Middle Miocene latitudinal climatic gradient in Western Europe: Evidence from pollen records

Gonzalo Jiménez-Moreno [a,b,*], Jean-Pierre Suc [a]

[a] *Laboratoire PaléoEnvironnements et PaléobioSphère (UMR CNRS 5125), Université Claude Bernard — Lyon 1, bâtiment Géode, 27-43 boulevard du 11 Novembre, 69622 Villeurbanne Cedex, France*
[b] *Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avda. Fuente Nueva S/N, 18002 Granada, Spain*

Abstract

Pollen analysis of sections spanning the Middle Miocene (Langhian and Serravallian) from southern Spain to Switzerland has been carried out with the aim of reconstructing the existing latitudinal environmental gradient.

Floral assemblages indicate a tropical–subtropical to warm–temperate climate for the entire area during the Middle Miocene. The presence, in all pollen spectra, of taxa with high temperature requirements demonstrates that the latitudinal gradient in temperature was relatively low. The development of a diverse subarid flora in southern Spain including *Neurada*, *Lygeum*, *Prosopis*, *Calligonum*, *Nitraria*, Caesalpiniaceae, etc., points to a very dry climate with a marked seasonality. These features clearly indicate that a very warm and dry climate (i.e. a steppe environment) was already present during the Langhian in the northwestern Mediterranean area. On the other hand, milder conditions are progressively inferred towards the north as subdesertic elements gradually disappeared and taxa with higher water requirements increased. The latter dominates the pollen assemblages in the eastern central part of France and Switzerland, thus precipitations would have been evenly distributed throughout the year. We interpret this gradient from subdesertic vegetation in the south to humidity-adapted plant environments in the north as the result of a latitudinal gradient in precipitation.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Palynology; Vegetation; Climate; Biogeography; Middle Miocene; Western Europe

1. Introduction

The modern distribution of plants in Southwestern Europe is very complex (Quézel and Médail, 2003). It is mainly controlled by the latitude, altitude, and the influence of the Atlantic Ocean or the Mediterranean Sea, as well as the position of the mountain ranges. However, the temperature gradient, from the very south of Spain and Italy, where summer drought and temperatures

are more pronounced, to the north, mainly controls the present-day latitudinal distribution of the vegetation. At the same time, the mountainous character of the Iberian and Italian peninsulas allows a marked southward extension of "boreal" assemblages (Quézel and Médail, 2003).

The Miocene is a key period in Cainozoic climatic and tectonic evolution. Indeed, the Middle Miocene represents one of the last warm episodes of the Neogene (Miocene Climatic Optimum, MCO) in a general cooling trend and development of major permanent Antarctic ice sheets (Flower and Kennett, 1994; Zachos

* Corresponding author. Tel.: +34 958243347; fax: +34 958248528.
E-mail address: gonzaloj@ugr.es (G. Jiménez-Moreno).

et al., 2001). The continents finally evolved toward their present-day configuration during Miocene–Pliocene times due to the uplift of the Alpine Chain and changes in sea-level (Meulenkamp and Sissingh, 2003).

Palynological studies carried out in order to understand vegetation and climate history during the Neogene in Europe are numerous. The most recent sediments are the most studied, therefore, the past dynamics of Pliocene vegetation and climate are well-known (Zagwijn, 1960; Pons, 1964; Suc, 1976, 1984; Suc and Cravatte, 1982; Diniz, 1984; Zheng and Cravatte, 1986; Bessais and Cravatte, 1988; Drivaliari, 1993; Bertini, 1994; Suc et al., 1995a,b; Popescu, 2001; Fauquette and Bertini, 2003). These studies suggest that, at least during the Early Pliocene (5.33–3.6 Ma), factors similar to those found today already played an important role in the organisation of the Mediterranean vegetation (Suc, 1989).

The Late Miocene is also well studied thanks to many studies that aimed at clarifying the climate forcing on the controversial Messinian Salinity Crisis (Suc and Bessais, 1990; Suc et al., 1995a,b; Bertini et al., 1998; Fauquette et al., 2006; Popescu, 2006).

However, Middle Miocene palynological studies in southwestern Europe are scarcer and have been geographically restricted (Bessedik, 1984, 1985; Zheng, 1990; Valle et al., 1995). These studies have proved beneficial by providing information mainly about the vegetation and climate of the different sites or relatively small areas (e.g. Catalonia and Southern France by Bessedik, 1984, 1985).

In order to fill this gap, several pollen records of Langhian and Serravallian ages from southern Spain to Switzerland have been compared in this paper. This was done to better understand the process and pattern of the Middle to Late Miocene climatic evolution in Western Europe.

2. Materials and methods

In this study, 74 samples of Langhian and Serravallian ages from different sections, that are today separated by about 11° in latitude (Spain, France and Switzerland), have been analysed. Samples are located in the north Mediterranean area, and originate from several Neogene basins that formed as a consequence of the African–Eurasian convergence (Meulenkamp and Sissingh, 2003).

The first 10 sections (Fig. 1) were analysed by one of the authors (G.J.-M.). They are (from south to north): Andalucía G1 (Alboran Sea), borehole (from Late Langhian to Early Tortonian; ELF, 1984); Alborán A1 (Alboran Sea), borehole (from Late Langhian to Early
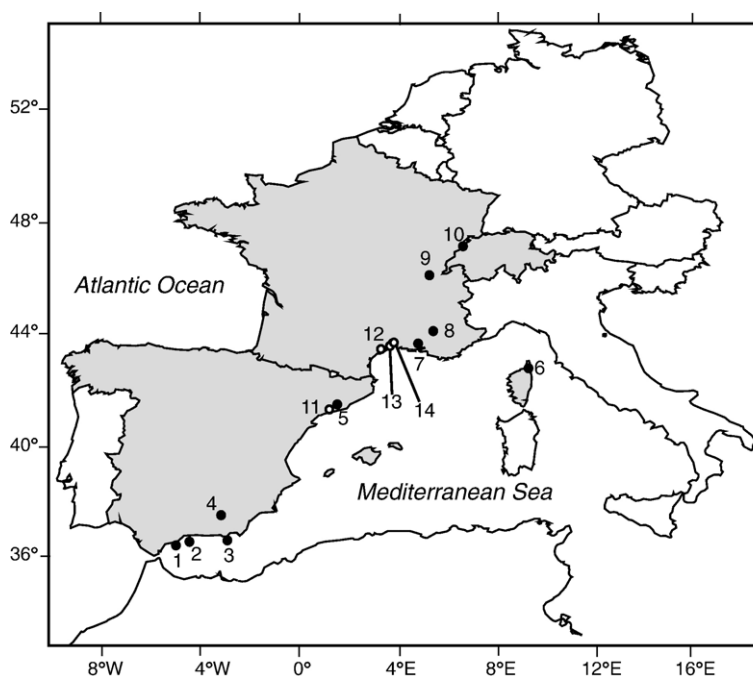

Fig. 1. Geographic position of the considered pollen localities. Black dots: new pollen localities acquired in this work; white dots: pollen spectra from Bessedik (1984, 1985). See text for a complete description of pollen localities and pollen records. (1) Andalucía G1; (2) Alborán A1; (3) Andalucía A1; (4) Gor; (5) La Rierussa; (6) Farinole; (7) Estagel–Bayanne; (8) Les Mées; (9) Ecotet; (10) Le Locle (Combe Girard); (11) Sant Pau d'Ordal; (12) Montady; (13) Poussan; (14) Issanka.

Tortonian; Chevron, 1986); Andalucía A1 (Alboran Sea), borehole (from Late Langhian to Early Tortonian; ELF, 1984; Rodríguez-Fernández et al., 1999); Gor (Spain), exposed section (Langhian; Martín Pérez and Viseras, 1994); La Rierussa (Spain), exposed section (Langhian; Magné, 1978; C. Müller *in* Bessedik, 1985); Farinole (France, Corsica), exposed section (Serravallian; Ferrandini et al., 1998, 2003); Estagel and Bayanne (France), exposed sections (Late Burdigalian and Langhian; Maurel-Ferrandini, 1976; Besson et al., 2002; Jiménez Moreno et al., 2002); Les Mées (France), borehole (from Late Burdigalian to Early Serravallian; Dubois and Curnelle, 1978); Ecotet (France), exposed section (Serravallian; Aguilar et al., 2004); Le Locle (Combe Girard locality) (Switzerland), exposed section (Serravallian; Kälin et al., 2001).

The remaining sections (11 to 14: Fig. 1) were studied by Bessedik (1985) and have been used here to refine the interpretations: Sant Pau d'Ordal (Spain), exposed section (Langhian), Montady (France), exposed section (Serravallian), Issanka (France), exposed section (Langhian), Poussan (France), and exposed section (Langhian).

Only the exposed section La Rierussa [Spain, Bessedik (1985)], was analysed again in order to refine the pollen record.

The Mid-Miocene palaeogeography is now relatively well-known and was relatively similar to the modern one in spite of the Late Miocene to Present change in latitude due to the subduction of the African plate. The latitudinal range between our two most distant localities (which is today a difference of 11°) may be estimated to have been about 12–

13° in the Mid-Miocene (Rögl, 1998; Goncharova et al., 2004; Ilyina et al., 2004; Harzhauser and Piller, 2007).

The sections studied (outcrops and boreholes) are well dated by planktonic foraminifera or nannoplankton and, in some cases, by mammals, all of which contain taxa that indicate a Middle Miocene age (Langhian and Serravallian stages; see references above and Fig. 2).

Sampling was done by taking ca. 150 g of sediment per sample. In the chemical treatment only a part (20–30 g of sediment) was used.

The samples were processed with cold HCl (35%) and HF (70%), removing carbonates and silicates respectively. Separation of the palynomophs from the rest of the residue was carried out using $ZnCl_2$ (density >2). Sieving was done using a 10 μm nylon sieve. The pollen residue, together with glycerine, was prepared on slides. A transmitted light microscope, using ×250 and ×1000 (oil immersion) magnifications, was used for identification and counting of palynomorphs.

