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Reconstruction of Mediterranean flora, vegetation and climate for the last 23 million years based on an extensive pollen dataset

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Abstract

In the last 46 years extensive effort has been devoted to the botanical identification of pollen grains from Neogene deposits. This robust approach is the only reliable way to reconstruct past flora and vegetation from pollen archives, additionally allowing fruitful comparisons with plant macroremains. Rich peri-Mediterranean fossil pollen data provide a comprehensive history of plant ecosystems during the last 23 million years. Successive disappearance of thermophilous-hygrophilous taxa has occurred. Severe changes affected the North Mediterranean vegetation which varied from prevalent forests to dominant open environments. *Avicennia* mangrove progressively perished from North to South and was replaced by *Glyptostrobus* swamps which in turn disappeared too in a diachronous way. Subtropical evergreen forests left room for Mediterranean sclerophyllous communities, and finally to *Artemisia* steppes which alternated with mesophilous forests during glacial-interglacial cycles. The South Mediterranean plant ecosystems contrasted with open subdesertic associations where *Avicennia* persisted up to the early Pliocene before the steppes invaded the lowlands. Neogene climate changes benefited the Mediterranean sclerophyllous plants that were already present in the early Miocene. Their subsequent fluctuations relate not only to temperature variations but maybe also to phases with high instability in seasonality and low variability in warmth. When present, *Microtropis fallax* is a serious candidate for identifying the primary Mediterranean sclerophyllous assemblages. Interpretation and climate quantification of the pollen data show a well-marked latitudinal contrast in the Mediterranean area both in temperature and humidity/dryness. The thermic latitudinal gradient is characterized by a significant increase in the late Miocene towards its modern value. In the late Pliocene, climate evolved from overall warm temperatures and dry seasons to cooler winters and dry summers. General dryness and colder conditions developed during glacial periods, alternating with moister and warmer conditions during interglacials. Present refuges of *Zelkova* and *Pterocarya* are discussed. Desiccation of the Mediterranean led subdesertic plants and cedar to migrate in opposite ways. The present distribution of *Cedrus* illustrates its weakness against coolings although it seems to have been saved by geodynamic events.

Key-words: Palynology and Botany, History of taxa and plant ecosystems, Climate quantifications.

Version abrégée

Cette synthèse, qui repose sur l'analyse de plus de 220 flores polliniques (Fig. 1), résume trente-sept années de collaboration avec Pierre Quézel (1926-2015), Professeur à l'Univesité d'Aix-Marseille, qui ont été marquées par vingt-huit travaux académiques (Tabl. 1). Après un effort unique en vue de l'identification botanique des grains de pollen du Néogène, plus de 260 taxa (dont 74 nouveaux) sont aujourd'hui inventoriés dans le Cénozoïque supérieur de Méditerranée (Tabl. 2). Il est désormais démontré qu'il s'agit de la meilleure approche à même de retracer l'histoire de la flore et de la végétation des derniers 23 millions d'années (Ma), favorisant en plus la comparaison avec les macroflores. Cet article se veut un plaidoyer pour l'abandon par quelques palynologues d'une approche inadaptée et dont on devrait mettre en cause la forte homogénéité des résultats incompatible avec l'hétérogénéité des paléoenvironnements.

Le caractère diachrone des extinctions de taxa thermophiles et hygrophiles est détaillé selon la latitude et la longitude. Les flores polliniques de Méditerranée nord-occidentale fournissent un exemple significatif des remplacements successifs des écosystèmes végétaux (Figs. 2 & 3) : la mangrove appauvrie à *Avicennia* remplacée sur les littoraux du Serravallien par les marécages à *Glyptostrobus* qui disparaîtront à leur tour au Pliocène ; le relais des forêts sclérophylles par les groupements xérophytiques au Pliocène supérieur ; l'invasion par les steppes à *Artemisia* signant les premières glaciations de l'hémisphère Nord à 2,6 Ma qui désormais alterneront avec les forêts mésophiles des interglaciaires. Le diachronisme latitudinal-longitudinal de ces remplacements est illustré à l'échelle de toute la région méditerranéenne (Fig. 4). Le domaine sud-méditeranéen était différent avec des environnements ouverts, subdésertiques (avec *Lygeum*, *Calligonum*, *Neurada*, *Nitraria*, *Ziziphus*), où *Avicennia* persista jusqu'au Pliocène inférieur avant l'invasion généralisée par les steppes à *Artemisia*. Les xérophytes méditerranéennes (*Olea*, *Phillyrea*, *Ceratonia*, *Pistacia*, *Nerium*, *Quercus* type *ilex*, etc.), présentes dès le début du Miocène, bénéficièrent de cette évolution puis, lors de refroidissements, tirèrent peut-être partie de certaines phases de grande instabilité dans la saisonnalité et de faible variabilité de la chaleur reçue en relation avec certains paramètres astronomiques (respectivement, forte amplitude de l'obliquité et faible amplitude de l'excentricité) (Figs. 5-7). Avant sa disparition du domaine nord-méditerranéen, *Microtropis fallax* (Celastraceae), vivant aujourd'hui dans la forêt sempervirente à larges feuilles du Viêt-Nam mais sous sécheresse estivale, doit être considéré pour illustrer les groupements xérophytiques primitifs. En Camargue, l'expansion des xérophytes méditerranéennes est intervenue plus de 2000 ans avant les premiers signes d'activité anthropique, apportant un nouvel argument dans le débat sur le rôle respectif du climat et de l'action humaine dans leur récente expansion qui, comme pour les steppes, peut être due d'abord au climat avant d'être encouragée par la pression anthropique (Fig. 8).

L'évolution climatique déduite des flores polliniques peut être subdivisée en trois phases majeures :

- du Miocène au début du Pliocène supérieur (23 – 3,37 Ma), un certain rythme climatique existait avec une saison sèche (avec des variantes selon l'âge et la situation géographique) dans un contexte subtropical à faible saisonnalité thermique ;

- la période 3,37 – 2,6 Ma peut être regardée comme une phase de transition au cours de laquelle un rythme saisonnier méditerranéen (à sécheresse estivale et froids hivernaux) a été expérimenté ;
- la mise en place des glaciations de l'hémisphère Nord à 2,6 Ma entraînèrent la généralisation de la xéricité et du froid avec des saisons très contrastées tandis que les interglaciaires étaient plus doux et plus humides.

Les quantifications confirment l'existence dès le Miocène moyen d'un gradient latitudinal très marqué, à la fois en température et sécheresse-humidité (Fig. 9). Peu après le gradient thermique latitudinal connut une augmentation vers sa valeur actuelle. La dessiccation quasi-totale de la Méditerranée à la fin du Miocène (5,6 – 5,46 Ma) ne s'est pas traduite par des bouleversements climatiques drastiques dans cette région et, du point de vue de la végétation, semble se résumer en l'état de nos connaissances encore partielles (1) à la migration des éléments subdésertiques vers des milieux septentrionaux moins défavorables et (2) à l'opportunité offerte à *Cedrus atlantica* d'un passage en Afrique du Nord.

L'aire relictuelle actuelle de *Zelkova* (Ulmaceae) est en adéquation complète avec les derniers témoignages polliniques recensés dans le Golfe du Lion et en Adriatique centrale. Au contraire, celle de *Pterocarya* (Juglandaceae) est sujette à discussion. La distribution très disjointe de *Cedrus* (Pinaceae) est le résultat des vicissitudes climatiques sur le continent eurasiatique où, semble-t-il, trois événements géodynamiques ont permis sa survie (Fig. 10) : le soulèvement du Tibet pendant l'orogenèse himalayenne pour *C. deodara*, l'extrusion de la péninsule anatolienne pour *C. libani*, la dessiccation momentanée de la Méditerranée pour *C. atlantica*. L'extinction du Cèdre sur le continent nord-américain demeure par contre très insuffisamment documentée et sans explication si ce n'est à cause des péjorations climatiques qui, pourtant, n'en ont pas éliminé *Tsuga*.

Introduction

This paper summarizes 37 years of collaboration with Pierre Quézel, former Professor at Aix-Marseilles University and famous specialist of ecology and biogeography of plants in the Mediterranean region (Médail, 2018), marked by several important papers aiming to decipher the onset of the modern Mediterranean flora, vegetation and climate on the basis of pollen records from the last 23 million years (Ma). Resulting from a new approach to Neogene palynology (Suc & Bessedik, 1981), this synthesis considers more than 220 localities (Fig. 1) studied within the frame of 29 analytic major analytical works (10 Master theses; 15 PhD theses; 4 State theses) (Table 1; see also: Suc *et al.*, 1999; Suc & Popescu, 2005; Jiménez-Moreno & Suc, 2007; Jiménez-Moreno *et al.*, 2007; Popescu *et al.*, 2010; Suc *et al.*, 2010). Collected data has increased in recent years (e.g.: Jiménez-Moreno *et al.*, 2009, 2013, 2015; Bertini, 2010; Combourieu-Nebout *et al.*, 2015; Suc & Popescu, studies in progress), making this school unquestionably the most suitable one for past reconstructions of the Neogene Mediterranean flora and vegetation. In addition, most of the data are quantified climatically by applying a method based on present-day pollen records and plant distribution (Fauquette *et al.*, 1998a & b, 2007). This paper does not aim to provide a complete review of all the available pollen data from the Late Cenozoic in the Mediterranean region. The displayed pollen records are all characterized by the same level of quality in identifying pollen grains and can be statistically analyzed as we have all the detailed counts. In particular, the Pleistocene and Holocene times are represented by only few (often long) records, covering the last 2.6 Ma. Overall, these data are the results of our intense collaboration with Pierre Quézel that justifies this synthesis in the issue dedicated to his memory.

After a recap of the main aspects of the methods used, we synthesize the most significant results at the whole Mediterranean scale with focus on (1) floral – vegetation changes, (2) quantified climatic evolution, and (3) biogeographical history of selected taxa.

Methods

Following Zagwijn (1960) and Pons (1964), the most impressive palaeoecological progress reached in the 1970's lies in the botanical identification of fossil pollen grains, which was possible due to detailed morphological analyses and accurate comparisons with modern taxa. In this way, identifications are usually done at the genus level for tree pollen with some examples at the species level, and at the family level for herb pollen except for some genera and species. This successful botanical approach severely contrasts with the previously used artificial nomenclature, which unfortunately is still considered by some palynologists for the Neogene (e.g. Bruch, 2004; Barron *et al.*, 2016). This artificial nomenclature supports the myth of a superficial morphological analysis of the pollen while the botanical approach is based on accurately documented pollen morphology. In addition, the artificial nomenclature keeps alive the faith in species level identification by using a pseudo-binomial such as *Subtriporopollenites simplex* (Pot.) Th. & Pf. or *Tetracolporopollenites manifestus* (Pot.) Th. & Pf. This method evokes only one simple morphological character (triporate pollen and tetracolporate pollen, respectively) so far from the complex morphological description of any one pollen grain. Sometimes, the used binomial directly recalls a botanical genus, for example *Caryapollenites simplex* Pot. or *Sciadopityspollenites tuberculatus* (Zakl.) W.Kr.: why attach the *pollenites* suffix plus useless pseudo-species name as the pollen is easily identifiable at the genus level and only at this level? In fact, the out-dated artificial nomenclature denotes an inadequate expertise in pollen morphology, especially the non-practice of the effective L.O. analysis of Erdtman (1952) and shows a lack of experience in pollen grains from the various modern vegetation realms of the Earth.

More than 260 taxa (determined to family and/or genus and/or sometimes species levels) identified in the Late Cenozoic (i.e. the last 23 Ma) of the Mediterranean region are listed in Table 2 with respect to their epochs of occurrence (Miocene, Pliocene or Quaternary) and their major chronostratigraphic subdivisions. Thanks to this unrivalled effort, 74 taxa have been indicated for the first time in the Mediterranean Late Cenozoic (Table 2). Any pollen analyst wishing to develop a robust botanical approach can find a complete documentation on fossil and modern pollen descriptions and photographs in the theses mentioned in Table 1 and following papers (Lobreau-Callen & Suc, 1972; Suc, 1973, 1974, 1976a, 1976b, 1978a, 1978b; Naud & Suc, 1975; Julià Bruguès & Suc, 1980; Cravatte & Suc, 1981; Bessedik, 1983; Suc *et al.*, 1986; Bessais & Cravatte, 1988; Zheng, 1990; Suc *et al.*, 2004; Jiménez-Moreno & Suc, 2007; Popescu *et al.*, 2010; Biltekin *et al.*, 2015).

For building synthetic pollen diagrams, taxa are mostly grouped according to a global "ecological niche" corresponding to the mean annual temperature (MAT) under which their present-day representatives are living (Nix, 1982) plus other climatic (mainly linked to xericity) or edaphic considerations, and their status that can be deduced from variations in their pollen records over time (Table 2):

- Megatherm plants inhabiting equatorial and tropical forests: MAT>24°C;
- Mega-mesotherm plants living in subtropical forests: 24°C>MAT>20°C;
- Mesotherm plants corresponding to warm-temperate forests: 20°C>MAT>14°C;
- Meso-microtherm plants growing in cool-temperate forests, including *Cathaya*, a relictuous altitudinal conifer in subtropical China: 14°C>MAT>12°C;
- Microtherm plants constituting the boreal coniferous forests: MAT<12°C;
- Cupressaceae: genera showing the *Cupressus-Juniperus* pollen-type cannot be identified, and cover a large temperature range;

- Aquatic plants living in freshwater environments;
- Mediterranean sclerophyllous plants, i.e. the trees, shrubs and herbs today characteristic of the thermo- and meso-Mediterranean ecosystems;
- Herbs that cannot be referred to the Mediterranean sclerophyllous plants with respect to the insufficient level of their pollen identification or by inhabiting different open environments;
- Steppe plants, i.e. *Artemisia*, *Ephedra* and *Hippophae*, characterizing the Mediterranean steppes and also including also some subdesertic plants (*Neurada*, *Nitraria*, *Calligonum*, *Lygeum*, *Ziziphus*);
- Plants without significance because they live under various environmental conditions or by considering the low potential of their pollen identification.

Additional improvements also contribute to an optimal achievement of pollen analysis such as gentle techniques in processing sediments, mounting of the residue between cover-slip and microscope slide in glycerol (allowing examination of all the pollen faces by rotation and thus its reliable botanical identification), development of extensive photographic databases and modern pollen collections, use of modern pollen atlases, and when necessary examination of the pollen using scanning electron microscope (SEM).

Finally, counting of at least 100-150 pollen grains, excluding *Pinus* because it is often over-represented in marine or lacustrine sediments, makes our palynological approach fully comparable to that performed for late Quaternary studies. The results are shown in synthetic pollen diagrams (with the above mentioned groups), which suitably illustrate the vegetation changes (Suc, 1984).

Most of the studied localities correspond to coastal marine (often prodeltaic) sediments supplied by rivers, which, in addition to their independent dating by marine microplankton, are very appropriate to record the Mediterranean sclerophyllous plants as they inhabited the nearby hinterland.

