

Neogene flora, vegetation and climate dynamics in southeastern Europe and the northeastern Mediterranean

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Abstract: Pollen analysis of Miocene and Pliocene sediments from southeastern Europe and the northeastern Mediterranean is represented in pollen synthetic diagrams based on ecological criteria in order to clearly visualize changes in the composition and structure of the vegetation through time. New pollen data, together with abundant existing palynological information from this area, show a progressive reduction in plant diversity caused by a decrease in the most thermophilous and high-water requirement plants and, on the contrary, an increase in warm-temperate (mesothermic) and seasonal-adapted taxa during the Middle–Late Miocene and Pliocene. At the same time, an increase in high-elevation trees and herbs has been recorded, with a strong augmentation in *Artemisia*, first in the eastern Mediterranean and later on in the western Mediterranean area. This has been interpreted as a response of the vegetation to global and regional processes, including climate cooling related to the development of the East Antarctic Ice Sheet (EAIS), uplift of regional mountains during Alpine orogenesis and progressive movement of Eurasia towards northern latitudes as a result of the northwards collision of Africa.

Pollen analyses dealing with Miocene–Pliocene sediments from the Paratethys are rare. Studies have focused on the Miocene and Pliocene palynology of the Central Paratethys (Petrescu *et al.* 1989a, b; Planderová 1990; Nagy 1991, 1992, 1999; Petrescu & Malan 1992) and Turkey (Benda 1971; Benda *et al.* 1975; Akgün & Akyol 1999), but the lack of any quantitative information render these analyses limited. However, palynological data, with reliable botanical identification, are available for the Miocene (Ivanov 1995; Ivanov & Koleva-Rekalova 1999; Palamarev & Ivanov 2001; Ivanov *et al.* 2002; Jiménez-Moreno *et al.* 2005) and the Pliocene (Drivaliari 1993; Drivaliari *et al.* 1999; Popescu 2001, 2002, 2006; Popescu *et al.* 2006a, b) of the same region. In these studies, pollen was not used for biostratigraphy but for climatic information, as independent biostratigraphic dating was available (see below). Pollen counts and a statistical treatment of the data were made to obtain reliable information about floral diversity, organization of the vegetation and to better visualize vegetation and climate change.

The geographical position of the studied area, between Africa and Eurasia and between a Mediterranean and temperate climate, makes this region of great interest for palaeobotanic studies. Today, the southeastern part of the area is mainly occupied by steppe vegetation rich in *Artemisia* (i.e. the central Anatolian steppes), that is the main refuge area of thermophilous plants (mostly along the Turkish coastlines: Zohary 1973; Quézel & Médail 2003). Alpine tectonics were active during the Neogene, producing uplift of the Carpathians, Dinarides, Balkan, Rhodope and Taurides mountains. Then, important palaeogeographical changes occurred (see below; Rögl 1998; Meulenkamp & Sissingh 2003; Popov *et al.* 2004) that may have contributed to the pattern of vegetation distribution seen today.

In this paper, we present a synthesis of palynological data, interpreted vegetation and climate dynamics based on Miocene and Pliocene deposits from Eastern Europe. New sections of Middle and Late Miocene age from this area have been analysed, adding new information to the already

published data. Changes in vegetation have been observed from the Langhian to the early Pliocene (16.3–3 Ma). These are mainly related to global climatic changes, in temperature and precipitation, that are linked to atmospheric and palaeogeographic changes that were of significant importance during the Neogene.

Regional setting

The studied area comprises Neogene basins formed within the Central–Eastern Paratethys Sea. They were generated during the Neogene, like the rest of the basins belonging to the Paratethys, as a product of the collision of the African plate and Eurasia. These basins are delimited by the Carpathians, Balkan, Dinarides and Taurides, occupying parts of Hungary, Romania, Bulgaria, Serbia,

Greece and Turkey (Fig. 1; Kojumdgieva & Popov 1989; Rögl 1998; Meulenkamp & Sissingh 2003; Goncharova *et al.* 2004; Ilyina *et al.* 2004; Paramonova *et al.* 2004; Khondkarian *et al.* 2004a, b). During the Neogene, the Paratethys displayed a long-term trend of decreasing marine influence and a correlative reduction in size with regard to the marine depositional domains. Marine deposition lasted throughout the Early and Middle Miocene up to approximately 12 Ma, when uplift caused the sea to retreat from the Pannonian basin complex where a brackish lake formed instead (Rögl 1998). However, during the Early and Middle Miocene, connection between the Mediterranean Sea and the Paratethys existed that allowed for a free marine faunal exchange (Harzhauser *et al.* 2003). The first impairment of marine connections is evident in the Late Badenian (Early Serravallian)



Fig. 1. Geographic map of the studied area and location of the sites. 1 Nireas-1; 2 Valea Morilor; 3 Ruzhintsi; 4 Catakbagyaka; 5 Hinova; Husnicioara and Valea Visenilor; 6 Lupoiaia; 7 Ticleni-1; 8 Ravno Pole and Lozenec; 9 Sandanski; 10 Lion of Amphipoli; 11 Nestos-2; 12 Site 380 A; 13 Aghios Vlassios; 14 Avadan; 15 Lataquie; 16 Drenovets C-1; 17 Deleina C-12; 18 Makrilia; 19 Tengelic-2.

