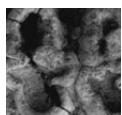


Palynofloras and vertebrates from Muğla-Ören region (SW Turkey) and palaeoclimate of the Middle Burdigalian–Langhian period in Turkey

MINE SEZGÜL KAYSERİ ÖZER, FUNDA AKGÜN, SERDAR MAYDA & TANJU KAYA



The Miocene is the last warm episode in Earth history, and this episode was well recorded in Turkey as shown by plant distribution and inferred numerical temperature values. In this study, Ören-Kultak, Hüssamlar and Karacaağac palynofloras from western Turkey, which are characterized by the thermophilous plants (*Engelhardia*, Sapotaceae, Cyrillaceae, *Avicennia*, Arecaceae, Palmae), are described. Age determinations of these palynofloras (middle Burdigalian–Langhian) are strengthened by the mammalian fossil record (MN4–5) and strontium isotope results. Palaeoclimate is humid and warm subtropical during the middle Burdigalian–Langhian time interval in Europe and Turkey. However, temperature difference has been observed between Europe and Turkey during this time interval and it could be explained by the palaeogeographic position of countries. Despite some discrepancies in the climatic values and palaeovegetation groups, warm climatic conditions are recorded, based on the palynofloras, in Turkey (Çayırhan, Havza, Çan, Etili, Gönen, Bigadiç, Emet, Kirka and Kestelek, Sabuncubeli, Soma, Tire, Kuloğulları, Başçayır, Hüssamlar and Karacaağac), Greece and elsewhere in Europe throughout the middle Burdigalian–Langhian period. This warming is related to the Middle Miocene Climatic Optimum period. Carbon and oxygen isotope values obtained from tooth enamel of *Gomphotherium* sp. from Kultak and Hüssamlar indicate similar ecological condition during the Burdigalian–Langhian time. This isotopic result and high MAP_{DRY} value from the Kultak locality are in agreement with ecological interpretation of mammalian fossils. Besides, according to the precipitation values, central and northwestern Anatolian sites provide more rainfall during the Burdigalian–Langhian time interval than the western Anatolian sites. • Key words: palynology, palaeoclimate, palaeovegetation, mammalian fossils, western Anatolia, Miocene.

KAYSERİ ÖZER, M.S., AKGÜN, F., MAYDA, S. & KAYA, T. 2014. Palynofloras and vertebrates from Muğla-Ören region (SW Turkey) and palaeoclimate of the Middle Burdigalian–Langhian period in Turkey. *Bulletin of Geosciences* 89(1), 137–162 (13 figures, 5 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received January 25, 2013; accepted in revised form August 6, 2013; published online January 6, 2014; issued January 21, 2014.

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Numerous coal bearing deposits in Turkey from the Burdigalian–Langhian time interval display clear palaeoenvironmental changes and in particular the record of the Middle Miocene Climatic Optimum (e.g. Akgün 1993; Gemici *et al.* 1991; Akgün & Akyol 1999; Akgün *et al.* 2000, 2002, 2004, 2007; Ediger 1990; Rögl 1998; Karayıgit *et al.* 1999; Zachos *et al.* 2001; Akgün & Kayseri 2004; Popov *et al.* 2004; Mosburgger *et al.* 2005; Kayseri *et al.* 2006; Kayseri & Akgün 2008; Fauquette *et al.* 2007; Yavuz-Işık 2007; Ivanov *et al.* 2011; Utescher *et al.* 2011; Kern *et al.* 2011). Sediments of the Milas-Ören Basin are known as potentially favorable to provide a well-controlled regional stratigraphy and lithostratigraphic correlation with the neighbour basins based on a few palaeontological studies (i.e. Nebert, unpublished report; Nakoman 1978, Kaya *et al.* 2001). In the Milas-Ören Basin, the Burdigalian is represented by

marine sediments in the Akbük region according to the previous studies (i.e. Görür *et al.* 1994, 1995). Besides, Kaya *et al.* (2001) reported on the late Langhian (MN5–6 boundary) mammalian fossils. However, fossil evidence from terrestrial and marine sediments in the Milas-Ören Basin is not adequately studied and also the biostratigraphy of this region is not yet well-established (Fig. 1).

Sedimentary rocks at the Kultak locality are characterized by clastic sediments, which are deposited in the delta environment (Görür *et al.* 1994, 1995; Kayseri 2010). Terrestrial sediments at the Karacaağac and Hüssamlar localities are represented by coal and marl alternations, and they yielded mammalian fossils. In addition, strontium analyses on mammalian teeth are used to support the age determination. Palaeoenvironmental data on these deposits were obtained from palynofloras of the Kultak, Karacaağac and



Figure 1. Main tectonic units of Turkey (after Görür & Tüysüz 2001) and the study areas.

Hüssamlar localities, and oxygen, carbon isotopes analyses applied on mammalian fossil teeth.

Vegetation and climate history of Turkey during the Burdigalian–Langhian time interval is revealed, in addition to the present study on the Ören-Kultak, Karacaağac, Hüssamlar localities, by the previous studies on the palynofloras from Ankara-Beypazarı correlated to “latest Burdigalian” (Güngör 1991, Whateley & Tuncalı 1995), from Çanakkale-Çan and Balıkesir-Gönen correlated to “latest

Burdigalian–?Serravallian” (Ediger 1990), from Aydin-Başçayır and Kuloğulları correlated to “Langhian” (Akgün & Akyol 1999), from İzmir-Sabuncubeli correlated to “latest Burdigalian”. In addition, palynofloras studies from Spanokhorion and Evia in Greece correlated to “latest Burdigalian” and from Kolivata in Greece correlated to “Langhian” (Benda *et al.* 1982) provided interesting results that can be compared to those from Turkey. Taking into consideration the palaeogeography of the Burdigalian and Langhian, palaeoclimatic records from Serbia, Ukraine, Germany, Austria and Bulgaria are compared with palaeoclimatic results from Turkey and Greece.

Geological setting

Mesozoic sediments of the Lycian Nappes cover a large area between the Menderes Massif to the north and the Bey Dağları autochthonous unit to the east. These formations form the basement of the Early–Middle Miocene deposits in the Gökova region (Görür *et al.* 1994, Yılmaz *et al.* 2000, Sözbilir *et al.* 2005; Fig. 1). The north-south trending Ören Basin, where crop out the Oligo-Miocene sedimentary deposits, is located to the north of the Gökova gulf (Yılmaz & Polat 1998, Querol *et al.* 1999, Yılmaz *et al.* 2000, Gürer & Yılmaz 2002). The sedimentary infill of the Ören Basin is represented by coal-bearing continental and shallow marine sediments (Gürer & Yılmaz 2002), in some places including reefal limestones.

The basement rocks Lycian Nappes are unconformably overlain by marine and terrestrial sediments, which are deposited during the Oligocene–Early Miocene in the Ören

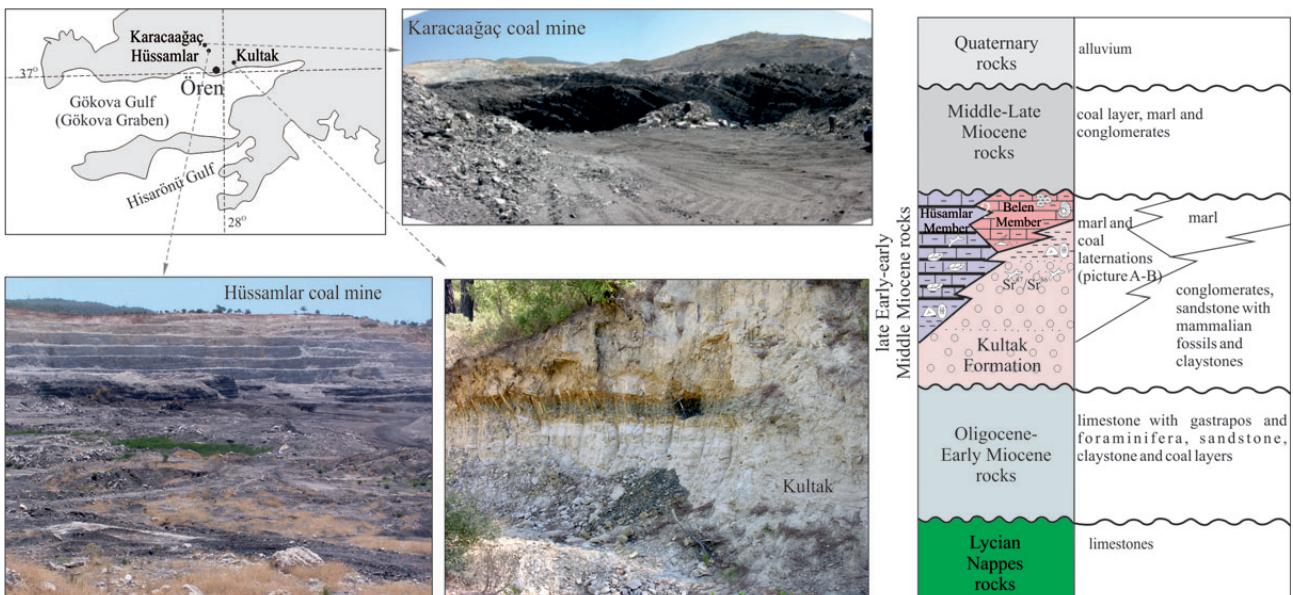


Figure 2. Generalized stratigraphic columnar section between the Kultak and Karacaağac localities.

region. The Kultak Formation unconformably overlies the basement and this formation laterally and vertically passes to the Hüssamlar and Belen members. The Kultak Formation is deposited during the late Early–early Middle Miocene interval based on palynological records, the mammalian fossil and strontium isotopic results. The Belen Member is characterized by marine sediments with foraminifers, gastropods, bivalves and corals in the Kultak area (Kayseri 2010, Kayseri & Akgün 2010). The Hüssamlar Member is represented by marls with leaf fossils and coal alternations in the Hüssamlar and Karacağaç areas (Fig. 2). Quaternary alluvial sediments cover on all the older units in the study area. The palynological data are obtained from the claystones of the upper part of the Kultak Formation (in the Kultak area) and claystones and coals of the Hüssamlar Member (in Hüssamlar and Karacağaç areas). Mammalian fossils are collected from the clastic rocks in the Kultak Formation and coal bearing sediments in the Hüssamlar Member (Kaya *et al.* 2001, Kayseri 2010; Fig. 2).

Material and methods

This study is based on sporomorphs extracted from the measured stratigraphic sections of the Kultak, Karacağaç and Hüssamlar localities. All samples were processed at the Dokuz Eylül University in İzmir using standard palynological preparation techniques, including treatment with HCl, HF and HNO₃. Separation of the spores and pollen from the rest of the residue was carried out using ZnCl₂ (2.0 g per cm³). Forty-seven samples from the terrestrial sediments in the Hüssamlar, Karacağaç and Kultak localities were found suitable for quantitative pollen analysis. Palynoflora description was carried out in the Senckenberg Museum in Frankfurt and Dokuz Eylül University. Changes of the palynomorph abundance are handled by the TILIA (2.0.2.) program. Besides, mammalian fossils are determined in the Aegean University.

The use of multivariate analytical methods in paleontological studies has become more widespread in the last twenty years (Kovach 1988, 1989). The choice of methods depends on the type of data and on the specific problems being solved (Kovach 1989). To interpret the faunal similarities, the statistical analyses were performed with the Paleontological Statistics Software (PAST), using the UPGMA (unweighted pair group method with arithmetic mean) cluster algorithm method and the Jaccard's similarity index (Hammer *et al.* 2001). Additionally, in this study, the isotopic results of oxygen and carbon are obtained from the first lower molar of *Gomphotherium* sp. Thus, the isotopic analyses results were combined with temperature and precipitation results evidenced by floral analyses to support the palaeovegetational investigations.

The coexistence approach (CA) method, which is developed by Mosbrugger & Utescher (1997), is used to obtain

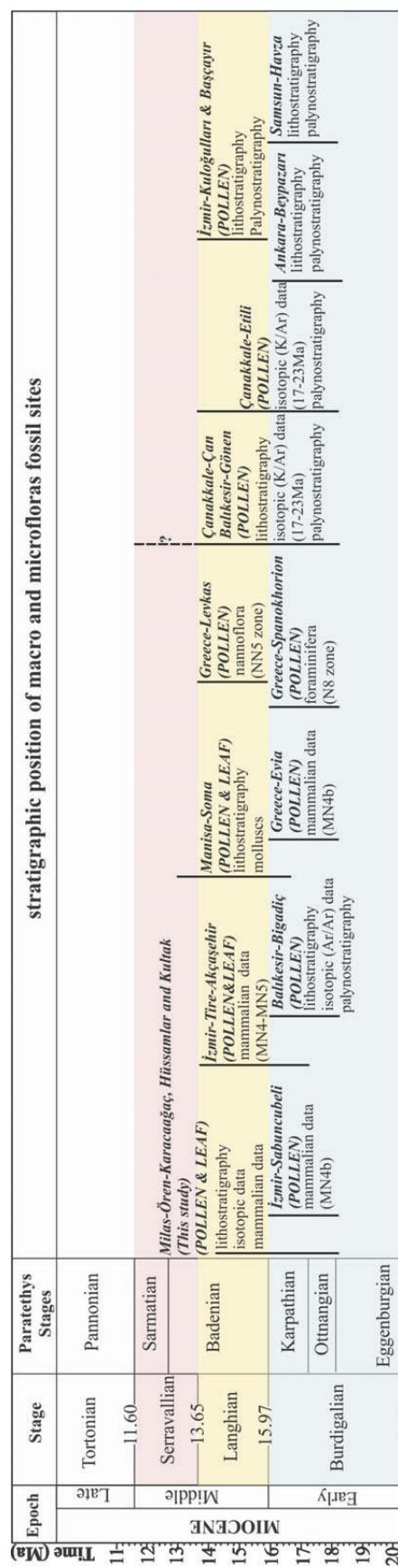


Figure 3. Stratigraphic ranges of previous the Burdigalian and Langhian palynofloras involved in the present study (Mediterranean and Paratethys stages columns after Harzhauser & Piller 2007).

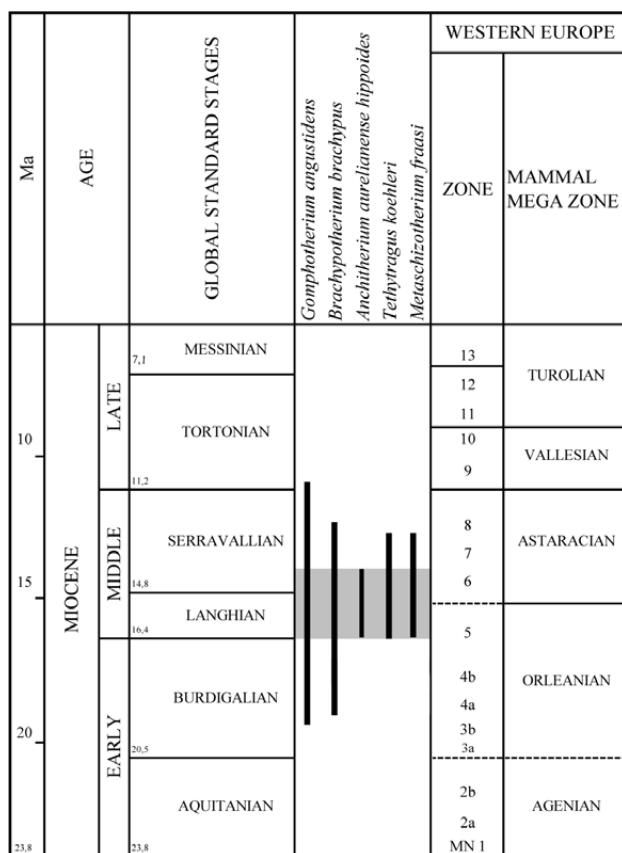


Figure 4. Faunal list and stratigraphic occurrences of the Kultak (light grey) vertebrate assemblage.

numerical palaeoclimatic results in different regions of Turkey and Greece during the late Early and early Middle Miocene periods. In this study, a total of 15 microfloras (Kultak, Karacağaç, Hüssamlar, Havza, Beypazarı (lower and upper coal seams), Çan, Gönen, Başçayır, Kuloğulları, Sabuncubeli in Turkey and Spanokhorion, Evia and Kolivata in Greece) are analyzed to calculate seven climate variables (Fig. 3). These are mean annual temperature (MAT), mean temperature of the coldest month (CMT), mean temperature of the warmest month (WMT), mean annual precipitation (MAP), mean annual range of temperature (MART = WMT-CMT) and precipitation in the warmest month (MAP_{WARM}), precipitation of the driest month (MAP_{DRY}) and precipitation of the wettest month (MAP_{WET}).