The “Climatic Amplitude Method” was developed to specifically quantify climatic parameters of the Mediterranean lowlands during the Late Cenozoic (Fauquette *et al*., 1998a). The method which also takes into account the modern bioclimatic requirements of taxa (Fauquette *et al*., 1998b), is built on the statistical comparison between each past pollen assemblage and a database of more than 8,000 modern pollen records from various latitudes and longitudes in the Northern Hemisphere, thus allowing the transposition of the relative abundances of each taxon into climatic values. The most probable climate (mean annual temperature, mean annual precipitation, temperature of the coldest and warmest months, available moisture) for a set of taxa corresponds to the climatic range suitable for the maximum number of taxa. The climatic estimate is obtained as a climatic range and a “most likely value”, which corresponds to a weighted mean. The “Climatic Amplitude Method” has been successfully tested several times on modern pollen records. Benefiting from high-quality pollen identifications (see above), the method is advantageous in comparison with another widely applied method, the “Coexistence Approach” (Mosbrugger & Utescher, 1997; Utescher *et al*., 2014) because of its dual traits, qualitative-quantitative consideration for each taxon allowing delimitation of thresholds, and statistical treatment allowing processing of large numbers resulting from pollen counts. Inadequacies, inconsistencies and errors of the “Coexistence Approach” are stressed by Grimm & Denk (2012) and Grimm *et al*. (2016) who notice the surprising uniformity of the climatic reconstructions for the Eurasian Cenozoic, continuously and everywhere qualified as “subtropical, per-humid or monsoonal conditions”. Such a matter is explainable: (1) supremacy of good quality macrofloras used by this approach is obvious although they are restricted to almost similar humid palaeoenvironments; (2) pollen floras used by this approach that could really document the regional heterogeneity are of very poor taxonomic quality (see above) and very homogenous with only a small number of omnipresent taxa. Pollen analysis is thus unfortunately underused in the "Coexistence Approach" method.

Main flora and vegetation changes

Flora

There has been a high diversity and heterogeneity of the Mediterranean flora since the beginning of Miocene, with a lot of megatherm and mega-mesotherm plants in addition to a large pool of taxa still present in the region today (Table 2). Extinction of 108 thermophilous and hygrophilous taxa from the Mediterranean region is recorded, mostly during the Miocene and Pliocene, a few during the Quaternary. At the scale of a long-time range as the entire Late Cenozoic, successive extinctions can be regarded to have occurred according to latitude mainly and to longitude secondarily, while some refuge areas were established and persisted up to nowadays (Médail & Diadema, 2009; Biltekin *et al*., 2015). Basically, extinctions were forced by repeated coolings in the mid-Miocene (13.6 Ma), just after the early-late Pliocene transition (3.6 Ma) and from the earliest Quaternary (onset of the Northern Hemisphere glaciations at 2.6 Ma) (e.g., Svenning, 2003; Suc *et al*., 2004). The Mediterranean physiography is characterized by West-East oriented barriers (mountains, the sea itself, and desert; Fig. 1). As a consequence, the thermophilous plants could not easily move southward during the climatic deteriorations and recolonize during the warmer phases the spaces previously abandoned. The Mediterranean floral history contrasts to that of North America where natural barriers are North-South oriented. Simultaneously, the East African monsoon exerted some influence that preserved some moisture in the Northeastern Mediterranean region (Popescu *et al*., 2006; Suc & Popescu, 2005; Biltekin *et al*., 2015). The Mediterranean sclerophyllous plants (*Olea*, *Ceratonia*, *Phillyrea*, *Pistacia*, *Nerium*, *Quercus ilex*-type, etc.) were already present in the earliest Miocene. According to several syntheses (Kovar-Eder *et al*., 2006; Barrón *et al*., 2010; Velitzelos *et al*., 2014; Martinetto *et al*., 2015), macrofloras (leaves, fruits, seeds, cuticle, wood) appear richer than pollen floras from the viewpoint of thermophilous taxa which inhabited the Mediterranean region during the Miocene and Pliocene. The macrofloras have, however, a significance mainly restricted to moist places and a relatively limited representation for the herbs.

Northwestern Mediterranean vegetation

The Northwestern Mediterranean region is rich in pollen data that can be used successfully for reconstructing the vegetation during the last 23 Ma (Fig. 1). Pollen counts provide reliable information for estimating palaeovegetation structures and the relative importance of ecological groups, supported by modern pollen records obtained from marine coastal deposits in the Gulf of Lions (Beaudouin *et al*., 2005b, 2007). Fifty-four localities were selected, distributed from the area between Barcelona and Nice (Fig. 2) and these are dated from the earliest Miocene to Holocene (Fig. 3). The following major vegetation changes can be addressed for this region (Fig. 3):

- The impoverished mangrove composed of *Avicennia* (megatherm element; Bessedik, 1981; Bessedik & Cabrera, 1985) disappeared in the earliest Serravallian (at ca. 13 Ma; Bessedik, 1984; Jiménez-Moreno & Suc, 2007);
- The swamps composed of *Glyptostrobus*[1] (mega-mesotherm element), which probably replaced the *Avicennia* mangrove along the shoreline, strongly decreased at about 3.6

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[1] *Glyptostrobus* was a member of the former Taxodiaceae family (as *Taxodium*, *Sequoia*, *Metasequoia*, *Sequoiadendron*, etc.) now included in the Cupressaceae family. Unidentified Taxodiaceae are listed as 'taxodioid' pollen. *Sciadopitys,* another genus previously incorporated into Taxodiaceae, now constitutes a new family, Sciadopityaceae.

Ma and disappeared at about 3 Ma from Southern France while they persisted up to at least 2 Ma in Catalonia; a difference in moisture probably appeared at 3 Ma between the northern and southern slopes of the Eastern Pyrenees as it exists today (appearance of the cold Tramontane and Mistral winds? Suc *et al.*, 1999);

- Although they existed before, the *Artemisia* steppes began to spread at about 3 Ma and significantly expanded at 2.6 Ma (Vilobi del Penedès, Papiol) (Suc, 1984);
- During the early and middle Miocene, the Mediterranean sclerophyllous plants show relatively important percentages in some places close to low carbonate reliefs (e.g.: Portel – Sigean, Narbonne, Poussan – Issanka – Montbazin, Fabrègues); their development seems to have increased in the coastal areas during the early Pliocene (e.g.: Garraf 1, Papiol, Torrente del Terme, Ciurana, Vivès, Le Boulou, Cap d'Agde 1); they probably already constituted sclerophyllous assemblages in some well-drained environments despite a climatic context that was, on the whole, humid (Suc *et al.*, 1999).

Vegetation of the entire Mediterranean region

This regional process of major vegetation changes and its timing must be reconsidered at the entire Mediterranean scale (Fig. 4):

- The *Avicennia* mangrove disappeared earlier from the North Hungarian – Austrian (i.e. Pannonian) Basin and later from the South Mediterranean shorelines, ending with some residual locations in the southern Black Sea (Biltekin *et al.*, 2015);
- Significantly younger, the disappearance of *Glyptostrobus* swamps followed in a similar way (Biltekin *et al.*, 2015);
- More or less simultaneously depending of the region, the *Artemisia* steppe spread over the lands bordering the Mediterranean Basin (Suc *et al.*, 1995; Popescu *et al.*, 2010; Feddi *et al.*, 2011).

Such a pattern of the main vegetation changes with a North-South succession implies a latitudinal organisation of the vegetation (i.e. zonation) since the earliest Miocene. The simultaneous presence of meso-microtherm (*Cathaya*, *Cedrus*, *Tsuga*) and microtherm (*Abies*, *Picea*) trees attests to an altitudinal belting of vegetation on higher ground (Suc, 1976a, 1989; Bessedik, 1984; Zheng, 1990; Jiménez-Moreno & Suc, 2007). In addition, the high heterogeneity in the Mediterranean physiography (Meulenkamp & Sissingh, 2003; Jolivet *et al.*, 2006) with coastal reliefs, large islands and/or long peninsulas and episodic wide oceanic connections infers a high diversity of landscapes, supported by a large variety of soils, and therefore probably some mosaic distribution of plant communities. For a large part, the Miocene and Pliocene Northern Mediterranean forests evoke the modern evergreen broad-leaved and mixed mesophytic forests of Southern China (Wang, 1961; Hou, 1983), the pollen representation of which is well-known today (Huang *et al.*, 2008; Zheng *et al.*, 2008). The Late Cenozoic Southern Mediterranean open vegetation evokes the modern vegetation of the Middle East (Zohary, 1973; White, 1983).

All throughout the last 23 Ma, lands bordering the northern part of the Mediterranean Sea were inhabited by forests while the southern part was occupied by open vegetation, emphasizing the longterm persisting contrast between these realms which probably results from the onset of the Sahara Desert prior to the early Miocene (Lancelot *et al.*, 1977; thesis n° 6, Table 1; Suc *et al.*, 1995; Fauquette *et al.*, 2007; Jiménez-Moreno *et al.*, 2007, 2010; Bachiri Taoufiq *et al.*, 2008; Feddi *et al.*, 2011). Such a contrasting context climatically predisposed the Mediterranean Sea to be desiccated as soon as the last gateway connecting to the Atlantic Ocean closed (Fauquette *et al.*, 2006) between 5.6 and 5.46 Ma due to tectonic activity (peak of the Messinian Salinity Crisis; Bache *et al.*, 2015). Ecological consequences of the sea-level drop of the Mediterranean Sea at this time are still poorly known due to the lack of sedimentary records. However, a significant northward migration of the subdesertic plants is documented as a response to desiccation of the central basins (Fauquette *et al.*, 2006; Popescu *et al.*, 2007). Only one deep pollen record provides information on the vegetation of desiccated lands near Sardinia at the last evaporitic episode (5.47 Ma): open vegetation rich in halophytes and subdesertic plants with Mediterranean sclerophyllous plants probably inhabited the lowlands while a forest cover existed on the nearby massifs (Popescu *et al.*, 2015).

Mediterranean steppes

Mediterranean steppes today constitute a crucial topic of discussion, probably because of their duality with respect to their xeric or thermic determinism (Quézel *et al.*, 1980; Subally & Quézel, 2002; Quézel & Médail, 2003). Evidence of steppe assemblages, mainly composed of *Ephedra*, is rare in the early Miocene of the Northwestern Mediterranean region, as illustrated at Vilobi del Penedès and at La Rierussa (Fig. 3). Such ecosystems were controlled by a xeric determinism. Later, a first discrete development of the Anatolian steppes, composed of *Artemisia* mainly and *Ephedra*, occurred at about 6.2 Ma and was followed by more pronounced expansion at 5.8 – 5.6 Ma, probably related to Antarctic glaciation and later with the desiccation phase of the Mediterranean Sea (Popescu, 2006; Popescu *et al.*, 2010, 2016). At 5.2 Ma, Anatolian steppes crossed a critical threshold in their spreading that probably transformed them into a “regional pool” for their forthcoming wide expansion around the Mediterranean Sea (Popescu, 2006; Popescu *et al.*, 2010, 2016). This affected the southern Mediterranean region at 3.34 Ma, related to cooling following the Zanclean – Piacenzian transition, then the northern Mediterranean region at 2.6 Ma when the Northern Hemisphere glaciations commenced (Fig. 4). As shown by some plants associated with *Artemisia* – *Ephedra* steppes, the turnover from steppes with xeric determinism into those with thermic determinism occurred at around 1 Ma (Suc *et al.*, 1995). This is also the age considered for the onset of modern steppic environments in the Iberian Peninsula (Gonzalez-Sampériz et al., 2010). Improvements are being made in the distinction of *Artemisia* species or species groups using pollen grains, as initiated by Suc *et al.* (2004). During glacial-interglacial cycles, *Artemisia* steppes and mesophilous forests were in competition for occupation of the lowlands.

Mediterranean sclerophyllous plants

Early Pliocene pollen floras from the eastern part of the Iberian Peninsula require special attention: they show a latitudinal succession of prevalent taxa among the Mediterranean sclerophyllous plants which resembles the present-day zonation of Mediterranean vegetation. From the Roussillon area southwards to Barcelona, *Quercus ilex*-type and *Phillyrea* are indicated by frequent pollen grains with few *Olea* and *Cistus* and rare *Pistacia* (Suc, 1976a; Suc & Cravatte, 1982). From Barcelona to south of the Ebre Delta, *Olea* is prevalent with *Phillyrea* and *Cistus*, *Quercus ilex*-type decreases and *Pistacia* is better represented in the pollen flora which also includes *Nerium* (Bessais & Cravatte, 1988). Some subdesertic elements, such as *Ziziphus*, *Calligonum*, *Lygeum* and *Nitraria* are also present and Arecaceae (maybe corresponding to *Chamaerops* and/or *Phoenix p.p.*) increase (Bessais & Cravatte, 1988). The pollen flora from Andalucia is similar and also includes *Ceratonia* (Feddi *et al.*, 2011). Equally, herbs increase from North to South (Jiménez-Moreno *et al.*, 2010). Such a latitudinal succession resembles the present-day replacement of meso-Mediterranean populations by thermo-Mediterranean populations, becoming progressively enriched in subdesertic plants (Quézel & Médail, 2003). According to pollen records, Mediterranean sclerophyllous plants increased when mega-mesotherm plants became progressively rarer and then disappeared: it has been hypothesized that sclerophyllous Mediterranean ecosystems somewhat similar to the modern ones developed for the first time in a sustained way between 3.34 and 2.6 Ma (Suc, 1984) but this time-interval is not yet well enough documented by pollen data to allow a detailed reconstruction of vegetation evolution at this time. However, according to Tzedakis (2007), several transient episodes with the Mediterranean seasonal pattern of rainfall may have occurred before the Pliocene that progressively led the sclerophyllous plants becoming more adapted to a dry season.