when dysaerobic bottom conditions and a stratified water column characterized the Paratethyan realm (Kovac *et al.* 2004). With the onset of the Sarmatian, marine connection to the Mediterranean almost completely ceased, and was reflected by the development of a highly endemic molluscan fauna (Harzhauser & Piller 2004). Finally, at the Sarmatian/Pannonian boundary (Serravallian/Tortonian boundary), the Central Paratethys became entirely restricted and the brackish Lake Pannon was established. Sporadic brief connections occurred during the Late Miocene and Pliocene between the Eastern Paratethys (Dacic and Euxinian basins) and the Mediterranean Sea as documented by nannoplankton influxes (Mărușeanu & Papaianopol 1998; Semenenko & Olejnik 1995). One of these short connections also concerned the southeastern Pannonian Basin during the so-called Portaferrian regional Stage (Pontian). Some of these connections occurred just before and just after the Messinian salinity crisis (Clauzon *et al.* 2005; Snel *et al.* 2006), resulting in the same responses (i.e. an intense erosion, then the construction of Gilbert-type fan deltas) to the Messinian desiccation and Zanclean flooding as in the Mediterranean Basin itself (Clauzon *et al.* 2005). However, during the late Neogene, most of the Paratethyan basins were disconnected and evolved as isolated lakes, some of them being temporarily connected with the Mediterranean Sea (Mărușeanu & Papaianopol 1995).

The independent evolution of the different sub-domains of the Paratethys led to the construction of several regional stratigraphies, constituted by stages based on diverse groups of organisms, mainly bivalves and ostracods, and benthic and planktonic foraminifera etc. (Marinescu 1978; Papaianopol & Motas 1978; Papaianopol & Marinescu 1995; Rögl 1998; Fig. 2). Reliable correlations are established between the Eastern Paratethys regional stratigraphy and the Mediterranean standard stratigraphy using nannoplankton (Papaianopol & Mărușeanu 1993; Mărușeanu & Papaianopol 1995, 1998; Drivaliari *et al.* 1999; Clauzon *et al.* 2005; Snel *et al.* 2006).

Chronological background

A total of 19 sections and a total of 680 samples have been studied for pollen. Of those 19 sections, 12 (or a part) belong to the Miocene and 14 (or a part) to the Pliocene (Fig. 2). As far as possible, an independent age control has been obtained; it is indicated in Table 1 with the authors of the pollen analyses. The timescale of Gradstein *et al.* (2004) has been used.

Methods

Identification was performed comparing the Neogene pollen grains with those of the living relative plants

using databanks of modern pollen grains and modern and past pollen grain photographs. Based on the results of the pollen spectra, standard synthetic diagrams (Suc 1984) with *Pinus* and Pinaceae have been constructed. In these pollen diagrams, taxa have been arranged into 12 different groups based on ecological criteria in order to obtain some visualization of the vegetation (see below) and more easily compare with reference oxygen isotopic curves. This method has been proven to be a very efficient tool for high-resolution climatic studies characterizing warm–cold alternations related to Milankovitch cycles for both the Miocene (Jiménez-Moreno *et al.* 2005) and the Pliocene (Popescu 2001, 2006; Popescu *et al.* 2006a, b).

Pollen data will be available, after publication, on the web from the 'Cenozoic pollen and climatic values' database (CPC) (<http://medias.obs-mip.fr/cpc>).

Results

Plant diversity and vegetation

Even if some parts of the studied region are characterized today by a very diverse flora and are main refuge areas of thermophilous plants (i.e. the Ponto-Euxinian area) (Quézel & Médail 2003), a richer and more diverse flora has been identified for the Mio-Pliocene that consisted of elements found presently in different geographic areas:

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

All of these taxa grew in the Eastern European area during the Miocene.

We use the Chinese flora as a present-day comparison for the southeastern Europe and Middle East flora during the Neogene as it is the closest living example of this floral inventory (Suc 1984). Flora of the broad-leaved evergreen forest was represented by 45 typical tropical and subtropical taxa (i.e. megathermic and mega-mesothermic elements, respectively) in the studied region during the middle Miocene's warmest phase; only 21 of them persisted until the early Pliocene and have presently disappeared from the area. Flora of the evergreen and deciduous mixed forest was represented by 21 subtropical and warm-temperate taxa (i.e. mega-mesothermic and mesothermic

