the Iberian Peninsula can be explained by a peculiar confluence of controls. Primarily, they result from a physical-environment conditioning, but then, they are also influenced by orbital and suborbital forcings.

5.2.- Generic extinctions

The Pleistocene involves genus and species extinction in the Iberian Peninsula, as with other regions of Europe, although certainly affecting less taxa and displaying some peninsular-specific asynchronies in respect to the rest of the continent (Postigo et al., 2007). Based on a database by Postigo et al. (2009) of the Cenozoic extinction, Carrión and Fernández (2009) have calculated the extinction rates of Iberian vascular plants during the last 65 Ma, concluding that, the Quaternary (13.29 taxa/Ma) is the period with highest phytodiversity loss, even higher than the Oligocene (10.67 taxa/Ma). Interestingly, the major biotic crisis is not indicated during the Plio-Pleistocene but rather at the Early-Middle Pleistocene transition, probably associated with the beginning of the 100 ka climatic cyclicity and a general cooling trend. This topic is widely discussed by Postigo et al. (2010, this issue). It is, nevertheless, essential to note that the Pleistocene extinctions are but a small sample of the longer-term disappearance trend that affected Palaeotropical and Arctotertiary plant species ever since the Eocene and with special strength since the Neogene.

Some genera, such as *Engelhardtia,* disappeared early during the Pleistocene, soon after 1.1 Ma, because it is still present in Bòbila Ordis sequence but absent afterwards. In other cases, the biochronological distribution through the Quaternary is poorly known, like in the case of *Aesculus,* which is an insect-pollinated tree, and therefore is always under-represented in pollen spectra. It was found, however, in fossil wood in Cal Guardiola (Postigo et al., 2007) during the Early-Middle Pleistocene transition. The case of *Parrotia* is also interesting. Its pollen morphology, not well known among palynologists due of its poor frequency, is illustrated in Leroy (2007) and Binka et al. (2003). In the Early Pleistocene samples, its occurrence is regular and sometimes reaches significant percentages (up to 9% in Bòbila Ordis; Leroy, 2008). It is not recorded in Middle Pleistocene sites. However, *Parrotia* is known in Northern Europe up to the Holsteinian (Binka et al., 2003); therefore it should also have maintained itself in southern Europe, including Iberia, in favourable locations until that time at least. It is therefore uncertain whether *Parrotia* disappeared from the Iberian Peninsula during the Early Pleistocene or later, and why. Its distribution may have been reducing progressively along the Quaternary dry spells, as currently, *Parrotia persica* is limited to the coastal area south of the Caspian Sea and to the Caucasus up to 1500 m altitude, where this deciduous tree lives in a mild and humid climate all the year (Davis et al., 1972).

During the Early Pleistocene, the pollen grain of *Ulmus* should be considered under the taxon *Ulmus-Zelkova* as the two genera were present as demonstrated in the leaf flora of the site of Incarcal at Crespià (Roiron, 1983) where *Zelkova crenata* was identified. In the late Early Pleistocene (or later) *Zelkova* disappeared from Iberia. The precise timing remains unknown, but the last certain appearance is in the sequence of Crespià (unprecised moment in between 2.1 and 1.6 Ma).

Other Tertiary taxa that disappeared later in the Quaternary occur in the palynoflora of the Iberian sites, more or less frequently: *Eucommia* (Garraf 1, Tres Pins, Bòbila Ordis)*, Cathaya* (Garraf 1, Tres Pins, Bòbila Ordis)*, Liquidambar* (Garraf 1, Tres Pins), *Nyssa* (Garraf 1, Tres Pins)*, Symplocos* (Garraf 1, Tres Pins, Bòbila Ordis) and *Parthenocissus* (Tres Pins, Bòbila Ordis) (Table 3). *Tsuga, Carya* and Taxodiaceae are present until the end of the Early Pleistocene. *Pterocarya* is still present during the Early (Tres Pins: Leroy, 1997, Crespià: Villalta and Vicente, 1972, Roiron, 1983, and Banyoles: Julià and Suc, 1980, Leroy, 1987) and Middle Pleistocene (MIS 11 or Holsteinian) in marine core MD01-2447 offshore NW Iberia (Desprat et al., 2005).