Conversely, data for analysing the development of the Mediterranean sclerophyllous ecosystems during glacial-interglacial cycles are abundant for the last 2.5 Ma. A lot of surface marine, lagoonal or lacustrine sediments from the Northwestern Mediterranean region illustrate that nowadays the Mediterranean sclerophyllous plants account for between 3 and 28% of the total pollen sum (*Pinus* excluded) (Cambon *et al*., 1997; Le Dantec *et al*., 1998; Suc *et al*., 1999; Beaudouin *et al*., 2007). A borehole covering the years 1950-1991, cored in the Rhône prodelta where sedimentation rate is fast (ca. 60 cm/year in the absence of disturbances as storms and/or floods), shows that the seasonal representation of Mediterranean sclerophyllous plants during their blooming period comprised between 3.79 and 8.52% of the total pollen sum, *Pinus* being excluded (Beaudouin *et al*., 2005b). Considering the large surface nowadays occupied by the meso-Mediterranean vegetation back of coastal ecosystems in Southern France, it is obvious that Mediterranean sclerophyllous plants are under-represented in coastal marine or lagoonal sediments. Therefore, we consider that a value higher than 3% in past pollen records is significant, outweighing potential biases due to pollen transport and/or preservation, and means an important development of Mediterranean sclerophyllous plants. In order to determine the relationship which may have existed since 3.6 Ma between climate evolution and development of the Mediterranean vegetation, we use the percentage curves in 13 accurately dated pollen localities (Fig. 5). These curves are plotted using the pollen ratio of "thermophilous/steppe elements" (Figs. 6-8), which is a reliable index of climatic changes in lowlands of the Mediterranean region as shown by long records, and correlated with reference to the oxygen isotope curve (Popescu *et al*., 2010; Joannin *et al*., 2008; Suc *et al*., 2010). Special attention is paid to significant peaks (>3%) of the Mediterranean sclerophyllous plants in Figures 6-8, indicated by grey bands. In particular, the isolated peaks significantly greater than 3% and those grouped in clusters, even though of brief duration, are examined (indexed 'a – i' in Figure 6; 'j – l' in Figure 7; 'm – r' in Figure 8):

- Time-interval 3.6 – 0.9 Ma (Fig. 6):
- peaks 'a – c' coincide with relative minima of the ratio of "thermophilous/steppe elements" and are thus correlated with cooler phases corresponding to marine isotope stages (MIS) M2, KM2 and G10, respectively;
- location of peak 'd' is somewhat ambiguous as it coincides with a minor maximum of the ratio of "thermophilous/steppe elements" within a general lowering trend, and is correlated with the warmer MIS G3;
- the cluster of peaks 'e' corresponds for the most prominent peaks to a colder phase identified as MIS 98;
- the cluster 'f' shows its most important maxima in its upper part, i.e. in correspondence with the minimum of the ratio of "thermophilous/steppe elements" correlated with MIS 86;
- the most important peaks of cluster 'g' belong to a colder phase correlated with MIS 82;
- cluster 'h' is located within a minor cooling during a warm phase identified as MIS 45;
- cluster 'i' shows its major peaks located within a warmer phase correlated with MIS 39 while minor peaks correspond to a cooling correlated with MIS 38;

- at least two isolated peaks (between ‘e’ and ‘f’ and above ‘i’) correspond to coolings, MIS 90 and 36 respectively.
- Time-interval 640 – 15 ka (Fig. 7):
  - cluster ‘j’ coincides with a warm period correlated with MIS 13;
  - cluster ‘k’ corresponds to a cold phase correlated with MIS 12;
  - cluster ‘l’ shows its minor peaks during a warm phase correlated with MIS 9 and its major peak during a warmer episode within MIS 8;
  - an isolated peak between clusters ‘k’ and ‘l’ belongs to a cold phase related to early MIS 10;
  - the three isolated and minor peaks following cluster ‘l’ occurred during moderate warmings within cold MIS 8 (lower peak) and MIS 6 (two upper peaks);
  - the last isolated minor peak is recorded in correspondence with a moderate warming correlated with MIS 5c (i.e. the Saint-Germain 1 interstadial).
- Time-interval 11,200 – 0 years for which climatic correlations are made with reference to the Greenland isotope curve GISP2 (Fig. 8):
  - cluster ‘m’ is located during a phase of weak decrease in temperature correlated with a transitional phase in the GISP2 curve characterized by low fluctuations around 4,500 yrs cal. BP;
  - each of the three peaks of cluster ‘n’ match a cooler episode within a fluctuating period with prevalent cooler episodes in the GISP2 curve between 4,000 and 3,600 yrs cal. BP;
  - the same observation is made for most of the peaks of cluster ‘o’ in relation with a phase of greater amplitude fluctuations in the GISP2 curve between ca. 3,500 and 2,900 yrs cal. BP;
  - a similar interpretation concerns peaks of cluster ‘p’ equating, on the whole, to a cooler period corresponding to prevalent coolings in the GISP2 curve (2,300 – 1,700 yrs cal. BP);
  - the two peaks of cluster ‘q’ correspond to a cooling trend expressed by the ratio of “thermophilous/steppe elements” and to repeated decreases in temperature in the GISP2 record between 800 and 500 yrs cal. BP;
  - peaks of cluster ‘r’ resemble those of cluster ‘p’ and are correlated with a cooler phase in the GISP2 curve between 400 and 200 yrs BP;
  - the four isolated peaks before cluster ‘m’ match relative cooler phases according to the ratio of “thermophilous/steppe elements” and are related to decreases in the GISP2 record at ca. 10,200, 8,700, 7,200 and 5,200 yrs cal. BP, respectively.

For the interval 3.6 – 0.9 Ma, the peaks or clusters are irregularly paced, but most of them occurred during periods with decreases in temperature (Fig. 6). In the Garraf 1 record, the main pollen contributors to peaks ‘a–d’ are *Olea*, *Phillyrea* and evergreen *Quercus* (Suc & Cravatte, 1982). In the lower part of the Crotone series (peaks ‘e–g’), they are *Pistacia*, *Olea* and evergreen *Quercus*; in its upper part (peak ‘h’), *Olea* and evergreen *Quercus* (Combourieu-Nebout, 1990). In the Camerota record (Brenac, 1984), the warm phase (lower part of cluster ‘i’) shows a predominance of *Ceratonia* and *Olea* replaced by that of *Olea*, *Phillyrea* and evergreen *Quercus*; the following cooler phase (middle part of cluster ‘i’) displays a minimum occurrence of *Olea* and evergreen *Quercus*; the uppermost warming phase (uppermost part of cluster ‘i’), shows a minor presence of evergreen *Quercus*. *Olea* is the main component of the minor peak of the lowermost part of the Montalbano Jonico series (Joannin *et al*., 2008).

Peaks or clusters from the interval 640 – 15 ka are also irregularly paced; some of them can be referred to a cooling period, others to a warming phase (Fig. 7). The upper interglacial phase of Vallo di Diano (cluster ‘j’) shows predominance of evergreen

Quercus and, at a lesser level, of *Pistacia* and *Olea* (Russo Ermolli, 1994). In the PRGL1-4 record, clusters 'k' and 'l' and secondary peaks show predominantly *Olea*, *Phillyrea* and evergreen *Quercus* (Suc *et al*., in progress).

Most of the isolated peaks and clusters from the interval 11,200 – 0 years are correlated with cooler episodes (Fig. 8). Evergreen *Quercus* prevails in the isolated peaks and in clusters 'm – o'. Subsequently, *Olea* and sometimes evergreen *Quercus* or *Phillyrea* are the most important representatives of Mediterranean sclerophyllous plants in clusters 'p – r'.

In a first approximation, it seems that the Mediterranean sclerophyllous plants were advantaged during cooling phases, maybe because of the opening of forested vegetation. However, these isolated peaks or clusters are not uniformly distributed through time (Figs. 6-8), indicating that temperature falls and correlative dryness increases are not the only forcings. Indeed, there is no direct relationship with the insolation curve at 60°N but some correlations coincide with phases of relative higher amplitude of obliquity and simultaneously with phases of relative lower amplitude of eccentricity: e.g. peaks or clusters 'c – g', 'i' and 'k' (Figs. 6-7). Such phases of increased instability in seasonality (high amplitude of obliquity) and low variability in heat (low amplitude of eccentricity) (Berger, 1990) may have advantaged the Mediterranean sclerophyllous plants competing with other ecosystems within opening low altitude landscapes during colder periods. Mediteranean sclerophyllous ecosystems were widely developed in the Southen Italian Peninsula between 2.6 and 1.2 Ma as illustrated by the Crotone and Camerota successions (Fig. 6). Pollen records from Crotone and Montalbano Jonico document a similar palaeoclimatic evolution to those from Camerota and Vallo di Diano although their sedimentary context differs. The younger records, Montalbano Jonico and Vallo di Diano, exhibit a distinct retreat of the Mediterranean sclerophyllous plants (Combourieu-Nebout *et al*., 2015). This retreat may be considered as a consequence of the mid-Pleistocene revolution (at about 1 Ma) during which prevalent 41 kyr glacial-interglacial cycles were replaced by 100 kyr ones (Head & Gibbard, 2005). As emphasized by Leroy (2007) and Tzedakis (2007), the relative shortness of glacials (although frequently repeated) compared to the length of interglacials before the mid-Pleistocene revolution may have advantaged the Mediterranean sclerophyllous plants in their expansion. Subsequently, during the last 900 ka, this expansion may have been slowed down by the significantly increased length of glacials with respect to interglacials (Leroy, 2007; Tzedakis, 2007). The Rhône Delta (Camargue) is rich in pollen records showing close and almost continuous climatostratigraphic relationships with the oxygen isotope curve of the GISP2 ice-core (Fig. 8). Percentages of Mediterranean sclerophyllous plants show episodic maxima in the lower part of the series which are clustering after 5,000 years cal. BP, the highest ones of which (mostly composed of *Quercus ilex*-type) precede, by more than 2,000 years the onset of human activity dated at 3245 years cal. BP in the area (Fig. 8) (Arnaud-Fassetta *et al*., 2000). This is in agreement with the observations in the nearby Languedoc by Jalut *et al*. (2009) who propose some aridification process since 5,500 years cal. BP. The new Camargue data contribute to the debate on the climatic vs. anthropogenic forcing of the recent spreading of Mediterranean sclerophyllous plants (Beaulieu *et al*., 2005). A similar contrast in the representation of Mediterranean sclerophyllous plants is obvious in Southern Spain between the early mid-Pleistocene (Joannin *et al*., 2011) and the Holocene (Combourieu-Nebout *et al*., 2009). As in the case of steppes, the development of Mediterranean sclerophyllous plants is probably first due to climatic forcing and then accentuated by anthropogenic pressure. One must note that the last 50 kyrs correspond to high amplitude of obliquity and low amplitude of eccentricity (Fig. 7; Laskar et al., 2004). As an additional argument, we emphasize that

Olea pollen is abundant in the youngest records from 92K08 and 92K04 cores (location in Fig. 5). These results highlight that pollen analyses at high time resolution are strongly needed.

The evolution of Mediterranean vegetation during the last 23 Ma can be summarized as follows: surface reduction of some plant ecosystems was counterbalanced by the spread of other ones: *Avicennia* mangrove vs. *Glyptostrobus* swamps, evergreen subtropical forests vs. Mediterranean sclerophyllous ecosystems, herb ecosystems vs. *Artemisia* steppes, and lastly mesophilous forests vs. *Artemisia* steppes during climatic cycles.

Climatic evolution

The climatic evolution of the Mediterranean region can be synthetically subdivided into three major phases:

- During the entire Miocene, the early Pliocene and the beginning of late Pliocene (i.e., from 23 to 3.37 Ma), a climatic rhythm existed with some seasonal dryness that could vary according to age and geography; low amplitude in seasonal temperature variation is also assumed in a subtropical context (Bessedik, 1984; Jiménez-Moreno & Suc, 2007; Jiménez-Moreno *et al*., 2007);
- The time interval 3.37 – 2.6 Ma can be regarded as a transitional period characterized by the emergence of a Mediterranean seasonal rhythm with summer drought and cooler winters (Suc, 1984; Popescu *et al*., 2010);
- From 2.6 Ma, the earliest glaciations in the Northern Hemisphere caused generalized dryness and colder conditions during glacials with highly contrasting seasons. On the contrary, moister and warmer conditions developed during interglacials. Such climatic trends were repeated during secondary fluctuations (Suc, 1978; Combourieu-Nebout *et al*., 2000).

A strong North-South gradient was continuously superimposed on this general context, characterized by a southward dryness and temperature increase during warmer periods, and a decreasing climatic contrast during colder periods (Suc et al., 1995; Jiménez-Moreno & Suc, 2007). Palaeoclimatic quantifications allow an estimation of this dual gradient, in humidity and temperature, over time (Fauquette *et al*., 2007). However, the precipitation seasonality is not quantified through this method.

The results of the climatic quantification based on pollen samples covering the middle Miocene period (15.97 – 11.63 Ma) show that mean annual temperatures (MAT) were higher than today at all sites (~2 to 8°C higher) and that mean annual precipitation (MAP) was higher than today in Southern France, Corsica and North Eastern Spain (between 400 mm and 700 mm higher) and almost equivalent to modern values (maximum 200 mm higher) in Southwestern Europe (Fig. 9a; Fauquette *et al*., 2007). From North to South, annual temperatures increased but annual precipitation decreased. The thermic gradient was clearly weaker than the modern one. On the basis of the reconstructed values from pollen data, the thermic gradient in Western Europe is estimated to have been around 0.48°C per degree in latitude during the middle Miocene (Fauquette *et al*., 2007).

During the Tortonian (11.63 – 7.24 Ma), the climate was warm and humid in Northwestern Europe (MAT 4 to 9°C and MAP 100 to 600 mm higher than today) and warm and dry in the South Mediterranean region (MAT 3 to 4°C higher and MAP less than 200 mm higher than today) (Fig. 9b). The climatic estimates show that the North-South climatic gradient that existed during the Tortonian was similar to that of the present-day, with increasing temperature and decreasing precipitation, but with higher temperatures. On the basis of the reconstructed MAT, Fauquette *et al*. (2007) showed that the thermic gradient was around 0.6°C per degree in latitude.

During the earliest Pliocene (5.3 – 5 Ma), the climatic reconstructions show that the average climate was warm and humid in Europe and the North Mediterranean region (MAT 1 to 4°C and MAP 400 to 700 mm higher than today), and warm and dry in the South Mediterranean region (1 to 5°C warmer and at least as dry as today) (Fig. 9c; Fauquette *et al*., 1998a, 1999, 2007; Fauquette & Bertini, 2003). A North-South climatic gradient existed at the beginning of the Pliocene with, as today, increasing temperatures and decreasing precipitation. The thermic gradient is estimated to have been around 0.6°C per degree in latitude (Fauquette *et al.,* 1999, 2007).

Our results thus confirm the existence of a North to South temperature gradient and a South to North precipitation gradient during the Neogene, but it appears that clearly the thermic gradient changed through time. Our results place the transition from the weak thermic gradient of the middle Miocene to the modern-like gradient of the Pliocene during the late Miocene, just before or during the Tortonian. The precipitation gradient was more pronounced during the Neogene than it is today. The transition to the modern gradient seems to have occurred during the lower Pleistocene, at the time of the earliest Northern Hemisphere glacial-interglacial cycles.

The climate of these first cycles has been reconstructed based on the Semaforo pollen sequence (lower part of the Crotone series: Figs. 5-6; Combourieu-Nebout, 1993) which covers the period between 2.46 and 2.11 Ma, i.e. nine glacial/interglacial cycles (Klotz *et al*., 2006). Our estimates indicate higher temperatures and precipitation than today during interglacials (MAT ~3°C higher, MAP 500 mm higher), but temperatures were equivalent to or lower than today and precipitation equivalent to modern levels during glacials. Moreover, throughout consecutive interglacials, a trend toward a reduction in annual and winter temperatures and toward higher seasonality is observed. During consecutive glacials, a trend toward a reduction in all temperature parameters is evident. Finally, the climatic amplitudes of the interglacial-glacial transitions progressively increased through time (Klotz *et al*., 2006). In the Rhône Delta, the last spreading of Mediterranean sclerophyllous plants due to climate significantly preceded the onset of human activity.

History of some emblematic plant taxa

This synthesis would not be complete without considering the biogeographical history of some woody taxa. As a complement to the reviews published by Biltekin *et al*. (2015) and Magri *et al*. (2017), we pay attention to three taxa, the behaviour of which over time may significantly complete our understanding of the history of peri-Mediterranean vegetation and the onset of the modern ecosystems.