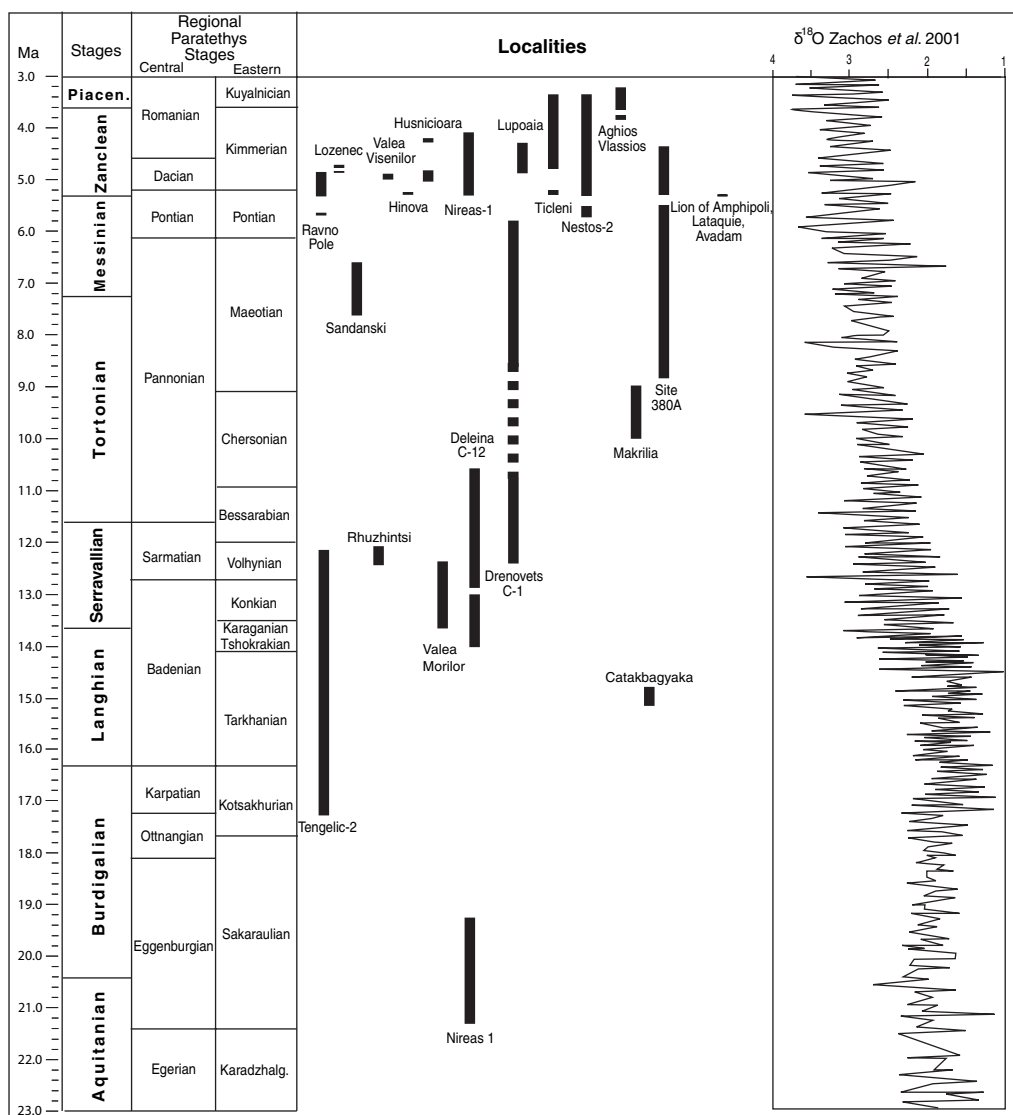


Fig. 2. Miocene and Pliocene chronostratigraphy and temporal situation of the studied sites. Correlations between standard stages and Paratethys stages by Harzhauser & Piller (in press) after data of Steininger (1999), Sprovieri (1992), Sprovieri *et al.* (2002), Fornaciari & Rio (1996) and Fornaciari *et al.* (1996). Oxygen isotope curve after Zachos *et al.* (2001); all stages recalibrated according to Gradstein & Ogg (2004), Gradstein *et al.* (2004) and Lourens *et al.* (2004).

elements, respectively) in the studied region during the Middle Miocene's warmest phase; they persisted here during the Early Pliocene and 17 among them are still living in the area.

The vegetation was characterized by a complex mosaic due to its dependency on several factors (water availability, characteristics of the soils, orientation of relief slopes, etc.) which superimposed its latitudinal–altitudinal organization. The most important factor, similar to

present day, would be altitude, controlling both temperature and precipitation. Therefore, the vegetation would be organized in altitude belts, which have been compared with those found today in subtropical to temperate southeastern China, the most reliable model. The following have been distinguished:

(1) a coastal marine environment characterized by the presence of an impoverished mangrove composed of *Avicennia* which is mainly

Table 1. Age control of the 19 considered pollen localities indicating the authors of the pollen analyses

#	Section	Location	Datation	Age	Pollen analysis by
1	Nireas 1	Greece	* Drivaliari 1993	Aquitanian-Burdigalian	Drivaliari, A.
2	Valea Morilor	Romania	*) Papatanopol <i>et al.</i> 1995	Zanclean	Jiménez-Moreno, G.
3	Ruzhintsi	Bulgaria) Kojumdjieva 1976; Palmarev & Ivanov 2001	Sarmatian	Jiménez-Moreno, G.
4	Catakbagyaka	Turkey	i Sickenberg <i>et al.</i> 1975; Heissig 1976	Langhian	Jiménez-Moreno, G.
5	Hinova	Romania) Marinescu 1978	Early Zanclean	Popescu, S.-M.
			* Clauzon <i>et al.</i> 2005	Bosphorlian	
5	Husnicioara	Romania	* § ♣ Popescu <i>et al.</i> 2006a	Early Zanclean	Popescu, S.-M.
			¶ Ticleanu & Diaconita 1997		
5	Valea Visenilor	Romania	§ ♣ Popescu <i>et al.</i> 2006b	Early Zanclean	Popescu, S.-M.
			¶ Ticleanu & Diaconita 1997		
6	Lupoaia	Romania	♣ Popescu <i>et al.</i> 2006b	Zanclean	Popescu, S.-M.
			i Radulescu <i>et al.</i> 1997; Apostol & Enache 1979		
			§ Radan & Radan 1998; Van Vugt 2001		
			¶ Ticleanu & Diaconita 1997		
			♣ Popescu S.-M. 2002; Popescu <i>et al.</i> 2006b		
7	Ticleni 1	Romania	*) ♣ Drivaliari <i>et al.</i> 1999	Zanclean	Drivaliari, A. 1993
8	Ravno Pole	Bulgaria) Drivaliari 1993	Pontian-Dacian	Drivaliari, A.
8	Lozenc	Bulgaria	i Gromolard & Guerin 1980; Thomas <i>et al.</i> 1986	Dacian	Drivaliari, A.
9	Sandanski	Bulgaria	i Kojumdjieva <i>et al.</i> 1982; Spassov N. (personal information)	Maeotian	Ivanov, D.
10	Lion of Amphipoli	Bulgaria	* Melinte, M.C. (personal information)	Early Zanclean	Suc, J.-P.
11	Nestos 2	Greece	* + Drivaliari 1993	Messinian-Zanclean	Drivaliari, A.
12	Site 380 A	Black Sea	¶ Hsü 1978; Hsü & Giovanoli 1979; Letouzey <i>et al.</i> 1978	Late Miocene-Early Pliocene	Popescu, S.-M.
			♣ Popescu 2006		
13	Aghios Vlassios	Greece	+ Spaak 1983; Drivaliari 1993	Early Pliocene	Drivaliari, A. 1993
14	Avadam	Turkey	¶ Robertson A.H.F. (personal information)	Early Zanclean	Suc, J.-P.
15	Latakie	Syria	¶ Rubino J.-L. (personal information)	Early Zanclean	Suc J.-P.
16	Drenovets C-1	Bulgaria	+) ^ Kojumdjieva <i>et al.</i> 1989	Sarmatian to Pontian	Ivanov, D.
17	Deleina C-12	Bulgaria	+) ^ Kojumdjieva & Popov 1989	Badenian to Pannonian	Ivanov, D.
18	Makrilia	Greece	* Sachse <i>et al.</i> 1999	Tortonian	Sachse, M.
19	Tengelic-2	Hungary	* +) Nagymarosi 1982; Bohn-Havas 1982; Korecz-Laky 1982	Burdigalian Ottnangian to Sarmatian	Jiménez-Moreno, G.