Palynomorphs are abundant in the sediments, which generally contain more than 2000 pollen grains/gram of sediment and in some cases many dinoflagellate cysts (concentrations were estimated according to the Cour's (1974) method). Spores have not been considered due to their sparse representation. Many of the pollen grains were identified by comparing them with published keys and the modern pollen reference collection at the pollen laboratory in Lyon, and also using the Photopal website (http://medias.obs-mip.fr/photopal). A minimum of 150 pollen grains was counted in each analysed sample. Generally samples were diverse, containing more than 30
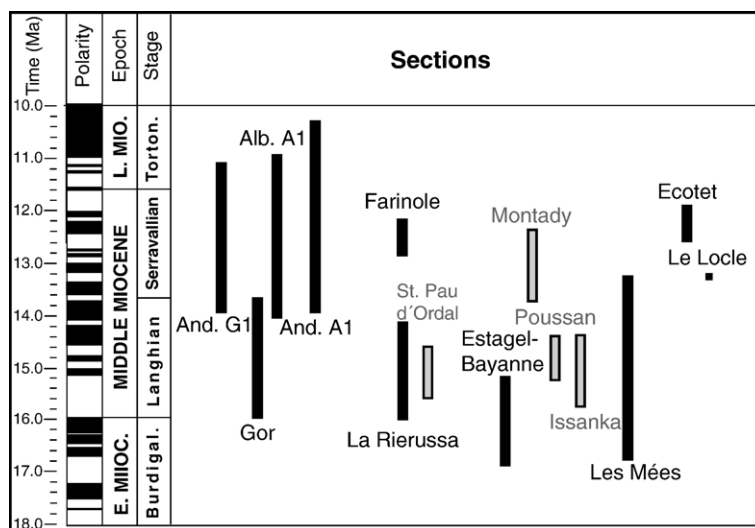

Fig. 2. Chronostratigraphic situation of the considered sections, according to the time-scale of Harzhauser and Piller, 2007. The sections are arranged from South (left) to the North (right). Black sections: pollen analyses done by G. Jiménez-Moreno; grey sections: pollen analyses done by M. Bessedik (1984, 1985).

different taxa. A total of 172 taxa have been identified. *Pinus* and Pinaceae and undetermined pollen grains were counted but excluded from the pollen sum. *Pinus* and Pinaceae are usually overrepresented because of their prolific production and the advantage they have in air and water transport, as well as in preservation.

Several studies (Turon, 1984; Hooghiemstra et al., 1986; Cambon et al., 1997) confirm that pollen content of modern coastal marine sediments, transported by air or rivers, reflects the regional vegetation, and therefore, environmental and climatic interpretations are possible using comparable Miocene sediments.

Based on the results of the pollen spectra, detailed pollen diagrams (Figs. 3–7; Table 1) and standard synthetic diagrams (Suc, 1984) without *Pinus* and Pinaceae have been constructed. In the synthetic pollen diagrams, taxa have been grouped into 12 different

groups based on ecological criteria in order to clearly visualise the composition of the past vegetation (see Table 2).

Complete pollen data will be available on the web from the "Cenozoic Pollen and Climatic values" database (CPC) (http://cpc.mediasfrance.org).

3. Results

Changes in vegetation can be observed in some of the sections covering a relatively long time frame, and they are likely to have been produced by climatic changes which occurred during the Mid-Miocene (e.g. the Antarctic glaciation at ca. 14 Ma; see Kennett, 1977; Miller et al., 1991; Flower and Kennett, 1994). Nevertheless, these changes produced mainly quantitative variations in the different taxa, and in only a few
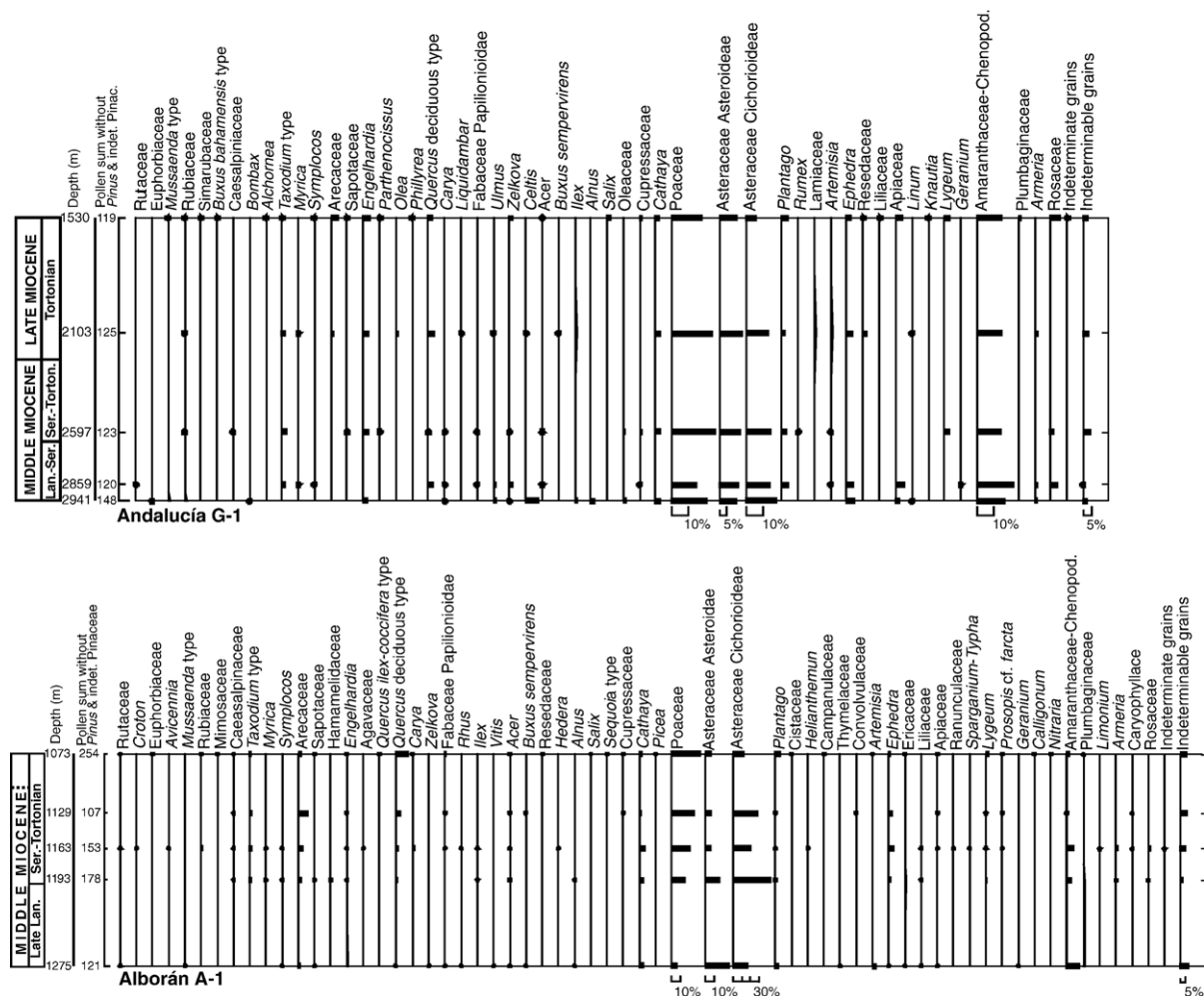