The Burdigalian and Langhian palaeobiogeography in Turkey based on the vertebrates

Although the Middle Miocene fossil localities known from Turkey are limited unlike the numerous Late Miocene localities, most of them were studied thoroughly thanks to well-organized studies dating back to early seventies

(Sickenberg *et al.* 1975, Gaziry 1976, Köhler 1987, Gentry 1990, Geraads *et al.* 1995, Kaya *et al.* 2001, Geraads 2003, Sarac, unpublished report, Mayda *et al.* 2006). The rich collections from Bursa-Paşalar, Ankara-Çandır and Ankara-İnönü localities as well as the remarkable İzmir-Mordoğan, Çanakkale-Nebisuyu and Milas-Kultak collections were subjected of detailed systematic studies on many paleontological papers. The Kultak faunal assemblage, previously described by Kaya *et al.* (2001) includes *Anchitherium aurelianense hippoides* (Lartet), *Ancylotherium* (*Metaschizotherium*) *fraasi* (Koenigswald), *Tethytragus koehlerae* (Azanza & Morales) and *Gomphotherium* sp. Recent field work in the Kultak locality has led to the discovery of additional fossils, which are under study.

The proboscidean remains, collected from the former studies were previously allocated to *Gomphotherium* sp. (Kaya *et al.* 2001). The rich proboscidean remains recovered during the latest excavations are now identified as *Gomphotherium angustidens* (Cuvier). *G. angustidens* (Cuvier) has been found in various Early and Middle Miocene localities of Eurasia, mainly from: Spain "Bunol" and "Corcoles" (MN4); Portugal "Quinta Grande" (MN4b); France "Sansan" (MN6) and Germany "Steinheim" (MN7–8) and Saudi Arabia "Al Jadidah (MN6) (Göhlich 1999). This species is also found in Anatolia, mainly from the Middle Miocene localities of Bursa-Paşalar, Muğla-Milas-Sarıçay and Çatakbağyaka, and also from the Early Miocene locality of Ankara-Kalecik-Hancılı (Gaziry 1976, Mayda *et al.* 2006, Sarac, unpublished report, Sickenberg *et al.* 1975). Well-preserved rhinocerotid remains that have been unearthed from the Kultak area were identified as *Brachypotherium brachypus* (Lartet). *B. brachypus* is a common element of Middle Miocene localities of Europe, such as Simorre (MN7), Sansan (MN6) and La Grive (MN7) in France, Thannhausen (MN6) and Massenhausen (MN8) in Germany (Heissig 1999). This species was found in the Middle Miocene localities of Turkey: Ankara-Çandır, İnönü-I, Tüney, Muğla-Yenieskihisar, Çatakbağyaka, Kütahya-Sofça, Edirne-Pişmanköy, Bursa-Paşalar and Orhaneli (Sarac, unpublished report; Fig. 4). *B. brachypus* is a short-legged rhino of hippo-like proportions, adapted to subtropical forested habitats and nearby lakes and rivers (Fortelius 1990). It has brachydont cheek teeth indicating a soft diet. However, the wear patterns of teeth indicate intermediate diet between browser and graser (Fortelius 1990). Comparing with the other Turkish and European samples, *Brachypotherium* materials from Kultak appear to be slightly larger. This feature shows that our sample is more advanced in terms of evolution than the classical forms of this species. *G. angustidens* remains from Kultak are morphologically identical with the Turkish and European Middle Miocene samples and but distinguished from the Early Miocene forms by its relatively simple molar pattern and larger size. *Tethytragus*

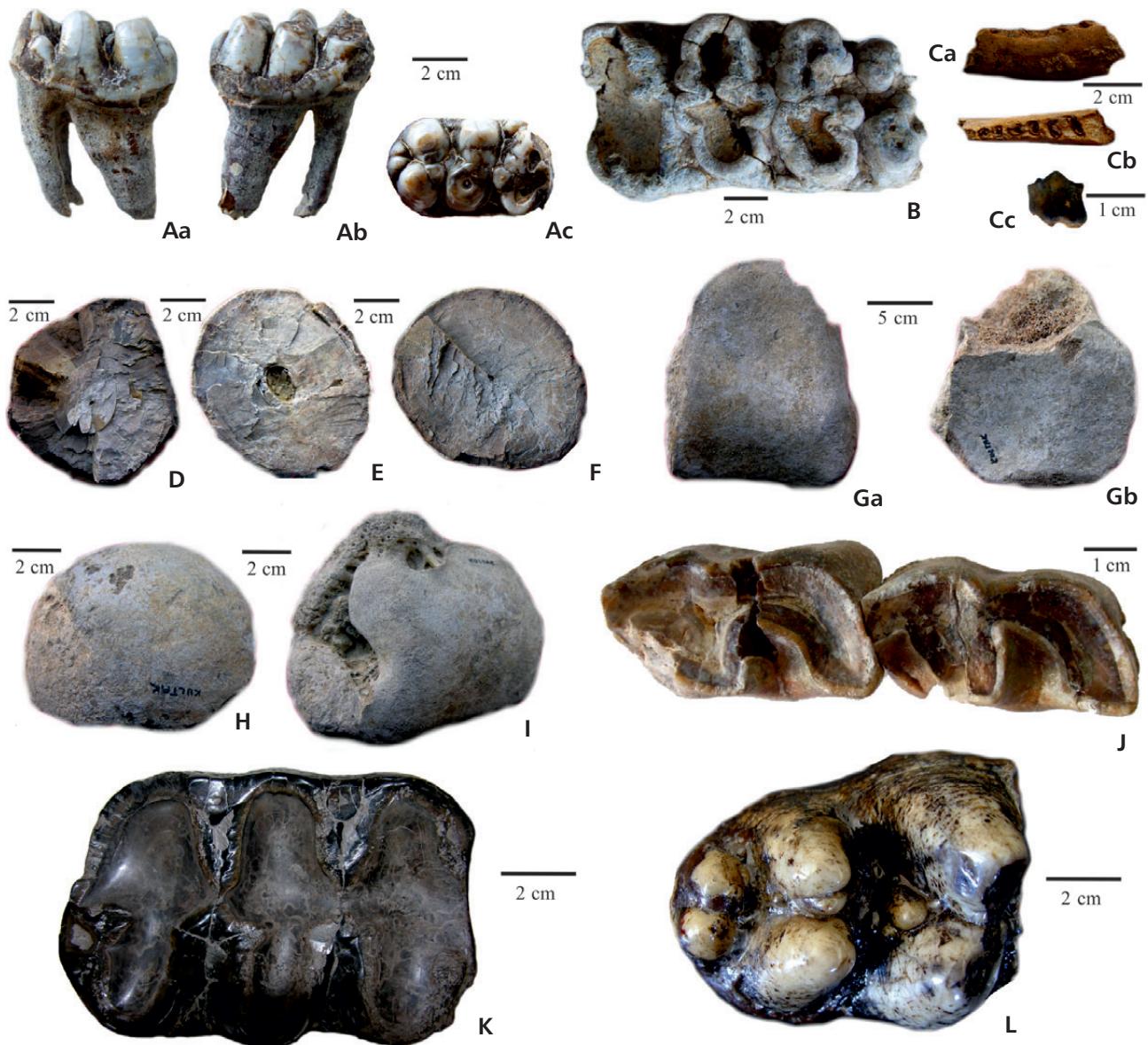


Figure 5. Mammalian fossils collected from the Hüssamlar (K, L) and Kultak (A–J) localities. • A, B, D–F – *Gomphotherium angustidens*: lower right m1 (Aa – lingual view, Ab – labial view, Ac – occlusal view); lower left m3 (B – occlusal view); upper tusk fragments in cross-section (D, E – proximal view, F – distal view). • C – *Tethytragus koehlerae*; left hemimandible with p4 (Ca – lingual view, Cb, Cc – labial view). • G–I – *Gomphotherium angustidens*; right cuneiform (Ga – proximal view, Gb – distal view), H – caput femoris, I – right astragalus (occlusal view). • J – *Brachytherium brachypus*: lower right m1–2 (occlusal view). • K, L – *Gomphotherium angustidens*: K – upper right M2, occlusal view; L – lower right m3, occlusal view.

koehlerae from the Kultak fauna (Kaya *et al.* 2001) is a species typical for the Middle Miocene and it has previously been known from Bursa-Paşalar, Muğla-Sarıçay, and Ankara-Çandır and İnönü localities (Köhler 1987, Gentry 1990, Geraads *et al.* 1995, Geraads 2003; Figs 4, 5).

Besides the systematic and taxonomic part, we have focused on the faunal similarity of Middle Miocene localities from Turkey and Europe, at genus level only, using the UPGMA (unweighted pair group method with arithmetic mean) cluster algorithm method on similarity indices based on the presence/absence data (Fig. 6A, B). Over 50 taxa

from the following mammalian faunas are analyzed by the Jaccard Index (Jaccard 1908) as a distance measure to examine palaeocommunity integrity, taking into consideration only the sites with at least ten species (except Çanakkale-Nebisuyu locality) that we also retained for this analysis. The sites from Turkey are Bursa-Paşalar (MN6, NW Anatolia), Ankara-Çandır (MN6, Central Anatolia), İzmir-Mordoğan (MN6, Western Anatolia); Ankara-İnönü (MN6, Central Anatolia), Muğla-Kultak (MN6; SW Anatolia), Nebisuyu (MN6–7/8, NW Anatolia), Muğla-Çatakbağyaka (MN6–7/8, SW Anatolia) and from

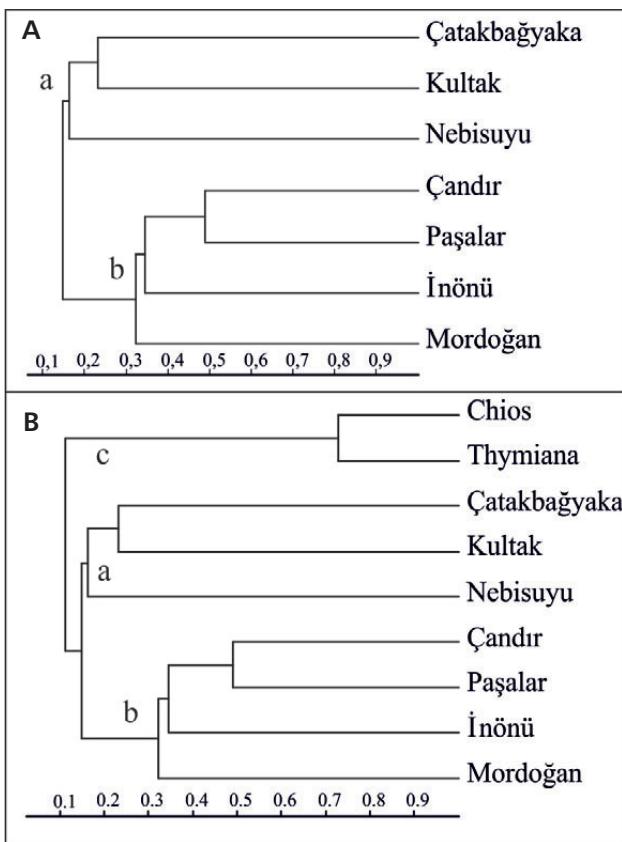


Figure 6. Cluster Analysis on presence/absence data at the genus level, using Jaccard's similarity index on Middle Miocene sites. A – Turkish, B – Greek and Turkish.

Greece Chios (MN5) and Thymiana (MN5) (Casanovas-Vilar *et al.* 2011). The Fig. 6 summarizes the result of the analysis carried out on the Middle Miocene taxa (Fig. 6A, B). Considering the Fig. 6A, the dendrogram based on the Jaccard index has grouped two major clusters: (1) the Central and NW Anatolian localities (Bursa-Paşalar, Ankara-Çandır, İnönü; cluster A) and (2) SW Anatolian localities (the others; cluster B). The first group is clearly separated from the second group except for the İzmir-Mordoğan site, which seems to close to Ankara-Inönü and Çandır respectively. Moreover, there is a clear separation between the Anatolian faunas correlated to MN6, MN6–7/8 and Greek faunas (Fig. 6B). Bursa-Paşalar and Ankara-Çandır localities match together as a result of high faunal similarity and Ankara-Inönü and İzmir-Mordoğan localities follow this conclusion. This arrangement of Kultak, Çatakbağyaka and Nebisuyu localities in the upper cluster (Fig. 6A) also marks a higher bovid diversity than the rest of the other Turkish faunas, which points out that a more open environment was dominant during the Middle Miocene in Central Anatolia.

Andrews & Kelley (2007) suggest a subtropical woodland or forest environment incorporating open areas with

abundant ground vegetation for the Middle Miocene at Bursa-Paşalar. Geraads *et al.* (2003) proposed a relatively dry, seasonal subtropical woodland habitat for Ankara-Çandır and Bursa-Paşalar and emphasized that Ankara-Çandır had a dominant open country biotope and Ankara-İnönü had an even more open environment compared to the former sites. This type of environment, which is lately documented at İzmir-Mordoğan (Geraads *et al.* 2002), is composed of a mixture of woodland and grassland habitats, which were widespread in the western part of Anatolia. Çanakkale-Nebisuyu differs significantly from the former localities by the absence of open environment elements, such as bovids. *Chalicotherium* and *Anchitherium* are regarded as being moist forest inhabitants. This is also consistent with the existence of more or less the same taxa at Kultak and Çatakbağyaka. Besides, the new Kultak rhino record, *Brachypotherium brachypus*, which is a short-legged brachydont rhino of hippo-like proportions, usually assumed to inhabit subtropical forested habitats and nearby lakes and rivers (Fortelius 1990). In summary, the mammalian data argue for the existence of a humid palaeoclimate in SW and NW Anatolia. On the contrary, Central Anatolia was under the influence of a dry phase throughout the Langhian.

The field work around the Hüssamlar lignite deposits in the last couple of years provided limited assemblage of a mammalian fauna in which two species can be determined. The first one is the common proboscidean, *Gomphotherium angustidens*, which is already recorded in Kultak. However, the Hüssamlar material differs from the Kultak one in its slightly smaller size and archaic occlusal pattern of teeth. The other record is a small European brachypothere *Prosantorhinus* sp., which also makes its first appearance in Turkey. According to Cerdeno (1996) this genus has a quite widespread distribution with two species, *Prosantorhinus germanicus* and *Prosantorhinus douvelli* in Western and Central Europe during the late Early (MN3) to latest Middle Miocene (MN7/8). We may well add the recently described *Prosantorhinus laubei* from the well-known locality Tuchořice (MN3) in Czech Republic to be the third species intermediate between the first two (Heissig & Fejfar 2007). The preliminary study of Turkish material reveals morphological and metrical similarities with the largest form, *Prosantorhinus douvelli* from Beaugency (MN5), which hosted the last appearance of this species. These taxa indicate a humid continental environment.

Considering the preliminarily studied new material mentioned above, we may suggest an age of "MN4b–5" for Hüssamlar, which refers to a slightly older age comparing to Kultak. According to whole data gathered from the preliminary faunal studies, the same type of ecological conditions might have occurred during the Middle Miocene in the Kultak and Hüssamlar areas, although shorter premolar

rows and more slender metapodials of *Prosantorhinus douvelli* compared to *Brachypotherium brachypus* may reflect drier local conditions in Hüssamlar than in Kultak.

Palynoflora of Milas-Ören Region

In this study, three palynofloras from the Kultak, Hüssamlar and Karacaağac localities are described. The diversity and percentages of spores are low, but the abundance of pollen is remarkable. While most the taxa are recorded in low frequencies, a few are abundant.

The Kultak microflora is characterized by the highest frequency of *Laevigatisporites haardti* (Polypodiaceae), *Laevigatosporites gracilis* (Polypodiaceae), *Pityosporites microalatus* (Pinaceae-Pinus haploxyton type), *Momipites punctatus* (Engelhardia), *Momipites quietus* (Engelhardia), *Polyporopollenites undulosus* (Ulmus), *Caryapollenites simplex* (Carya), *Subtriporopollenites anulatus nanus* (Juglandaceae), *Tricolpopollenites densus* (*Quercus* sp.), *Tricolpopollenites microhenrici* (*Quercus*), *Tricolporopollenites cingulum* (Castaneae), *Tricolporopollenites megaexactus* (Cyrillaceae), represented by the values from 5 to 20%. *Pinus haploxyton* type and indeterminate Pinaceae are characterized with higher values of 5 to 10%. *Cupressacites cuspidateformis* (Cupressaceae) appears regularly with values of 4 to 9%. Spores are represented by scarce grains of *Baculatisporites primarius* (Osmundaceae), *Verrucatosporites favus* (Davalliacae), *Leiotriletes maxoides minoris* (Schizaceae), *Leiotriletes maxoides maxoides* (Schizaceae) and *Leiotriletes tranquillus* (Schizaceae) (Fig. 7). Open vegetation elements, *Graminidites gramineoides* (Poaceae) and *Umbelliferaepollenites* sp. (Apiaceae), are found in minor quantities. *Inaperturopollenites dubius* (Cupressaceae-Taxodoioidea), *Polyporopollenites stellatus* (Pterocarya), *Triatriopollenites rurensis* (Myricaceae-Myrica), *Tricolpopollenites retiformis* (Platanus/Salix), *Tricolporopollenites pacatus* (Simaroubaeae), *Oleoidearumpollenites microreticulatus* (Oleaceae) scarcely and *Dicolpopollenites kockelii* (Calamus), *Zonolapollenites verrucatus* (Tsuga), *Inaperturopollenites polyformosus* (Sequoia), *Plicapollis plicatus* (Juglandaceae), *Quercopollenites robur* (*Quercus* deciduous type), *Tricolpopollenites librarensis librarensis* (Fagaceae), *Tricolpopollenites librarensis fallax* (Fagaceae), *Polyporopollenites undulosus* (Ulmaceae-Ulmus/Zelkova), *Tetralcoporopollenites* spp., Cyperaceae sp., and *Avicennia* rarely or sporadically recorded in this microflora (Fig. 7, Table 1).