+ Foraminifera ^ Ostracods i Mammals ♣ Climatostratigraphy * Nanoplankton) Bivalves § Palaeomagnetism ¶ Lithostratigraphy

accompanied by halophytes (Amaranthaceae–Chenopodiaceae, *Armeria*, etc.);

(2) a broad-leaved evergreen forest, from sea level to around 700 m altitude characterized by *Taxodium* or *Glyptostrobus*, *Myrica*, *Rhus*, Theaceae, Cyrillaceae–Clethraceae, *Bombax*, Euphorbiaceae, *Distylium*, *Castanopsis*, Sapotaceae, Rutaceae, *Mussaenda*, *Ilex*, *Hedera*, *Ligustrum*, *Jasminum*, Hamamelidaceae, *Engelhardia*, *Rhoiptelea*, etc.;

(3) an evergreen and deciduous mixed forest, above 700 m altitude; characterized by deciduous *Quercus*, *Engelhardia*, *Platycarya*, *Carya*, *Pterocarya*, *Fagus*, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis*, *Acer*, etc. Within this vegetation belt, riparian vegetation has been identified, composed of *Salix*, *Alnus*, *Carya*, *Carpinus*, *Zelkova*, *Ulmus*, *Liquidambar*, etc. The shrub level was dominated by Ericaceae, *Ilex*, Caprifoliaceae, etc.;

(4) above 1000 m, a mid-altitude deciduous and coniferous mixed forest with *Betula*, *Fagus*, *Cathaya*, *Cedrus*, *Tsuga*.

(5) above 1800 m altitude, a coniferous forest with *Abies* and *Picea*.

Vegetation dynamics

The following description of the Miocene and Pliocene vegetation dynamics in the southern Forecarpathian Basin and Greece–Turkey is a brief summary of the pollen analysis of Drivaliari (1993), Ivanov (1995), Drivaliari *et al.* (1999), Popescu (2001, 2006), Popescu *et al.* (2006a, b), Jiménez-Moreno *et al.* (2005) and Jiménez-Moreno (2005).

Burdigalian–Langhian (20.4–13.6 Ma). The regular occurrence and abundance of thermophilous species typical of the lowest altitudinal belts described above and the relative scarcity of altitudinal elements (Fig. 3) are characteristic for vegetation of this time. The coastal marine environment was then occupied by an impoverished *Avicennia* mangrove and several halophytes (Nagy & Kóky 1991; Nagy 1999; Plaziat *et al.* 2001; Jiménez-Moreno 2005). In the hinterland, lowlands were populated by a broad-leaved evergreen forest, characterized by *Alchornea*, Passifloraceae, *Pandanus*, *Rhus*, Theaceae, Cyrillaceae–Clethraceae, *Bombax*, Rubiaceae, Chloranthaceae, *Reevesia*, Euphorbiaceae, *Distylium*, *Castanopsis*, Sapotaceae, Rutaceae, *Mussaenda*, *Ilex*, *Hedera*, *Itea*, *Alangium*, cf. Mastixiaceae, *Ligustrum*, *Jasminum*, Hamamelidaceae, *Engelhardia*, *Rhoiptelea*, Schizaeaceae, Gleicheniaceae, etc. Within this vegetation belt, swamp forests were also well developed during this time period. Its components, such as *Taxodium* or *Glyptostrobus*, *Nyssa*, *Myrica*, *Planera*, show

comparatively high values in the pollen spectra. Probably the low elevation palaeogeography and very humid conditions at that time in the studied area favoured the wide distribution of swamp forests and of ecologically related riparian forests with *Platanus*, *Liquidambar*, *Zelkova*, *Carya*, *Pterocarya* and *Salix*.