Fig. 3. Detailed pollen diagrams without *Pinus* and indeterminable Pinaceae of the boreholes Andalucía G-1 and Alborán A-1. Black dots mean values lower than 1%.
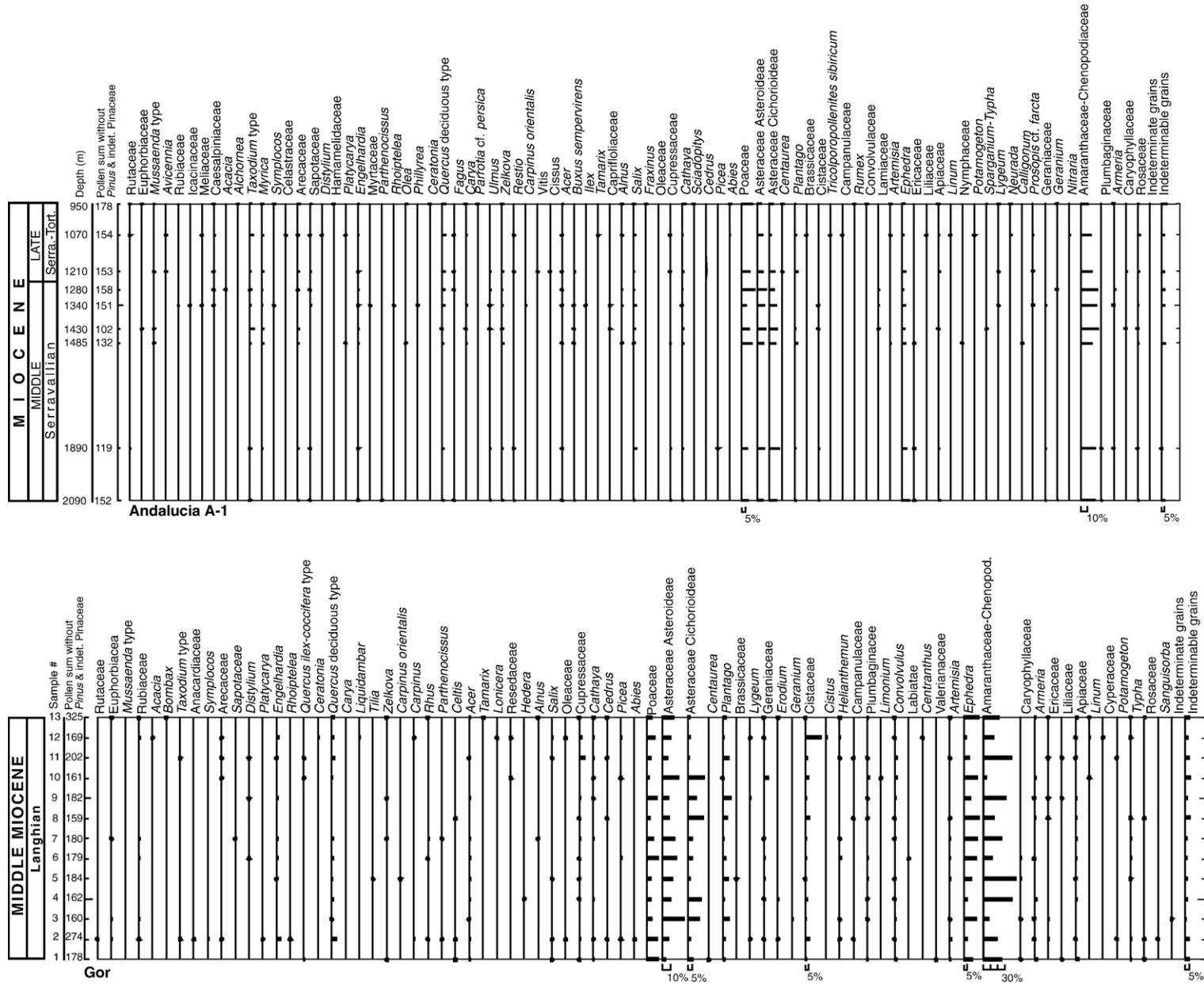
Fig. 4. Detailed pollen diagrams without *Pinus* and indeterminable Pinaceae of the sections Andalucía A-1 and Gor. Black dots mean values lower than 1%.
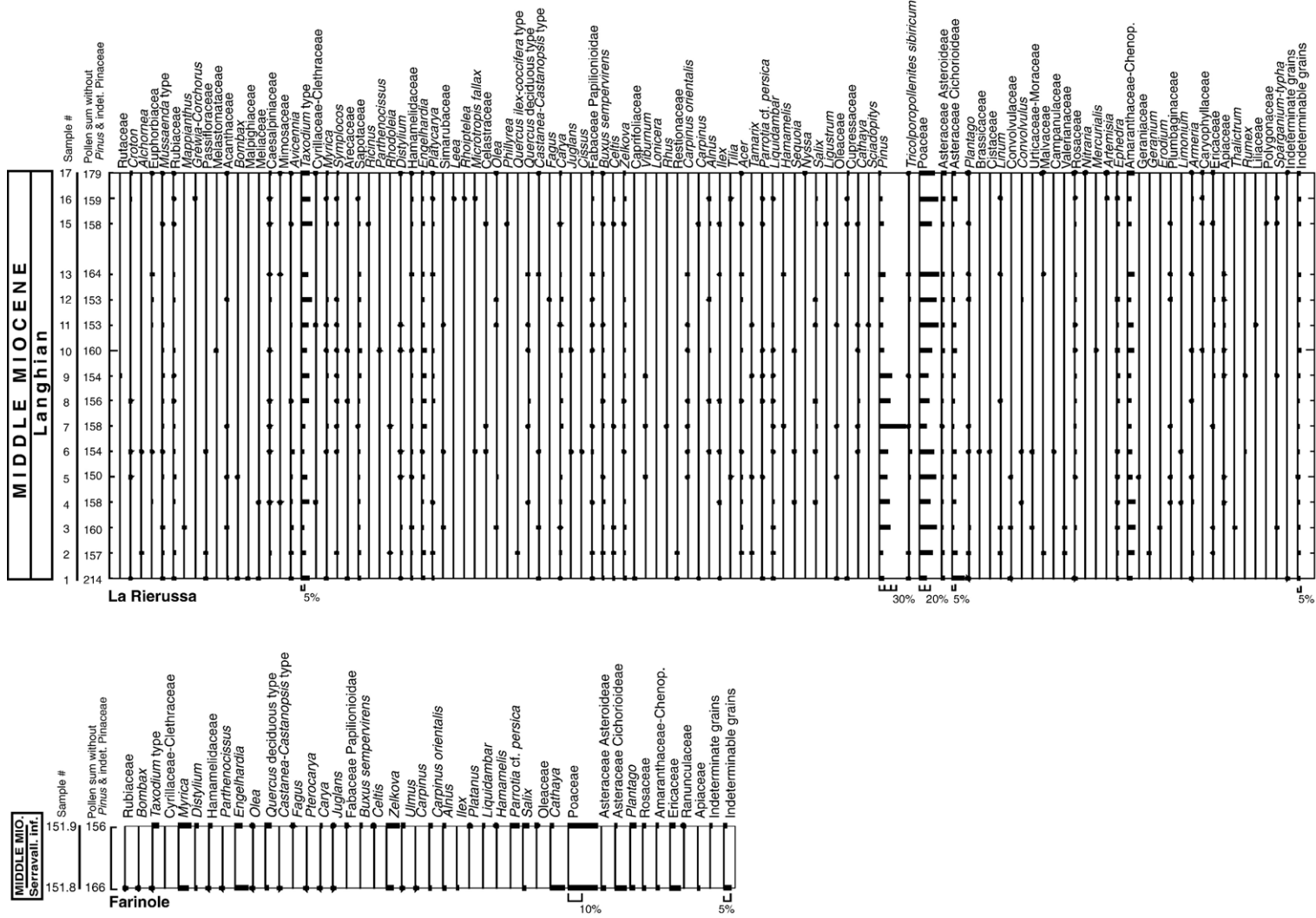
Fig. 5. Detailed pollen diagrams without *Pinus* and indeterminable Pinaceae of the La Rierussa and Farinole outcrops. Black dots mean values lower than 1%.
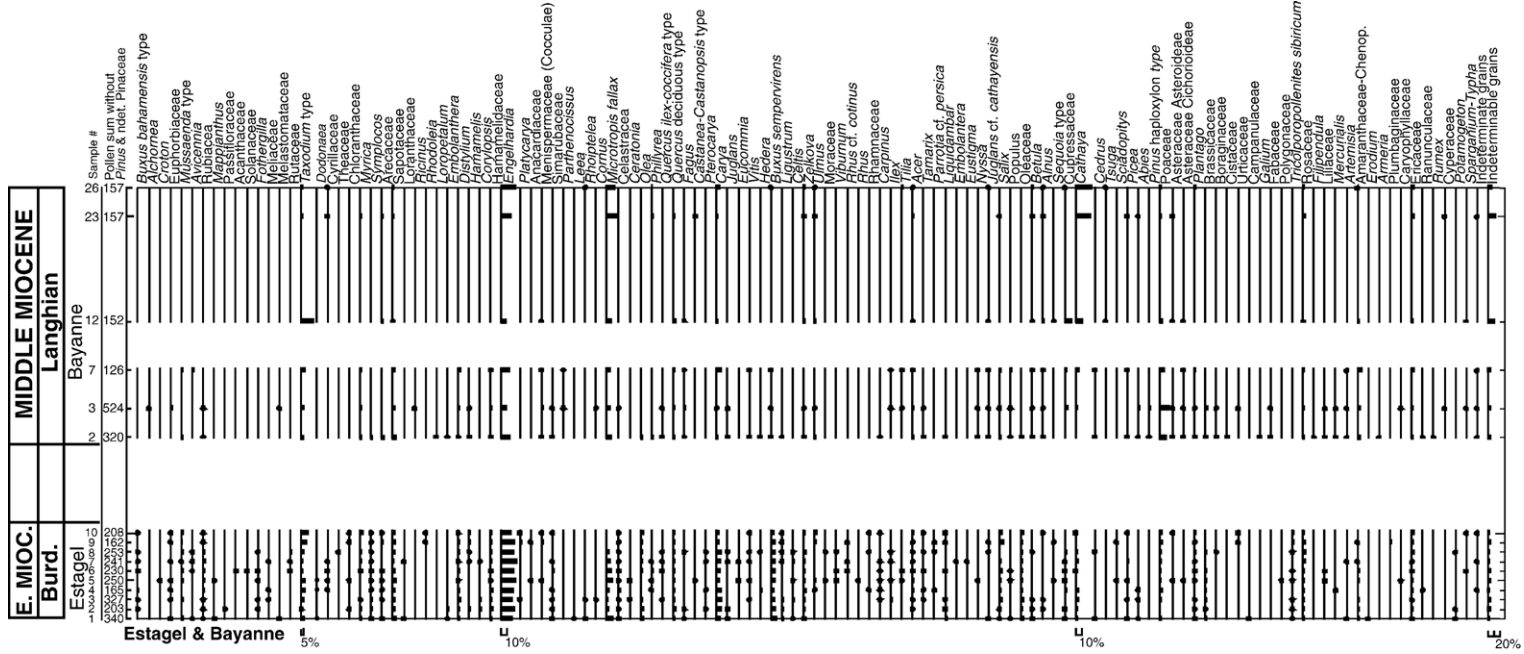
Fig. 6. Detailed pollen diagrams without *Pinus* and indeterminable Pinaceae of the Estagel and Bayanne outcrops. Black dots mean values lower than 1%.
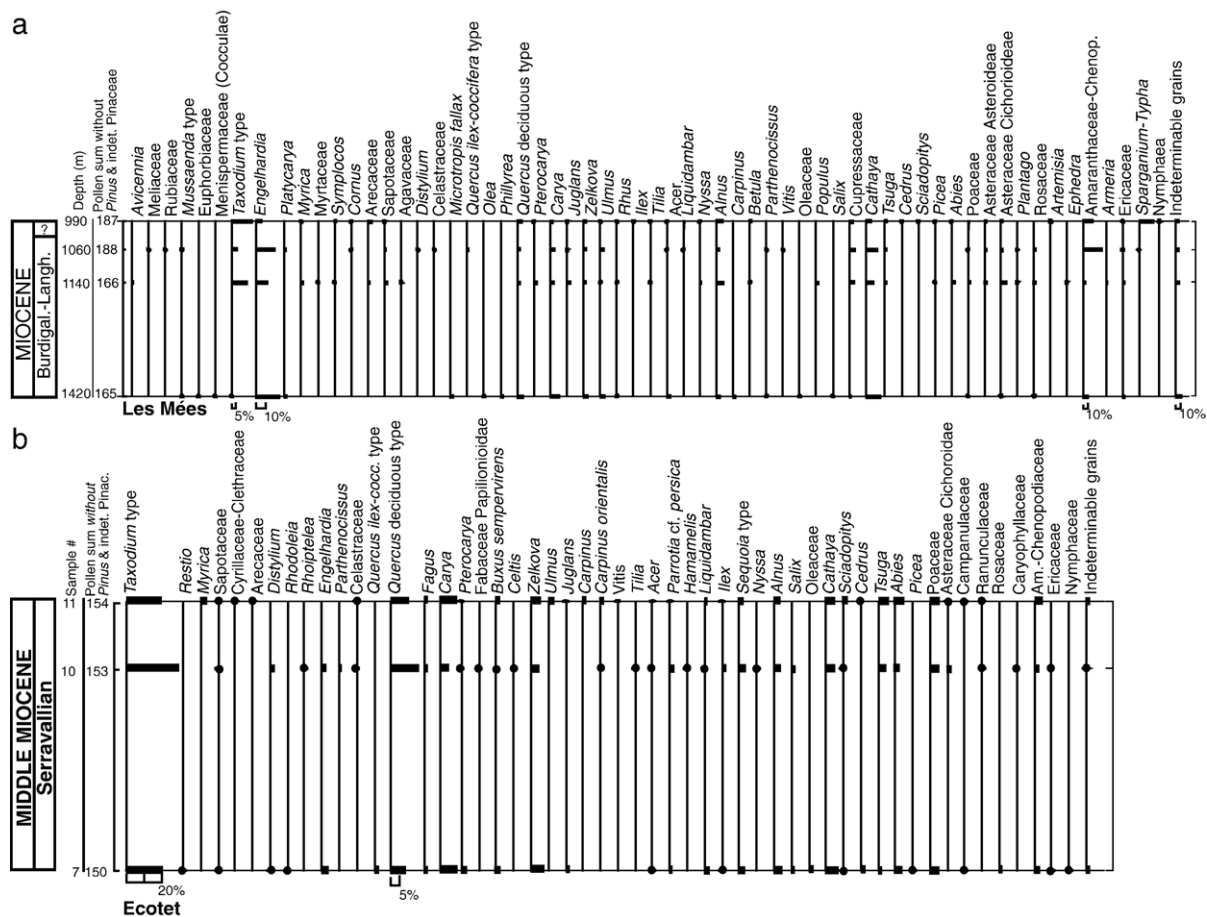
Fig. 7. (a) Detailed pollen diagrams without *Pinus* and indeterminable Pinaceae of the borehole Les Mées and (b) detailed pollen diagrams without *Pinus* and indeterminable Pinaceae of the Ecotet outcrop. Black dots in both diagrams mean values lower than 1%.

cases, extinction of some of the taxa, such as *Avicennia*, a mangrove element, from the northwestern Mediterranean shorelines. In this study, general and detailed pollen assemblages of each site are used to compare different sites to each other.