Microtropis fallax Pitard (Celastraceae)

This pollen grain is one of the few to benefit from identification at the species level because its morphology is very specific within the genus *Microtropis* and itself within the Celastraceae family, as argued by Lobreau-Callen & Suc (1972). That fact should not be lost by Bertini & Martinetto (2011: p. 240) in their claim that the correct identification of this taxon may require observation by SEM. Although we have SEM photographs, their publication is of little value in the identification of pollen of *Microtropis fallax* because the decisive characters concern the inner structure of the pollen membrane and not its surface ornamentation. The species is rarely but continuously recorded around the entire Mediterranean Sea *s.l.* (Fig. 1) from the early Miocene to early Pleistocene inclusive (Table 2) (detailed distribution in theses n° 2-4-5-6-7-9-10-13-14-16-17-21-23-25-26-29: Table 1). Today, *Microtropis fallax* is confined to two localities from Vietnam (Merrill & Freeman, 1940) where it is a constituent of the evergreen broad-leaved forest living under warm climate with dry summer (3 months) and very moist autumn, strongly influenced by the nearby sea (Vidal, 1960). It can be hypothesized that *M. fallax* participated with Mediterranean sclerophyllous plants within ecosystems adapted to dry soils during the Miocene and early Pliocene, then disappeared when the temperature fall became too intense. *M. fallax* is not reported in the European macrofloras that are mainly documenting the moister forest ecosystems. Its absence may be explained by its ecological requirements for seasonally dry environments.

Zelkova (Ulmaceae)

The history of *Zelkova* was reported at the Northeastern Mediterranean scale by Biltekin *et al.* (2015). The recent discovery of the living plant in Sicily (*Z. sicula* di Pasquale, Garfi & Quézel: di Pasquale *et al.*, 1992; Quézel *et al.*, 1993) requires us revisit its pollen records in the Northwestern Mediterranean region. Follieri *et al.* (1986) provided evidence of its last record in pollen successions from the Rome area at about 31,000 years BP. Recently, two offshore cores provided long pollen records, PRGL1-4 in the Gulf of Lions (Suc *et al.*, in progress) and PRAD1-2 near the Gargano Peninsula (thesis n° 12: Table 1) (Fig. 5). In the PRGL1-4 core, *Zelkova* occurs during each warm phase whatever its intensity, accompanied by *Pterocarya*, up to the end of the Last Interglacial (ca. 70 ka). They are both absent from all the colder phases since 500 ka, and that shows their extreme frailty during the recent glacial-interglacial cycles. In the PRAD1-2 core, at a latitude closer to Sicily, they are both present during the Last Interglacial and recorded episodically during the Last Glacial and the Holocene up to 6,000 years cal. BP., a little younger age than considered by Magri *et al.* (2017), suggesting its elimination in the Gargano Peninsula was caused by Man. Such recent evidence supports the continued survival of *Zelkova* up until today in Sicily. Quézel *et al.* (1993) were surprised by the modern occurrence of *Zelkova* in Sicily. Surprising too is the present-day absence of living remnants of *Pterocarya* in the Central Mediterranean region.

Cedrus (Pinaceae)

Three species are now accepted within the *Cedrus* genus: *C. deodara* (Roxb. Ex D. Don) G. Don, *C. atlantica* (Endl.) Manetti ex Carrière, and *C. libani* A. Rih. (The Plant List, 2013). These species live today in disjunct distribution areas (Quézel, 1998): *C. deodara* in the Himalayas realm, from Afghanistan to Nepal; *C. atlantica* in Northern Africa (Morocco and Algeria); *C. libani* in the Eastern Mediterranean region (Turkey to Lebanon) including *C. brevifolia* (Hook. f.) Henry, a taxon restricted to Cyprus (Fig. 10). Such a distribution has never been successfully explained. According to molecular clock estimates, *C. deodara* diverged at about 55 Ma, *C. atlantica* between 20 and 17 Ma while *C. libani* and *C. brevifolia* separated between 8 and 5 Ma (Qiao *et al.*, 2007).

A first synthesis of the history of *Cedrus* was attempted by Pons (1998) despite only a limited documentation of macroremains and insufficient information from pollen records. However, the ancient origin (Lower Cretaceous?) of the genus seems to be established as attested by the occurrence of some *Cedrus*-like pollen grains in Upper Cretaceous deposits from central France (Bassil *et al.*, 2016). The *Cedrus* bisaccate pollen is easily identifiable thanks to the jointed shape of its air-sacs and thickness of its cappa (Van Campo-Duplan, 1950) and the long walls of the large alveoli of the air-sacs (Sivak, 1975). Such an homogenous pollen morphology makes it difficult to identify isolated pollen grains at the species level for which Aytug (1961), however, indicated some distinctive characters: slightly thicker cappa in *C. deodara*, thinner cappa in *C. atlantica*, and with lateral crests in *C. libani*. In addition, the longest walls of the large alveoli of the air-sacs can be observed in *C. deodara*.

Now we have at disposal enough high-quality pollen data to reconstruct a reliable history of *Cedrus* for the Late Cenozoic, particularly for the Mediterranean region *s.l.* A thorough review of Quaternary *Cedrus* records (pollen grains and macroremains) in Southern Europe was provided by Magri (2012) and completed by Magri *et al.* (2017), leading to a reconstruction of its history around the Mediterranean Basin. A few *Cedrus* pollen grains have been recorded on both sides of the Arctic Ocean, in the New Siberian Islands (Suan *et al*., 2017) and the Mackenzie Delta (Salpin *et al*., accepted) where it confirms a first presence, observed by Rouse & Srivastava (1972), during cooler phases surrounding the early Eocene Climatic Optimum, i.e. at 58 – 54 Ma and 50 – 38 Ma (Suc, unpublished). These findings reveal a high potential on the American and Eurasian continents for unravelling the history of *Cedrus* (Fig. 10).

North America

The Cenozoic history of *Cedrus* in North America is poorly documented: about ten localities are reported by Thompson (1991) and Graham (1999), mostly in the Western USA along the Rocky Mountains, the most important of them concerings the late Miocene (Leopold & Denton, 1987) and the youngest the mid-Pliocene (Graham, 1999). The conditions and timing of the extinction of *Cedrus* from North America are enigmatic. Is there some relationship with the North-South alignment of the Rocky Mountains? Was the competition too hard with *Tsuga* still alive on the two sides of the continent?

Eastern Asia

The history of *Cedrus deodara*, today restricted to the southern slope of the Himalayas, is better constrained (Fig. 10). According to Hsü (1983), *Cedrus* seems to have been widespread during the Paleogene (from the Sakhalin Island to Inner Mongolia and Eastern China) and Miocene (from the Tibet Plateau to Eastern China). It has also been recorded from the early Miocene of Southern Myanmar (Popescu, unpublished). Hsü (1983) showed the restriction of *Cedrus* to the Tibet Plateau during the Pliocene and early Pleistocene and discussed its migration to the southern slopes of the Himalayas during the Pliocene. However, *Cedrus* could have occupied a larger area on both sides of the Himalayas before the uplift of the Tibet Plateau. Uplift started in the mid-Eocene, with repeated strong phases, mainly in the early Oligocene and since the mid-Miocene (15 Ma; Wang *et al*., 2012), during which time *Cedrus* was eliminated from the northern part of the mountain chain. *Cedrus* persisted in Southwestern China up until the late Pliocene from where it was probably eliminated by the onset of dry winters and early springs (Zhou *et al*., 2018). In addition, it cannot be excluded that this cedar may have had a larger extent to the West according to the occurrence of some pollen grains close to those of *C. deodara* up to the early Pliocene in the Northwestern Mediterranean region. Accordingly, a reduction of area similar to that of *Cathaya* and *Tsuga* may have affected this species.

Western Asia

Biltekin *et al*. (2015) assume that the early to mid-Miocene cedar from Anatolia refers to the *C. libani* – *C. brevifolia* lineage while the late Miocene – early Pliocene cedar is referable to *C. libani*. They show that *Cedrus* continuously inhabited the Anatolian reliefs up until the development of *Artemisia* steppes that probably fragmented the tree populations. Maybe the Middle East cedar resulted from an isolation process of the Anatolian Peninsula forced by intense tectonic extrusion since ca. 10 Ma (Fig. 10; Barka, 1992; Meulenkamp & Sissingh, 2003; Jolivet *et al*., 2006). During the late Miocene, propagation of the North Anatolian fault halted, that resulted in relief uplift (Armijo *et al*., 1999; Karacaş *et al*., 2018). This hypothesis is supported by spreading of *Cedrus* pollen in late Messinian sediments from the Dardanelles Strait (Melinte-Dobrinescu *et al*., 2009). It is also consistent with the proposed age of genetic divergence of *C. libani* between 8 and 5 Ma (Qiao *et al*., 2007).

Located at the junction between the Middle East and Asian realms, the South Caucasus area (Georgia) displays a dual history of *Cedrus*, mainly based on pollen grains, since the mid-

Eocene. A fossil species and probably *C. deodara* and *C. libani* co-existed from the latest Miocene to mid-Pleistocene (Shatilova *et al.*, 2011). *C. atlantica* is also indicated by the same authors as present during the late Miocene and early Pliocene. *C. deodara* would have persisted in the South Caucasus area up to the Last Glaciation (Shatilova *et al.*, 2011) and is replaced today by re-introduced *C. libani* (Denk *et al.*, 2001). This illustrates how complex the history of *Cedrus* is in Eurasia due to the co-existence of fossil species and the emergence of the modern ones; the history is arduous to decipher because of the lack of fossil macroremains and difficulty in distinguishing the species using pollen morphology alone.

Europe and North Africa

The history of cedar in Europe is also complex. *Cedrus* was pointed out in relation to the occurrence of Mediterranean massifs since the Oligocene (Fauquette *et al.*, 2015), that confirms its ancient presence on the continent (Ferguson, 1967). In Southern France (Languedoc), a rich early Pliocene assemblage suggests the existence of a dominant fossil *Cedrus* species, indicated by a coarser pollen grain (with thick cappa and dense alveolate network in the air-sacs) (Suc, 1981), consistent with the assumption of Pons (1964). In addition, several other pollen grains show a morphology close to that of *C. atlantica* and rare specimens are similar to *C. deodara*. Progressively, *Cedrus* disappeared during the Neogene from the higher latitudes to survive at lower latitudes, especially in some islands (Corsica, Sardinia) and the Hellenic, Italian and Iberian peninsulas where the species *C. atlantica* prevailed and persisted in this area up to the mid-Pleistocene (Fig. 10). Abundant pollen data from the Moroccan depression between the Rif and Atlas mountains and from the Chelif Basin in Algeria, do not show the occurrence of *Cedrus* during the Tortonian and early Messinian (thesis n° 2, Table 1; Chikhi, 1992). First occurrences of cedar in North Africa are indicated in the latest Messinian (i.e. during the desiccation phase of the Mediterranean) and earliest Zanclean in West Morocco (thesis n° 28, Table 1; Warny *et al.*, 2003) and the early Pliocene of Northern Tunisia (thesis n° 24, Table 1) and Northern Morocco (Jiménez-Moreno & Fauquette, unpublished). We can hypothesize that the paroxysmal desiccation phase of the Messinian Salinity Crisis (5.6 – 5.46 Ma; Bache *et al.*, 2015) offered *Cedrus* the opportunity to migrate to North Africa, maybe from the Sardinian highlands considering the large amount of cedar pollen (including *C. atlantica*) in latest Messinian – earliest Zanclean deposits offshore of this island (Popescu *et al.*, 2015). A second possibility is migration from the Calabrian and/or Sicilian mountains (Suc and Bessais, 1990; Fauquette *et al.*, 2006), despite the substantial distance to cross (Fig. 10). Contrasting with the hypothesis of Qiao *et al.* (2007) and Alba-Sánchez *et al.* (2018), migration of *Cedrus* to North Africa was probably impossible via the Alboran domain because it was partly covered by oceanic waters during the paroxysm of the Messinian Salinity Crisis (Bache *et al.*, 2012, 2015) probably because of the pre-existence of the Gibraltar Strait (Capella *et al.*, 2018). As a last hypothesis, *Cedrus* could have already existed, albeit not significantly, in the Rif Mountains (a pollen grain was recorded in the Tortonian sediments of the Irhachâmene section, in Northern Morocco; Achalhi *et al.*, 2016) and would have benefited from the closure of the Rifian corridor at about 7 Ma (Capella *et al.*, 2018) for colonizing the Middle and Tell Atlas mountains (Fig. 10). In this particular case, movement of *Cedrus* into North Africa could have occurred prior to the Messinian Salinity Crisis, and would have been assisted by the Rif orogen (Capella *et al.*, 2017). In the Alboran Sea, there is weak evidence of *Cedrus* pollen offshore Algeria and Morocco in the latest Pliocene (Suc, 1989; Feddi *et al.*, 2011) while it is rarely recorded in Southern Spain since the mid-Miocene (thesis n° 17, Table 1; Jiménez-Moreno *et al.*, 2010; Suc, unpublished). This hypothesis, supported by new data, offers reliable solutions to the questions asked by Magri (2012) and Magri *et al.* (2017). Especially, it provides robust information because most of the pollen data come from prodeltaic sediments forced by river supply and undisturbed by long-distance wind transport, suspected to have biased some late Quaternary European lacustrine records (Magri & Parra, 2002; Magri, 2012; Magri *et al.*, 2017). Otherwise, the persistence of *Cedrus* in Southern Spain during the late Pleistocene is still debated (Postigo-Mijarra *et al.*, 2010; Joannin *et al.*, 2011; Alba-Sánchez *et al.*, 2018).

Once established in Morocco, *Cedrus* was helped by the uplifting Rif Mountains that peaked during the Pliocene (Romagny *et al.*, 2014) and led, at mid to high altitude, to wetter and cooler climatic conditions more suitable for this conifer. *Cedrus atlantica* was probably saved from extinction by its migration from Europe to North Africa which offered new habitats protecting it from the forthcoming glacials (Fig. 10), especially from those of the late Pleistocene which decimated the European cedar populations and made the North African ones highly unstable (Cheddadi *et al.*, 2009). *Cedrus* almost disappeared during medieval times from most of the pollen records, indicating its regression to its present-day stands on mountain crests in the Rif and Atlas (Muller *et al.*, 2015).

To summarize, it appears that the greatly disconnected geographic distribution of *Cedrus* species mainly results from the progressive but unavoidable restriction of their habitat area caused by decreasing temperatures in the Northern Hemisphere (Fig. 10). However, it seems that the three surviving species may have been saved by strong geodynamic events: uplift of the Himalayas (including the Tibet Plateau) for *C. deodara*, extrusion of the Anatolian Peninsula for *C. libani*, and brief desiccation of the Mediterranean Sea and maybe Rif orogen for *C. atlantica* (Fig. 10). Maybe the geodynamical passive the North American craton did not provide sufficient mountain habitats and boost enough cedar populations there to allow its survival during the Northern Hemisphere glaciations.

Conclusion

This review shows how much high quality pollen records are needed for reliable past reconstructions of flora, vegetation and climate. In this synthesis, the pollen data show that large number of thermophilous (from megatherm to mesotherm) and hygrophilous taxa successively disappeared from the Mediterranean area throughout the Neogene. However, the great plant biodiversity was not really affected because plant extinctions were rapidly balanced by diversification of new taxa, especially among herbs and shrubs, that maintained the region as an hotspot of plant diversity (Médail & Quézel, 1997; Médail & Myers, 2004).