The diversity and percentages of spores (*Baculatisporites primarius* (Osmundaceae) and *Leiotriletes* sp. (Schizaceae)) in the Karacaağac palynoflora are low, except for *Laevigatisporites haardti* (Polypodiaceae), which is recorded abundantly in all samples (20–40%). Indeterminate Pinaceae and *Pinus haploxyton* type species are

more abundant (10–25%). The pollen of *Inaperturopollenites dubius* (Taxodoioidea), *Tricolpopollenites microhenrici* (*Quercus*) and *Polyvestibulopollenites verus* (*Alnus*) appear in high amounts (5–15%). Gymnosperm pollen of *Pityosporites labdacus* (*Pinus silvestris* type), *Pityosporites libellus* (*Podocarpus*), *Pityosporites macroinsignis* (*Pinus haploxyton* type), *Cedripites miocenicus* (*Cedrus*), *Cathaya* sp., *Cupressacites cuspidateformis* (Cupressaceae) are also less abundantly recorded (2–5%). Herbs such as *Graminidites gramineoides* (Poaceae), *Ephedripites* spp. (Ephdraceae), *Periporopollenites multiporatus* (Amaranthaceae-Chenopodiaceae), *Cichoreacidites* sp. (Asteraceae-Cichorioideae-Liguliflorae type) and *Tricoporopollenites* sp. (Asteraceae-Asteroideae-Tubulifloreae type) are scarcely observed (1–4%). *Betulopollenites betulooides* (Betulaceae), *Quercopollenites robur* (*Quercus* deciduous type), *Tricolpopollenites densus* (*Quercus*), *Arecipites* sp. (Arecaceae), *Polyporopollenites undulosus* (Ulmaceae-Ulmus), *Triatriopollenites rurensis* (Myricaceae-Myrica), *Triatriopollenites coryphaeus* (Engelhardia), *Momipites punctatus* (Engelhardia), *Momipites quietus* (Engelhardia), *Lonicerapollis* sp. (*Lonicera*), *Tricolporopollenites megaexactus exactus* and *brühlensis* (Cyrillaceae), *Polycolporopollenites* sp., *Inaperturopollenites laevigatus* (Cupressaceae-Taxodoioidea), *Sparganiapollenites neogenicus* (Sparganiaceae), *Liriodendriopollis semiverrucatus* (Magnoliaceae-Liriodendron), *Polygalacidites* sp. (Polygalaceae) and *Magnolipollis* sp. (Magnoliaceae-Magnolia) is scarcely or rarely present in the Karacaağac palynoflora (Fig. 8, Table 1).

The high percentages of ferns in the Hüssamlar palynospectra [*Laevigatisporites haardti* (Polypodiaceae), *Sparganiapollenites neogenicus* (Sparganiaceae), and *Baculatisporites primarius* (Osmundaceae), 5–30%] recall that of the Karacaağac palynoflora. Gymnosperm pollen – *Pityosporites microalatus* (*Pinus haploxyton* type), *Cathaya* and indeterminate Pinaceae – achieve their highest percentages of 10–43%. The highest abundance of the *Tricolpopollenites microhenrici* (*Quercus*) and *Inaperturopollenites hiatus* (Taxodoioidea) is observed in this palynoflora (10–33%). The pollen of *Inaperturopollenites dubius* (Taxodoioidea), *Polyvestibulopollenites verus* (*Alnus*), *Tricolporopollenites cingulum oviformis* (Castanea), *Ineperturopollenites laevigatus* (Taxodoioidea) are observed in reliable percent (2–15%). Grassland species (*Graminidites gramineoides* (Poaceae) and *Periporopollenites multiporatus* (Amaranthaceae-Chenopodiaceae)) are not various in this palynoflora but these are regularly present (1–5%). *Quercopollenites robur* (*Quercus* deciduous type), *Tricolpopollenites densus* (*Quercus*), *Cupressacites cuspidateformis* (Cupressaceae), *Momipites punctatus* (Engelhardia), *Tricolporopollenites megaexactus exactus* and *brühlensis* (Cyrillaceae), *Tricolporopollenites microreticulatus* (Oleaceae) barely (3–5%) and

Table 1. Ecological requirement and climatic character of extant taxa represented by sporomorphs of the Kultak, Karacaağac and Hüssamlar regions (i.e. Kovar-Eder 1987; Planderová 1991; Nagy 1990, 1999, 1992; Akgün & Akyol 1999).

Taxa		Preferable habitat	Climatic distribution	Deciduous-evergreen/sclerophyllous trees
Spores				
Schizaeaceae- <i>Lygodium</i>	<i>Leiotriletes</i> sp., <i>L. maxoides minoris</i> , <i>L. microadrienni</i> , <i>L. traquillus</i>	Cosmopolitan	Subtropical to tropical	Fern
Polypodiaceae- <i>Pteridoidreae</i>	<i>Laevigatosporites haardti</i> , <i>L. gracilis</i>	Cosmopolitan	Cosmopolitan	Fern
Davalliaceae	<i>Verrucatosporites favus</i>	Cosmopolitan	Subtropical to tropical	Fern
Osmundaceae- <i>Osmunda</i>	<i>Baculatisporites primarius</i>	Cosmopolitan	Cosmopolitan	Fern
Pollen				
Gymnosperm				
<i>Pinus</i> (haploxyylon type)	<i>Pinuspollenites microalatus</i> , <i>Pinuspollenites macroinsignis</i>	Conifer forest	Warm temperate	Evergreen
<i>Pinus</i> (silvestris type)	<i>Pinuspollenites labdacus</i>	Conifer forest	Temperate	Evergreen
<i>Pinus</i>	<i>Pityosporites</i> spp.	Conifer forest	Temperate	Evergreen
Podocarpaceae- <i>Podocarpus</i>	<i>Podacarpidites libellus</i>	Conifer forest	Subtropical to tropical	Evergreen
<i>Tsuga</i>	<i>Zonolapollenites verrucatus</i>	Conifer forest	Subtropical to tropical	Evergreen
<i>Cedrus</i>	<i>Cedripites miocaenicus</i>	Conifer forest		Evergreen
<i>Cathaya</i>	<i>Cathayapolitis</i> sp.	Conifer forest		Evergreen
Cupressaceae-Taxodoioideae	<i>Cupressacites cuspidataeformis</i> , <i>Inaperturopollenites dubius</i>	Conifer forest	Warm temperate to temperate	Evergreen/deciduous
Taxodoioideae	<i>Inaperturopollenites laevigatus</i> , <i>Inaperturopollenites hiatus</i>	Swamp forest	Warm temperate to temperate	Evergreen/deciduous
Ephedraceae- <i>Ephedra</i>	<i>Ephedripites</i> sp.	Herbs and shrubs	Temperate	Shrub
Angiosperm				
Monocotyledoneae Pollen				
Poaceae (= Gramineae)	<i>Graminidites gramineoides</i> , <i>Graminidites laevigatus</i>	Herbs and shrubs	Cosmopolitan	Shrub
Sparganiaceae	<i>Sparganiapollenites neogenicus</i>	Aquatic vegetation	Temperate	Aquatic plant
Cyperaceae	<i>Cyperaceae</i> sp.	Aquatic vegetation	Cosmopolitan	Aquatic plant
Nymphaeaceae	<i>Nymphaepollenites minor</i> , <i>Monogemmites pseudosetarius</i>	Aquatic vegetation	Cosmopolitan	Aquatic plant
Cycadaceae- <i>Cycas</i>	<i>Cycadopites</i> spp.	Conifer forest	Subtropical to tropical	Evergreen
Palmea	<i>Monocolpopollenites triangulus</i>	Evergreen and deciduous mixed forest	Subtropical to tropical	Evergreen
Arecaeae	<i>Arecipites</i> sp.	Evergreen and deciduous mixed forest	Subtropical to tropical	Evergreen
Magnoliaceae- <i>Magnolia</i>	<i>Magnolipollis</i> sp.	Herbs and shrubs	Subtropical to tropical	?Evergreen
Magnoliaceae- <i>Liriodendron</i>	<i>Liriodendrioipollis semiverrucatus</i>	Evergreen and deciduous mixed forest	Subtropical to tropical	?Evergreen
Dicotyledoneae Pollen				
Myricaceae- <i>Myrica</i>	<i>Triatriopollenites rurensis</i>	Swamp forest	Warm temperate	Evergreen
Juglandaceae- <i>Engelhardtia</i>	<i>Momipites punctatus</i> , <i>Momipites quietus</i> , <i>Triatriopollenites coryphaeus</i> , <i>Plicapollis plicatus</i>	Evergreen and deciduous mixed forest	Subtropical to tropical	Evergreen
Betulaceae	<i>Betulapollenites betuloides</i>	Evergreen and deciduous mixed forest	Temperate	Deciduous
Carya Juglandaceae	<i>Subtriporopollenite simplex</i> , <i>Subtriporopollenites anulatus nanus</i>	Riparian forest	Temperate	Deciduous
Myrtaceae	<i>Myrtaceoidites mesonensis</i>	Evergreen and deciduous mixed forest	Subtropical to tropical	?Evergreen

Table 1. continued

Taxa		Preferable habitat	Climatic distribution	Deciduous-evergreen/sclerophyllous trees
<i>Calamus</i>	<i>Dicolpopollis kockelii</i>	Swamp vegetation	Subtropical to tropical	?Evergreen
Betulaceae- <i>Alnus</i>	<i>Polyvestibulopollenites verus</i>	Riparian forest	Temperate	Deciduous
Ulmaceae- <i>Ulmus</i>	<i>Polyporopollenites undulosus</i>	Riparian forest	Temperate	Deciduous
<i>Pterocarya</i>	<i>Polyporopollenites stellatus</i>	Evergreen and deciduous mixed forest	Warm temperate	
Fagaceae- <i>Quercus</i>	<i>Tricolporopollenites microhenrici</i> , <i>Quercus robur</i> (deciduous type), <i>Tricolporopollenites densus</i> , <i>Quercus</i> sp. (evergreen type), <i>Tricolporopollenites liblarensis</i>	Evergreen and deciduous mixed forest	Warm temperate to temperate	Deciduous/evergreen
Aceraceae	<i>Aceripollenites striatus</i>	Evergreen and deciduous mixed forest	Warm temperate to temperate	Deciduous
<i>Platanus</i>	<i>Tricolporopollenites retiformis</i>	Riparian forest	Temperate	Deciduous
<i>Salix</i>	<i>Tricolporopollenites retiformis</i>	Riparian forest	Temperate	Deciduous
<i>Castanea</i>	<i>Tricolporopollenites cingulum</i> <i>oviformis</i>	Evergreen and deciduous mixed forest	Warm temperate	Deciduous
Simaroubaceae	<i>Tricolporopollenites pacatus</i>	Evergreen and deciduous mixed forest	Subtropical to tropical	Evergreen
Cyrillaceae	<i>Tricolporopollenites megaexactus</i> <i>exactus</i> , <i>T. megaexactus brühlensis</i>	Evergreen and deciduous mixed forest	Subtropical to tropical	Evergreen
Nyssaceae- <i>Nyssa</i>	<i>Tricolporopollenites kruschi</i>	Swamp forest	Subtropical to tropical	Cosmopolitan tree
Oleaceae- <i>Olea</i> sp.	<i>Tricolporopollenites</i> <i>microreticulatus</i> , <i>Oleoidearumpollenites</i> <i>microreticulatus</i>	Evergreen and deciduous mixed forest	Subtropical to tropical	Evergreen
Sapotaceae	<i>Tetracolporopollenites biconus</i>	Evergreen and deciduous mixed forest	Subtropical to tropical	Evergreen
<i>Avicennia</i>	<i>Avicennia</i>	Back mangrove	Subtropical to tropical	Evergreen
<i>Lonicera</i>	<i>Lonicerapollenites</i> sp.	Herbs and shrubs	Temperate to tropical	Sclerophyllous
Asteraceae, Asteroideae-Tubulifloreae type Asteraceae, Cichorioideae-Liguliflorae type	<i>Tricolporopollenites</i> spp. <i>tubuliflora/liguliflora</i> types	Herbs and shrubs	Cosmopolitan	Shrub
Polygonaceae	<i>Polygonacoidites</i> sp.	Herbs and shrubs	Cosmopolitan	Cosmopolitan tree/shrub/herb
Umbelliferae (= Apiaceae)	<i>Umbelliferaepollenites</i> sp.	Herbs and shrubs	Cosmopolitan	Cosmopolitan tree/shrub/herb
Amaranthaceae-Chenopodioideae	<i>Periporopollenites multiporatus</i>	Herbs and shrubs	Cosmopolitan	Cosmopolitan shrub/herb

Triatriopollenites rurensis (*Myrica*), *Subtriporopollenites simplex* (*Carya*), *Subtriporopollenites anulatus nanus* (Juglandaceae), *Momipites quietus* (*Engelhardia*), *Polyporopollenites undulosus* (*Ulmus*), *Tricolporopollenites retiformis* (*Platanus/Salix*) rarely (1–3%) recorded in the Hüssamlar palynospectra (Fig. 9, Table 1).

Palaeovegetation

In the hinterland of the Kultak locality, a broad-leaved evergreen forest, represented by *Myrica*, Cyrillaceae, Sapotaceae, *Castanea*, *Engelhardia* and Gleicheniaceae was

widespread in the lowland area. In this vegetation belt, swamp forests were also well developed during the late Burdigalian–Langhian period. Its components (*Sequoia*, Cupressaceae–Taxodoidea, Polypodiaceae, Davalliaceae, Gleicheniaceae, Osmundaceae, Schizaeaceae and *Myrica*) indicate relatively high percentages in the palynospectra. The presence of swamp vegetation, which is supported by the lowland topography and humid conditions, was confirmed by mammalian fossils. The swamp and broad-leaved evergreen forests were accompanied by the riparian forest elements such as *Platanus*, *Salix*, *Ulmus* and *Zelkova*, *Carya* and *Pterocarya*. The occurrence of Fagaceae like *Castanea* and *Quercus* (deciduous and evergreen types),

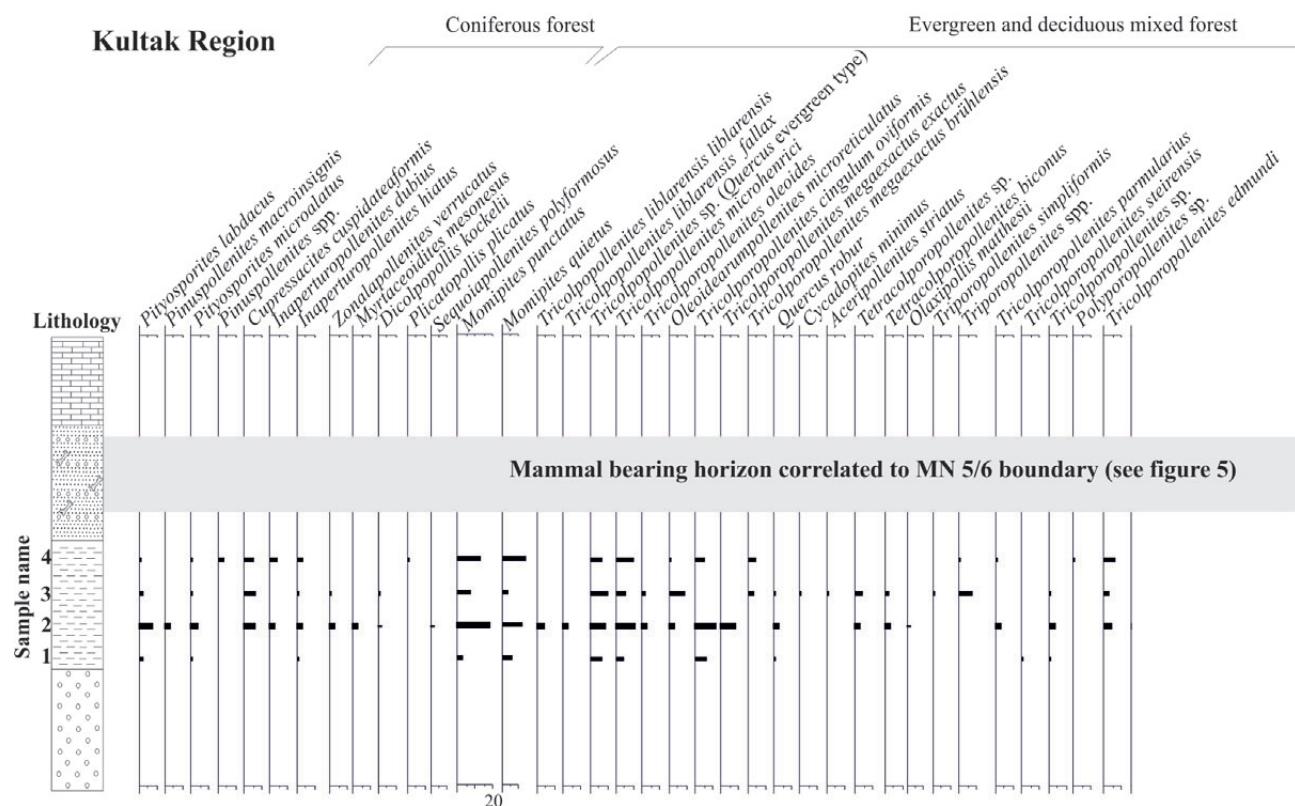


Figure 7. Detailed microfloras diagram of the studied part of the Kultak stratigraphic section. Black dots indicate percentage lower than 1%.