The pollen content of the considered localities allows the subdivision of the area into four flora-vegetation domains from south to north. The same general features, even if some changes occurred, are observed during the Langhian and Serravallian stages.

1) Southern Spain. (localities: Andalucía G1, Alborán A1, Andalucía A1, Gor; Figs. 3, 4 and 8).
Herbs and shrubs are clearly dominant in the pollen spectra with Poaceae, and halophytes such as Amaranthaceae–Chenopodiaceae, Plumbaginaceae *p.p.*, Caryophyllaceae *p.p.*, as the most representative. The pollen spectra are also characterized by the abundance of subdesertic elements since the Lan-

ghian, such as *Nitraria*, *Lygeum*, *Prosopis*, *Neurada*, and *Calligonum* (see Fig. 9).

Thermophilous (i.e. tropical and subtropical) elements [*Taxodium* type[1], *Engelhardia*, Sapotaceae, *Myrica*, *Alchornea*, *Mussaenda* type, Melastomataceae, Rutaceae, *Avicennia* (which constituted an impoverished mangrove in the coastal area) and *Sindora*] and mesothermic (i.e. warm–temperate) elements (such as *Quercus* deciduous type, *Carya*, *Zelkova*, etc.) contribute to such a pollen assemblage. *Cathaya*, a gymnosperm today restricted to some subtropical mid-altitude forests of southeastern China, is also present but generally in very low percentages. Mid-altitude (*Cedrus*, *Tsuga*) and high-altitude (*Abies*, *Picea*) elements appear only occasionally.

---

[1] A pollen type including the genera *Taxodium* and *Glyptostrobus*, both being regularly recorded among the Neogene plant macroremains in Europe.

Table 1

Pollen spectra of the Combe Girard (Le Locle) section

Combe Girard — Le Locle (Serravallian)	
Taxodium type	1
Arecaceae	3
Myrica	52
Distylium	7
Hamamelis	1
Hamamelidaceae	7
Platycarya	1
Engelhardia	140
Olea	7
Quercus ilex-coccifera type	1
Quercus deciduous type	8
Carya	14
Pterocarya	4
Juglans	5
Juglans cf. *cathayensis*	25
Carpinus orientalis	47
Buxus sempervirens	1
Zelkova	3
Ulmus	2
Celtis	1
Carpinus	6
Alnus	7
Tilia	1
Parthenocissus	1
Acer	7
Tamarix	3
Liquidambar	8
Salix	21
Ligustrum	1
Oleaceae	4
Cupressaceae	4
Cathaya	1
Picea	2
Abies	1
Indeterminable Pinaceae	13
Pinus	22
Poaceae	7
Plantago	4
Geraniaceae	1
Fabaceae	2
Ericaceae	1
Potamogeton	2
Rosaceae	3
Indeterminable grains	12

The vegetation, according to the high percentage of herbs in the pollen spectra, is typical of an open environment. Percentages of the remaining groups are very low. The mesothermic trees were probably restricted to mid- to high-altitude environments.

2) NE Spain and Corsica. (Localities: La Rierussa and Farinole; Figs. 5 and 8).

In this area, pollen spectra are rich in herbs and shrubs, mainly made up of Poaceae, Asteraceae, and halophytes such as Amaranthaceae–Chenopodiaceae, Plumbaginaceae *p.p.* Thermophilous elements are abundant in all the samples and *Avicennia* still plays a very important role in this area, representing the impoverished mangrove in the coastal area. However, many of the subdesertic elements are not present in the pollen spectra and Caesalpiniaceae and *Acacia* were recorded in very low percentages. The rest of the assemblage is characterized by temperate elements (*Carya*, *Zelkova*, *Buxus sempervirens* type, etc.). Mid- and high-altitude elements are very scarce in these samples.

This is in agreement with the pollen data of Bessedik (1985) for the same area (La Rierussa and Sant Pau d'Ordal sections).

Such pollen spectra suggest scattered forests developing at a low altitude along humid places (rivers, lakes) or at mid-altitude, but in general, not as open as in southern Spain.

3) Southern France (localities: Estagel, Bayanne, Les Mées; Figs. 6, 7a, and 8).

This domain is characterized by the dominance of thermophilous elements (Sapotaceae, *Myrica*, *Engelhardia*, *Taxodium* type, Hamamelidaceae, Simarubaceae, Chloranthaceae, *Avicennia*, etc.) as well as mesothermic elements such as *Carya*, *Buxus sempervirens* type, *Zelkova*, *Quercus* deciduous type, Oleaceae, *Liquidambar*, etc. Percentages of herbs and shrubs are sometimes important; however they do not dominate the pollen spectra. This group is mainly made up of Poaceae, Amaranthaceae–Chenopodiaceae, Plumbaginaceae, Geraniaceae, Ericaceae, etc. Very low percentages of semiarid taxa such as *Acacia*, Caesalpiniaceae or *Prosopis* are noted (see Fig. 9).

The same results were obtained by Bessedik (1985) within the same area of study (Montady, Poussan and Issanka sections) during the Middle Miocene and suggest more developed forest vegetation in this area.

4) Eastern-central part of France and Switzerland. (Localities: Ecotet and Le Locle; Figs. 7b and 8; Table 1).

In this region, the pollen flora is characterized by the high abundance of thermophilous elements and predominantly by *Taxodium* type and *Engelhardia* and by high percentages of mesothermic elements mainly made up of *Quercus* deciduous type. *Avicennia* has not been recorded in this area and percentages of herbs and shrubs and other groups are very low.

This kind of pollen assemblage is very similar to the one which characterized the Middle Miocene in the Pannonian basin and the Middle Miocene environment of Central Europe (Gregor et al., 1989; Ashraf and Mosbrugger, 1996; Jiménez-Moreno et al., 2005) and even though some species of Caesalpiniaceae or Mimosaceae were observed, they occur in small proportions and would appear to

Table 2
List of the taxa identified in this study grouped by ecological requirements in order to plot the synthetic diagrams

Thermophilous elements
    Rutaceae
    Croton
    Alchornea
    Mussaenda type
    Mappianthus
    Grewia–Corchorus
    Passifloraceae
    Melastomataceae
    Acanthaceae
    Bombax
    Icacinaceae
    Malpighiaceae
    Avicennia
    Meliaceae
    Fothergilla
    Simarubaceae
    Buxus bahamensis type
    Dodonaea
    Myrica
    Symplocos
    Arecaceae
    Sapotaceae
    Loranthaceae
    Engelhardia
    Platycarya
    Parthenocissus
    Leea
    Cornus
    Microtropis fallax
    Celastracea
    Rhoiptelea
    Restio
    Anacardiaceae
    Taxodiaceae
    Taxodium type
    Cyrillaceae—Clethrac.
    Theaceae
    Distylium
    Embolanthera
    Rhodoleia
    Loropetalum
    cf. *Corylopsis*
    Hamamelidaceae
    Menispermaceae
    Agavaceae
    Chloranthaceae
    Ricinus
Cathaya
  Mesothermic elements
    Fagus
    Quercus – deciduous type
    Castanea–Castanopsis type
    Pterocarya
    Carya
    Juglans cf. *cathayensis*
    Juglans

Table 2 (*continued*)

Cathaya
  Mesothermic elements
    Nyssa
    Betula
    Alnus
    Carpinus
    Carpinus orientalis
    Sequoia
    Tamarix
    Fabaceae—Papilion.
    Buxus sempervirens
    Restio
    Celtis
    Zelkova
    Ulmus
    Cissus
    Vitis
    Ilex
    Oleaceae
    Ligustrum
    Fraxinus
    Caprifoliaceae
    Lonicera
    Viburnum
    Rhus cf. *cotinus*
    Rhus
    Salix
    Eucommia
    Populus
    Rhamnaceae
    Sequoia type
    Hedera
    Hamamelis
    Parrotia
    Parrotia cf. *persica*
    Eustigma
    Platanus
    Liquidambar
    Hamamelis
    Tilia
    Acer
    Moraceae
    Resedaceae
Meso-microthermic elements
    Cedrus
    Sciadopitys
    Tsuga
Microthermic elements
    Abies
    Picea
Non-significant elements
    Indet. grains
    Indeterminable grains
    Rosaceae
    Ranunculaceae
    Euphorbiacea
    Rubiaceae
    Myrtaceae

Table 2 (*continued*)

Solanaceae
Cupressaceae
Mediterranean xerophytes
Olea
Phillyrea
Ceratonia
Quercus ilex—coccifera type
Herbs and shrubs
Poaceae
Asteraceae—Aster.
Asteraceae—Cichor.
Convolvulaceae
Convolvulus
Plantago
Cistaceae
Helianthemun
Cistus
Thymelaceae
Brassicaceae
Centaurea
Geraniaceae
Erodium
Geranium
Campanulaceae
Tricolpor. sibiricum
Rumex
Mercurialis
Knautia
Nymphaceae
Potamogeton
Sparganium–Typha
Boraginaceae
Galium
Linum
Lamiaceae
Centranthus
Valerianaceae
Artemisia
Ephedra
Caryophyllaceae
Urticaceae
Malvaceae
Cyperaceae
Potamogeton
Liliaceae
Apiaceae
Thalictrum
Polygonaceae
Ericaceae
Sanguisorba
Filipendula
Subdesertic elements
Lygeum
Neurada
Calligonum
Caesalpiniaceae
Prosopis cf. *farcta*
Mimosaceae
Acacia
Nitraria

Table 2 (*continued*)

Halophytes
Amaranthaceae–Chenopodiaceae
Plumbaginaceae
Limonium
Armeria

represent small patches of dry adapted subtropical taxa. In general, the pattern record points to a forest vegetation.