Palaeogeographical models for *Cedrus* are subject of controversy. Its pollen is frequent in a variety of the sediments of the Iberian Pleistocene, and, while long-distance pollen transport from northern African locations is shown even today (Magri and Parra, 2002), the possibility that local populations of *Cedrus* survived in the Iberian Peninsula up to the Lateglacial or thereafter cannot be ruled out, like profusely discussed by Postigo et al. (2010, this issue). The abundance of *Cedrus* pollen in the Early Pleistocene is certainly supporting its occurrence in the Iberian Peninsula (Joannin, 2007). In fact, the *Cedrus-Abies* assemblages are probably related to a relatively high level of precipitation not only in altitude but also in the lowlands, where the ratio Asteraceae liguliflorae to *Artemisia* is higher during the Early than during the Late Pleistocene.

The case of *Picea* is pertinent to northern Iberia during the Late Pleistocene. While today it is extinct, the pollen sequence of Area Longa (Gómez-Orellana et al., 2007) and charcoal analyses from three archaeological sites located on the Cantabrian shoreline (La Pila and Santa Catalina caves, and Peña del Perro rockshelter: see Table 1) yielded evidence of *Picea*, even until the Early Holocene (Uzquiano, 1995). *Picea* pollen is no longer recorded: in the Area Longa sequence, from AREL-6e zone (1460 cm depth) upwards, during the Lower Pleniglacial, while anthracological data show a continuous but decreasing presence between 12.5-11.7 uncal. ka BP from La Pila cave (see Fig. 1). Santa Catalina cave has one charcoal fragment of *Picea* in bed 27 (12.7 uncal. ka BP) and La Peña del Perro rockshelter another one in bed 2A, dated at 10.1 uncal. ka BP, so in the Early Holocene. All these data suggest the maintenance of *Picea* relict clusters along different areas of the Cantabrian shoreline (Uzquiano, 1998). The main cause of its disappearance is difficult to understand (Postigo et al., 2009), and it is for other taxa like *Platanus* (García-Antón et al., 1990), which nevertheless may have disappeared due to natural causes (Postigo et al., 2008).

In the leaf flora of Incarcal at Crespià, *Laurus nobilis* and *L. canariensis* have also been noted (Roiron, 1983). Their pollen grains do not preserve well, neither survive well pollen extraction; therefore we have no record of any change in their area of distribution over time.

5.3.- Survival of temperate, Mediterranean, and Ibero-North African woody species

Ever since the first investigations in southern Europe (Beug, 1968, Van Campo, 1969, Jalut et al., 1975), the composition, structure and location of glacial refugia of temperate tree species has been a subject of devoted research. Using pollen records, Huntley and Birks (1983) hypothesized the prevalence of migrational patterns of tree expansions from glacial refugia, which would have been largely located in the eastern Mediterranean. A similar perspective was adopted by Bennett et al. (1991), although these last authors predicted that this situation could change as new data were acquired. In a seminal work, Costa Tenorio et al. (1990) had already suggested that lowlands and mid-altitude mountain regions of Iberia could have served as refugia for tree taxa. These authors based their speculation in the current distribution of tree species, and in the observation that Lateglacial forest developments were relatively rapid as observed in pollen diagrams, an approach also adopted by Willis (1994) in the Balkans.