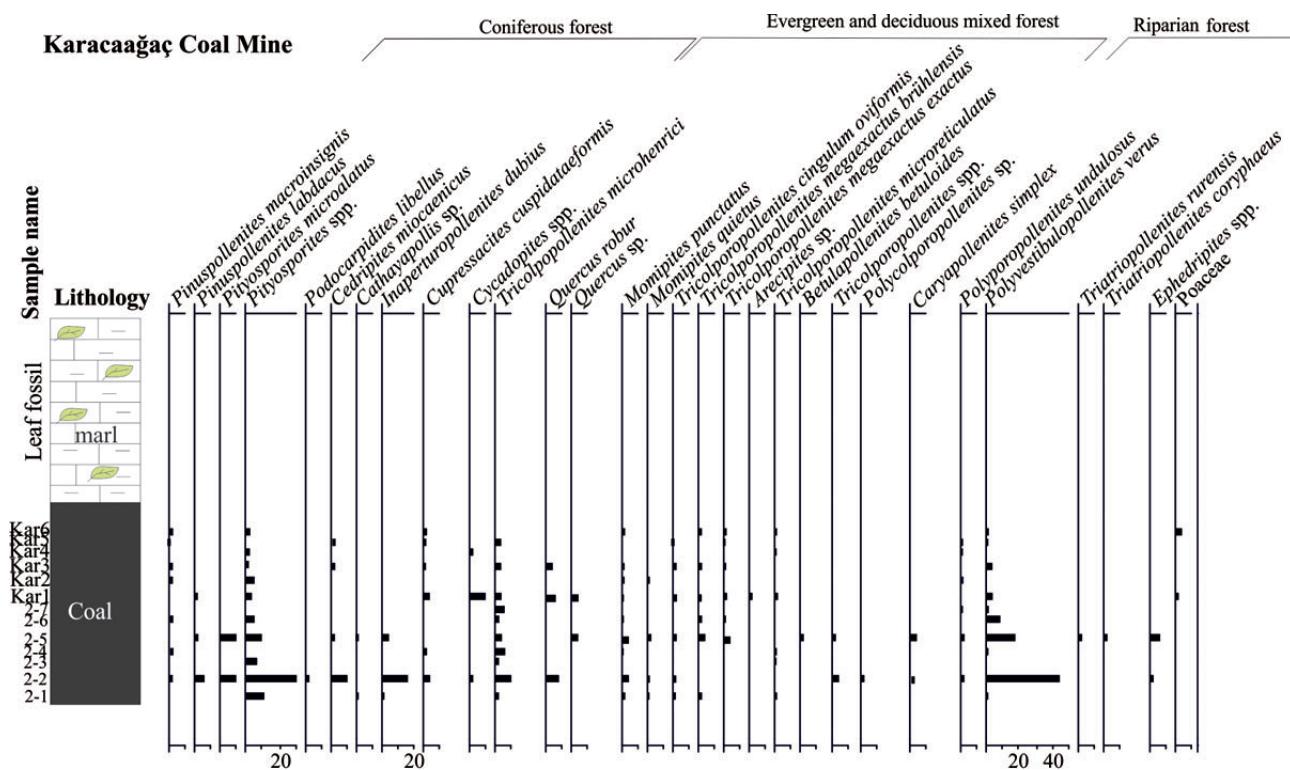


Figure 8. Detailed microfloras diagram of the studied part of the Karacaagaç stratigraphic section. Black dots indicate percentage lower than 1%.

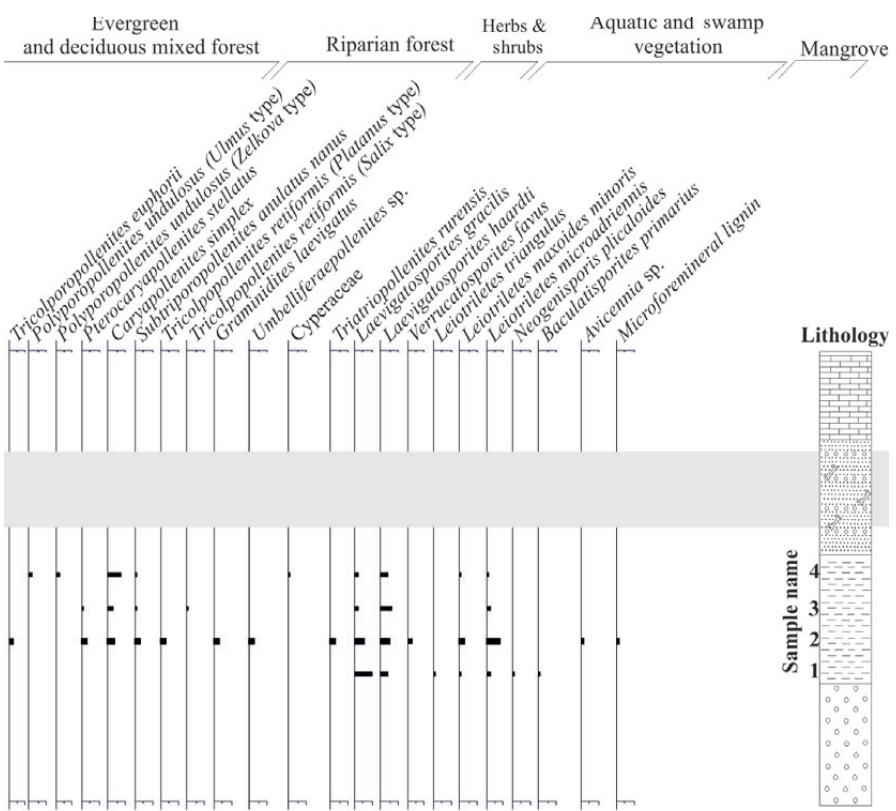


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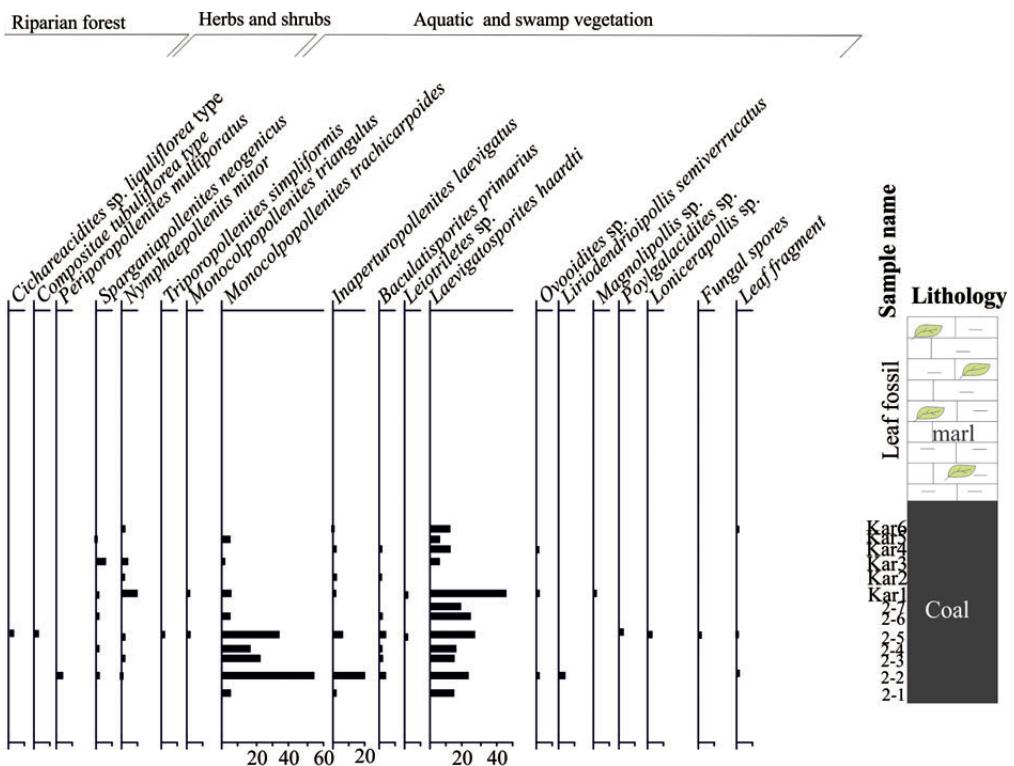


Figure 8. continued

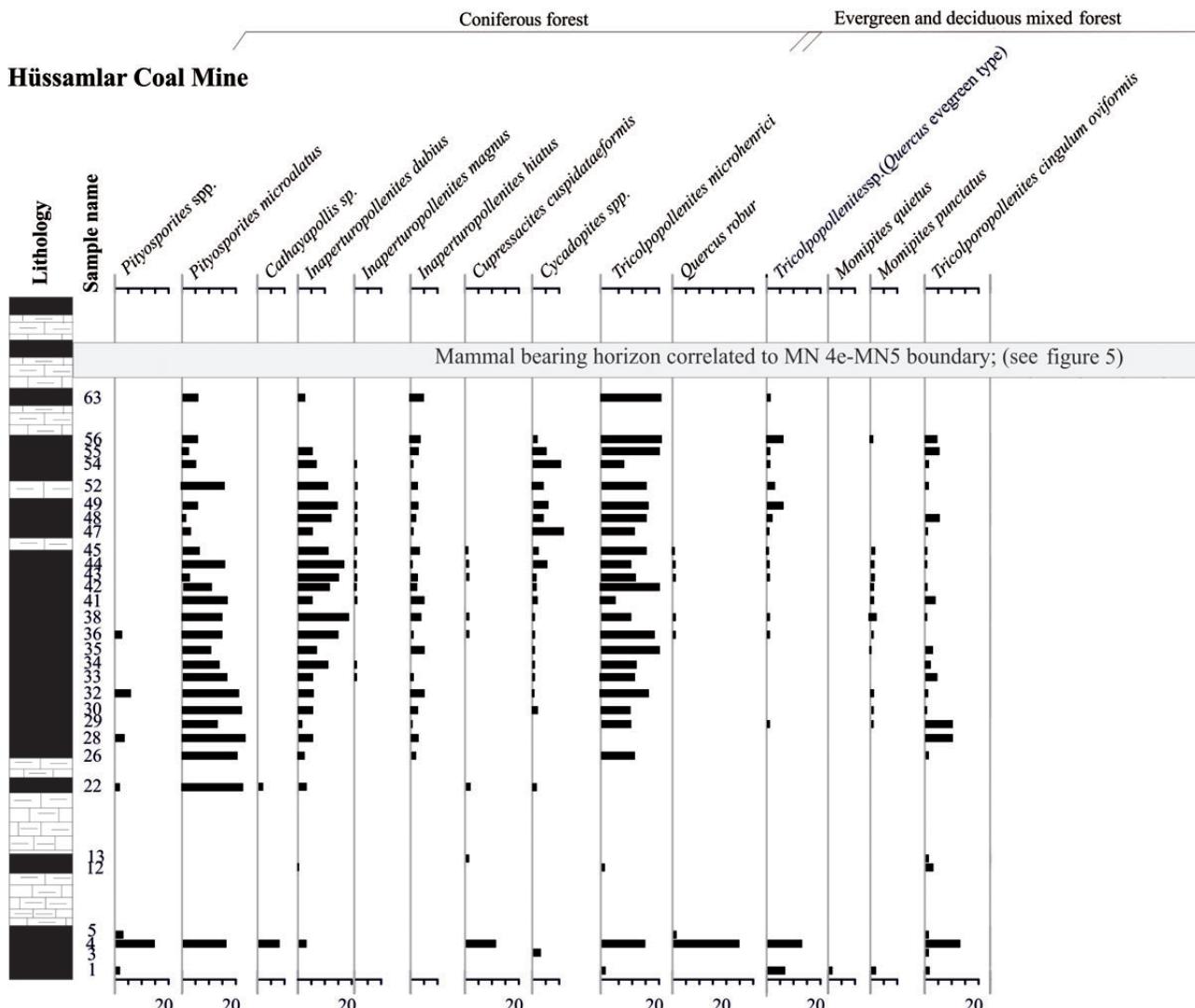


Figure 9. Detailed microfloras diagram of the studied part of the Hüssamlar stratigraphic section. Black dots indicate percentage lower than 1% and mammalian data level in the Hüssamlar section.

Juglandaceae likes *Pterocarya* and *Engelhardia*, Betulaceae, *Acer*, Cyrillaceae, Oleaceae and Sapotaceae indicates evergreen and deciduous mixed forests. Gymnosperm pollen mainly that of *Pinus haploxyylon* type and other indeterminate Pinaceae are found less abundantly, presumably because of the capacity of saccate pollen for long-distance transport, and also because of differentiation of palaeotopography and/or taphonomy (Heusser 1988, Suc & Drivaliari 1991, Cambon *et al.* 1997, Beaudouin 2003). Additionally, mid and high altitude elements are characterized by *Pinus* pollen of the *diploxyylon* and *haploxyylon* types and *Tsuga* in the Kultak locality (Fig. 7; Ivanov *et al.* 2012). Microforaminiferal lignin and *Avicennia* pollen are also recorded in the Kultak palynospectra and these palynomorphs indicate marine effect in the region during the late

Burdigalian–Langhian time interval (MN4–5 boundary). Besides, the finding of corals, bivalves, and foraminifer fossils in Kultak (Kayseri 2010, Kayseri & Akgün 2010) strengthens the presence of marine effect.