4. Discussion

4.1. Flora and vegetation

According to pollen data, numerous Mediterranean Middle Miocene taxa (mostly identified at the genus level) show close affinities to modern species nowadays growing in:

1. Eastern Asia (*Avicennia*, *Distylium*, *Engelhardia*, *Platycarya*, *Cathaya*, *Symplocos*, *Eucommia*, etc.),
2. Central America (*Avicennia*, *Engelhardia*, *Symplocos*, etc.),
3. Tropical Asia, Africa and America (*Avicennia*, *Alchornea*, *Bombax*, Celastraceae, Meliaceae, Icacinaceae, Arecaceae, etc.),
4. Persian Gulf and the Red Sea coastlines (*Avicennia marina* which represents here the closest present-day occurrence to Europe, *Neurada*, *Prosopis*, etc.) under subtropical climates.

As has been shown, Middle Miocene pollen assemblages denote the juxtaposition of greatly contrasted environments. The presence of subdesertic taxa (*Nitraria*, *Lygeum*, *Prosopis*, *Neurada*, *Calligonum*, Caesalpiniaceae, etc.), which grow conditioned by a long dry season, together with others showing very high water requirements (like *Engelhardia*, *Platycarya*, *Taxodium* type, Sapotaceae, *Myrica*, etc.), needing constant water, has two possible explanations. This could be due to the structure of the vegetation in altitudinal belts and the effect of humid cloud masses, which cling to the mountains at an altitude of ca. 400–500 m (Bessedik, 1984), similar to the Canary Islands today (Rivas-Martínez, 1987). Secondly, there may have been significant availability of water sources along the rivers or around the lakes, as has been interpreted as the cause of such a floral assemblage in the Rubielos de Mora (Burdigalian) lacustrine basin in Spain (Jiménez-Moreno, 2005) and which frequently occurs in subtropical and tropical Africa, for instance around Lake Tanganyika. In both situations water availability clearly controls the vegetation and would compensate for the lack
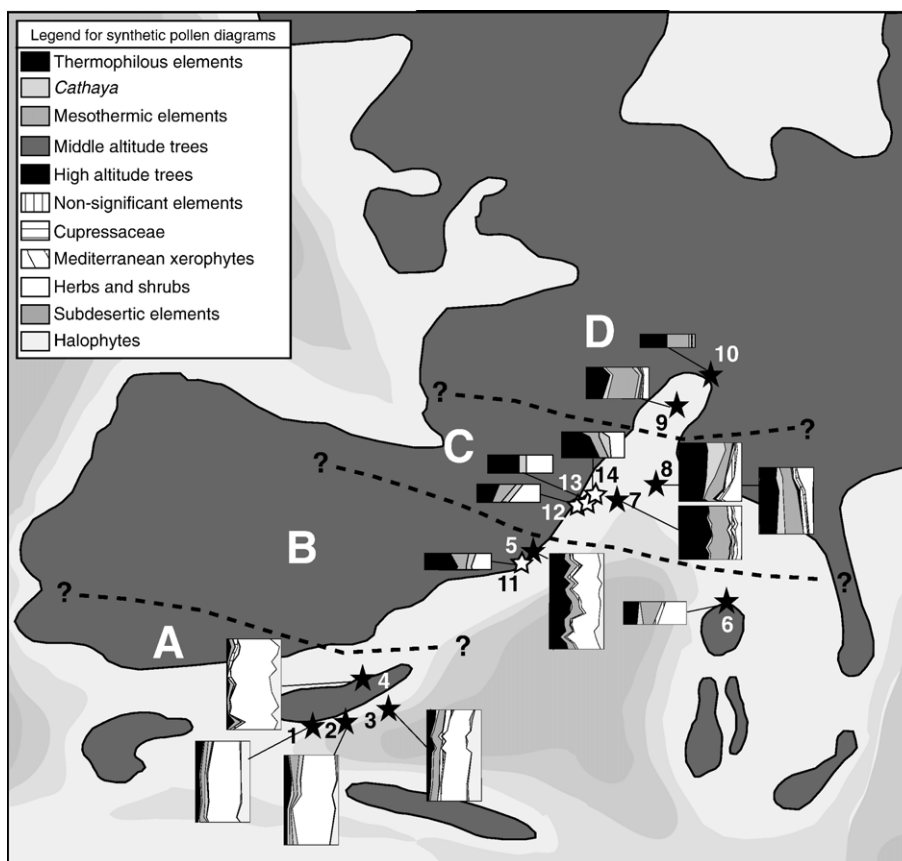
Fig. 8. Synthetic pollen diagrams of the new pollen localities acquired in this work (sites 1 to 10: see Fig. 1) and of the pollen localities already studied by Bessedik (1984, 1985) (sites 11 to 14; see Fig. 1), according to their geographic distribution on the palinspastic map of Harzhauser and Piller (2007) for the Mid-Miocene (Serravallian). Four distinct flora and vegetation latitudinal domains have been identified, from the South to the North: Domain A, dominated by herbs and shrubs, subdesertic elements such as *Nitraria*, *Calligonum*, *Lygeum*, *Prosopis*, *Neurada*, etc., denoting warm and dry conditions with a marked seasonality; Domain B, characterized by a strong decrease in herbs and shrubs and the absence of subdesertic elements except for Caesalpiniaceae, also by an important increase in elements with high-water requirements, indicative of a less pronounced seasonality; Domain C, where plants with high-water requirements dominate the pollen spectra with very small percentages of elements still indicating some seasonality; Domain D, characterized by prevalent plants with heavy water requirements, and by the absence of taxa suggesting some seasonality.

of precipitations in the summer time. This compensation would result from the duality of the gradual disappearance of a humid climate with summer rainfall ("Asian" climate type), which prevailed during the Paleogene in this area, and the episodic appearance of a subtropical climate with a dry season which progressively became established, responsible for the semiarid zone in the lowlands during the Miocene (Bessedik, 1984).

As a large number of taxa have been identified in this study, they can also be compared to the organisation of the present-day plant ecosystems in altitudinal belts. Reconstructions are mainly done by comparing data to the present-day forest of southeastern China (Wang, 1961), the closest living analogue for the Mid-Miocene South European flora (Suc, 1984; Axelrod et al., 1996). Vegetation along the Red Sea (presence of the mangrove of *Avicennia marina* for example) (White, 1983; Audru et al.,

1987) and from the Canary Islands (Rivas-Martínez, 1987), is very informative for such a reconstruction, in the latter because of the proximity of the laurel forest and xeric belts.

Therefore, the vegetation can be grouped into ecologically different environments, arranged mostly from the coastal area to higher elevation, but also according to the presence of humid places at low altitudes (evergreen broad-leaved forest within our latitudinal domain A, evergreen and deciduous mixed forest within our latitudinal domain B):

1. Coastal environments were represented by the impoverished mangrove (*Avicennia*) and saline bearing elements such as Amaranthaceae–Chenopodiaceae, *Ephedra*, Plumbaginaceae, *Plantago* and *Tamarix*. Today, this kind of impoverished mangrove vegetation represents the high latitude limit of mangroves
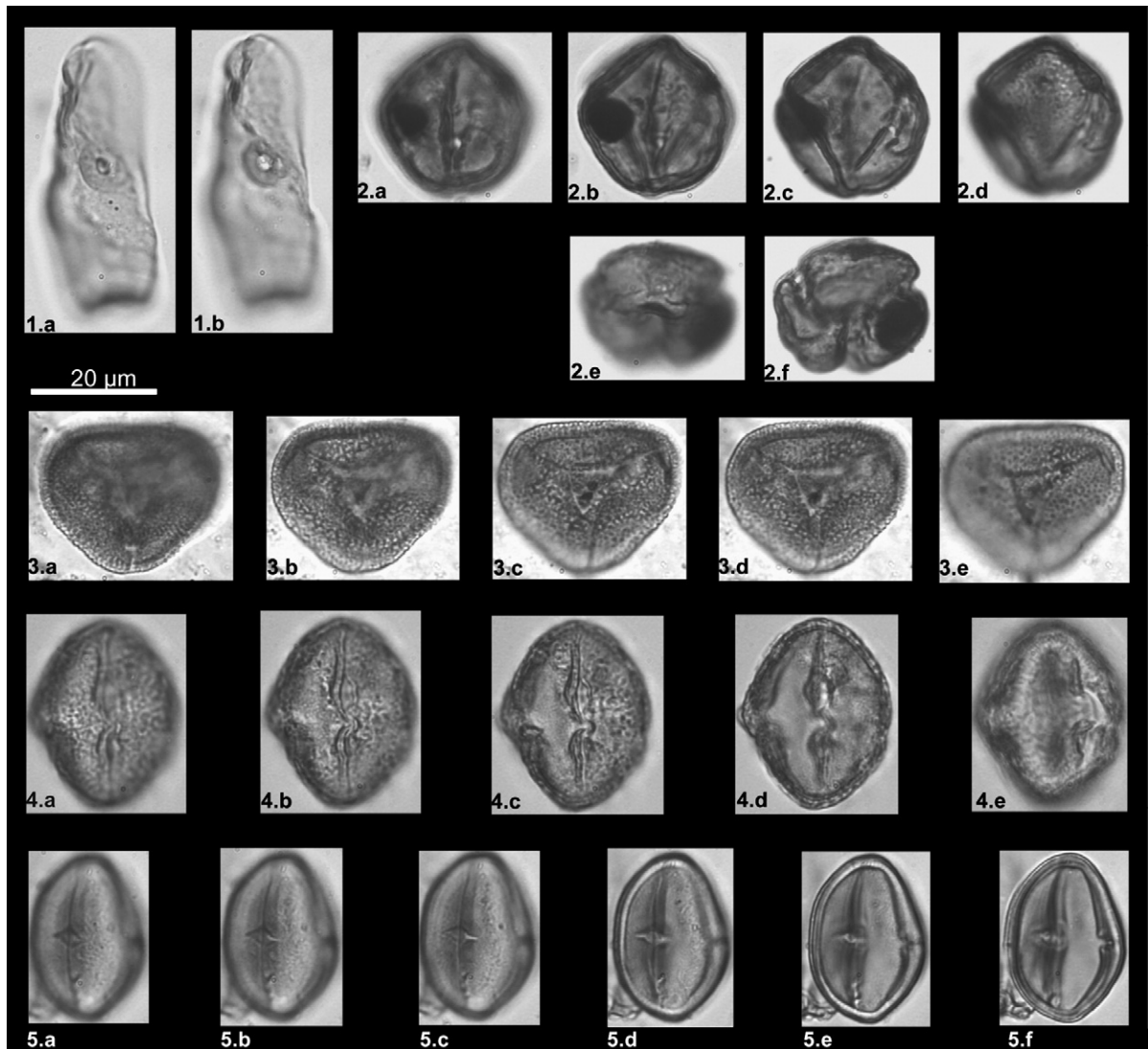
Fig. 9. Photographs of various pollen grains from the Mid-Miocene of the studied area. The presence of these plants implies warm and dry conditions and a marked seasonality in dryness. 1, *Lygeum* (Poaceae), monoporate pollen grain from the Andalucía A1 borehole, at 1340 m depth: a, surface scabrate ornamentation; b, view of the typical pore with a thick annulus. 2, *Prosopis* (Caesalpiniaceae), tricolporate pollen grain from the Andalucía A1 borehole, at 1340 m depth: a to d, L.O. analysis of the ovoid equatorial view: a and b, verrucate surface with perforations and a psilate margo, front views of the meridionally lengthened ectoaperture bordered by thick costae and of the circular endoaperture; c and d, profile views of the ecto- and endoaperutres; c, optical section; e and f, L.O. analysis of the triangular polar view of the same grain: e, verrucate sculpture with perforations; f, optical section. 3, *Neurada* (Rosaceae), tricolporate–syncolpate pollen grain from the Andalucía A1 borehole, at 1070 m depth: a to e, L.O. analysis of the subtriangular polar view of this heteropolar pollen: a, finely reticulate sculpture; b to d, successive views showing the three syncolpate apertures and the exine structure; e, optical section. 4, Caesalpiniaceae, tricolporate pollen grain from the Bayanne section (sample 7); a to e, L.O. analysis of the elliptical equatorial view; a, reticulate sculpture with a wide margo; b and c, front views of the meridionally lengthened ectoaperture bordered by thick costae and of the diffuse endoaperture, L.O. analysis of the exine structure; d, optical section; e, profile view of the ecto- and encoapertures. 5, *Nitraria* (Zygophyllaceae), tricolporate pollen grain from the Alborán A1 borehole, at 1193 m depth; a to f, L.O. analysis of the elliptical equatorial view; a, rugulate sculpture with a psilate margo; b to d, front views of the meridionally lengthened ectoaperture bordered by thick costae and of the elliptical equatorially lengthened endoaperture, L.O. analysis of the exine structure; e, optical section (note the thick endexine); g, profile view of the ecto- and endoapertures.