An evergreen and deciduous mixed forest mainly composed of mesothermic elements such as *Quercus*, *Carya*, *Pterocarya*, *Fagus*, Ericaceae, *Ilex*, Caprifoliaceae, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis*, *Acer*, but also *Engelhardia*, *Platycarya*, etc., characterized areas of higher altitude. Within this vegetation belt, riparian vegetation has been identified, composed of *Salix*, *Alnus*, *Carya*, *Carpinus*, *Zelkova*, *Ulmus*, etc.

It should also be mentioned that conifer pollen, mainly *Pinus* and indeterminate Pinaceae, can be particularly abundant, presumably because of the capacity of saccate pollen for long-distance transport (Heusser 1988; Suc & Drivaliari 1991; Cambon *et al.* 1997; Beaudouin 2003): during the Badenian, the basin developed its largest extension so that the studied sections had the maximum distance from the coastline (Fig. 3). Mid- and high-altitude elements (*Tsuga*, *Cedrus*, *Abies* and *Picea*) and *Cathaya* seem not to vary significantly in sections of this age (Fig. 3).

Serravallian–Tortonian–Messinian (13.6–5.3 Ma). During this time-interval, important changes in the vegetation are observed: *Avicennia*, which populated the coastal areas in previous times, is not found commonly and several megathermic elements (*Buxus bahamensis* group, *Alchornea*, *Bombax*, Iacacinaceae, *Croton*, Melastomataceae, etc.), typical from the broad-leaved evergreen forest, became rare and most of them disappeared (Fig. 3). The evergreen–deciduous mixed forest suffered a great transformation due to the loss and decrease in the abundance of several megamesothermic evergreen plants. This kind of vegetation was progressively enriched by deciduous mesothermic plants, such as deciduous *Quercus*, and *Fagus*, *Alnus*, *Acer*, *Eucommia*, *Betula*, *Alnus*, *Carpinus*, *Ulmus*, *Zelkova*, *Tilia*, etc. Thus, the vegetation shows a tendency towards increasing proportions of mesothermic deciduous elements coming from higher altitudes.

Even if the thermophilous elements decreased during this period, the swamp forest continued to be well developed. At the same time, the vegetation from mid- (*Cathaya*, *Tsuga* and *Cedrus*) and high-altitude (*Picea* and *Abies*) belts clearly strengthened. For instance, *Tsuga* (mid-altitude indicator) is absent in the Badenian (Langhian and Early Serravallian) or very rare, it is still rare at the base of the Volhynian (approx. 12.7 Ma), but reaches