The aquatic and swamp palaeovegetation was represented by Sparganiaceae, Nymphaeaceae, Osmundaceae, Poypodiaceae, Taxodioidea, *Myrica*. The abundance of these taxa indicates the presence of shallow lake environments in the Karacağaç and Hüssamlar localities during the Burdigalian–Langhian time interval. The plants of the riparian forest elements (*Alnus*, *Ulmus* and *Carya*) are also abundantly recorded in both palynospectras. Coniferous forest elements are recorded more abundantly in Karacağaç and Hüssamlar microfloras, accompanied by evergreen-deciduous mixed mesophytic forest elements. This

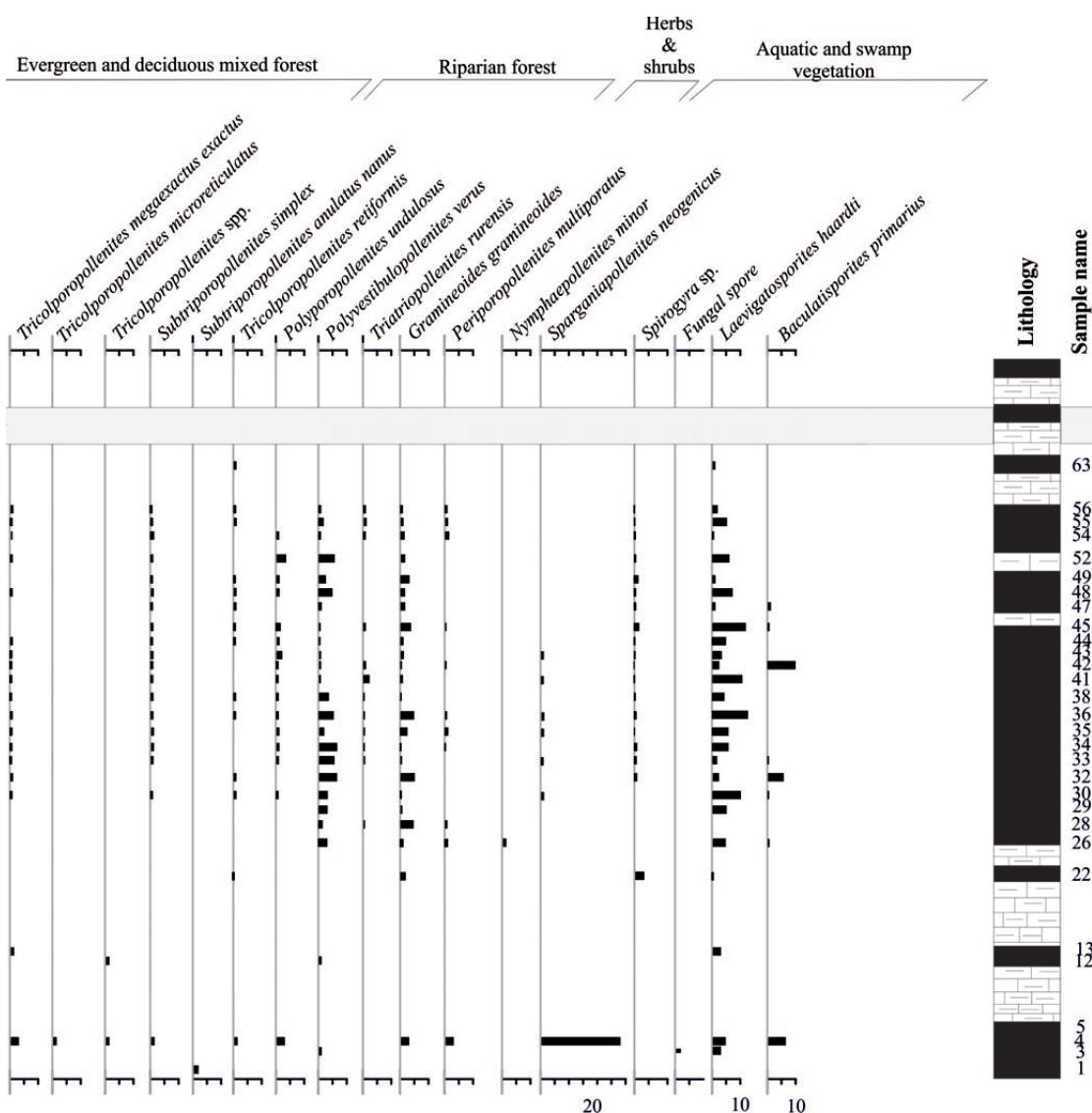


Figure 9. continued

abundance could be interpreted as the presence of high topographic areas around the lacustrine depositional area during the middle Burdigalian–Langhian period (MN4–5 boundary). Although the percentage of herb and shrubs species (*i.e.* Ephedraceae, Poaceae, Chenopodiaceae, Asteraceae-Asteroideae-Tubulifloreae type and Cichorioideae-Liguliflorae type) in the Hüssamlar and Karacaağac palynospectras is low, their percents varied in all samples (Figs 8, 9). This result suggests the presence of the narrow open vegetational areas at Karacaağac and Hüssamlar throughout the middle Burdigalian–Langhian time interval. These grassland areas are also supported by the mammalian fossil records of the Hüssamlar locality.

The significant difference between the Kultak, Hüssamlar and Karacaağac palynofloras is mainly environmental: while clastic sediments in the Kultak locality

indicate deltaic conditions, the coal bearing sediments in the Hüssamlar and Karacaağac localities were deposited in a lacustrine environment. In the Hüssamlar and Karacaağac localities freshwater swamp was existed during the middle Burdigalian–Langhian period together with a high topographic condition surrounding of the swampy area as shown by the abundance of gymnosperm pollen. The Kultak locality is located southern to Hüssamlar and Karacaağac, and it is characterized by the effect of brackish marine conditions. This marine condition is supported by the foraminifers, corals, bivalves, and also back mangrove plants (Fig. 10). This marine palaeoenvironmental evidence based on faunal and floral data could indicate that the land-sea line in the middle Burdigalian–Langhian time could be near the Kultak locality.

In Turkey, the palynoflora of the Burdigalian-

Table 2. CA_{palynoflora} results (MAT, CMT, WMT and MAP) of the Burdigalian–Langhian time interval in Turkey.

Location	Climate	References	MAT (°C)	CMT (°C)	WMT (°C)	MAP (mm)	MART(°C)
This study Ören-Karacaağç Ören-Hüssamlar Ören-Kultak	Warm subtropical	This study	17.0–18.4	6.2–12.5	26.5–28.1	1146–1322	17.95
			17.0–21.3	6.2–13.3	27.3–28.1	1146–1322	17.95
			15.7–18.8	9.6–13.1	24.7–27.7	1122–1520	13.5
Ankara-Çayırhan (upper coal seam)	Warm subtropical	Güngör (1991), Whateley & Tuncalı (1995)	16.5–20.8	4.8–13.3 or 0.9–1.1	26.0–27.9	735–1520	17.9 or 25.95
Ankara-Çayırhan (lower coal seam)			17.0–21.3	7.7–13.3	27.3–28.1	1146–1322	17.2
Samsun-Havza	Warm subtropical	Kayseri (2002), Kayseri & Akgün (2008)	17.2–20.8	6.2–13.3	27.3–27.9	1217–1322	17.45
Çanakkale-Çan	More temperate to subtropical	Ediger (1990)	15.7–21.3	9.6–13.3	22.8–28.1	735–1520	14
Çanakkale-Etili	Warm subtropical	Akgün <i>et al.</i> (2008)	17.2–18.4	6.2–7.4	27.3–27.9	1146–1151	20.8
Balıkesir-Gönen	More temperate to subtropical	Ediger (1990)	15.7–21.3	9.6–13.3	22.8–28.1	437–1520	14
Balıkesir-Bigadiç	Warm subtropical	Akyol & Akgün (1990), Akgün <i>et al.</i> (2007)	17.2–21.3	6.2–13.3	26.5–27.9	1217–1322	17.45
Manisa-Soma	Warm subtropical	Akgün <i>et al.</i> (2007)	16.5–21.3	4.8–13.3	26–27.9	629–1520	17.9
İzmir-Sabuncubeli	Warm subtropical	Kayseri <i>et al.</i> (2007)	17.0–18.8	6.2–13.1	27.3–27.7	1146–1322	17.85
Aydın-Kuloğulları	Warm subtropical	Akgün <i>et al.</i> (2007)	13.5–21.3	1.8–13.3	25.4–28.1	1183–1520	19.2
Aydın-Başçayır	Warm subtropical	Akgün <i>et al.</i> (2007)	12.9–21.7	0.9–15.6	23.6–28.1	735–1574	17.6

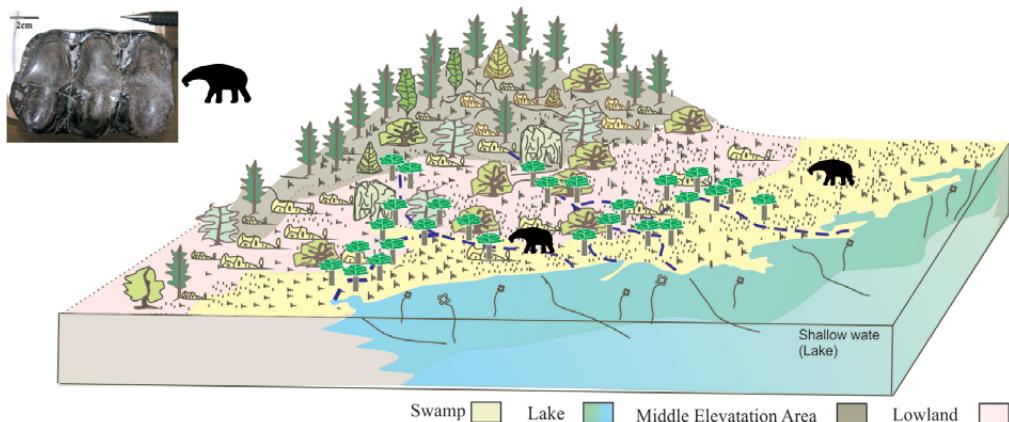
Langhian transition is well-documented from Bey-pazarı-Çayırhan, Havza, Çan, Etili, Gönen, Bigadiç, Emet, Kırka and Kestelek, Sabuncubeli, Soma, Tire, Kuloğulları, Başçayır, Kultak, Hüssamlar and Karacaağç localities. It includes thermophilous taxa (*e.g.* Palmae, *Engelhardia*, Schizaceae, *Castaneae*, Cyrillaceae, Sapotaceae), which could be observed in different palaeovegetational group, *e.g.* swamp, mixed mesophytic forest (Ediger 1990; Gemici *et al.* 1991, 1992; Güngör 1991; Whateley & Tuncalı 1995; Akgün & Akyol 1999; Akgün *et al.* 2007, Kayseri *et al.* 2007; Kayseri & Akgün 2008, 2010). During this time interval, swamp palaeovegetation represented with Schizaceae, Sparganiaceae, *Nyssa*, Taxodioidea, *Myrica* and the diversity fungal spores was widespread in the central part of western Anatolia. However, abundance of mid and high altitude elements such as the gymnosperm pollen (*e.g.* *Pinus diploxyylon* and *haploxyylon* types and *Abies*) in the northwestern Anatolia (Çan, Etili, Gönen localities) and in northern Central Anatolia (Ankara and Samsun localities) may suggest the presence of high topographies in these areas during the Burdigalian–Langhian period. In central and western Anatolia, the evergreen and deciduous mixed forests were mainly represented by *Castanea* and *Quercus* (deciduous and evergreen types), *Ulmus* and *Zelkova*, *Carya*, *Tilia*, Cyrillaceae. Elements of the riparian forest (*Alnus*, Simaroubaceae, *Platanus* and *Salix*) are also observed in palynospectra of all localities during this period. Besides, species of open vegetation (*e.g.* Asteraceae-Asteroideae-Tubulifloreae type and Cichorioideae-Liguliflorae type, Chenopodiaceae and Poaceae) are

generally observed in low percentage in the palynofloras of Central and Western Anatolia.

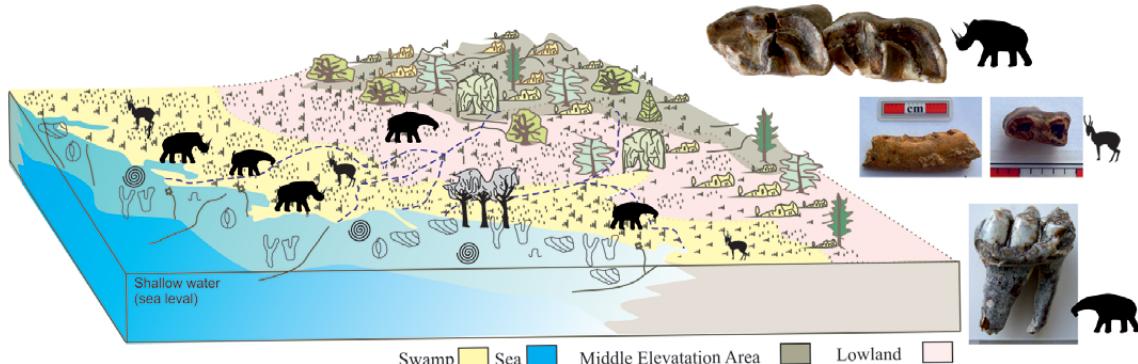
The palynofloras of Kolivata and Spanokhorion in Greece, correlated to the latest Burdigalian (lower part of N8 zone) thanks to the planktonic foraminiferal association from the same deposits, are characterized by abundant mixed mesophytic and coniferous forests elements, *i.e.* *Pinus* spp., *Pinus haploxyylon* group and rarely *Pinus silvestris* group, *Quercus*, *Castanea* (Benda *et al.* 1982). The swamp forest is also well developed in Kolivata-Spanokhorion as indicated by the occurrence of the Taxodioidea, *Nyssa* and Myricaceae. The Kolivata-Spanokhorion palynospectra also includes some open area elements represented by herb and shrubs species such as Poaceae, Asteraceae-Asteroideae-Tubulifloreae type and Cichorioideae-Liguliflorae type, Cyperaceae and Chenopodiaceae.

Another late Burdigalian palynoflora is recorded from the Marmarenia Formation in the southern part of the Aliveri Basin in the Evia Island, Greece by Reigel *et al.* (1989). This palynoflora is correlated to the mammalian zone MN4a and includes abundant thermophilous elements (*Engelhardia*, Sapotaceae, *Platycarya* and Palmae). Palaeovegetation also includes swamp forest elements such as *Spirogyra*, Cupressaceae-Taxodioidea, Cupressaceae-*Sequoia*, Taxodioidea-*Glyptostrobus* and Nymphaeaceae. In Greece, Benda *et al.* (1982) also recorded a Langhian (NN5 zone) microflora and nannoflora at Kolivata-Levkas. This palynoflora is characterized by the abundance of mixed mesophytic forest elements such as Cyrillaceae, *Engelhardia*, Cupressaceae-Taxodioidea, *Pinus haploxyylon* type and *Quercus*.

Palaeoenvironment of the Karacaağac-Hüssamlar area as indicated by palynofloras



Palaeoenvironment of the Kultak area as indicated by palynofloras



	<i>Salix</i>		Herbs and shrubs
	<i>Quercus</i> spp.		<i>Spargania</i>
	<i>Alnus</i>		Back mangrove plant (<i>Avicennia</i>)
	<i>Pinus</i> spp.		Corals
	<i>Castaneae</i>		Bivalves
	Cupressaceae		Algae
			Miliolidae
			Microforaminiferal linings



Figure 10. Reconstructed palaeobiogeography of the Kultak, Karacaağac and Hüssamlar localities during the middle Burdigalian–Langhian period.

The herb and shrubs represented with Poaceae, Cyperaceae and Chenopodiaceae are rare in the palaeovegetation of Kolivata-Levkas (2% or less).

Palaeoclimate and CA results

Palaeoclimatic interpretation of the Burdigalian–Langhian

palynofloras of the Kultak, Karacaağac and Hüssamlar localities is based on the results obtained using the CA analysis method. Besides, temperature values of other localities in Anatolia and Greece are calculated using the published palynospectra of the Burdigalian–Langhian. Numerical climatic variables from Turkey and Greece are correlated with those from European countries (Germany, Serbia, Bulgaria and Ukraine).

Turkey

The Late Burdigalian is characterized by a temperature increase, and a significantly warm climate persisted through the late Burdigalian and Langhian. This period of high temperature corresponds to the Middle Miocene Climatic Optimum, which is also globally observed based on the isotopic, faunal and floral data (e.g. Zachos *et al.* 2001, Mosbrugger *et al.* 2005). This important palaeoclimatic event in the Miocene could be evaluated using the CA method in Turkey based on the palynofloras from Karacaağac, Kultak and Hüssamlar in the Milas region (SW Turkey, Middle Burdigalian–Langhian), from Beypazarı (latest Burdigalian), Bigadiç (latest Burdigalian), Sabuncubeli (late Burdigalian) Tire (latest Burdigalian), Soma (late Burdigalian–Langhian), Etili (late Burdigalian–Langhian), Çan and Gönen (latest Burdigalian–?Serravallian) and Başçayır and Kuloğulları (Langhian) (Table 2).

In the middle Burdigalian, the CMT value of Kultak is higher than in the other localities in Turkey. This higher value indicates the palaeoclimatic condition in the Kultak locality warmer than the others. Additionally, MART value of this locality is lower than in the other localities in Turkey and this could be interpreted as the presence of a low palaeotopographic condition in Kultak during the middle Burdigalian–Langhian time interval. Besides, the CMT and MART values of Karacaağac and Hüssamlar localities are similar and the MART values of these localities are higher than the MART values of Kultak. This different CMT and MART values could be interpreted as indicative of different palaeogeographic conditions in the Karacaağac, Hüssamlar and Kultak localities during the Burdigalian–Langhian period. This evidence is supported by the low altitude deltaic conditions observed in the middle Burdigalian–Langhian period in Kultak while a lowland and middle altitude area with lacustrine condition is observed in the Hüssamlar and Karacaağac localities based on their faunal and floral fossil contents and sedimentary facies. The palynoflora of the Kultak locality reinforced this palaeoenvironmental evidence thanks to presence of plants growing in mangrove environment (*Avicennia*), foraminifers, bivalves and corals.

The highest MART values and lower CMT values are calculated for the Etili and Çayırhan localities and these data could be interpreted as resulting from high palaeotopographic condition in the late Burdigalian–Langhian period in these localities. Despite some environmental differences (e.g. palaeotopography, palaeogeographic position), temperature values are high, and warm subtropical climatic condition inferred from these values dominated in the all localities, and this led to the development of thermophilous plants (*Engelhardia*, *Sapotaceae*, *Cyrillaceae*, *Avicennia*, *Palmae* etc.).