The North Mediterranean plant ecosystems have been deeply modified during the last 23 Ma, evolving from forest conditions to open landscapes: *Avicennia* mangrove disappeared, *Glyptostrobus* swamps disappeared later too, Mediterranean sclerophyllous ecosystems replaced subtropical evergreen forests, and lastly *Artemisia* steppes alternated with mesophilous forests during glacial-interglacial cycles. In contrast, the South Mediterranean plant ecosystems continuously sustained an open structure of vegetation with subdesertic associations where the *Avicennia* mangrove persisted up to the early Pliocene before invasion by the *Artemisia* steppe. The Mediterranean sclerophyllous plants, already present in the early Miocene, benefited first from the extinction of thermophilous-hygrophilous elements, then fluctuated in relation with temperature variations. They appear, however, to have been advantaged during some phases of high instability in seasonality (high amplitude of obliquity) and low variability in heat (low amplitude of eccentricity). Before its regional extinction, *Microtropis fallax* can be regarded as a reliable indicator of primitive Mediterranean sclerophyllous populations. At the scale of the whole Late Cenozoic, plant extinctions appear to have been mostly driven along a North-South latitudinal gradient despite some influence of longitude effects (e.g. diversification of rainfall). This general process cannot hide more complex modes that the detailed study of Quaternary glacials-interglacials allows us to decipher (Magri *et al.*, 2017). These include the protective or destructive effects of peculiar geographic situations (e.g. some azonal and irregular strengthening of continental ice during glacials; Tzedakis *et al*., 2013) or progressively acquired ability of some plants or ecosystems to survive in hard conditions (Svenning *et al*., 2015).

Climatic interpretation of pollen records and their quantification in terms of palaeoclimate parameters emphasize a latitudinal contrast in temperature and in humidity/dryness, the thermic latitudinal gradient being characterized by a significant increase in the late Miocene towards its modern value. Characterized by elevated temperatures and some seasonality in dryness from 23 to 3.37 Ma, climate evolved with cooler winters and drought concentrated in summers when earliest glacials occurred at 2.6 Ma with generalized dryness and colder conditions alternating with moister and warmer conditions during interglacials. The present-day refuges of some mesophilous taxa, such as the "climate relicts" *Zelkova* and *Pterocarya*, may be considered as representative of this highly contrasted history, both from a biogeographical and climatic point of view. The desiccation phase of the Messinian Salinity Crisis did not severely impact the region but forced the subdesertic elements to momentarily migrate northward (Fauquette *et al*., 2006; Popescu *et al*., 2007) and offered cedar the opportunity to reach North Africa. The present-day patchy distribution of *Cedrus* seems to have been influenced by geodynamic events, which offered opportunities to persist, despite repeated coolings.

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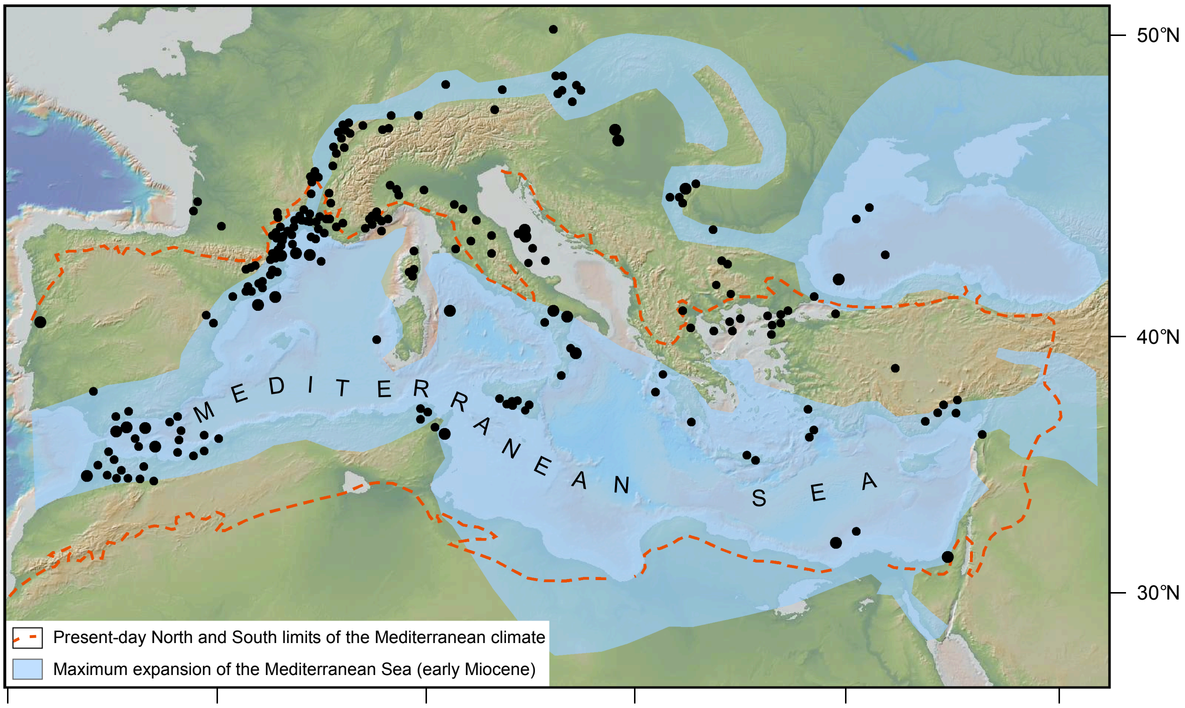

Fig. 1. Geographic location of the studied Late Cenozoic pollen floras in the Mediterranean region considered in this paper.
Larger dots correspond to long pollen records.
The present-day limits of the Mediterranean climate are from Quézel & Médail (2003). The maximum expansion of the Mediterranean Sea (early Miocene) is from Meulenkamp & Sissingh (2003).
All the maps are elaborated using GeoMapApp from Ryan *et al*. (2009).

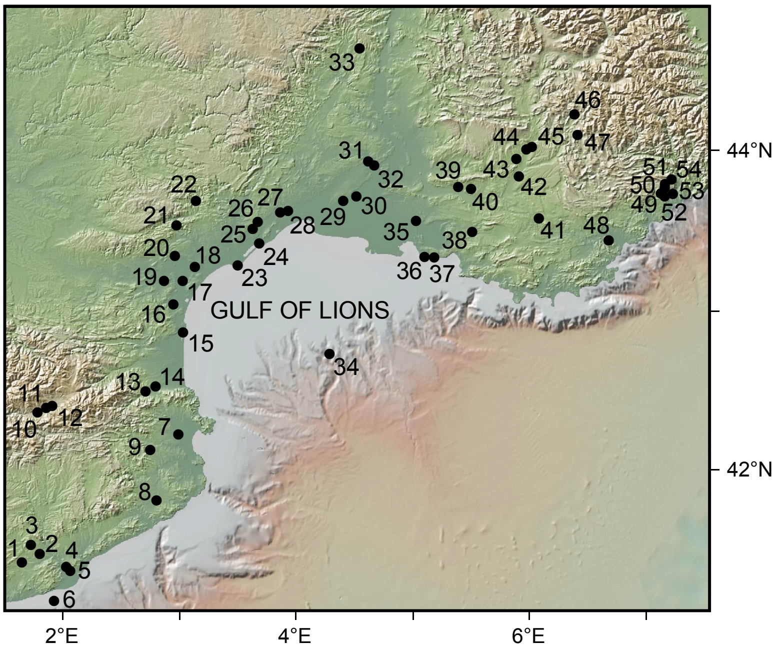

Fig. 2. Location map of selected significant pollen floras from the Northwestern Mediterranean region. From Northeastern Spain to Southeastern France: 1, Vilobi del Penedès; 2, Sant Pau d'Ordal; 3, La Rierussa; 4, Papiol; 5, Torrente del Terme; 6, Garraf 1; 7, Ciurana; 8, Can Cateura; 9, Banyoles; 10, Can Vilella; 11, Sampsor; 12, Sanavastre; 13, Vivès; 14, Le Boulou; 15, Leucate SC1; 16, Portel – Sigean; 17, Narbonne: V. Hugo College; 18, Lespignan; 19, Montredon; 20, Montady; 21, Cessenon; 22, Bernasso; 23, Cap d'Agde 1; 24, Issanka; 25, Poussan; 26, Montbazin; 27, Caunelle; 28, Montpellier; 29, Pichegu; 30, Pierrefeu 1; 31, Fournès; 32, Vacquières; 33, Mirabel; 34, Autan 1; 35, Estagel – Bayanne; 36, Les Tamaris; 37, Carry le Rouet; 38, Aix en Provence – Venelles; 39,Vaugines; 40, La Motte d'Aigues; 41, Fabrègues; 42, Oraison (Flour); 43, Villeneuve; 44, Les Mées (Périgoite); 45, Les Mées 1; 46, Le Rochassas; 47, Châteauredon; 48, Escaravatier; 49, Vence; 50, Le Gourg; 51, Carros; 52, Saint-Paul de Vence; 53, Saint-Isidore; 54, Saint-Martin du Var.

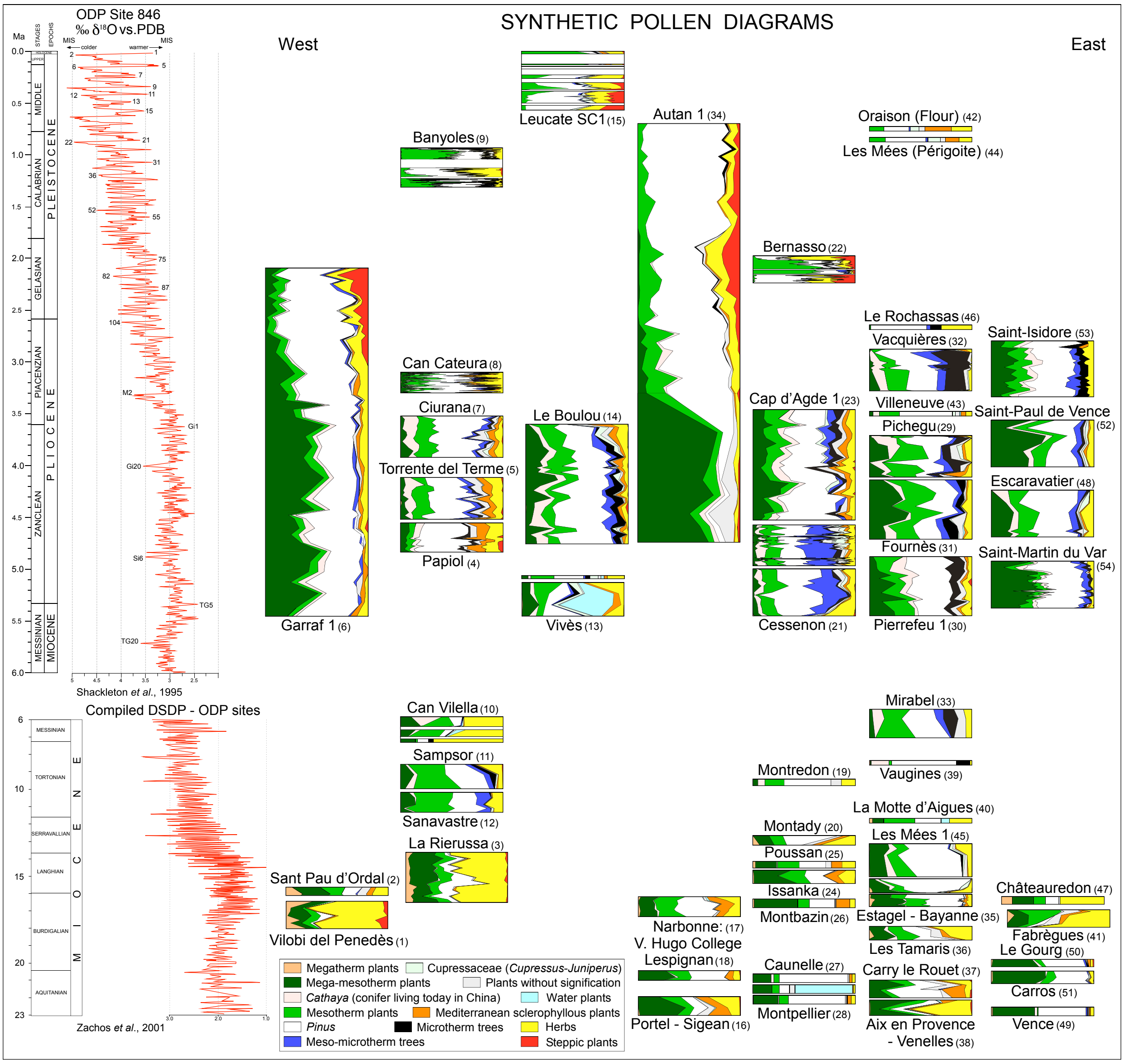

Fig. 3. Synthetic pollen diagrams distributed from West to East with respect to chronology and climatostratigraphy correlated with the reference oxygen isotope records.
MIS, Marine isotope stages.
Site numbers in brackets refer to Figure 2.

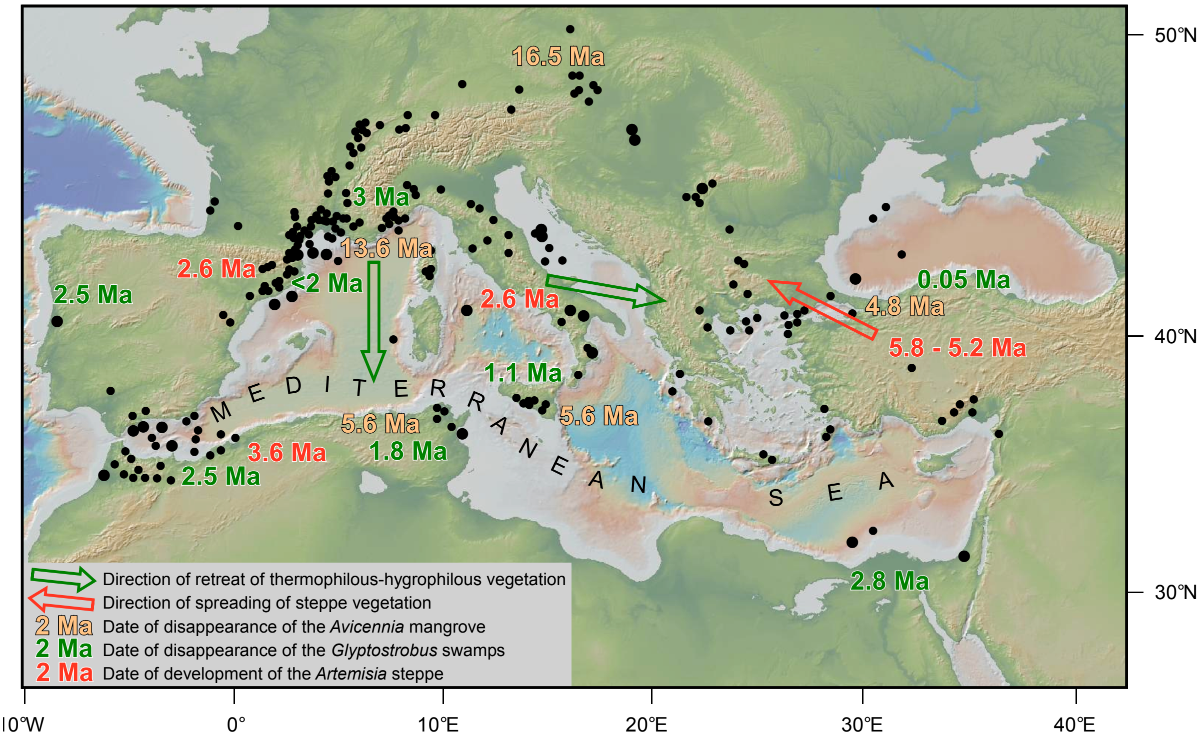

Fig. 4. Heterogeneity of the Mediterranean region with regard to the evolution of some plant ecosystems.