For the Iberian Peninsula, Figure 13 drafts the available evidences for broad-leaf and evergreen trees and shrubs, as well as the Mediterranean sclerophyllous elements, during MIS 4, MIS 3 and MIS 2. The evidences (the data themselves) for the two first stages are sparse and those maps should be taken, more like accounts of findings, than as distribution maps. Yet, they should not be taken to infer distribution changes from the Early to Middle, then to the Late Pleistocene. Some patterns can be notwithstanding assessed. During the coldest episodes of the MIS 3 and MIS 2, the occurrence of Ibero-North African xerothermic scrub is noticeable in coastal Murcia, Málaga and the southernmost extreme in the Gibraltar Peninsula. But the most striking feature is the broad occurrence of tree populations throughout the whole region, including continental territories. Genera like *Corylus, Quercus, Fraxinus, Alnus, Betula, Castanea,* and *Fagus,* among others, are common components of the Pleistocene pollen assemblages not only in the south, but also in the northwest (*i.e.* Gómez-Orellana et al., 2007), Cantabrian Mountains and Central Iberia (Uzquiano, 1992b, López-Merino et al., 2008), Pyrenees (Montserrat, 1992, González-Sampériz et al., 2005, 2006) pre-Pyrenees (Pérez-Obiol and Julià, 1994, González-Sampériz et al., 2003, 2005), north-eastern areas (Ros Mora, 1987, Burjachs and Julià, 1994, Burjachs and Allué, 2003), Central Ebro Basin (Valero-Garcés et al., 2000a, 2000b, González-

Sampériz, 2004), Iberian Range and Central system (Peñalba, 1994, Uzquiano, unpublished data).

It seems, therefore, that the Iberian Peninsula was covered by patches of vegetation types with more or less abundant woody plant taxa during the Pleistocene, including relicts from the Middle or the Late Pleistocene (*i.e. Juglans, Carpinus, Fagus, Castanea, Celtis,* and *Platanus*: Postigo et al., 2008) up to present (*i.e. Prunus lusitanica*: Pulido et al., 2008, Calleja et al., 2009). It is also worth mentioning (Table 1, Fig. 13) that Iberian refugia could have been at relatively high-altitude in mountain areas. This is confirmed in some outstanding pollen records such as the site of Siles, at 1400 m a.s.l., in the Segura Mountains of southern Spain (Carrión, 2002a).

It cannot be sufficiently stressed that the location of Iberian glacial refugia is not limited to the southern territories, because it follows that the conventional picture of long-distance migration since southern coastal areas is loosing its explanatory power. Data are now converging to depict a different picture in which a mosaic of forests, savannahs, and sparse stands of small populations of woody plant species scattered in multiple regions would have taken the main role (Carrión et al., 2008). Phylogeographical models based on the genetic structure of current populations (Taberlet et al., 1998, Hewitt, 1999, Olalde et al., 2002, Petit et al., 2002, Provan and Bennett, 2008, Bhagwat and Willis, 2008), and climate modelling of potential refuge areas (Benito Garzón et al., 2006, 2007, Leroy and Arpe, 2007, Médail and Diadema, 2009, Tzedakis, 2009, see Rodríguez-Sánchez et al., 2010, this issue, for further detail), support this view and postulates, in addition, that the most continental and northern Peninsula served yet as an area of secondary refugia and/or microrefugia during diverse unfavourable regional environmental conditions.

Concerning this topic, we are only starting to build methodological and conceptual connections between ecology, palaeoecology and evolution. It bears emphasis that changes in atmospheric CO_2 content may also have added to the effects of aridity in vegetation composition and fluctuations. The amplitude of millennial-scale changes in CO_2 has been traditionally considered too small to imply any really relevant contribution in Mediterranean vegetation changes (Stauffer et al., 1998, Tzedakis et al., 2003). However, experiments on *Ambrosia artemisiaefolia* in greenhouses have shown that when CO_2 is low, the pollen production is low too (Ziska and Caulfield, 2000). Low CO_2 during glacial times might have been an important factor for the underestimation of the number of trees surviving harsh times in sheltered positions (Leroy, 2007). Owing to this under-representation of trees in the pollen record, the interpretation of several pollen diagrams during the strong glacial times of the Middle and the Late Pleistocene could therefore be revisited.