Greece

Detailed palynological records from the Miocene of Greece were obtained by Benda (1971) and Benda *et al.* (1982). They observed warm subtropical palaeoclimatic conditions for the latest Burdigalian and Langhian time interval in Greece (Benda *et al.* 1982) based on the palynofloras, which are characterized by the thermophilous elements (e.g. *Cyrillaceae*, *Engelhardia*). Using these data, we calculated the numerical climatic values for Spanokhorion in Greece, which are the MAT 9.10–10.8 °C or 15.6–21.3 °C, the CMT (−2.7)–1.1 °C (−0.8 °C) or 5.0–13.3 °C (9.15 °C), the WMT 24.7–43.0 °C (33.85 °C), the MAP 823.0–1520.0 mm and the MART 34.65 °C or 24.7 °C. The presence of two intervals of the MAT, CMT and MART could be interpreted as due to two different palaeotopographic conditions at Spanokhorion during the late Burdigalian period. The palaeogeography of this period supports this interpretation (Pindos uplift and opening of the Ionian Basin) and this different palaeotopographic condition could have been caused microclimatic condition in Greece (Popov *et al.* 2004; Fig. 11). Evia Island is located east to Spanokhorion, and the parameters for Evia for the late Burdigalian are calculated from Reigel *et al.* (1989). These parameters are the MAT of 17.0–18.4 °C, the CMT and WMT of 6.2–12.5 °C (9.35 °C) and 26.5–32.0 °C, the MAP 1146–1322 mm, and the MART 19.9 °C. The palaeotopography of the Evia locality differs from Spanokhorion and it should be lowland based on the MART values (Popov *et al.* 2004; Figs 11, 12, Table 3). Numerical climatic data for the Langhian of Kolivata western Greece) are calculated based on the palynofloras described by Benda *et al.* (1982). The results from Kolivata are the MAT 15.6–21.7 °C, the CMT 5.0–15.6 °C (10.3 °C), the WMT 24.7–27.9 °C (26.3 °C), the MAP 823.0–1520.0 mm and the MART 16 °C. According to the CA results and palynological data, the palaeoaltitude has declined from the late Burdigalian (MART values of the Spanokhorion; 34.65 °C or 24.7 °C) to Langhian (MART values of Kolivata; 19.9 °C) in the western part of the Greece (Fig. 11).

Germany

Mosbrugger *et al.* (2005) recorded the palaeoclimatic evolution during the Eocene–Pliocene interval based on the macro and microfloras from Germany and central Europe. The climatic curves of central Europe (Mosbrugger *et al.* 2005) are correlated with the climatic curves of oxygen and carbon isotopes (Zachos *et al.* 2008). For MAT and WMT, similar values are obtained from the floras of different Cenozoic basins during this period. However, these authors observed the peak in the curve of CMT values (9–13 °C) for the Burdigalian–Langhian interval, and this increase of

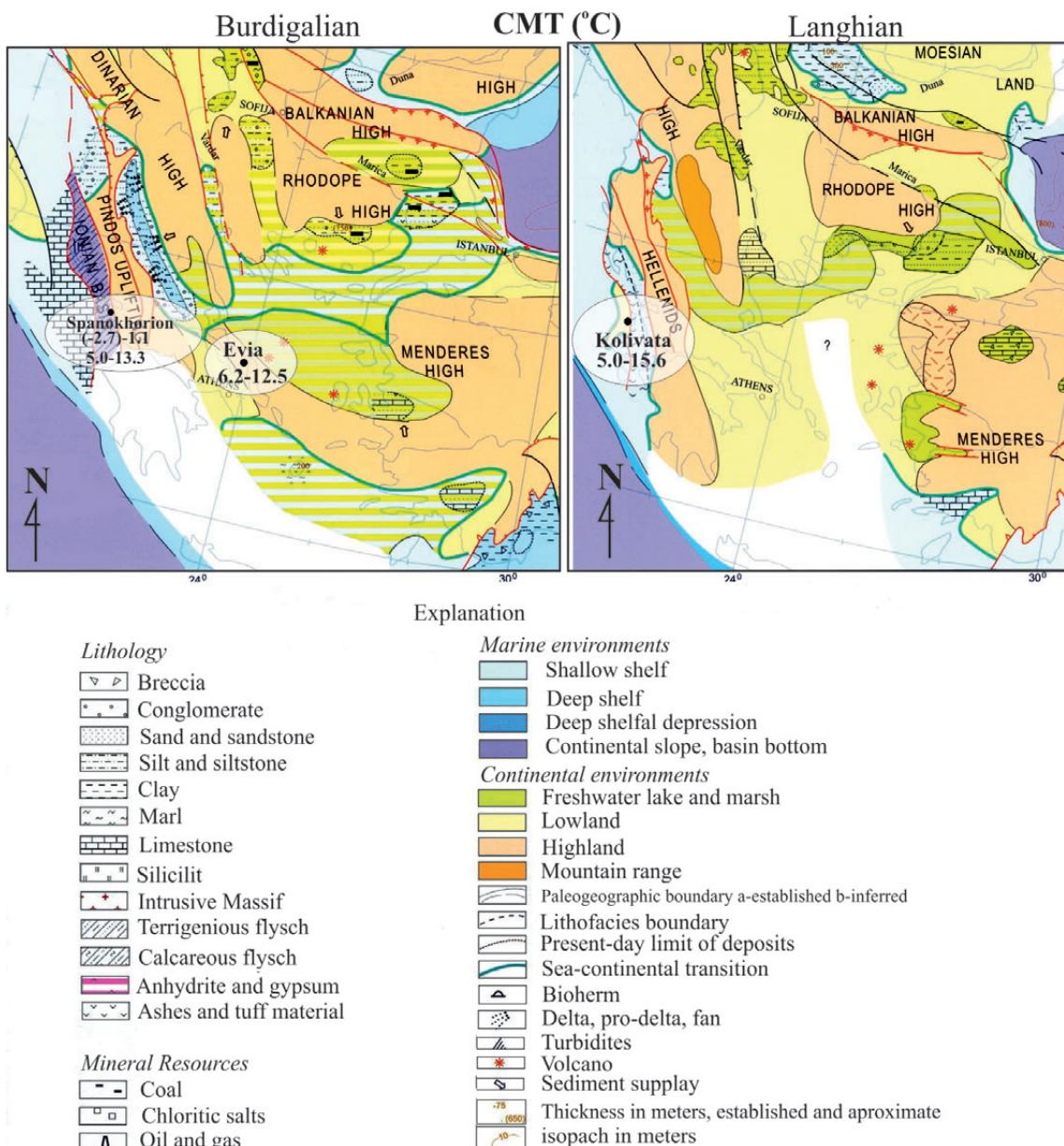


Figure 11. CA_{palynoflora} results (MAT, CMT, WMT, MAP and MART) of Greece for the Burdigalian–Langhian time interval and palaeogeography of Greece and western Turkey.

temperature is related to the warm climatic conditions (Mosbrugger *et al.* 2005). Besides, these authors emphasized that regional differences of climatic values are probably caused by palaeogeographic settings. For example, the Lower Rhine and the Weisselster-Lausitz basins are close to the Cenozoic North Sea, moderating the climate during the cold season. In the case of the Molasse Basin, orographic movements in the nearby area might be also influenced the palaeoclimate of this basin. The onset of the Miocene cooling seems to be between 13.0 and 14.0 my when considering all of the different records and climate variables analyzed. In the Molasse Basin, the CMT decreased

more rapidly than in the other regions at the end of the middle Miocene and it dropped below 4 °C (Fig. 12).

Bulgaria

The palynoflora of the Langhian period in northeast Bulgaria was studied by Ivanov *et al.* (2007, 2011). During the Tarkhanian stage (Langhian), mixed mesophytic forests appear to have been widespread in the lowlands and mid-altitude uplands surrounding the deposition area in Bulgaria. *Quercus* and *Ulmus* are recorded abundantly in these

forests, accompanied by *Castanea*, *Carya*, *Pterocarya*, *Juglans*, *Ilex*, *Eucommia*, *Betula*, *Carpinus* and *Corylus* etc. Elements of the thermophilous plants such as *Platycarya*, *Engelhardia*, *Symplocos*, *Reevesia*, Sapotaceae, Araliaceae and Arecaceae are also abundantly present in the pollen spectra (Ivanov 1995; Palamarev & Ivanov 1998; Palamarev et al. 1999; Stuchlik et al. 1999; Ivanov et al. 2002, 2007; Palamarev & Ivanov 2004). Additionally, Ivanov et al. (2007, 2011) obtained numerical climatic results using the CA analysis of the Langhian for the northeast Bulgaria: the MAT 13.6–17.2 °C (20.4 °C), the CMT 2.4–7.0 °C (7.5 °C), the WMT 24.7–27.8 °C (26.25 °C), the MAP 823–1206 mm and the MART 18.75 °C (Fig. 12). According to Meulenkamp & Sissingh (2003) and Ivanov et al. (2007), a tectonic controlled reorganization in the latest Early to earliest Middle Miocene in the Eastern Paratethys resulted in the emergence of the Greater Caucasian archipelago and this tectonic uplift was followed by a transgression in the territories west to the Black Sea. These authors hypothesized that tropical and subtropical water, which came by way of transgression from Black Sea affected the climate of the terrestrial areas in Bulgaria and thermophilous elements become abundant in the palynospectra of the Tarkhanian time. Additionally, the highland areas in northeast Bulgaria are known as existing since the Early Miocene and they were covered by the mixed mesophytic forest. Besides, the Balkan Peninsula apparently played a significant role in the origin, evolution, and migration of the Mediterranean vegetation during the Miocene, being situated between the Tethyan and Paratethyan realms (Palamarev 1989, Rögl 1998, Ivanov et al. 2007).

Serbia

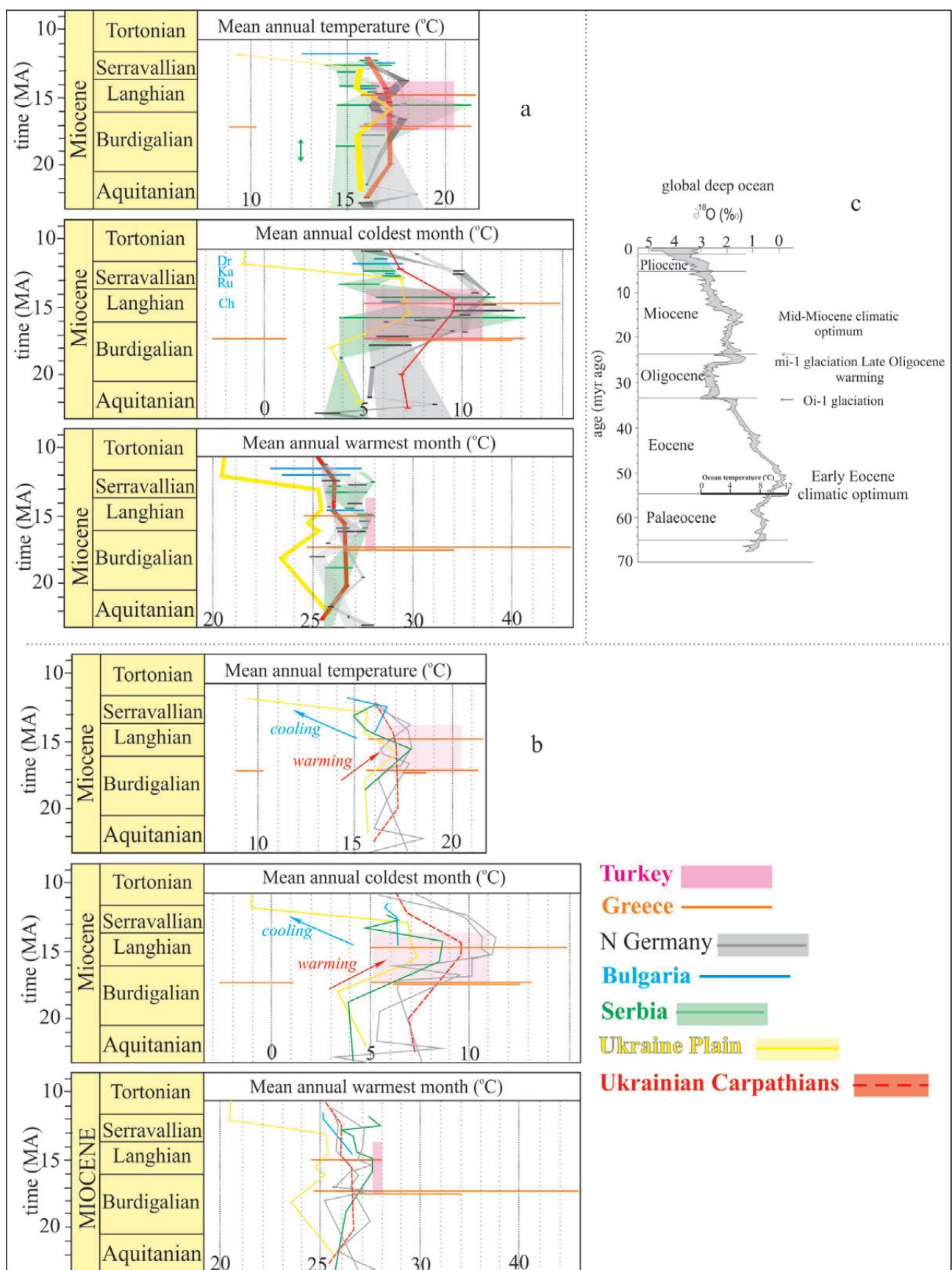
Langhian floras in Serbia (Popovac, Slanci and Misaca floras) are recorded by Utescher et al. (2007). The Popovac palynoflora is represented by the deciduous plants (*i.e.* *Acer*, *Rhamnus*) and their presence indicates highland areas in Serbia during the Langhian–early Serravallian. Utescher et al. (2007) emphasize that the Slanci palynoflora is dominated by the species of Lauraceae family. Typical temperate deciduous taxa, such as *Salix*, *Alnus*, *Populus* and *Acer*, but also *Engelhardia*, *Zelkova* and conifers, reach minor percentages in the Slanci palynoflora. In the Misaca palynoflora, the arctotertiary elements (temperate elements; Mai 1981, 1991) *Acer*, *Ulmus* and *Carpinus* are well-represented. According to Utescher et al. (2007) these taxa migrated to Serbia across the higher altitudes of the ri-

sing Carpathian mountain range. Additionally, these authors stated that deciduous and arctotertiary taxa form an important component of the mixed mesophytic vegetation of Central Europe during the Langhian–early Serravallian. Utescher et al. (2007) calculated palaeoclimatic data from Serbia by the CA. Resulting coexistence intervals of the Popovac flora are for the MAT 14.4–21.3 °C, CMT 3.7–13.3 °C (8.5 °C), WMT 27.2–28.1 °C (27.65 °C) and MART 19.15 °C. The coexistence intervals of the Slanci flora are the MAT ranges from the 15.6–16.5 °C, the CMT 7–7 °C, the WMT 25.6–27 °C, the MART 19 °C and the MAP 823–1237 mm. The values of the Misaca flora are 14.4 to 16.6 °C for the MAT, 5.6 to 11.7 °C (8.65 °C) for the CMT, 25.7 to 28.1 °C for the WMT, 18.25 °C for the MART and 867 to 1018 mm for the MAP (Fig. 12). These authors suggested that these coexistence intervals of the Popovac, Misaca and Slanci floras are higher than that of the early Burdigalian palynoflora and these high values point to the Mid-Miocene climatic optimum (Zachos et al. 2001, Utescher et al. 2007).

Ukraine

The palaeovegetation types and palaeoclimatic interpretations for the Langhian were separately defined for the Ukrainian Carpathian region and Ukraine Plain based on the macroflora. The Langhian–early Serravallian in the Carpathian Basin is characterized by a transgressive cycle according to Venglinsky (1975) and Syabryaj et al. (2007). These authors emphasized that a seaway existed between the Central Paratethys and Tethys, and warm oceanic waters stimulated the presence of thermophilous ferns. Expanding broad-leaved forest includes *Ulmus*, *Castanea* and frequent *Engelhardia* in the Ukrainian Carpathian region. Langhian palaeovegetation of the elevated and slope areas in the Ukrainian Carpathian region, which is characterized by *Picea* and *Ulmus*, differs from the palaeovegetation of the inner zone of the Ukrainian Carpathians. The CA results of the Ukrainian Carpathian region display the MAT values between 15.6 and 18.4 °C, the CMT between 6.6 to 12.5 °C (9.55 °C), the WMT values between 25.4 to 27.9 °C, the MART value of 17.1 °C and the MAP between 1122 and 1213 mm (Syabryaj et al. 2007; Fig. 12). In the early Middle Miocene, the Ukrainian Plain was characterized by a regressive phase. The continental areas of this region were covered by pine forests (*Keteleeria*, *Tsuga*, *Cedrus*, *Picea*, *Ginkgo* and *Podocarpus*). The swamp forest

Figure 12. A – climatic records (MAT, CMT and WMT) for the Miocene of the Central and Eastern Paratethys (Serbia: Utescher et al. 2007a, modified; Ukraine, Syabryaj et al. 2007, modified, and Bulgaria, Ivanov et al. 2011, modified) and the eastern Mediterranean regions (Greece and Turkey: this study) compared to the continental climatic record of northern Germany (Utescher et al. 2009). • B – climatic curve based on the average climatic values. • C – the marine oxygen isotope record (Zachos et al. 2001). Abbreviations: Ch – Chukourovo, Ru – Ruzhints, Ka – Koshava, Dr – Drenovets.