and can occur under arid or semiarid conditions as in the Red Sea and Persian Gulf (White, 1983; Audru et al., 1987).

2. An open vegetation with subdesertic plants such as *Nitraria*, *Neurada*, *Ephedra*, *Convolvulus*, *Lygeum, Prosopis*, Caesalpiniaceae, *Acacia*, etc., which are

representative of a steppe or a wood–shrub vegetation, characterized the lowlands. Similar modern assemblages are present on the Red Sea coasts, on the shorelines of the Arabian Peninsula, and in North Africa (Quézel, 1965; Quézel and Médail, 2003).

3. An evergreen broad-leaved forest existed, characterized by the presence of Theaceae, Clethraceae, *Bombax*, Sapotaceae, Rutaceae, Moraceae, Iacacinaceae, Simarubaceae, Meliaceae, Melastomataceae, Arecaceae, *Ilex*, *Hedera*, *Olea*, *Ligustrum*, *Jasminum*, Hamamelidaceae, *Rhoiptelea*, etc. This forest is known as the "Oak-Laurel" forest in eastern Asia (Wang, 1961) and constitutes the "palaeo-origin" of the present-day residual laurel forest in the Canary Islands (Quézel and Médail, 2003).

4. Evergreen and deciduous mixed forest developed at a higher altitude, mainly composed of *Quercus* deciduous type, *Engelhardia*, *Platycarya*, *Carya*, *Pterocarya*, *Fagus*, *Distylium*, *Liquidambar*, *Parrotia*, Hamamelidaceae, *Carpinus*, *Celtis* and *Acer*. Within this vegetational belt, a riparian plant association has been identified with *Salix*, *Alnus*, etc. The shrub level was dominated by Ericaceae, *Ilex*, Caprifoliaceae, Rhamnaceae, etc. This kind of mesophytic forest today appears above 700–800 m in altitude in eastern China (at 30° N latitude) (Wang, 1961).

5. Mid-high altitude forest attested by small amounts of pollen grains of gymnoperms such as *Cathaya*, *Sciadopitys*, *Cedrus* and *Tsuga*, and *Abies* and *Picea*. The small percentages of mid-high altitude taxa represented in the pollen records during the Middle Miocene in the entire area can be interpreted as due to the low altitude of the surrounding mountains. This is normal as the Alpine Chain was still not well developed therefore high relief cannot be expected during that time.

4.2. Climate

In the global context of the late Early Miocene and Middle Miocene (Burdigalian, Langhian and Serravallian stages; Woodruff and Savin, 1989; Flower and Kennett, 1994; Zachos et al., 2001), the climate in the European mid-latitudes was mainly subtropical (Bessedik, 1985; Lécuyer et al., 1996; Utescher et al., 2000; Agustí and Antón, 2002; Böhme, 2003). This is supported at the South European scale by the abundance of thermophilous elements with high temperature requirements in the pollen spectra. The same interpretations were made by other authors working on palynology (Ivanov et al., 2002), macrofloras (Sanz de Siria Catalan, 1993), corals (Bessedik and Cabrera, 1985;

Braga et al., 1996; Saint-Martin et al., 2000) or molluscs (Harzhauser et al., 2003) from equivalent latitudes.

4.3. Latitudinal gradient

The absence of several thermophilous indicators (i.e. *Bombax*, *Buxus bahamensis* type or *Croton*) northward from southern Spain and the coeval lower percentage of the thermophilous group indicate that a latitudinal temperature gradient existed over the studied area during the Mid-Miocene. However, the presence, in the entire area, of several taxa with similar temperature requirements such as *Engelhardia*, *Myrica*, *Taxodium* type, *Mussaenda* type, *Avicennia*, etc., suggests that this temperature gradient was relatively low. This is consistent with the presence of some thermophilous taxa during the same time-span, very high in latitude in the European area (Jiménez-Moreno, unpublished data) and Asia (i.e. occurrence of Taxodiaceae, *Pterocarya* or *Hamamelis* in Kamchatka; Brattseva, 1993). This phenomenon was also observed in North America by Liu and Leopold (1994) who estimated a value of just 0.3 °C per degree in latitude for North America and China (between 35°N–65°N) during the Middle Miocene.

Important differences in vegetation in terms of precipitation requirement have been observed in this study from south to northwestern Europe. An increase in rainfall gradually occurred between southern Spain and Switzerland over about 12–13° of past latitudinal difference. The lowland vegetation in southern Spain was dominated by herbs and shrubs, and within this group a high presence of subdesertic taxa such as *Nitraria*, *Neurada*, *Prosopis*, Caesalpiniaceae, *Acacia*, *Ephedra*, Convolvulus, *Lygeum*, etc. has been found. On the contrary, a gradual disappearance of these elements going northward can be observed. They have not been found in the eastern-central part of France or Switzerland. This fact has been interpreted as the consequence of a strong latitudinal gradient in precipitation. The Mid-Miocene latitudinal gradient between southern Spain and Switzerland would have been stronger than the present-day gradient moving from a Saharan-like climate to a very humid situation in only 12–13° in latitude.

Previous palynological studies have shown that subdesertic plants already existed in southwestern Europe and North Africa during the Messinian or previously (Suc and Bessais, 1990; Chikhi, 1992; Bertini et al., 1998; Bachiri Taoufiq et al., 2001; Fauquette et al., 2006) and, later on, during the Pliocene (Bessais and Cravatte, 1988; Suc, 1989; Suc et al., 1995a). Modern floras show that these subdesertic elements grow in North Africa, including the Sahara

Desert (Quézel, 1965). In this study we show that these taxa, and therefore a Saharan type of climate, already existed in the south of the northern Mediterranean area during at least the Langhian (Middle Miocene). The gradual disappearance of most of these elements from the northern Mediterranean area towards the south, during the late Miocene and Pliocene, was due to a climatic cooling and the beginning of an Atlantic climatic influence (Bessedik, 1985; Suc et al., 2004).

As mentioned previously, four different domains have been differentiated with respect to the pollen assemblages (Fig. 8). Because climate controls vegetation organisation, four climatic zones can be estimated for the study area:

1) Zone A, Southern and central Spain: southern Spain is characterized by the high presence of herbs and shrubs and the remarkably high presence of sub-desertic taxa (Fig. 9). Very dry conditions are inferred for this area with a marked seasonality in a subtropical climate. Present-day climate in southern Spain is in some areas very arid (i.e. the Almería area), however most of the subdesertic taxa previously mentioned, such as *Prosopis*, *Neurada* or *Acacia*, are not growing in this area today. Therefore, the climate inferred for the Middle Miocene in southern Spain would be more arid than the present-day situation.
2) Zone B, Northeastern Spain: herbs and shrubs are abundant; however, there is a lack of most of the subdesertic taxa. The occurrence of Caesalpiniaceae and *Acacia* (Mimosaceae) is interpreted as the result of high seasonality. Wetter and/or cooler conditions during the summer time are inferred for this region, preventing the development of subdesertic taxa.
3) Zone C, Southern France: Even though a very few semiarid taxa have been found in this study by Bessedik (1984, 1985), the vegetation was dominated by thermophilous elements requiring high humidity all year (*Engelhardia*, *Platycarya*, *Taxodium* type, *Myrica*, etc.). Therefore seasonality in terms of precipitation is less marked in this area.
4) Zone D, central-eastern part of France and Switzerland: in this area the vegetation characterized a climate with high precipitations, well distributed throughout the year, as high percentages of high-humidity indicators are recorded and no taxa indicating precipitation seasonality have been observed.