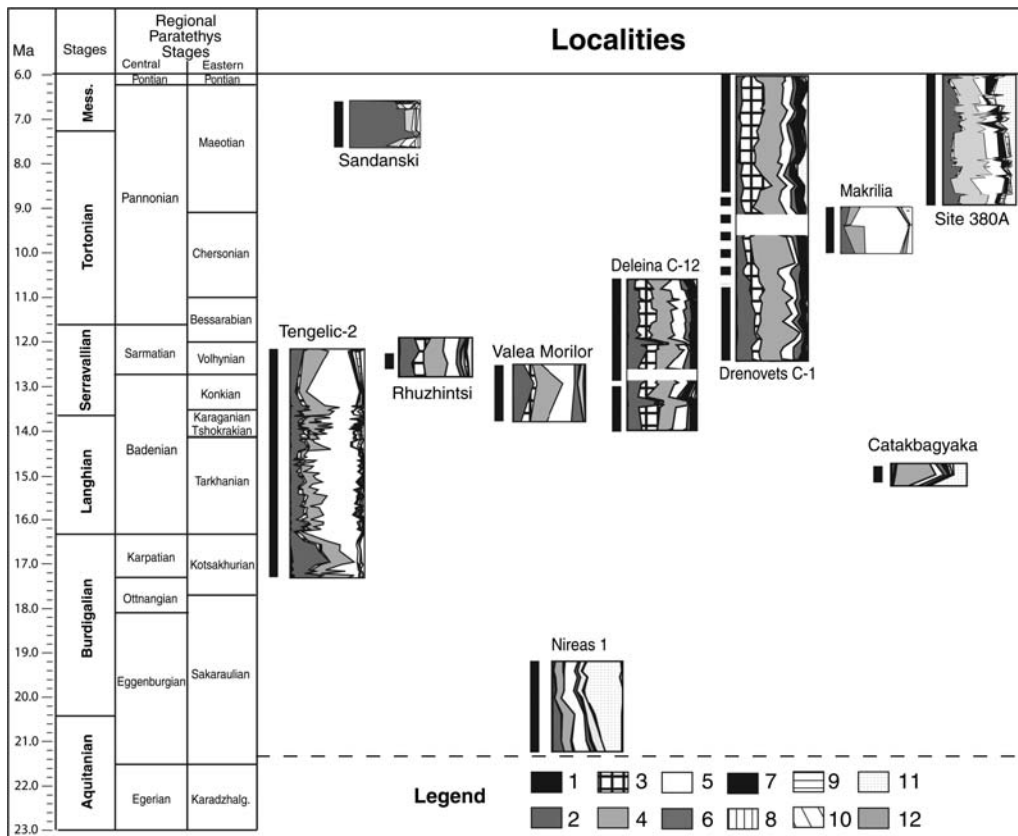


Fig. 3. Synthetic pollen diagrams of the sections spanning the Miocene until 6 Ma. Taxa have been grouped according to their ecological significance as follows: 1 Megathermic (= tropical) elements (*Avicennia*, *Amanoa*, *Alchornea*, *Fothergilla*, *Exbucklandia*, Euphorbiaceae, Sapindaceae, Loranthaceae, Arecaceae, Acanthaceae, *Canthium* type, Passifloraceae, etc.). 2 Mega-mesothermic (= subtropical) elements (Taxodiaceae, *Engelhardia*, *Platycarya*, *Myrica*, Sapotaceae, *Microtropis fallax*, *Symplocos*, *Rhoiptelea*, *Distylium* cf. *sinensis*, *Embolanthera*, *Hamamelis*, Cyrillaceae–Clethraceae, Araliaceae, *Nyssa*, *Liriodendron*, etc.). 3 *Cathaya*, an altitudinal conifer living today in Southern China. 4 Mesothermic (= warm-temperate) elements (deciduous *Quercus*, *Carya*, *Pterocarya*, *Carpinus*, *Juglans*, *Celtis*, *Zekkova*, *Ulmus*, *Tilia*, *Acer*, *Parrotia* cf. *persica*, *Liquidambar*, *Alnus*, *Salix*, *Populus*, *Fraxinus*, *Buxus sempervirens* type, *Betula*, *Fagus*, *Ostrya*, *Parthenocissus* cf. *henryana*, *Hedera*, *Lonicera*, *Elaeagnus*, *Ilex*, *Tilia*, etc.). 5 *Pinus* and poorly preserved Pinaceae pollen grains. 6 Meso-microthermic (= mid-altitude) trees (*Tsuga*, *Cedrus*). 7 Microthermic (= high-altitude) trees (*Abies*, *Picea*). 8 Non-significant pollen grains (undetermined ones, poorly preserved pollen grains, some cosmopolitan or widely distributed elements such as Rosaceae and Ranunculaceae). 9 Cupressaceae. 10 Mediterranean xerophytes (*Quercus ilex* type, *Carpinus* cf. *orientalis*, *Olea*, *Phillyrea*, *Ligustrum*, *Pistacia*, *Ziziphus*, *Cistus*, etc.). 11 Herbs (Poaceae, *Erodium*, *Geranium*, *Convolvulus*, Asteraceae Asteroideae, Asteraceae Cichorioideae, Lamiaceae, *Plantago*, *Euphorbia*, Brassicaceae, Apiaceae, *Knautia*, *Helianthemum*, *Rumex*, *Polygonum*, *Asphodelus*, Campanulaceae, Ericaceae, Amaranthaceae–Chenopodiaceae, Caryophyllaceae, Plumbaginaceae, Cyperaceae, *Potamogeton*, *Sparganium*, *Typha*, Nymphaeaceae, etc.) including some subdesertic elements (*Lygeum*, *Neurada*, *Nitraria*, *Calligonum*). 12 Steppe elements (*Artemisia*, *Ephedra*).

up to 10% in the middle and upper part of the Volhynian (Fig. 3). This palaeofloristic change occurs slowly and gradually without major fluctuations. A similar vegetation change is observed during the same time-interval in other areas of Europe (e.g. Spain, southern France, Switzerland and Austria: Bessedik 1985; Jiménez-Moreno 2005).

The herbs (mainly Poaceae, Amaranthaceae–Chenopodiaceae, *Artemisia*, Caryophyllaceae, Polygalaceae, Lamiaceae, Asteraceae Asteroideae and Asteraceae Cichorioideae) also became more abundant (Fig. 3). This may be due to a somewhat drier climate during that time as is also indicated by macrofloras of the same area (Palamarev 1991; Palamarev &

Ivanov 2004) and confirmed by sedimentological data (Koleva-Rekalova 1994; Ivanov & Koleva-Rekalova 1999): in Bessarabian to Chersonian sediments (12–9.1 Ma) of northeast Bulgaria, aragonite sediments occur which are assumed to have been formed under a seasonally dry climate. This trend continued during the Late Miocene. Presumably, open landscapes covered by more xerophytic herbaceous communities existed during that time.

Pliocene (5.3–c. 3.2 Ma). The vegetation was then characterized by a mosaic of different plant associations inherited from the Miocene. The same vegetation dynamics marked by disappearance of thermophilous plants and increase in mesothermic and micro-mesothermic plants continued. Some of the coastal areas of this region were still inhabited by *Avicennia* mangrove (*Avicennia* pollen at Site 380A at 781.63 m) and several megathermic elements typical from the broad-leaved evergreen forest occupying the lowlands, such as *Amanoa*, *Pachysandra*, *Entada*, Meliaceae, Mimosaceae, Sapindaceae, Tiliaceae, Euphorbiaceae, Acanthaceae and *Fothergilla*, are sporadically present. They disappeared during the early Pliocene (between 4–3.5 Ma) (Popescu 2001). The mega-mesothermic plants, belonging to these plant associations, such as *Engelhardia*, *Microtropis*, *Distylium*, *Parthenocissus*, Sapotaceae, Arecaceae, etc., are still abundant and persisted through the Pliocene (Fig. 4). Swampy (mainly *Taxodium* or *Glyptostrobus*, *Nyssa*, *Myrica*) and marshy (Cyperaceae, Poaceae, Cyrtaceae–Clethraceae, *Myrica*) elements, populating deltaic areas, were very abundant. Trees from the family Taxodiaceae did not disappear from this area until the middle Pleistocene (Mamatsashvili 1975).

The mixed deciduous forest (mainly made up of conifers like *Pinus*, and several deciduous trees such as *Quercus*, *Acer*, *Carpinus*, *Parrotia*, *Carya*, *Pterocarya*, *Liquidambar*, *Platanus*, *Tilia*, *Ulmus*, *Zelkova*, etc.), situated at higher altitude, as well as the trees belonging to the highest altitudinal belts, become more abundant during this period (*Cathaya*, *Cedrus*, *Tsuga*, *Picea* and *Abies*) (increasing percentages of these elements are compared on Fig 3 and 4).