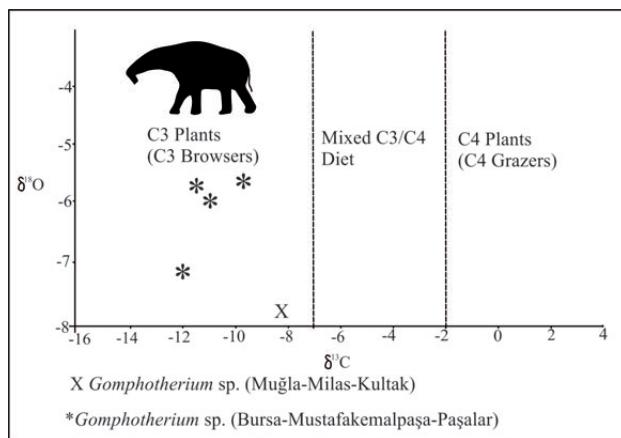


Figure 13. Stable carbon and oxygen isotope values of Kultak and Paşalar localities (Quade *et al.* 1995).

with *Taxodium* occurred in the most humid continental areas of the Ukrainian Plain. The broad-leaved forest was characterized by *Quercus*, *Ulmus*, *Zelkova*, *Castaneae*, *Liquidambar*, *Fagus*, *Pterocarya*, *Juglans*, *Carpinus* and *Betula*. In the undergrowth of this forest, *Corylus*, *Erica*, *Lauraceae*, *Buxus*, *Ilex*, *Palmae* and *Theaceae* occurred; this plant community points to the subtropical climatic conditions in the Ukrainian Plain. *Salix* and *Alnus* cloaked the river valleys and lakes. Furthermore, some herb species were recorded in samples from Ukrainian Plain. The resulting coexistence intervals of the Ukrainian Plain are calculated by Syabryaj *et al.* (2007) as the MAT ranges from the 17–17.1 °C, the CMT 6.6–7.1 °C (6.85 °C), the WMT 24.7–25.9 °C, the MART 18.45 °C and the MAP 1146–1322 mm (Fig. 12).

The MAT, CMT and WMT values indicate some differences between the different regions of Europe due to their palaeogeographic position and the palaeotopography during the Burdigalian–Langhian period. However, climatic curves of these countries show some similarities. For instance, numerical climatic values decrease from the Early to Middle Miocene in all these regions. The starting of this decline generally begins in the Langhian. Climatic values from Turkey and Greece for the Burdigalian–Langhian periods are high as in Europe. While the CMT values resemble the values of European countries, the MAT and WMT values are higher than in these countries (Fig. 12). The effects of the Middle Miocene Climatic Optimum, which covers the Burdigalian–Langhian time interval, are observed as well in the palaeoclimatic records of Europe, Turkey and Greece (Fig. 12). The differences of the mean annual range of the temperature values (MART) were used as indicators for continental climatic condition and/or seasonality (see Bruch *et al.* 2004, Yao *et al.* 2011). Based on the high MART values from Turkey for the Burdigalian–Langhian period, the presence of a high seasonality (warmer summers and colder winters) could be deduced. As a result,

the high seasonality in Turkey could be related to influences of the continental climate (Table 2; Yao *et al.* 2011).

Stable isotope analysis and precipitation records of Turkey and Europe

The carbon isotopic composition of carbonate in biogenic apatites and in most soils is dependent upon the carbon isotopic composition of the local vegetation. C3 plants include nearly all trees, most shrubs and herbs, and grasses that favor cool growing seasons. Regions receiving dominantly winter rains, such as the modern Mediterranean, are vegetated largely by C3 plants. Modern C3 plants average $-27 \pm 5\text{\textperthousand}$ for $\delta^{13}\text{C}$. The $\delta^{13}\text{C}$ value of C4 plants averages about $-13 \pm 3\text{\textperthousand}$. C4 plants include grasses that favor warm growing seasons, as well as a few desert shrubs and herbs. C4 grasses are common in tropical, subtropical and temperate climates dominated by warm summer rainfall (Quade *et al.* 1995). The $\delta^{13}\text{C}$ value of fossil tooth enamel from Kultak and Hüssamlar is $-8.32\text{\textperthousand}$ (Table 4). This value indicates that herbivorous mammals from Kultak and Hüssamlar mainly consumed C3 plants as those of the Bursa-Paşalar mammal locality (Quade *et al.* 1995).

The oxygen isotopic composition of bone phosphate is largely defined by the $\delta^{18}\text{O}$ value of environmental water, and metabolic processes which vary from species to species (Luz & Kolodny 1995, Quade *et al.* 1995). Of the two, the $\delta^{18}\text{O}$ value of environment water has been shown to be the most important, and this is controlled by the $\delta^{18}\text{O}$ value of local precipitation and by the extent to which rainfall is later modified by evaporation. Leaves can be strongly enriched in $\delta^{18}\text{O}$ due to evaporation from leaf surface, the more so in an unshaded setting like a clearing or a forest canopy (Quade *et al.* 1995). Sternberg *et al.* (1989) documented systematic enrichment in $\delta^{18}\text{O}$ of foliage upward through a tropical forest. This isotopic stratification appears to be reflected in the $\delta^{18}\text{O}$ value of mammals that consume such vegetation. The $\delta^{18}\text{O}$ value is low in *Gomphotherium* sp. from Ören and Bursa-Paşalar (Table 4). This result could indicate that this large elephantoid was eating plants shielded from sunlight, as in a shaded forest setting (Fig. 13). Carbon and oxygen values of the Kultak, Hüssamlar and Paşalar localities are located in the range of C3 plants as shown in Fig. 13. This indicates similar ecological conditions during the Burdigalian–Langhian time. This isotopic result and high MAP_{DRY} value of Kultak are in agreement with ecological interpretation from mammalian fossils. However, according to the isotopic results, the Kultak and Hüssamlar localities are more shaded than Bursa-Paşalar. Negative $\delta^{18}\text{O}$ values could be indicative of less humidity in the Ören region (Table 3).

The MAP, MAP_{WET} and MAP_{WARM} values of Karaağaç, Hüssamlar and Kultak localities in the SW Anatolia

Table 3. CA_{palynoflora} results (MAT, CMT, WMT and MAP) of the Burdigalian–Langhian time interval in Greece.

Location	Climate	References	MAT (°C)	CMT (°C)	WMT (°C)	MART(°C)	MAP (mm)
Greece – Spanokhorion	Warm subtropical	Benda (1971) Benda <i>et al.</i> (1982)	9.1–10.8 or 15.6–21.3 (−2.7)–1.1 or 5.0–13.3	24.7–43.0	34.65 or 24.7	823–1520	
Greece – Evia	Warm subtropical	Reigel <i>et al.</i> (1989)	17.0–18.4	6.2–12.5	26.5–32.0	19.9	1146–1322
* Greece – Kolivata	Warm subtropical	Benda (1971) Benda <i>et al.</i> (1982)	15.6–21.7	5.0–15.6	24.7–27.9	16	823–1520

Table 4. Stable carbon and oxygen value of Kultak fossil site.

Sample	CO ₃ -content (%CaCO ₃)	δ ¹³ C (‰ VPDB)	δ ¹⁸ O (‰ VPDB)	
<i>Gomphotherium</i> sp.	12.4	−8.32	−7.75	Milas-Hüssamlar and Kultak (MN4e–6)
<i>Gomphotherium</i> sp.	–	(−10) and (−12)	(−5) and (−8)	Bursa-Paşalar (MN6)

Table 5. CA_{palynoflora} results (MAP, MAP_{WET}, MAP_{DRY} and MAP_{WARM}) of the Burdigalian–Langhian time interval in Turkey and Greece (“**” symbolized the palynoflora of the Langhian time).

Location	MAP (mm)	MAP _{WET} (mm)	MAP _{DRY} (mm)	MAP _{WARM} (mm)	MART (°C)
This study	Ören-Karacağaç	1146–1322	225–227	7–32	79–125
	Ören-Hüssamlar	1146–1322	225–227	8–32	79–125
	Ören-Kultak	1122–1520	204–227	19–43	79–125
	Ankara-Çayırhan (upper coal seam)	735–1520	134–180	26–27.9	17.9 or 25.95
	Ankara-Çayırhan (lower coal seam)	1146–1322	225–245	19–32	79–154
	Samsun-Havza	1217–1322	236–255	19–32	118–125
	Çanakkale-Çan	735–1520	175–180	8–43	45–163
	Çanakkale-Etili	1146–1151	–	–	20.8
	Balıkesir-Gönen	437–1520	175–180	8–43	45–61
	Balıkesir-Bigadiç	1217–1322	109–180 or 204–227	16–43	118–125
Anatolia	Manisa-Soma	629–1520	134–180	8–43	51–63
	İzmir-Sabuncubeli	1146–1322	–	–	18.3
	Aydın- Kuloğulları	1183–1520	107–180 or 205–245	8–43	85–163
	Aydın-Başçayırlı	735–1574	107–323	5–43	51–180
	Spanokhorion	823–1520	204–227	8–43	79–125
	Evia	1146–1322	225–227	8–32	79–125
	*Kolivata	823–1520	107–180 or 204–227	8–43	79–125
Greece					34.65 or 24.7
					19.9
					16

resemble each other. However, the MAP_{DRY} values of these localities indicate differences. This value of Kultak is distinctly higher than the MAP_{DRY} values for the two other localities. Thus Kultak has moist areas during the Burdigalian–Langhian time interval according to the high MAP_{DRY} value, while the low MAP_{DRY} values from Karacağaç and Hüssamlar indicate the presence of drier areas. These discrepancies of precipitation between the different localities in the Ören region may have affected the faunal composition. For example, drier local conditions at Hüssamlar compare to Kultak are evidenced based on physical properties of *Prosantorhinus douvillei* and *Brachypotherium brachypus*.

Several MAP values are recorded in central, northwest

and western Anatolia for the Burdigalian–Langhian time interval. The MAP values of certain localities are low (Table 5). This low precipitation values could be interpreted as the occasional existence of quite dry periods. The MAP_{WET} and MAP_{WARM} values of these localities do not show reliable differences. However, there are noticeable changes in the MAP_{DRY} values and these values for the central Anatolia and Bigadiç locality in western Anatolia are higher than the MAP_{DRY} values of other localities. This difference of the MAP_{DRY} values could indicate more rainfall, seasonality and/or presence of different palaeotopographic conditions in central Anatolia during the Burdigalian–Langhian time interval.

Conclusion

1. In this study, Kultak, Hüssamlar and Karacaağac palynoflora are described. These floras are dominated by the thermophilous plants (*Engelhardia*, Sapotaceae, Cyrillaceae, *Avicennia*, Palmae etc.).

2. In the middle Burdigalian–Langhian time interval, palaeoclimatic condition at the Kultak locality is warmer than in the other localities of Turkey (Çayırhan, Havza, Çan, Etili, Gönen, Bigadiç, Emet, Kirka and Kestelek, Sabuncubeli, Soma, Tire, Kuloğulları, Başçayır, Hüssamlar and Karacaağac) based on the CMT values. This warming could be related to the different depositional systems at the Kultak locality, which is represented by deltaic sedimentary environments. The lower MART value, the composition of its mammalian fauna and its palynoflora support this environmental evidence. Climatic variables of Karacaağac and Hüssamlar are different from the variable of Kultak because of widespread terrestrial condition in the Hüssamlar and Karacaağac areas. Based on Kultak, Hüssamlar and Karacaağac palynofloral evidences and physical properties of mammalian taxa, palaeotopography of the Hüssamlar and Karacaağac localities should be higher and drier than in the Kultak locality. Besides, although there is a presence of environmental discrepancy, temperature values are high and humid warm subtropical climatic condition is prevalent in Turkey.

3. The fossil assemblages from the two main localities (Kultak and Hüssamlar), described briefly here below, are formed of terrestrial vertebrates;

– *Brachypotherium brachypus* is the first rhinoceros record at Kultak, associated to the proboscideans, bovids and equids collected during the former field seasons; this species is still poorly documented in Anatolia.

– The small sized rhino *Prosantorhinus* cf. *douvillei* from Hüssamlar, encountered in Anatolia for the first time, is also the earliest record of the subtribe *Teleoceratina* in Turkey.

– The occurrence of *Prosantorhinus* and *Gomphotherium* at Hüssamlar is the further evidence for the forested environment in the Hüssamlar area in agreement with palynological results of this paper.

– *Prosantorhinus douvillei* known in several Middle Miocene (MN5) localities in Europe is interpreted as inhabiting the areas with hard soil and dry climatic conditions because of the slender morphology of its limb bones.

4. According to the palynological studies for the Burdigalian–Langhian periods, vegetational groups are represented in Greece and Turkey by a similar plant distribution (*Pinus haploxyylon* type, Cyrillaceae, *Engelhardia*, Cupressaceae-Taxodioidea, *Castanea*, Sapotaceae and *Quercus*). Palaeoclimatic values from Turkey resemble that of Greece and several European countries. However,

palaeogeography has a strong effect on the palaeoclimatic condition in Greece during the Burdigalian–Langhian time interval.

5. The temperature difference between different regions during the middle Burdigalian and Langhian periods could be explained by the palaeogeographic position of countries. Despite some differences in the climatic values and plant distribution, warm climatic conditions dominated, based on the palynofloras, in Turkey, Greece and elsewhere in Europe during this time interval. This warming is related to the Middle Miocene Climatic Optimum period.

6. The MAP, MAP_{WET} and MAP_{WARM} values of the Karacaağac, Hüssamlar and Kultak localities resemble each other. However the MAP_{DRY} of Kultak is distinctly higher than the MAP_{DRY} values of other Ören region localities. The high MAP_{DRY} value could be indicative of the humid climatic condition at Kultak during the Burdigalian–Langhian time interval and also low MAP_{DRY} values could be interpreted as indicative of drier areas at Karacaağac and Hüssamlar. The MAP_{WET} and MAP_{WARM} values of these localities are not distinctly differentiated. Furthermore, the MAP_{DRY} values of central Anatolia (Ankara-Çayırhan and Samsun-Havza) and of Bigadiç in western Anatolia are higher than the MAP_{DRY} values of other localities in Turkey. This could be interpreted as the more rainfall in central Anatolia during the Burdigalian–Langhian time interval.

7. Carbon and oxygen isotope values obtained from the tooth enamel of *Gomphotherium* sp. from the Kultak, Hüssamlar and Paşalar localities indicate that this elephantoid preferably consumed C3 plants. This isotopic result and high MAP_{DRY} value from the Kultak locality are in agreement with ecological interpretation of mammalian fossils.

Acknowledgements

This study was financially supported by Dokuz Eylül University, Graduate School of Natural and Applied Sciences (AFS, high licenses project numbers: 04 KB FEN 031) and Scientific and Technical Research Council of Turkey (TUBİTAK grant code 104Y297), DAAD and the Senckenberg Museum in Frankfurt. Authors thank to the Aegean University projects (TTM/001/2011, TTM/002/2011) and the TUBITAK-RFBR grant code 111Y192 for the mammalian fossil study. We would like to thank Volker Wilde, Angela Bruch, Ayhan İlgar, Sükrü Yurtsever, Bora Sonuvar and Serkan Özer for help through the course of this work. We are grateful to Şevket Şen and anonymous referees for their critical and constructive reviews that significantly improved the manuscript. Special thanks to Šárka Doležalová, who is executive editor of the Bulletin of Geosciences, for all suggestions, and Alexey Tesakov for English improvements.