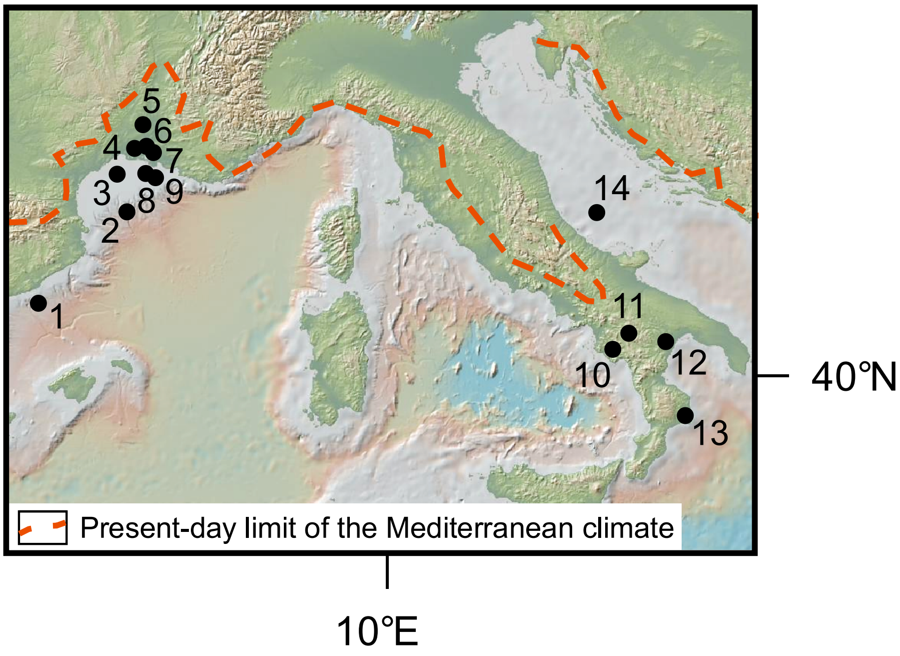

Fig. 5. Location map of pollen sites considered for reconstructing the history of the Mediterranean sclerophyllous plants since 3.6 Ma and the two sites showing last occurrences of *Zelkova*.
1, Garraf 1; 2, MD99-2348 and PRGL1-4; 3, 92K19; 4, Saint-Ferréol; 5, Piton; 6, Fangassier; 7, BF6; 8, 92K04; 9, 92K08; 10, Camerota; 11, Vallo di Diano; 12, Montalbano Jonico; 13, Crotone; 14, PRAD1-2.

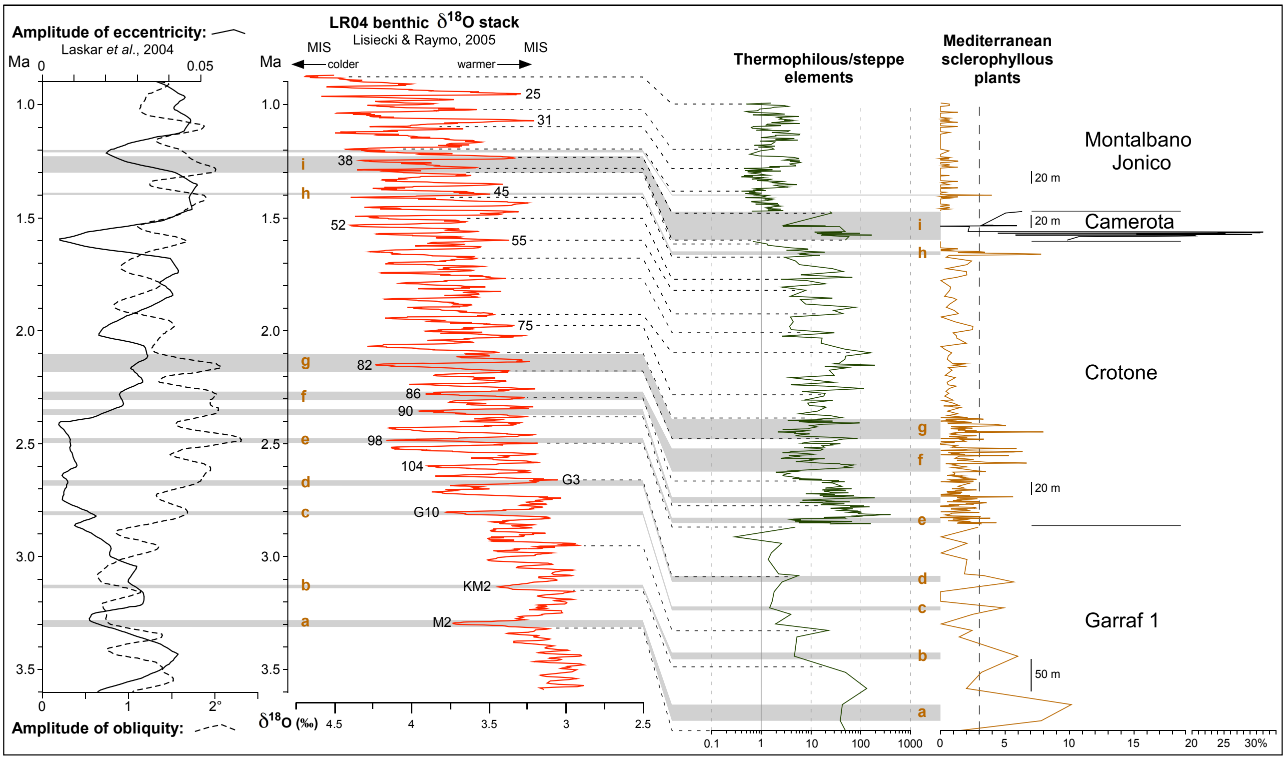

Fig. 6. History of the Mediterranean sclerophyllous plants between 3.6 and 0.9 Ma according to pollen records from four localities: Garraf 1 (Cravatte & Suc, 1981), Crotone (Suc *et al*., 2010), Camerota (Brenac, 1984), Montalbano Jonico (Joannin *et al*., 2008).

The curve of percentages of Mediterranean sclerophyllous plants (*Ceratonia*, *Nerium*, Myrtaceae, *Olea*, *Quercus ilex*-type, Rhamnaceae, *Pistacia*, *Phillyrea*, *Cistus*, *Phlomis* cf. *fruticosa*, *Rhus* cf. *cotinus*), based on the total pollen sum (*Pinus* excluded), is plotted with the curve of the ratio “thermophilous/steppe elements”, a reliable indicator of climatic changes.

Chronostratigraphic relationships with the reference oxygen isotope curve are indicated by dotted lines according to already established cyclostratigraphic correlations (Suc & Popescu, 2005; Joannin *et al*., 2008; Suc *et al*., 2010).

Grey bands display isolated peaks or clusters of peaks of Mediterranean sclerophyllous plants exceeding 3% of the pollen sum and correlate them with the other proxies.

The amplitude curves of eccentricity and obliquity are constructed thanks to a mathematical calculation of their envelope, respectively.

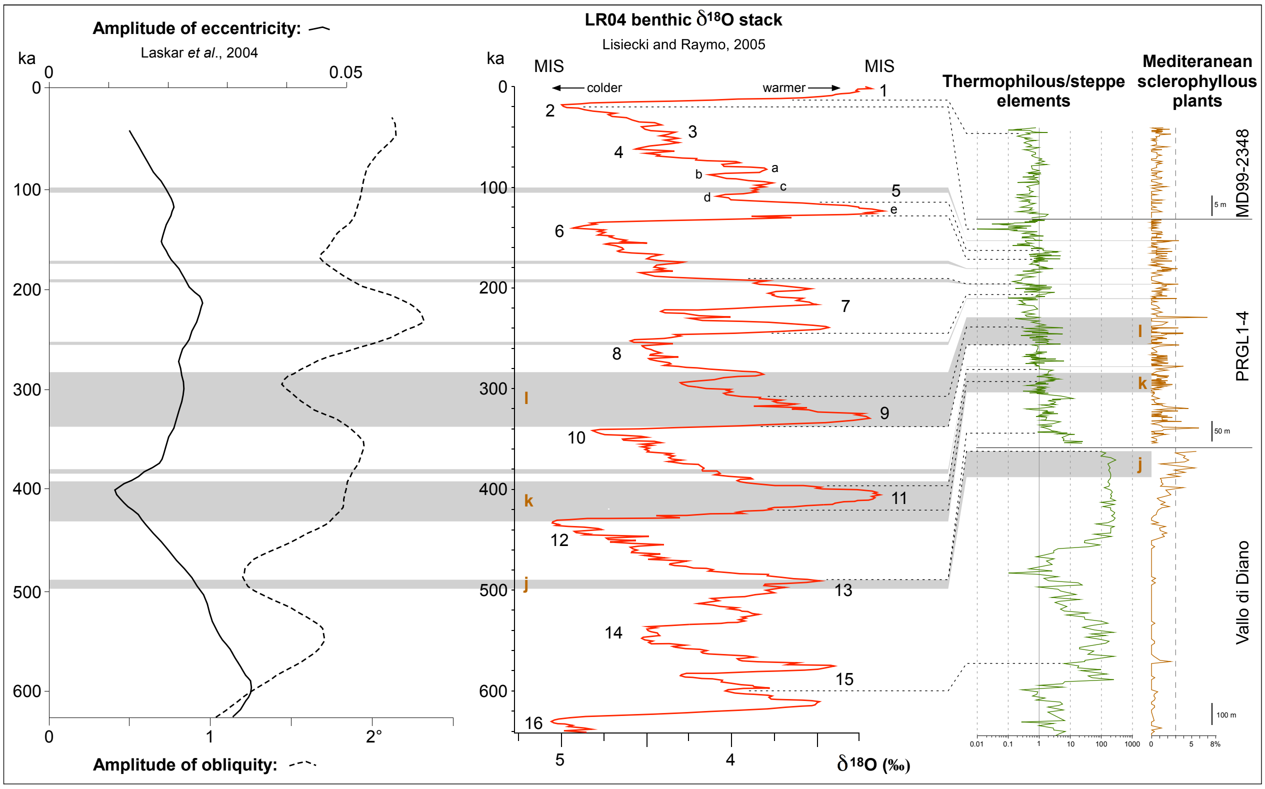

Fig. 7. History of the Mediterranean sclerophyllous plants between ca. 600 and 0.013 ka according to pollen records from three localities: Vallo di Diano (Russo Ermolli, 1994; Russo Ermolli & Cheddadi, 1997), PRGL1-4 (Suc *et al.*, in progress), MD99-2348 (Beaudouin *et al.*, 2005a).
Same explanations as for Figure 6.

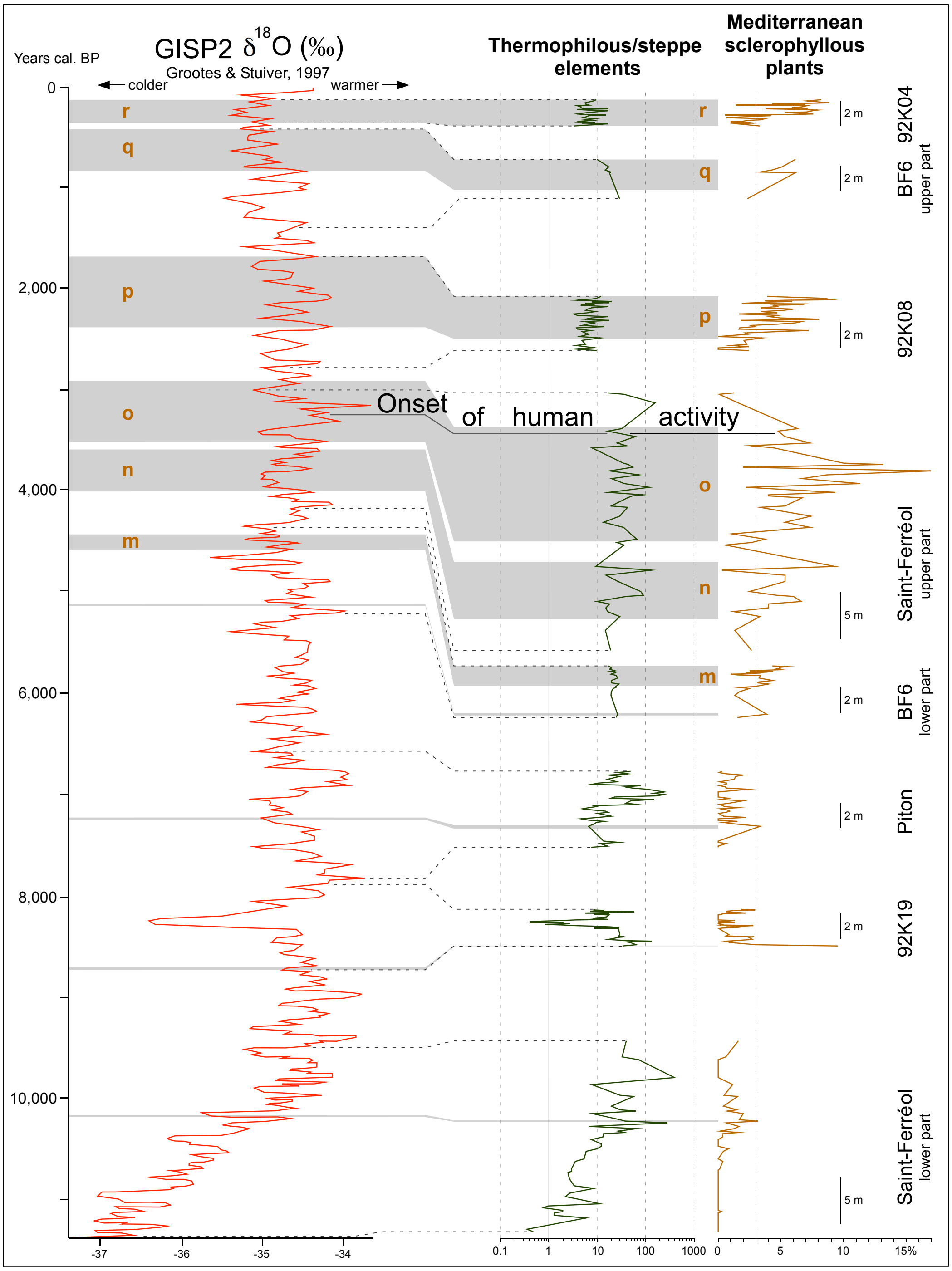

Fig. 8. History of the Mediterranean sclerophyllous plants since ca. 11,2000 years cal. BP according to pollen records from six localities: 92K19 (Beaudouin *et al.*, 2005a); 92K08 and 92K04 (thesis n° 1), Piton (thesis n° 3); Saint-Ferréol (thesis n° 11), BF6 (thesis n° 27) – thesis references are in Table 1.
Same explanations as for Figure 6 without the eccentricity and obliquity amplitudes not illustrated here.