This change of paradigm is also stimulated by neontological advances in biogeography. Médail and Diadema (2009) infer the putative location of plant refugia in the Mediterranean Basin on the basis of current chorological data. They show that a robust biogeographical congruence exists between the plausible location of refuge areas and the Mediterranean regions with highest biodiversity values. Refugia would fall entirely within areas with an endemism rate > 10%. At this point, and after the palaeobotanical data showed in Fig. 13 for the whole Iberian territory, it must be remembered that the Iberian peninsula has an endemicity index between 25 and 30% (Castroviejo, 2002, Sainz-Ollero and Moreno, 2002), which would confirm that the history of the Pleistocene Iberian flora is, at least partially, the result of a particular geographical position. So, Iberia represents a Quaternary hotspot, as it is still crucial in today's context of Global Change.

Gaining further detail in the interpretation of the controls of the distribution of glacial refugia as seen in Fig. 13, is challenging. The chronological control and spatial coverage are clearly insufficient to achieve that task. Climatic heterogeneity and climate change itself may have been important. Thus, in the knowledge that aridity of the southeastern is a feature ever since the late Miocene and Pliocene (Carrión et al., 2009, in press), the survival of Ibero-North African xerothermic scrub in the coastal territories is not surprising. Other southeastern pollen records, especially inland, even marine cores, fail to show these taxa (such as *Maytenus, Periploca,* and *Withania*), most likely because they are strictly insect-pollinated and their dispersal and input on the sediment of open-air sites is extremely deficient, as shown by Carrión (2002b). But they are present in cave minerogenic sediment and coprolites under depositional circumstances suitable for biotic transport (Carrión et al., 2008).

The integration of genetic and palaeobotanical data in other regions of southern Europe (*i.e.* Magri, 2008) has provided similar conclusions to this paper. What this involves is more complexity in the patterns of postglacial development. This complex network of glacial populations may have brought about competition, facilitation, and genetic flow to overlap with migrational patterns and bottlenecks as historical constraints for the modern genetic and distributional pathways. A note of singularity: in comparison with other Mediterranean peninsulas (Magri and Sadori, 2005, Tzedakis, 2009), Iberia was, doubtless, particularly suitable for the survival of sclerophyllous elements of any kind during glacial stages of the Pleistocene. Overall, and dealing with plant species, the Iberian Peninsula is more a land of survival than extinction for the whole Cenozoic (Postigo et al., 2009, this issue), but especially for the Pleistocene.

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Figure captions

Figure 1: Map of the bioclimatic zones of Iberia with the main Pleistocene sites cited in the text. Correspondence names to numbers are included in Table 1.

Figure 2: Ages of the main Early Pleistocene sites in Iberia. Limits of the Early Pleistocene (beginning of the Quaternary): Gelasian (Late Pliocene) and Calabrian periods (most of the Early Pleistocene). Ages of the limits after Gibbard and van Kolfschoten (2004) and Head and Gibbard (2005). Some marine isotopic stages (MIS) are given in the third and fourth column. CM: Cobb Mountain subchron. M: Matuyama chron. Garraf 1 sequence after Suc and Cravatte (1982), and Suc and Popescu (2005); Crespià site after Roiron (1992); Tres Pins after Leroy (1997); Bòbila Ordis after Leroy (2008); Cal Guardiola after Postigo et al. (2007); ODP site 976 after Combourieu-Nebout et al. (1999); Atapuerca after Burjachs (2001) and Berger et al. (2008).

Figure 3: Selected taxa from the pollen diagram of the Late Pliocene site of Garraf (modified from Fauquette et al., 1998a)

Figure 4: Selected pollen taxa from the pollen histogram of Bòbila Ordis, lake 2 (modified from Leroy, 1988). The sequence of lake 2 (sequence BOC4) represents a very open landscape. It is not directly dated. However stratigraphically it is between lake 1 (BOIV, Leroy, 2008) and lake 3 (BOII and BOIII, Leroy, 1987).

Figure 5: Pollen diagram of the Middle Pleistocene site of Atapuerca (modified from García-Antón and Sainz-Ollero, 1991).