The presence of a subdesertic vegetation, already containing C4 grasses (such as *Lygeum*) in southern Spain during the Middle Miocene, supports the proposal for subdesertic conditions for this area.

The development of C4-rich grasslands has traditionally been associated with late Cainozoic climate change, decreasing temperatures, increase in aridity and increase in seasonality of temperature and/or precipitation (Axelrod, 1985; Cerling et al., 1997; Fox and Koch, 2004). However, such a subdesertic vegetation is not expected to be found in this area until the late Middle Miocene or Late Miocene, when the development of the East Antarctic Ice Sheet around 14 Ma and the lowering of the atmospheric concentration of CO_2, produced mainly by the increase in weathering of the recently uplifted Himalayan–Tibetan region, have been shown to have a global impact on the Middle Miocene ecosystems (Flower and Kennett, 1994; Cerling et al., 1997; Fox and Koch, 2004). In addition, this event strengthened existing climatic belts and triggered a global mid-latitude desertification and increasing seasonality (Flower and Kennett, 1994). This study shows that increasing xericity in southern Spain during the Miocene may have occurred before it occurred in the rest of the northern latitudes (Axelrod, 1985; Cerling et al., 1997; Fox and Koch, 2004).

The observed latitudinal climatic gradient is consistent with a recent study on the distribution of air-breathing fish which are limited by the amount of summer precipitation (they are found where summer rainfall exceeds 150 mm) (Böhme, 2004). This study shows that their Mid-Miocene spatial distribution did not reach the southern parts of western Eurasia (i.e. Spain). This would imply an arid climate with dry summers in this area. Conversely, they were present in France and central Europe, reflecting wetter summers there. This pattern of distribution of summer precipitations in the European area closely matches the results presented here.

5. Conclusions

The Middle Miocene pollen records considered for the present study allow us to document the presence of a latitudinal climatic gradient from southern Spain to Switzerland.

The results demonstrate that, in a general European subtropical frame, taxa such as *Calligonum*, *Neurada*, *Nitraria*, *Prosopis* and *Lygeum*, that are linked to a very dry climate, were already present during the Middle Miocene in the northwestern Mediterranean area.

The gradual loss of these subdesertic elements and the progressive increase in taxa with higher water requirements, from the very south of Spain to Switzerland, is interpreted as reflecting a strong latitudinal gradient in precipitation. Consequently, four different types of

pollen assemblages corresponding to four climatic domains have been differentiated. It is nevertheless noteworthy that the presence of similar thermophilous taxa in the pollen spectra from all the localities shows that the latitudinal gradient in terms of temperature was not very large.

Middle Miocene pollen assemblages evidence, therefore, the juxtaposition of very contrasted environments; the presence of subdesertic taxa, which grew in lowlands characterized by a long dry season, together with others with very high water requirements throughout the year, can be explained by the presence of coastal ranges and of humid environments such as rivers or lakes providing local conditions for developing riparian forests in the lowlands. In both cases, vegetation was controlled by water availability under a subtropical and dry-seasonal climate.

Acknowledgments

References

Aguilar, J.-P., Berggren, W.A., Aubry, M.-P., Kent, D.V., Clauzon, G., Benammi, M., Michaux, J., 2004. Mid-Neogene Mediterranean marine-continental correlations: an alternative interpretation. Palaeogeography, Palaeoclimatology, Palaeoecoloy 204 (1–2), 165–186.

Agustí, J., Antón, M., 2002. Mammoths, Sabertooths, and Hominids. 65 Million Years of Mammalian Evolution in Europe. Columbia University Press. 313 pp.

Ashraf, A.R., Mosbrugger, V., 1996. Palynologie und palynostratigraphie des Neogens der Niederrheinischen Bucht. Teil 2: Pollen. Palaeontografica B 241, 1–98.

Audru, J., Cesar, G., Forgiarini, G., Lebrun, J., 1987. La végétation et les potentialités pastorales de la République de Djibouti. Institut d'Elevage et de Médecine Véterinaire des Pays Tropicaux, Maisons Alforts, France. 384 pp.

Axelrod, D.I., 1985. Rise of the grassland biome, central North America. Botanical Review 51, 163–201.

Axelrod, D.I., Al-Shehbaz, I., Raven, P., 1996. History of the modern flora of China. In: Zhang Aoluo, Wu Sugong (Eds.), Floristic characteristics and diversity of East Asian plants. Springer-Verlag, Berlin, pp. 43–55.

Bachiri Taoufiq, N., Barhoun, N., Suc, J.-P., Meon, H., Elaouad, Z., Benbouziane, A., 2001. Environment, végétation et climat du Messinien au Maroc. Paleontologia i Evolució 32–33, 127–138.

Bertini, A., 1994. Messinian–Zanclean vegetation and climate in North-Central Italy. Historical Biology 9, 3–10.

Bertini, A., Londeix, L., Maniscalco, R., Di Stefano, A., Suc, J.-P., Clauzon, G., Gautier, F., Grasso, M., 1998. Paleobiological evidence of depositional conditions in the Salt Member, Gessoso–Solfifera Formation (Messinian, Upper Miocene) of Sicily. Micropaleontology 44 (4), 413–433.

Bessais, E., Cravatte, J., 1988. Les Écosystèmes Végéteux Pliocènes de Catalogne Méridionale. Variations Latitudinales dans le Domaine Nord-Ouest méditerranéen. Geobios 21 (1), 49–63.

Bessedik, M., 1984. The Early Aquitanian and Upper Langhian–Lower Serravalian environments in the Northwestern Mediterranean region. Paléobiologie Continentale 15 (2), 153–179.

Bessedik, M., 1985. Reconstitution des environements Miocenes des regions nord-ouest Mediterraneennes à partir de la palynologie. Ph. D. Thesis. University Montpellier 2, France, 162 pp.

Bessedik, M., Cabrera, L., 1985. Le couple récif-mangrove à Sant Pau d'Ordal (Vallès-Pénédes, Espagne), témoin du maximum transgressif en Méditerranée nord occidentale (Burdigalien supérieur-Langhien inférieur). Newsletter Stratigraphy 14 (1), 20–35.

Besson, D., Clauzon, G., Coueffé, R., Dexcoté, Y., Ferry, S., Jiménez, G., Parize, O., Rubino, J.-L., Suc, J.-P., Tessier, B., 2002. Le Neogène du bassin d'avant pays rhodano-provençal. Field trip guide book, 3rd French Congress on Stratigraphy, Lyon (France). 162 pp.

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

Böhme, M., 2004. Migration history of air-breathing fishes reveals Neogene atmospheric circulation patterns. Geology 32 (5), 393–396.

Braga, J.C., Jiménez, A.P., Martín, J.M., Rivas, P., 1996. Middle Miocene coral–oyster reefs, Murchas, Granada, southern Spain. Models for Carbonate Stratigraphy from Miocene Reef Complexes of Mediterranean Regions. SEPM Concepts in Sedimentology and Paleontology 5, 131–139.

Brattseva, G., 1993. Cenozoic Kamchatka Pollen flora and climate. Proceedings of the international symposium Paleofloristic and paleoclimatic changes during Cretaceous and Tertiary. Bratislava, Slovakia, pp. 141–143.

Cambon, G., Suc, J.-P., Aloisi, J.-C., Giresse, P., Monaco, A., Touzani, A., Duzer, D., Ferrier, J., 1997. Modern pollen deposition in the Rhône delta area (lagoonal and marine sediments), France. Grana 36, 105–113.

Cerling, T.E., Harris, J.M., Mac Fadden, B.J., Leakey, M.G., Quade, J., Eisemann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene–Pliocene boundary. Nature 389, 153–158.

Chevron, 1986. Final Report Borehole Alborán A-1. Internal report. 24 pp.

Chikhi, H., 1992. Une palynoflore méditerranéenne à subtropicale au Messinien pré-evaporitique en Algérie. Géologie Méditerranéenne 19 (1), 19–30.

Cour, P., 1974. Nouvelles techniques de detection des flux et des retombées polliniques: Etude de la sédimentation des pollens et des spores à la surface du sol. Pollen et Spores 16 (1), 103–141.

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. Thesis, University Montpellier 2, France, 230 pp.

Drivaliari, A., 1993. Images polliniques et paléoenvironnement au Néogène supérieur en Méditerranée orientale. Aspects climatiques et paléogéographiques dún transect latitudinal (de la Roumanie au Delta du Nil). Ph.D. Thesis, University Montpellier 2, France, 333 pp.

Dubois, P., Curnelle, R., 1978. Résultats apportés par le forage Les Mées n°1 sur le plateau de Valensole (Alpes-de-Haute-Provence). Comptes Rendus Sommaire de seances de la Societé Géologique de France 4, 181–184.

ELF, 1984. Final Report Borehole Andalucía G1. Internal report. 18 pp.

Fauquette, S., Bertini, A., 2003. Quantification of the northern Italy Pliocene climate from pollen data — evidence for a very peculiar climate pattern. Boreas 32 (2), 361–369.

Fauquette, S., Suc, J.-P., Bertini, A., Popescu, S.-M., Warny, S., Bachiri Taoufiq, N., Perez Villa, M.-J., Chikhi, H., Subally, D., Feddi, N., Clauzon, G., Ferrier, J., 2006. How much did climate force the Messinian salinity crisis? Quantified climatic conditions from pollen records in the Mediterranean region. Palaeogeography, Palaeoclimatology, Palaeoecology 238, 281–301.

Ferrandini, M., Ferrandini, J., Loye-Pilot, M.-D., Butterlin, J., Cravatte, J., Janin, M.-C., 1998. Le Miocène du bassin de Saint-Florent (Corse): modalités de la transgression du Burdigalien supérieur et mise en évidence du Serravallien. Geobios 31 (1), 125–137.

Ferrandini, J., Gattacecca, J., Ferrandini, M., Deino, A., Janin, M.-C., 2003. Chronostratigraphie et paléomagnetisme des dépôts oligo-miocènes de Corse: implications géodynamiques pour l'ouverture du bassin liguro-provençal. Bulletin Societé Géologique de France 174 (4), 357–371.

Flower, B.P., Kennett, J.P., 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. Palaeogeography, Palaeoclimatology, Palaeoecology 108, 537–555.

Fox, D.L., Koch, P.L., 2004. Carbon and oxygen isotopic variability in Neogene paleosol carbonates: constraints on the evolution of the C4-grasslands of the Great Plains, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 305–329.