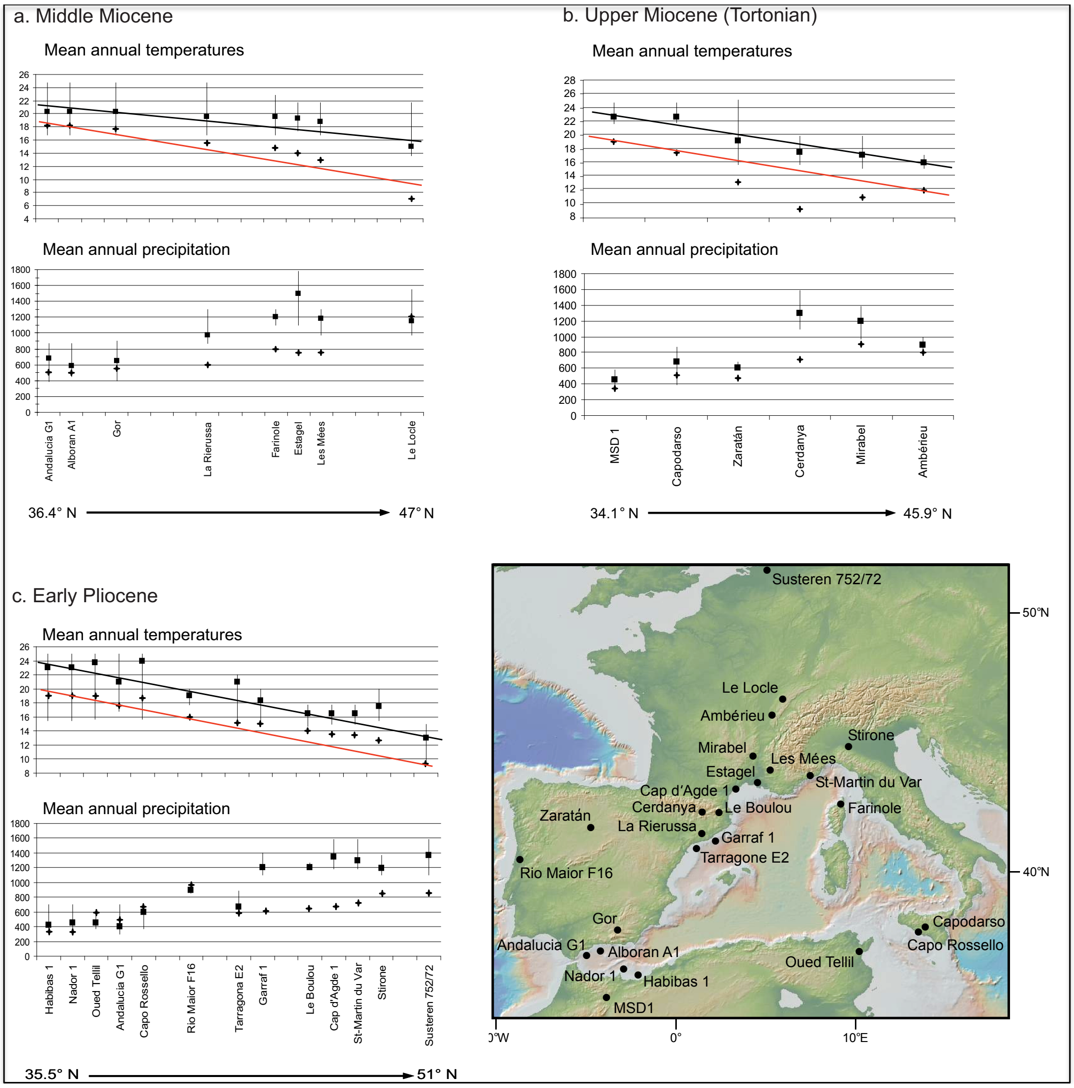

Fig. 9. Climatic reconstructions from pollen data (climatic interval and most likely value) in Western Europe and Mediterranean region showing the gradients of temperature (mean annual temperature in °C) and precipitation (mean annual precipitation in mm) for (a) the middle Miocene (Langhian/Serravallian, ~14 – 15 Ma), (b) the late Miocene (Tortonian, ~10 Ma), (c) the early Pliocene (Zanclean, ~5.3 – 5 Ma). Modern values are indicated by a cross to show the differences between modern and past latitudinal gradients (modified from Fauquette *et al*., 2007).

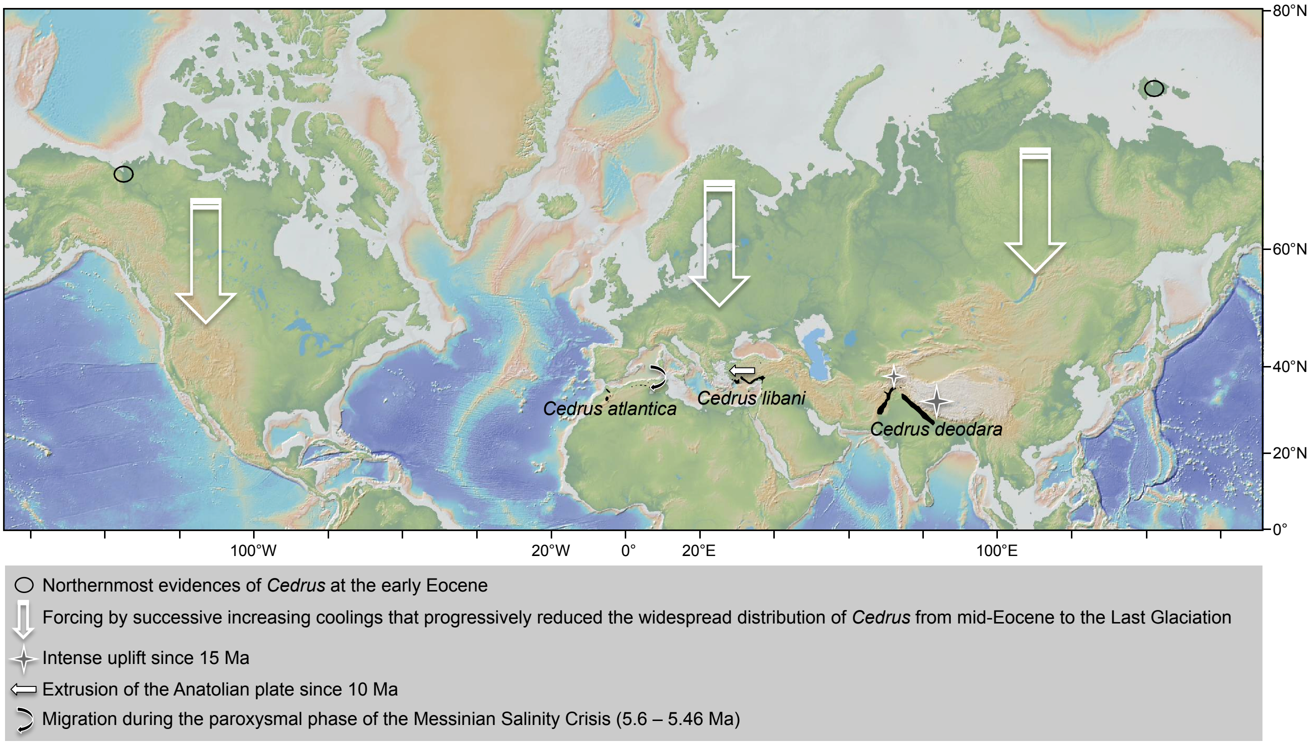

Fig. 10. North planisphere showing (1) the present-day distribution (in black) of the three living species of *Cedrus*, (2) the highest latitudinal places where the genus is recorded from early Eocene deposits, (3) the climatic forcing causing its weakening and surface regression, and (4) the intense geodynamic events which could be at the origin of the present refuges.

Thesis N°	Name	Year	Title	University
1	Acherki N.	1997	Analyse palynologique de quatre carottes du golfe du Lion. Application à la restitution de la végétation et du climat du midi de la France pendant le dernier cycle climatique et à la stratigraphie marine	Montpellier II, France
2	**Bachiri Taoufiq N.**	2000	Les environnements marins et continentaux du corridor rifain au Miocène supérieur d'après la palynologie	Casablanca, Morocco
3	Beaudouin C.	2003	Effets du dernier cycle climatique sur la végétation de la basse vallée du Rhône et sur la sédimentation de la plate-forme du golfe du Lion d'après la palynologie	Lyon I, France
4	Bertini A.	1992	Palinologia ed aspetti ambientali del versante adriatico dell'Appennino centro-settentrionale durante il Messiniano e lo Zancleano	Florence, Italy
5	Bessais E.	1984	Etude palynologique du Pliocène du sondage Tarragone E2	Montpellier II, France
6	**Bessedik M.**	1985	Reconstitution des environnements miocènes des régions nord-ouest méditerranéennes à partir de la palynologie	Montpellier II, France
7	Biltekin D.	2006	Vegetation and climate of North Anatolian and North Aegean region since 7 Ma according to pollen analysis	Lyon I, France Istanbul, Turkey
8	Brenac P.	1983	Analyse pollinique des dépôts lacustres de Camerota (Plio-Pléistocène inférieur) - Italie méridionale	Montpellier II, France
9	Chikhi H.	1992	Palynoflore du Messinien infra-évaporitique de la série marno-diatomitique de Sahaouria (Beni-Chougrane) et de Chabet Bou Seter (Tessala), bassin du Chelif, Algérie	Oran, Algeria
10	Combourieu-Nebout N.	1987	Les premiers cycles glaciaire-interglaciaire en région méditerranéenne d'après l'analyse palynologique de la série plio-pléistocène de Crotone (Italie méridionale)	Montpellier II, France
11	Cuinet J.	2007	Végétation, climat, incendies dans le Bas-Rhône depuis 12.000 ans. Etude palynologique de la carotte SF (Cacharel)	Lyon I, France
12	Dalibard M.	2007	Végétation et climat du Dernier Cycle Climatique en Italie centrale. Analyse pollinique de la carotte PRAD1-2 (mer Adriatique)	Lyon I, France
13	**Diniz F.**	1984	Apports de la palynologie à la connaissance du Pliocène portugais. Rio Maior : un bassin de référence pour l'histoire de la flore, de la végétation et du climat de la façade atlantique de l'Europe méridionale	Montpellier II, France
14	Drivaliari A.	1986	Sédimentation pollinique dans le paléogolfe de l'Orb : corrélations avec la végétation et le climat	Montpellier II, France
15	Drivaliari A.	1993	Images polliniques et paléoenvironnements au Néogène supérieur en Méditerranée orientale. Aspects climatiques et paléogéographiques d'un transect latitudinal (de la Roumanie au delta du Nil)	Montpellier II, France
16	Dubois J.-M.	2001	Cycles climatiques et paramètres orbitaux vers 1 Ma. Etude de la couoe de Monte San Giorgio (Caltagirone, Sicile) : palynologie, isotopes stables, calcimétrie	Lyon I, France
17	Jiménez-Moreno G.	2005	Utilización del análisis polínico para la reconstrucción de la vegetación, clima y estimación de paleoaltitudes a lo largo de arco alpino europeo durante el Mioceno (21 - 8 Ma)	Granada, Spain Lyon I, France
18	Joannin S.	2007	Changements climatiques en Méditerranée à la transition Pléistocène inférieur-moyen : pollens, isotopes stables et cyclostratigraphie	Lyon I, France
19	Leroy S.	1990	Paléoclimats plio-pléistocènes en Catalogne et Languedoc d'après la palynologie de formations lacustres	(Roman) Louvain, Belgium
20	Mrioo Z.	2010	La végétation et le climat du golfe d'Hammamet (Tunisie) du Miocène terminal au Pliocène supérieur d'après l'analyse pollinique	Casablanca, Morocco
21	Popescu S.-M.	2001	Végétation, climat et cyclostratigraphie en Paratéthys centrale au Miocène supérieur et au Pliocène inférieur d'après la palynologie	Lyon I, France
22	Russo Ermoli E.	1995	Analyse pollinique des dépôts lacustres pléistocènes du Vallo di Diano (Campanie, Italie) : cyclicités et quantification climatiques	Liège, Belgium
23	Sachse M.	1997	Die Makrilia-flora (Kreta, Griechenland) - Ein beitrag zur Neogenen klima- und vegetationsgeschichte des Östlichen Mittelmeergebietes	Zurich, Switzerland
24	Safra A.	2007	Flore et climat de la Tunisie nord-orientale au Messinien et Pliocène	Tunis, Tunisia
25	Suballyova D.	1997	Expression palynologique en Méditerranée des cycles glaciaire-interglaciaire arctiques anciens et cyclostratigraphie	Lyon I, France
26	**Suc J.-P.**	1980	Contribution à la connaissance du Pliocène et du Pléistocène supérieur des régions méditerranéennes d'Europe occidentale par l'analyse palynologique des dépôts du Languedoc - Roussillon (sud de la France) et de la Catalogne (nord-est de l'Espagne)	Montpellier II, France
27	Tinacci D.	2005	La registrazione pollinica in un sistema prodeltaico come strumento per la riconstruzione paleoambientale della bassa valle del Rodano durante l'Olocene	Florence, Italy
28	Warny S.	1999	Mio-Pliocene palynology of the Gibraltar Arc: A new perspective on the Messinian Salinity Crisis	(Roman) Louvain, Belgium
29	Zheng Z.	1986	Contribution palynologique à la connaissance du Néogène du Sud-Est français et de Ligurie	Montpellier II, France

Table 1. Listing of the 29 pollen analytic theses that contributed to establish the Mediterranean flora during the Late Cenozoic.

Authors of Master theses are underlined, those of PhD theses are in normal characters, those of State theses are in bold characters.