Another important fact that makes a difference between the Pliocene and the Miocene is the strong development of the steppe with *Artemisia* in the Ponto-Euxinian region since the early Pliocene (Site 380A, Fig. 4).

Climatic evolution: regional vs. global climatic change

The high presence of mega- and mega-mesothermic elements during the Early and early Mid-Miocene suggests the existence of a warm, subtropical

climate and a tendency towards slightly cooler conditions in the late Mid-Miocene. Climate was also quite humid, to support the development of such a large association of thermic elements (of present-day 'Asiatic' affiliation and climate) which require very humid conditions all year (Wang 1961). The major change is the impoverishment in plant diversity produced by the disappearance of the most thermophilous plants and the consequent enrichment in mesothermic plants (mainly deciduous *Quercus*, *Alnus*, etc.) and high-elevation conifers, from the Serravallian to the Pliocene.

The floral assemblages during the Early and early Mid-Miocene clearly reflect the Miocene Climatic Optimum (MCO: Zachos *et al.* 2001; Shevenell *et al.* 2004) well-recorded at Tengelic-2 (Jiménez-Moreno *et al.* 2005). The major change registered in plant diversity is related to a gradual decrease in temperature and precipitation after the MCO (Ivanov *et al.* 2002; Jiménez-Moreno *et al.* 2005). This fact is well documented on a worldwide scale and has been correlated with the general decrease in temperature observed by several authors as a gradual increase in the isotopic $\delta^{18}\text{O}$ values of foraminifera from deep-sea sediments (DSDP Sites 608: Miller *et al.* (1991) and 588: Zachos *et al.* (2001)) during this timespan and related to an increase in the size of the EAIS (East Antarctic Ice Sheet) (Zachos *et al.* 2001) (Fig. 2). The isotopic values also indicate that this cooling continued during the Late Miocene and Pliocene (Zachos *et al.* 2001) (Fig. 2).

High-elevation conifers seem not to vary along the sections of early and early Mid-Miocene; however, these elements are abundant in the samples and indicate that the surrounding mountains were already significantly uplifted. Mid- (including *Cathaya*) and high-elevation conifers clearly increase during the late Mid-Miocene and Late Miocene. This can be observed in the boreholes Deleina C-12 and Drenovets C-1 (Fig. 3).

In addition, an augmentation in herbs, mainly *Artemisia*, Amaranthaceae–Chenopodiaceae, Poaceae, Asteraceae, etc., during the Late Miocene and Pliocene, indicates more open vegetation, and drier conditions. Supporting this interpretation is the substitution of thermophilous elements with high humidity requirements all year (Asiatic-like vegetation) by mesothermic (mainly deciduous) elements which can survive under seasonal climate with respect to the precipitation (Popescu 2001; Ivanov *et al.* 2002; Jiménez-Moreno *et al.* 2005).

The noticeable increase in mesothermic plants and high-elevation conifers can be interpreted as a result of climate cooling, or by uplift of surrounding mountains (Kuhlemann & Kempf 2002). In both situations, altitudinal elements would increase.