Goncharova, I.A., Shcherba, I.G., Khondkarian, S.O., Gürs, K., Losifova, Ju.I., Jakubovskaja, T.V., Kovac, M., Krasheninnikov, V.A., Pinchuk, T.N., Pinkhasov, B.I., Popov, S.V., Popescu, G., Rögl, F., Rusu, A., Zajtsev, A.V., Zastrozhnov, A.S., 2004. Lithological–Paleogeographic maps of Paratethys. Map 5: Early Middle Miocene. Courier Forschungsinstitut Senkenberg 250, 19–21.

Gregor, H.-J., Hottenrott, M., Knobloch, E., Planderova, E., 1989. Neue mega-und mikrofloristische Untersuchengen in der jungter-tiären Molasse Bayerns. Geologica Bavarica 94, 281–369.

Harzhauser, M., Piller, W., 2007. Benchmark data of a changing sea – Palaeogeography, Palaeobiogeography and Events in the Central Paratethys during the Miocene. Palaeogeography, Palaeoclima-tology, Palaecology 253, 8–31.

Harzhauser, M., Mandic, O., Zuschin, M., 2003. Changes in Parathethyan marine molluscs at the Early/Middle Miocene transition: diversity, palaeogeography and palaeoclimate. Acta Geologica Polonica 53 (4), 323–339.

Hooghiemstra, H., Agwu, C.O.C., Beug, H.J., 1986. Pollen and spore distribution in recent marine sediments: a record of NW-African seasonal wind patterns and vegetation belts. Meteor Forschung-sergeb. Reihe C 40, 87–135.

Ilyina, L.B., Shcherba, I.G., Khondkarian, S.O., Goncharova, I.A., Gürs, K., Losifova, Ju.I., Jakubovskaja, T.V., Kovac, M., Krasheninnikov, V.A., Nagymarosy, A., Pinchuk, T.N., Popov, S.V., Popescu, G., Rusu, A., 2004. Lithological–Paleogeographic maps of Paratethys. Map 6: Mid Middle Miocene. Courier Forschungsinstitut Senkenberg 250, 23–25.

Ivanov, D., Ashraf, A.R., Mosbrugger, V., Palmarev, E., 2002. Palynological evidence for Miocene climate change in the Forecarpathian Basin (Central Paratethys, NW Bulgaria). Palaeogeography, Palaeoclimatology, Palaeoecology 178, 19–37.

Jiménez-Moreno, G., 2005. Utilización del análisis polínico para la reconstrucción de la vegetación, clima y estimación de paleoalti-tudes a lo largo del arco alpino europeo durante el Mioceno (21–8 Ma). Ph.D. Dissertation. Universidad de Granada, Spain, 313 pp.

Jiménez Moreno, G., Iaccarino, S., Rubino, J.-L., 2002. Miocene of the Berre lagoon area (southern France): palynology and biostratigraphy. Documents des Laboratoires de Géologie de Lyon 156, 136.

Jiménez-Moreno, G., Rodríguez-Tovar, F.-J., Pardo-Igúzquiza, E., Fauquette, S., Suc, J.-P., Müller, P., 2005. High-resolution palynological analysis in late early-middle Miocene core from the Pannonian Basin, Hungary: climatic changes, astronomical forcing and eustatic fluctuations in the Central Paratethys. Palaeogeography, Palaeoclimatolology, Palaeoecology 216 (1–2), 73–97.

Kälin, D., Weidmann, M., Engesser, B., Berger, J.-P., 2001. Paléontologie et âge de la Molasse d'eau douce supérieure (OSM) du Jura neuchâtelois. Mémoires suisses de Paléontologie 121, 66–99.

Kennett, J.P., 1977. Cenozoic evolution of Antarctic glaciation, the circum Antarctic Ocean and their impact on global palaeo-oceanography. Journal of Geophysical Research 82, 3843–3860.

Lécuyer, C., Grandjean, P., Paris, F., Robardet, M., Robineau, D., 1996. Deciphering "temperature" and "salinity" from biogenic phosphates: the $\delta^{18}O$ of coexisting fishes and mammals of the Middle Miocene sea of western France. Palaeogeography, Palaeoclimatoloy, Palaeoecology 126, 61–74.

Liu, G., Leopold, E.B., 1994. Climatic comparison of Miocene pollen floras from northern East-China and south-central Alaska, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 108 (3–4), 217–228.

Magné, J., 1978. Etudes microstratigrafiques sur le Néogène de la Méditerranée nord-occidentale. Les Bassins néogènes catalans. Edit. CNRS, Paris. 259 pp.

Martín Pérez, J.A., Viseras, C., 1994. Sobre la posición estratigráfica de las "Margas de Gor", Sierra de Baza, Cordillera Bética. Geogaceta 15, 63–66.

Maurel-Ferrandini, M., 1976. Reconstitution paléogéographique du Burdigalien du littoral de la châine de la Nerthe et de la Région des Etangs (Bouches du Rhône, France). Travaux du Laboratoire de Géologie Historique et de Paléontologie Université de la Provence, vol. 7. 133 pp.

Meulenkamp, J.E., Sissingh, W., 2003. Tertiary palaeogeography and tectonostratigraphic evolution of the Northern and Southern Peri-Tethys platforms and the intermediate domains of the African–Eurasian convergent plate boundary zone. Palaeogeography, Palaeoclimatology, Palaeoecology 196 (1–2), 209–228.

Miller, K.G., Feigenson, M.D., Wright, J.D., Clement, B.M., 1991. Miocene isotope reference section, DSDP Site 608: an evaluation of isotope and biostratigraphic resolution. Paleoceanography 6 (1), 33–52.

Pons, A., 1964. Contribution palynologique à l'étude de la flore et de la végétation pliocènes de la région rhodanienne. Annales des Sciences Naturelles, Botanique 12 (5), 499–722.

Popescu, S.-M., 2001. Repetitive changes in Early Pliocene vegetation revealed by high-resolution pollen analysis: revised cyclostratigraphy of southwestern Romania. Review of Palaeobotany and Palynology 120 (3–4), 181–202.

Popescu, S.-M., 2006. Late Miocene and Early Pliocene environments in the southwestern Black Sea region from high-resolution palynology of DSDP Site 380A (Leg 42B). Palaeogeography, Palaeoclimatology, Palaeoecology 238, 64–77.

Quézel, P., 1965. La végétation du Sahara, du Chad à la Mauritanie. G. Fischer, Stuttgart. 333 pp.

Quézel, P., Médail, F., 2003. Ecologie et biogéographie des forêts du bassin méditerranéen. Elsevier, France. 571 pp.

Rivas-Martínez, S., 1987. Memoria del mapa de las series de vegetación de España. Icona, Madrid. 268 pp.

Rodríguez-Fernández, J., Comas, M.C., Soría, J., Martín-Pérez, J.A., Soto, J.I., 1999. In: Zahn, R., Comas, M.C., Klaus, A. (Eds.), The sedimentary record of the Alboran Basin: an attempt at sedimentary sequence correlation and subsidence analysis. Proceedings of the Ocean Drilling Program Scientific Results, vol. 161, pp. 69–76.

Rögl, V.F., 1998. Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). Annals of the Natural History Museum Vienna 99A, 279–310.

Saint-Martin, J.-P., Müller, P., Moissette, P., Dulai, A., 2000. Coral microbialite environment in a Middle Miocene reef of Hungary. Palaeogeography, Palaeoclimatology, Palaeoecology 160, 179–191.

Sanz de Siria Catalan, A., 1993. Datos sobre la paleoclimatología y paleoecología del Neógeno del Vallès-Penedès según las macrofloras halladas en la cuenca y zonas próximas. Paleontologia i Evolució 26–27, 281–289.

Suc, J.-P., 1976. Apports de la Palynologie a la Connaissance du Pliocène du Roussillon (Sud de la France). Geobios 9 (6), 741–771.

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

Suc, J.-P., 1989. Distribution latitudinale et étagement des associations végétales au Cenozoique superieur dans láire ouest-mediterranénne. Bulletin de la Societé Géologique de France 8 (3), 541–550.

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

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

Suc, J.-P., Bertini, A., Comborieu-Nebout, N., Diniz, F., Leroy, S., Russo-Eromolli, E., Zheng, Z., Bessais, E., Ferrier, J., 1995b. Structure of West Mediterranean vegetation and climate since 5.3 ma. Acta zoologica Cracoviensia 38 (1), 3–16.

Suc, J-P., Bessais, E., 1990. Pérennité d'un climat thermo-xérique en Sicile avant, pendant et après la crise de salinité messiniense. Comptes Rendus de l'Academie des Sciences Paris 310 (2), 1701–1707.

Suc, J.-P., Fauquette, S., Popescu, S.-M., 2004. L'investigation palynologique du Cénozoïque passe par les herbiers. Actes du Colloque "Les herbiers: un outil d'avenir. Tradition et modernité", Villeurbanne. Edit. Association française pour la Conservation des Espèces Végétales, Nancy, pp. 67–87.

Turon, J.-L., 1984. Le palynoplancton dans l'environnement actuel de l'Atlantique nord-oriental. Evolution climatique et hydrobiologique depuis le dernier maximum glaciaire. Thesis, University Bordeaux 1, 313 pp.

Utescher, T., Mosbrugger, V., Ashraf, A., 2000. Terrestrial climate evolution in Northwest Germany over the last 25 million years. Palaios 15, 430–449.

Valle, M.F., Alonso Gavilán, G., Rivas Carballo, M.R., 1995. Analyse Palynologique Préliminare du Miocène dans le NE de la Dépresion du Duero (aire de Belorado, Burgos, España). Geobios 28 (4), 407–412.

Wang, C.W., 1961. The Forests of China with a Survey of Grassland and Desert Vegetation. Maria Moors Cabot Foundation, vol. 5. Harvard University, Cambridge, Massachusetts. 313 pp.

White, F., 1983. The vegetation of Africa, a decriptive memoire to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. Natural Resources Research, vol. 20. UNESCO, Paris. 356 pp.

Woodruff, F., Savin, S.M., 1989. Miocene deep water oceanography. Paleoceanography 4 (1), 87–140.

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

Zagwijn, W.H., 1960. Aspects of the Pliocene and early Pleistocene vegetation in the Netherlands. Mededelingen Geologische Stichting Serie C 3 (5), 78.

Zheng, Z., 1990. Végétations et climats neogénes des Alpes Maritimes Franco-Italiennes d'après les donnes de l'analyse palynologique. Paléobiologie Continentale 17, 217–244.

Zheng, Z., Cravatte, J., 1986. Etude palynologique du Pliocène de la Côte d'Azur (France) et du littoral Ligure (Italie). Geobios 9 (6), 815–823.