Figure 6: Selected taxa from the pollen diagram of the Middle Pleistocene sequence of marine core MD01-2443 (modified from Roucoux et al., 2006).

Figure 7: Chronological distribution of the main continental full glacial Iberian sites of the Late Pleistocene (MIS 4, MIS 3 and MIS 2).

Figure 8: Pollen diagram of the Würm phase of the Late Pleistocene site of Area Longa (modified from Gómez-Orellana et al., 2007)

Figure 9: Anthracological synthesis of the Late Pleistocene data from Cantabrian and Mediterranean regions. Cantabrian Region: *Pinus* and *Betula* are the most representative taxa along MIS 4 and MIS 3 besides *Sorbus aria* that are important in MIS 3. *Juniperus, Salix* and Heathland shrubs (*Cytisus, Ulex, Erica*) are characteristic during MIS 2 before the Lateglacial. *Betula* reappears since this event. Karstic shrubs consist on spiny deciduous shrubs (*Sambucus, Crataegus, Prunus* spp., *Hippophae rhamnoides*) and Mediterranean shrubland (*Rhamnus alaternus, Phillyrea* sp., *Arbutus unedo*) and Meso-thermophilous trees group is composed by deciduous *Quercus*, *Castanea*, *Fagus, Corylus* and *Fraxinus*. *Quercus ilex* Pleistocene occurrences are noticed, as well as *Abies* and *Picea*. Mediterranean Region: *Pinus*, shrubs (*Rhamnus cathartica, R. alaternus, Prunus* spp., *Buxus, Phillyrea* sp.) and deciduous trees (deciduous *Quercus, Corylus, Fagus, Sorbus sp., Acer* spp., *Betula*) are the most representative taxa during the MIS 3 in NE Iberia. *Pinus-Juniperus* alternations are the main vegetation trend in S/SE Iberia during the MIS 2. Besides *Olea*, deciduous trees (deciduous *Quercus, Q. faginea* type, *Fraxinus ornus*, *F. oxyphylla, Acer* spp., *Salix-Populus*) and a more varied shrub vegetation cover (*Crataegus, Sambucus, Prunus* spp., *Rhamnus alaternus, Phillyrea* sp., *Pistacia lentiscus, P. terebinthus, Buxus, Cistus* sp., *Rosmarinus*, Fabaceae, *Viscum*, *Ephedra* and Chenopodiaceae) are recorded. *Quercus ilex-coccifera* is always present but in small amounts.

Figure 10: Selected taxa of the pollen diagram from the Late Pleistocene site of Abric Romaní (modified from Burjachs and Julià, 1994).

Figure 11: Comparison pollen diagram of Late Pleistocene sequence from Padul peatbog and Carihuela cave (modified from Fernández et al., 2007).

Figure 12: Selected taxa of the pollen diagram from the Late Pleistocene sequence of marine core MD95-2042 (modified from Sánchez-Goñi et al., 1999).

Figure 13: Full glacial (MIS 4 to MIS 2) distribution of: i) Mesothermophilous taxa (deciduous *Quercus*, *Corylus, Alnus, Tilia*, *Fagus*); ii) Mesothermophilous taxa including

Sclerophyllous elements (evergreen *Quercus, Olea, Pistacia, Phillyrea, Myrtus, Buxus, Rhamnus*); and iii) Mesothermophilous taxa including sclerophyllous elements and Ibero-Maghrebian scrub (*Maytenus, Periploca, Ziziphus, Withania, Lycium, Calicotome*).

Tables

Table 1: List of Pleistocene Iberian sites, location, type of data (pollen, charcoal), chronology and references.

Table 2: List of Late Pliocene-Early Pleistocene sites with altitude, number and type of samples, type of floral remains preserved, ages, and source of information (*pre-cyclostratigraphy ages).

Table 3: Occurrence of some taxa that have disappeared in the Quaternary in Late Pliocene-Early Pleistocene sites. In order of possible disappearance, with the earliest to the left (sp: species not precised; *: morphology unknown to the palynologist; always maximum amounts noted).