Family	**Genus**	**Species**	**Miocene**			**Pliocene**		**Quaternary**			
			early	**middle**	**late**	**early**	**late**	**early**	**middle**	**late**	**Holocene**
Megatherm plants:											
Acanthaceae			+	+	+	+	+	+			
	Avicennia		+	+	+	+		+			
	Blepharis							+			
Bombacaceae	*Bombax*		+	+	+	+		+			
Buxaceae	*Buxus*	*bahamensis*-type	+	+	+	+					
Cucurbitaceae						+					
Euphorbiaceae			+	+	+	+	+				
	Alchornea		+	+	+	+	+				
	Amanoa				+	+					
	Claoxylon-type		+	+							
	Croton		+	+	+	+	+	+			
	Jatropha		+	+							
	Phyllanthus-type			+	+						
Leguminosae Caesalpinioideae			+	+	+						
	Sindora			+	+	+					
Leguminosae Mimosoideae			+	+	+	+					
	Acacia		+	+							
	Prosopis	cf. *farcta*	+	+	+	+	+	+			
Hamamelidaceae	*Altinghia*				+						
	Fothergilla		+	+	+	+					
Icacinaceae			+	+	+	+					
	Mappianthus		+	+							
Malpighiaceae			+	+	+			+			
	Malpighia		+	+							
Malvaceae	*Grewia - Corchorus*		+	+	+						
Melastomataceae			+	+	+						
Meliaceae			+	+	+	+					
Passifloraceae			+	+	+	+	+				
Rubiaceae			+	+	+						
	Canthium-type				+		+				
Rutaceae			+	+	+	+					
Simaroubaceae	(*Pentapollenites*: fossil genus)		+	+	+						
	Picrasma		+	+							
Mega-mesotherm plants:											
Asparagaceae				+	+	+					
	Cordyline		+	+							
	cf. *Dracaena*					+					
	Nolina				+	+		+			
Alangiaceae	*Alangium*			+		+					
Anacardiaceae			+	+	+	+	+	+	+		
Aquifoliaceae	*Ilex*	*floribunda*-type			+	+		+			
Araliaceae			+		+	+	+	+	+		
Arecaceae			+	+	+	+	+	+	+		
Berberidaceae			+		+	+					
Bignoniaceae			+								
Celastraceae			+	+	+	+	+	+			
	Microtropis	*fallax*	+	+	+	+	+	+			
		cf. *fokienensis*			+	+					
Chloranthaceae			+	+							
Convolvulaceae	*Ipomoea*		+	+							
Coriariaceae	*Coriaria*				+			+	+		
Cornaceae			+								
	Cornus		+	+		+		+	+		+
	Nyssa	cf. *sinensis*	+	+		+	+	+			
Cupressaceae	Unidentified 'taxodioid' pollen		+	+	+	+	+	+			
	Sequoia-type		+	+	+	+	+	+	+		
	Taxodium-type (*Glyptostrobus*)		+	+	+	+	+	+	+	+	+
Cyrillaceae - Clethraceae			+	+	+	+	+	+			
Euphorbiaceae	*Mallotus*			+	+						
	Ricinus		+	+	+	+	+	+			
Gingkoaceae	*Gingko*			+	+	+	+				
Hamamelidaceae			+	+	+	+	+	+	+		
	Corylopsis		+	+	+						
	Dicoryphe-type				+						
	Disanthus		+								
	Distylium	cf. *chinensis*	+	+	+	+	+	+			
	Embolanthera		+		+	+	+				
	Eustigma		+	+							
	Exbucklandia		+		+						
	Hamamelis	cf. *mollis*	+	+	+	+	+	+			
	Loropetalum		+		+	+		+			
	Rhodoleia		+	+	+						
	cf. *Trichocladus*		+	+							
Iteaceae	*Itea*				+						
Juglandaceae	*Engelhardia*		+	+	+	+	+	+	+		
	Platycarya		+	+	+	+	+	+			
Loranthaceae			+	+	+	+	+	+			
Lythraceae	*Decodon*				+	+	+				
Magnoliaceae					+	+		+			
	Liriodendron				+	+					
Malvaceae	*Craigia*				+	+		+			
Menispermaceae tribe Cocculae			+	+	+	+	+	+			
Myricaceae	*Myrica*		+	+	+	+	+	+	+	+	+
Poaceae	cf. *Bambusa*		+		+						
Rhoipteleaceae	*Rhoiptelea*		+	+	+	+	+	+			
Rubiaceae	*Mussaenda*-type		+	+	+	+					
	Uncaria-type		+			+					
Sapindaceae			+	+	+	+		+			
	Dodonaea		+	+	+						

Sapotaceae			+	+	+	+	+	+			
Symplocaceae	*Symplocos*		+	+	+	+	+	+	+		
		cf. *paniculata*	+	+		+	+				
Sciadopityaceae	*Sciadopitys*		+	+	+	+	+	+	+		
Theaceae			+	+	+						
Vitaceae	*Leea*		+	+	+	+	+	+			
Mesotherm plants:											
Aceraceae	*Acer*		+	+	+	+	+	+	+	+	+
Anacardiaceae	*Rhus*		+	+	+	+		+			+
Aquifoliaceae	*Ilex*		+	+	+	+	+	+	+		+
Araliaceae	*Hedera*	cf. *helix*	+	+	+	+	+	+	+	+	+
Betulaceae	*Alnus*		+	+	+	+	+	+	+	+	+
	Betula		+	+	+	+	+	+	+	+	+
	Carpinus		+	+	+	+	+	+	+	+	+
		cf. *betulus*	+		+	+	+	+	+	+	+
		cf. *orientalis*	+	+	+	+	+	+	+	+	+
	Corylus		+	+	+	+	+	+	+	+	+
	Ostrya		+	+	+	+	+	+	+		+
Buxaceae	*Buxus*	cf. *sempervirens*	+	+	+	+	+	+	+	+	+
Cannabaceae	*Celtis*		+	+	+	+	+	+	+	+	+
Caprifoliaceae	*Lonicera*		+	+	+	+		+	+		+
	Sambucus				+	+		+	+	+	+
	Viburnum		+	+	+	+	+	+	+	+	+
Celastraceae	*Evonymus*				+	+		+	+	+	+
Cornaceae	*Nyssa*	cf. *aquatica*			+	+	+	+	+		
Elaeagnaceae	*Elaeagnus*		+	+	+			+	+		+
Ericaceae			+	+	+	+	+	+	+	+	+
Eucommiaceae	*Eucommia*		+	+	+	+	+	+	+	+	
Fagaceae	*Castanea*-type (*Castanopsis*?)		+	+	+	+	+	+	+	+	+
	Quercus (deciduous)		+	+	+	+	+	+	+	+	+
Hamamelidaceae	*Liquidambar*		+	+	+	+	+	+	+	+	
	Parrotia	cf. *persica*	+	+	+	+	+	+	+	+	
	Parrotiopsis	cf. *jacquemontiana*	+		+	+	+	+			
Juglandaceae	*Carya*		+	+	+	+	+	+	+	+	
	Juglans		+	+	+	+	+	+	+	+	+
		cf. *cathayensis*	+	+	+	+	+	+			
	Pterocarya		+	+	+	+	+	+	+	+	+
Malvaceae	*Tilia*		+	+	+	+	+	+	+	+	+
Oleaceae	*Fraxinus*		+	+	+	+	+	+	+	+	+
	Ligustrum		+	+	+	+	+	+	+	+	+
Platanaceae	*Platanus*		+	+	+	+	+	+	+	+	+
Salicaceae	*Populus*		+		+	+	+	+	+	+	+
	Salix		+	+	+	+	+	+	+	+	+
Santalaceae	*Arceuthobium*		+		+						
Sapindaceae	*Aesculus*	cf. *hippocastanum*	+			+				+	+
Tamaricaceae	*Tamarix*		+	+	+	+	+	+	+	+	+
Taxaceae			+		+	+	+	+	+		+
Ulmaceae	*Ulmus*		+	+	+	+	+	+	+	+	+
	Zelkova		+	+	+	+	+	+	+	+	+
Vitaceae	*Cissus*		+	+	+						
	Parthenocissus	cf. *henryana*	+	+	+	+	+	+	+		
		cf. *quinquefolia*				+			+	+	
	Vitis		+	+	+	+	+	+	+	+	+
Meso-microtherm plants:											
Fagaceae	*Fagus*		+	+	+	+	+	+	+	+	+
Pinaceae	*Cathaya*		+	+	+	+	+	+	+	+	
	Cedrus		+	+	+	+	+	+	+	+	+
	Keteleeria			+	+	+	+	+			
	Tsuga		+	+	+	+	+	+	+	+	
Microtherm plants:											
Pinaceae	*Abies*		+	+	+	+	+	+	+	+	+
	Picea		+	+	+	+	+	+	+	+	+
Cupressaceae	*Cupressus*-*Juniperus* pollen-type		+	+	+	+	+	+	+	+	+
Aquatic plants:											
?	*Aglaoreidia*: fossil genus		+								
Alismataceae	*Alisma*				+	+		+	+	+	+
Gunneraceae	*Gunnera*			+							
Haloragaceae	*Myriophyllum*		+		+	+	+	+	+	+	+
Lentibulariaceae	*Utricularia*					+					
Lythraceae					+	+		+	+		+
	Trapa		+			+					
Menyanthaceae									+		
Nymphaeaceae			+	+	+	+	+	+	+		+
Onagraceae			+	+	+	+	+	+	+	+	+
Potamogetonaceae	*Potamogeton*		+	+	+	+	+	+	+	+	+
Restionaceae			+	+	+	+	+	+			
	Restio		+	+	+	+					
Rubiaceae	*Cephalanthus*				+	+	+	+			
Ruppiaceae	*Ruppia*		+	+							+
Typhaceae	*Sparganium*		+	+	+	+	+	+	+	+	+
	Typha		+	+	+	+	+	+	+	+	+
Mediterranean sclerophyllous plants:											
Anacardiaceae	*Pistacia*		+	+	+	+	+	+	+	+	+
	Rhus	cf. *cotinus*	+		+	+	+	+	+		+
Apocynaceae	*Nerium*		+		+	+	+	+	+		
Cistaceae	*Cistus*		+	+	+	+	+	+	+	+	+
		cf. *monspeliensis*				+	+	+	+		
		cf. *salvifolius*			+	+			+		+
Ericaceae	*Erica*	cf. *arborea*				+	+	+	+		+
Fabaceae Caesalpinioideae	*Ceratonia*		+	+	+	+		+	+	+	+
Fagaceae	*Quercus*	*ilex*-type	+	+	+	+	+	+	+	+	+
Lamiaceae	*Phlomis*	cf. *fruticosa*	+		+	+	+	+	+	+	+

Myrtaceae			+	+	+	+	+	+	+		
Oleaceae	*Olea*		+	+	+	+	+	+	+	+	+
	Phillyrea		+	+	+	+	+	+	+	+	+
Rhamnaceae	*Rhamnus*		+	+	+	+	+	+	+	+	+
Herbs:											
Acanthaceae	*Acanthus*							+	+		
Amaranthaceae (including the former Chenopodiaceae)			+	+	+	+	+	+	+	+	+
Apiaceae			+	+	+	+	+	+	+	+	+
	Eryngium		+	+	+	+			+		
Apocynaceae	*Periploca*				+	+					
Asteraceae Asteroideae			+	+	+	+	+	+	+	+	+
	Ambrosia				+	+		+			+
	Centaurea		+	+	+	+	+	+	+	+	+
	Echinops				+				+	+	+
	Xanthium							+			+
Asteraceae Cichorioideae			+	+	+	+	+	+	+	+	+
Boraginaceae					+	+	+	+	+	+	+
	cf. *Anchusa*							+			+
	Borago			+	+	+	+		+		
	Echium				+						
	Lithospermum							+			
	Symphytum				+	+					
Brassicaceae			+	+	+	+	+	+	+	+	+
Campanulaceae			+	+	+	+	+	+	+	+	+
	Campanula					+			+		
Cannabaceae					+	+	+	+	+	+	+
Caprifoliaceae	*Centranthus*			+				+	+		
	Knautia		+	+	+	+	+	+	+	+	+
	Scabiosa		+	+	+	+	+	+	+	+	+
Caryophyllaceae			+	+	+	+	+	+	+	+	+
	Polycarpaea					+	+	+			
Cistaceae	*Helianthemum*		+	+	+	+	+	+	+	+	+
Convolvulaceae	*Calystegia*			+		+		+	+		
	Convolvulus		+	+	+	+	+	+	+	+	+
Crassulaceae			+		+	+	+	+	+	+	+
Cyperaceae			+	+	+	+	+	+	+	+	+
Euphorbiaceae			+	+	+	+	+	+			+
	Euphorbia		+	+	+	+	+	+	+	+	+
	Mercurialis		+	+	+	+	+	+	+	+	+
Fabaceae Papilionoidaeae			+	+	+	+	+	+	+	+	+
Gentianaceae					+	+	+	+	+	+	+
Geraniaceae	*Erodium*		+	+	+	+	+	+	+		+
	Geranium		+	+	+	+	+	+	+	+	+
Globulariaceae						+					
Grossulariaceae	*Ribes*		+			+		+	+	+	+
Iridaceae					+						
Lamiaceae			+	+	+	+	+	+	+	+	+
Liliaceae			+	+	+	+	+	+	+	+	+
	Colchicum								+		+
Linaceae	*Linum*		+	+	+	+	+	+	+	+	
		usitatissimum									+
Malvaceae			+	+	+	+	+	+		+	+
Papaveraceae			+		+	+		+	+	+	+
Plantaginaceae	*Plantago*		+	+	+	+	+	+	+	+	+
Plumbaginaceae			+	+	+	+	+	+	+	+	+
Poaceae			+	+	+	+	+	+	+	+	+
Cerealia											+
Polygalaceae			+	+	+	+		+			
Polygonaceae	*Polygonum*		+	+	+	+	+	+	+	+	+
	Rumex		+	+	+	+	+	+	+	+	+
Primulaceae					+	+			+		+
Ranunculaceae	*Thalictrum*		+	+	+	+		+	+	+	+
Resedaceae			+	+	+	+	+	+		+	+
Rosaceae	*Filipendula*		+	+		+	+		+		+
	Sanguisorba-type		+	+	+	+	+	+	+	+	+
Rubiaceae	*Galium*		+	+	+	+		+	+	+	+
Saxifragaceae			+	+	+	+	+	+	+	+	+
Scrophulariaceae						+	+	+	+	+	+
Solanaceae			+	+	+	+		+	+	+	+
Thymelaeaceae			+	+	+	+	+	+	+	+	+
Urticaceae			+	+	+	+	+	+	+	+	+
Valerianaceae			+	+	+	+		+			
Xanthorrhoeaceae	*Asphodelus*		+	+	+	+	+	+	+		+
Steppe plants:											
Arecaceae	*Chamaerops*	cf. *humilis*			+	+					
Asteraceae	*Artemisia*		+	+	+	+	+	+	+	+	+
Elaeagnaceae	*Hippophae*	*rhamnoides*		+	+	+	+	+	+	+	+
Ephedraceae	*Ephedra*		+	+	+	+	+	+	+	+	+
Neuradaceae	*Neurada*				+		+	+			
Nitrariaceae	*Nitraria*		+	+	+	+	+	+	+		
Poaceae	*Lygeum*	cf. *spartum*	+	+	+	+	+	+	+	+	+
Polygonaceae	*Calligonum*			+	+	+	+	+		+	+
Rhamnaceae	*Ziziphus*				+	+			+		
Plants without signification:											
Pinaceae	*Pinus* diplostellate-type		+	+	+	+	+	+	+	+	+
	Pinus haplostellate-type		+		+	+	+	+	+	+	
	Pinus haploxylon-type		+	+	+	+	+	+	+		
Ranunculaceae			+	+	+	+	+	+	+	+	+
Rosaceae			+	+	+	+	+	+	+	+	+
Rutaceae			+	+	+				+	+	
?	*Gymnocardiidites*: fossil genus	*subrotunda*: fossil species			+	+	+	+			
?	*Tricolporopollenites*: fossil genus also called: *Fupingopollenites*	*sibiricum*: fossil species *wackersdorfensis*: fossil species	+	+	+	+		+	+		

Table 2. Listing of taxa (at the family, genus and sometimes species level) identified at the Mediterranean scale according to pollen grains from the Late Cenozoic deposits, distributed according to the main chronostratigraphic subdivisions.

Taxa identified for the first time in the Mediterranean Late Cenozoic are underlined in grey.