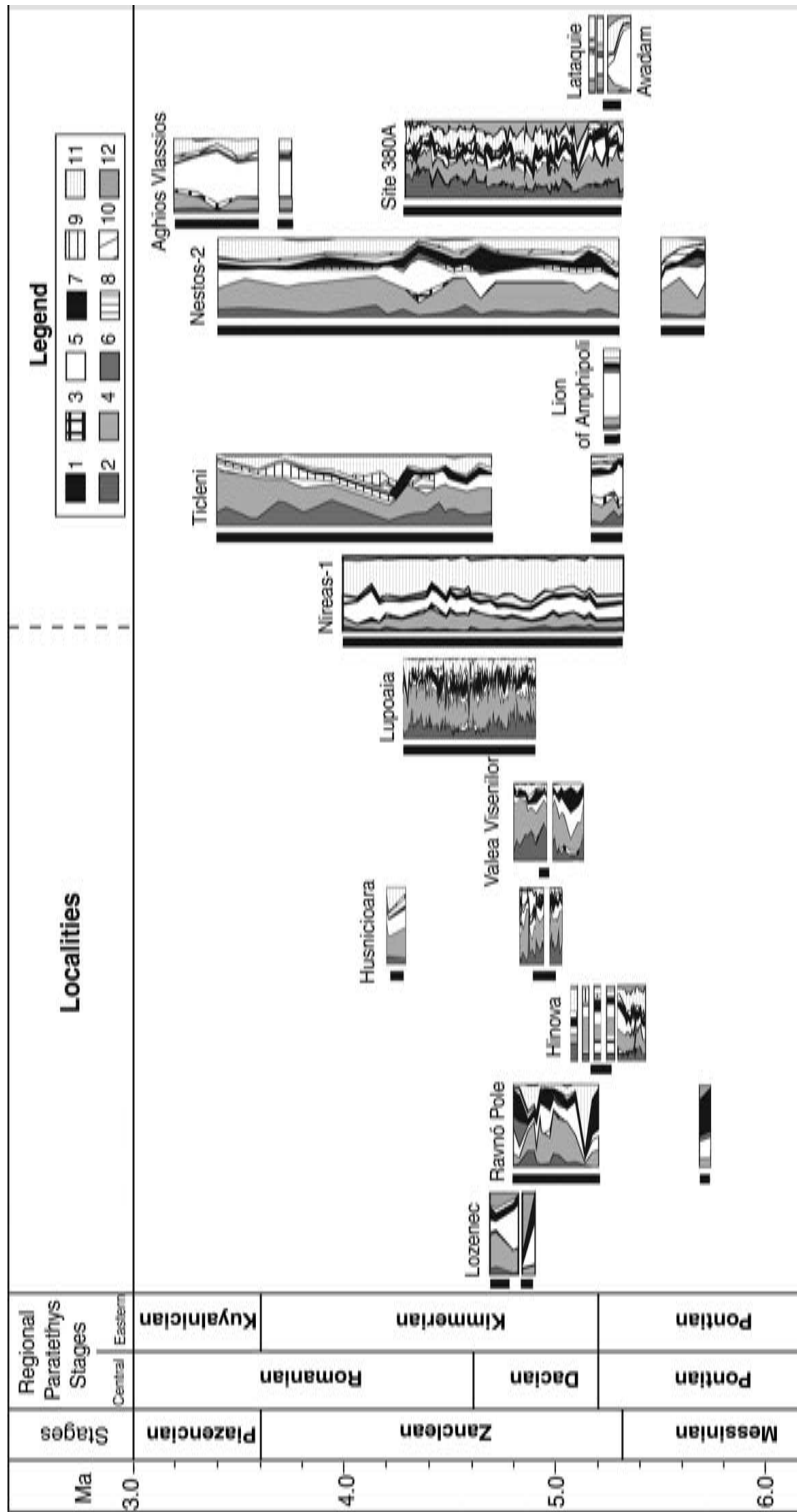


Fig. 4. Synthetic pollen diagrams of the studied sections spanning the Late Miocene (from 6 Ma) and Pliocene. For legend of plant groups, see Figure 3.

It is quite difficult to separate one process from another (global climatic forcing vs. the regional one), due to the tectonic situation of the studied area and the fact that they may have interfered. However, the vanishing of several thermophilous plants, which lived at low elevations and thus were not affected by the regional uplift, and the climate reconstructions using mainly taxa growing at low to middle–low altitude confirm a decrease in mean annual temperatures (Ivanov *et al.* 2002; Jiménez-Moreno *et al.* 2005; Mosbrugger *et al.* 2005). Then, it is clear that even if the uplift of the surrounding mountains may have influenced the regional climate, the evolution of the vegetation during both the Miocene and Pliocene was very dependent on the global climatic signal as shown in previous studies (Popescu 2001, 2002; Ivanov *et al.* 2002; Jiménez-Moreno *et al.* 2005). Hence, according also to the rapid nature of the recorded change in vegetation, we consider that global cooling was the most efficient forcing.

The origin of the steppe with *Artemisia*

Open herbaceous formations in the southern Mediterranean area are known since the Burdigalian (Suc *et al.* 1995a, b; Bachiri Taoufiq *et al.* 2001; Jiménez-Moreno 2005; Jiménez-Moreno & Suc in press). They were already well-developed during the Zanclean in other regions of the Mediterranean area (Suc *et al.* 1999) but were relatively poor in *Artemisia*. It is at the end of the Pliocene, as the climate got cooler and glacial–interglacial cycles appeared in the Northern Hemisphere, when the steppes with *Artemisia* became of significant importance (Suc *et al.* 1995b) during the glacial periods (Suc & Cravatte 1982; Combourieu-Nebout & Vergnaud Grazzini 1991; Beaudouin 2003) and even during interglacials (Subally *et al.* 1999) because of the ambivalent significance of *Artemisia* from the temperature viewpoint (cold vs. warm species: Subally & Quézel 2002).

The presence of steppe vegetation with *Artemisia* in the Ponto-Euxinian region (i.e. in Anatolia according to Site 380A pollen record; Popescu 2001, 2006) in the Late Miocene and their significant strengthening in the Early Pliocene is very informative. Their early presence and development in this region, contrary to the extreme scarcity of *Artemisia* in the Moroccan steppes in the Late Miocene and Early to Middle Pliocene (Bachiri Taoufiq 2000; Suc *et al.* 1999), indicates that Anatolia and neighbouring areas could have been the source area of this kind of vegetation for the rest of the Mediterranean region, a style of vegetation that became very abundant during the cold periods of the Quaternary (Popescu 2001; Suc & Popescu

2005). The early settlement and then development of *Artemisia* steppe vegetation in Anatolia may have resulted from migration from the east of this genus as a consequence of uplift of the Tibetan Plateau (where *Artemisia* species are still abundant today) and the succeeding reinforced Asiatic monsoon (Zhisheng *et al.* 2001).

Conclusions

Pollen data show a progressive reduction in the most thermophilous and high-water requirement plants typical of a broad-leaved evergreen forest and, in contrast, an increase in seasonal-adapted plants coming from higher altitude belts, including mesothermic (mainly deciduous) elements, altitudinal trees and herbs, during the Middle–Late Miocene and Pliocene. This has been interpreted as the response of the vegetation to global climate cooling, accentuated by the regional uplift of the surrounding mountains during Alpine tectonics. This process may also have been favoured by progressive movement of Eurasia towards northern latitudes.

The appearance of steppe vegetation with *Artemisia* on the Anatolian Plateau since the Late Miocene and its development in the Early Pliocene, significantly earlier than in the rest of Southern Europe, is informative. This suggests that the Anatolian *Artemisia*-rich steppes could have been the source area of this kind of open vegetal formation for the rest of the Mediterranean area during the Quaternary.

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