References

- AKGÜN, F. 1993. Palynological age revision of the Neogene Soma coal basin. *Bulletin of the Geological Society of Greece* 28, 151–170.
- AKGÜN, F., AKAY, E. & ERDOĞAN, B. 2002. Terrestrial to shallow marine deposition in central Anatolia: a palynological approach. *Turkish Journal of Earth Sciences* 11, 1–7.
- AKGÜN, F., AKKIRAZ, M. S., MOSBRUGGER, V., BRUCH, A., UTESCHER, T., WILDE, V. & BOZCU, M. 2008. Early–Middle Miocene palynostratigraphy and palaeoclimate of the Biga Peninsula, Northwest Turkey. *Terra Nostra* 2, *IPC–XII/IOPC–VIII Bonn, Germany Abstract Volume*, p. 9.
- AKGÜN, F. & AKYOL, E. 1999. Palynostratigraphy of the coal-bearing Neogene deposits in Büyük Menderes Graben, Western Anatolia. *Geobios* 32, 367–383.
DOI 10.1016/S0016-6995(99)80013-8
- AKGÜN, F., KAYA, T., FORSTEN, A. & ATALAY, Z. 2000. Biostratigraphic data (Mammalia and palynology) from the Upper Miocene Incesu Formation at Duzyayla (Hafik-Sivas, central Anatolia). *Turkish Journal of Earth Sciences* 9, 57–67.
- AKGÜN, F. & KAYSERI, M.S. 2004. Climatic evolution and vegetational changes during the Miocene period in central Anatolia (Turkey). *NECLIME Annual Meeting, Island of Crete (Greece)*, p. 7.
- AKGÜN, F., KAYSERI, M.S. & AKKIRAZ, M.S. 2004. Paleoclimatic evolution and vegetational changes from the Oligocene to Miocene in Turkey. *NECLIME Annual Meeting, Island of Crete (Greece)*, p. 7.
- AKGÜN, F., KAYSERI, M.S. & AKKIRAZ, M.S. 2007. Paleoclimatic evolution and vegetational changes during the Late Oligocene–Miocene period in western and central Anatolia (Turkey). *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 56–106. DOI 10.1016/j.palaeo.2007.03.034
- ANDREWS, P. & KELLEY, J. 2007. Middle Miocene dispersals of apes. *Folia Primatologica* 78, 328–343.
DOI 10.1159/000105148
- 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*. 403 pp. PhD thesis, Université Claude Bernard Lyon 1, France.
- BENDA, L. 1971. Grundzüge einer pollenanalytischen Gliederung des türkischen Jungtertiärs (Känozoikum und Braunkohle der Türkei 4). *Beihhefte zum Geologischen Jahrbuch* 113, 1–46.
- BENDA, L., MEULENKAMP, J.E. & SCHMIDT, R.R. 1982. Biostratigraphic correlations in the eastern Mediterranean Neogene; 6, Correlation between sporomorph, marine microfossil and mammal associations from some Miocene sections of the Ionian islands and Crete (Greece). *Newsletters on Stratigraphy* 11, 83–93.
- BRUCH, A.A., UTESCHER, T., ALCALDE-OLIVARES, C., DOLAKOVA, N., IVANOV, D. & MOSBRUGGER, V. 2004. Middle and Late Miocene spatial temperature patterns and gradients in Europe: preliminary results based on palaeobotanical climate reconstructions. *Courier Forschungsinstitut Senckenberg* 249, 15–27.
- CAMBON, G., SUC, J.-P., ALOISI, J.-C., GIRESSE, P., MONACO, A., TOUZANI, A., DUZER, D. & FERRIER, J. 1997. Modern pollen de-
- position in the Rhône delta area (lagoonal and marine sediments), France. *Grana* 36, 105–113.
DOI 10.1080/00173139709362596
- CASANOVAS-VILAR, I., ALBA, D.M., GARCÉS, M., ROBLES, J.M. & MOYÀ-SOLÀ, S. 2011. Updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proceedings of the National Academy of Sciences* 108, 5554–5559.
DOI 10.1073/pnas.1018562108
- CERDENO, E. 1996. *Prosantorhinus*, the small teleoceratine rhinocerotid from the Miocene of western Europe. *Geobios* 29, 111–124. DOI 10.1016/S0016-6995(96)80077-5
- EDIGER, V.Ş. 1990. Tortonian–Messinian palynomorphs from the easternmost Mediterranean region around İskenderun, Turkey. *Micropaleontology* 42, 189–205.
DOI 10.2307/1485870
- FAUQUETTE, S., SUC, J.-P., JIMÉNEZ-MORENO, G., MICHEELS, A., JOST, A., FAVRE, E., BACHIRI-TAOUIQ, N., BERTINI, A., CLET-PELLERIN, M., DINIZ, F., FARJANEL, G., FEDDI, N. & ZHENG, Z. 2007. Latitudinal climatic gradients in the Western European and Mediterranean regions from the Mid-Miocene (c. 15 Ma) to the Mid-Pliocene (c. 3.5 Ma) as quantified from pollen data, 481–502. In WILLIAMS, M., HAYWOOD, A.M., GREGORY, F.J. & SCHMIDT, D.N. (eds) *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies. The Micropalaeontological Society, Special Publications*. The Geological Society, London.
- FORTELJUS, M. 1990. Rhinocerotidae from Pasalar, Middle Miocene of Anatolia (Turkey). *Journal of Human Evolution* 19, 489–508. DOI 10.1016/0047-2484(90)90061-F
- GAZIRY, A.W. 1976. Jungtertiäre Mastodonten aus Anatolien (Turkei). *Geologisches Jahrbuch, Reihe B* 22, 3–143.
- GEMICI, Y., AKGÜN, F. & YILMAZER, Ç. 1992. Akçaşehir (Tire–İzmir) Neojen havzası fosil makro ve mikroflorası. *Doğa, Türk Botanik Dergisi* 16, 383–393.
- GEMICI, Y., AKYOL, E., AKGÜN, F. & SEÇMEN, Ö. 1991. Soma kömür havzası fosil makro ve mikroflorası [Fossil macro- and micro-flora of Soma coal basin]. *General Directorate of Mineral Research and Exploration of Turkey (MTA) Bulletin* 112, 161–178. [in Turkish with English abstract]
- GENTRY, A.W. 1990. Ruminant artiodactyls of Pasalar, Turkey. *Journal of Human Evolution* 19, 529–550.
DOI 10.1016/0047-2484(90)90063-H
- GERAADS, D. 2003. Ruminants, other than Giraffidae from the Middle Miocene hominoid locality of Candır (Turkey). *Courier Forschungsinstitut Senckenberg* 240, 181–199.
- GERAADS, D., GULEC, E. & SARAC, G. 1995. Middle Miocene ruminants from Inönü, central Turkey. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 8, 462–474.
- GÖHLICH, U.B. 1999. Order Proboscidea, 157–168. In RÖSSNER, G. & HEISSIG, K. (eds) *The Miocene land mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.
- GÖRÜR, N., ŞENGÖR, A.M.C., SAKINÇ, M., TÜYSÜZ, O., AKKÖK, R., YİĞİTBAS, E., OKTAY, F.Y., BARKA, A.A., SARICA, N., ECEVITOĞLU, B., DEMİRBAĞ, E. & AKYOL, A. 1994. Cross-cutting rift systems of the Gökova region, SW Anatolia: Implications for the formation of the Aegean Sea. *Bulletin of the Technical University of Istanbul* 47, 275–292.

- GÖRÜR, N., ŞENGÖR, A.M.C., SAKINÇ, M., TÜYSÜZ, O., AKKÖK, R., YİĞİTBAS, E., OKTAY, F.Y., BARKA, A.A., SARICA, N., ECEVITOĞLU, B., DEMIRBAĞ, E., ERSOY, S., ALGAN, O., GÜNEYSU, C. & AKYOL, A. 1995. Rift formation in the Gökova region, southwest Anatolia: implications for the opening of the Aegean Sea. *Geological Magazine* 132, 637–650.
DOI 10.1017/S0016756800018884
- GÖRÜR, N. & TÜYSÜZ, O. 2001. Cretaceous to Miocene palaeogeographic evolution of Turkey: Implications for hydrocarbon potential. *Journal of Petroleum Geology* 24, 119–146.
DOI 10.1111/j.1747-5457.2001.tb00664.x
- GÜNGÖR, H.Y. 1991. *Ankara (Beypazarı) Kömürlerinin Palinolojisi ve Paleokolojisi*. 38 pp. Licence thesis, Dokuz Eylül University, İzmir.
- GÜRER, Ö.F. & YILMAZ, Y. 2002. Geology of the Ören and surrounding areas, SW Anatolia. *Turkish Journal of Earth Sciences* 11, 1–13.
- HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontology Electronica* 4, 9 pp.
- HARZHAUSER, M. & PILLER, W.E. 2007. Benchmark data of a changing sea – palaeogeography, palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 8–31.
DOI 10.1016/j.palaeo.2007.03.031
- HEISSIG, K. 1999. Family Rhinocerotidae, 175–188. In RÖSSNER, G. & HEISSIG, K. (eds) *The Miocene land mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.
- HEISSIG, K. & FEJFAR, O. 2007. The mammals from Utermiozaen of Tuchorice in Northwest Bohemia – 1. The fossils of rhinoceros (Mammalia, Rhinocerotidae). *Sborník Národního muzea v Praze, Řada B – přírodní vědy* 63, 19–66.
- HEUSSER, L. 1988. Pollen distribution in marine sediments on the continental margin of Northern California. *Marine Geology* 80, 131–147. DOI 10.1016/0025-3227(88)90076-X
- IVANOV, D.A. 1995. Palynological data about the presence of the family Symplocaceae in the Miocene of Northwestern Bulgaria. *Geologica carpathica* 46, 37–40.
- IVANOV, D., ASHRAF, A.R. & MOSBRUGGER, V. 2007. Late Oligocene and Miocene climate and vegetation in the Eastern Paratethys area (northeast Bulgaria), based on pollen data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255, 342–360. DOI 10.1016/j.palaeo.2007.08.003
- IVANOV, D., ASHRAF, A.R., MOSBRUGGER, V. & PALAMAREV, E. 2002. Palynological evidence for Miocene climate change in the Forecarpathian Basin (Central Paratethys, NW Bulgaria). *Palaeogeography, Palaeoclimatology, Palaeoecology* 178, 19–37. DOI 10.1016/S0031-0182(01)00365-0
- IVANOV, D., UTESCHER, T., ASHRAF, A.R., MOSBRUGGER, V., BOZUKOV, V., DJORGOVA, N. & SLAVOMIROVA, E. 2012. Late Miocene palaeoclimate and ecosystem dynamics in Southwestern Bulgaria – A study based on pollen data from the Gotse Delchev Basin. *Turkish Journal of Earth Sciences* 21, 187–211.
- IVANOV, D., UTESCHER, T., MOSBRUGGER, V., SYABRYAJ, S., DJORDJEVIC-MILUTINOVIC, D. & MOLCHANOFF, S. 2011. Miocene vegetation and climate dynamics in Eastern and Central Paratethys (Southeastern Europe). *Palaeogeography, Palaeoclimatology, Palaeoecology* 304, 262–275.
DOI 10.1016/j.palaeo.2010.07.006
- JACCARD, P. 1908. Nouvelles recherches sur la distribution florale. *Bulletin de la Société vaudoise des sciences naturelles* 44, 223–270.
- KERN, A., HARZHAUSER, M., MANDIC, O., ROETZEL, R., CORIC, S., BRUCH, A.A. & ZUSCHIN, M. 2011. Millennial-scale vegetation dynamics in an estuary at the onset of the Miocene Climate Optimum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304, 247–261.
DOI 10.1016/j.palaeo.2010.07.014
- KARAYİĞİT, A.İ., AKGÜN, F., GAYER, R.A. & TEMEL, A. 1999. Quality, palynology, and palaeoenvironmental interpretation of the Ilgın lignite, Turkey. *International Journal of Coal Geology* 38, 219–236. DOI 10.1016/S0166-5162(98)00015-9
- KAYA, T., TUNA, V. & GERAADS, D. 2001. A new late Orleanian/early Astaracian mammalian fauna from Kultak (Milas-Mugla), southwestern Turkey. *Geobios* 34, 673–680.
DOI 10.1016/S0016-6995(01)80028-0
- KAYSERI, M.S. 2010. *Oligo-Miocene Palynology, Palaeobotany, Vertebrate, Marine Faunas, Palaeoclimatology and Palaeo-vegetation of the Ören Basin (North of the Gökova Gulf), Western Anatolia*. PhD thesis, Dokuz Eylül University, İzmir.
- KAYSERI, M.S. & AKGÜN, F. 2008. Late Burdigalian-Langhian time interval in Turkey – palaeoenvironment and palaeoclimatic implications and correlation of Europe and Turkey. *Terra Nostra* 2008/2, IPC-XII/IOPC-VIII, p. 138.
- KAYSERI, M.S. & AKGÜN, F. 2010. The Late Burdigalian–Langhian time interval in Turkey and the palaeoenvironment and palaeoclimatic implications and correlation of Europe and Turkey: Late Burdigalian–Langhian palynofloras and palaeoclimatic properties of the Muğla-Milas (Kultak). *Geological Bulletin of Turkey* 53, 1–44.
- KAYSERI, M.S., AKGÜN, F., KAYA, T. & MAYDA, S. 2006. Palynological and faunal inventories of the Oligo-Miocene period in the Muğla-Kultak region, Western Anatolia (Turkey); preliminary results. *7th European Palaeobotany and Palynology Conference (Prague)*, p. 63.
- KAYSERI, M.S., AKGÜN, F. & ÖRÇEN, S. 2007. Stratigraphy and microfaunal data of the Oligocene and Miocene ages in the Alakilise and Kultak regions (Gökova region). *NECLIME Annual Meeting (Slovakia)*, p. 15.
- KOVACH, W.L. 1988. Multivariate methods of analyzing paleoecological data, 72–104. In DiMICHELE, W.A. & WING, S.L. (eds) *Methods and Applications of Plant Paleoecology. The Paleontological Society, Special Publication* 3.
- KOVACH, W.L. 1989. Comparisons of multivariate analytical techniques for use in pre-Quaternary plant paleoecology. *Review of Palaeobotany and Palynology* 60, 255–282.
DOI 10.1016/0034-6667(89)90046-8
- KOHLER, M. 1987. Boiden des türkischen Miozans (Kanozoikum und Braunkohlen der Turkei 28). *Paleontologia i Evolucion* 21, 133–246.
- MAYDA, S., SARAÇ, G. & KAVUŞAN, G. 2006. ‘*Gomphotherium angustidens* (Cuvier)’ (Proboscidea, Mammalia) from the

- Hancılı Formation (Kalecik, Ankara): oldest Neogene Pro-boscidea record from Turkey. 55. *Turkish Geology Symposium, Ankara*, 254–255.
- MAI, D.H. 1981. Entwicklung und klimatische Differenzierung der Laubwaldflora Mitteleuropas im Tertiär. *Flora* 171, 525–582.
- MAI, D.H. 1991. Palaeofloristic changes in Europe and the confirmation of the Arcto-Tertiary-Palaeotropical geofloral concept. *Review of Palaeobotany and Palynology* 68, 29–36. DOI 10.1016/0034-6667(91)90055-8
- 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, Paleoecology* 196, 209–228. DOI 10.1016/S0031-0182(03)00319-5
- MOSBRUGGER, V. & UTESCHER, T. 1997. The coexistence approach, a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 134, 61–86. DOI 10.1016/S0031-0182(96)00154-X
- MOSBRUGGER, V., UTESCHER, T. & DILCHER, D.L. 2005. Cenozoic continental climatic evolution of Central Europe. *Proceedings of the National Academy of Sciences* 102(42), 14964–14969. DOI 10.1073/pnas.0505267102
- NAKOMAN, E. 1978. *Investigation of coal deposits Tinas, Bağyaka, Bayır, Eskihisar, Sekkoy and Hüsamilar in SW Turkey*. 140 pp. Tübitak project, İzmir. [in Turkish]
- QUADE, J., CATER, J.M.L., OJHA, T.P. & HARRISON, T.M. 1995. Paleodietary reconstruction of Miocene faunas from Paşalar, Turkey using stable carbon and oxygen isotopes of fossil tooth enamel. *Journal of Human Evolution* 4, 373–384. DOI 10.1006/jhev.1995.1029
- QUEROL, X., ALASTUEY, A., PLANA, F., LOPEZ-SOLER, A., TUNCALI, E., TOPRAK, S., OCAKOĞLU, F. & KOKER, A. 1999. Coal geology and coal quality of the Miocene Muğla Basin, southwestern Anatolia, Turkey. *International Journal of Coal Geology* 41, 311–332. DOI 10.1016/S0166-5162(99)00025-7
- PALAMAREV, E. 1989. Palaeobotanical evidences of the Tertiary history and origin of the Mediterranean sclerophyll dendroflora. *Plant Systematic Evolution* 162, 93–107. DOI 10.1007/BF00936912
- PALAMAREV, E. & IVANOV, D. 1998. Über einige Besonderheiten der tertiären Floren in Bulgarien und ihre Bedeutung für die Entwicklungsgeschichte der Pflanzenwelt in Europa. *Acta Palaeobotanica* 38, 147–165.
- PALAMAREV, E. & IVANOV, D. 2004. Badenian vegetation of Bulgaria: biodiversity, palaeoecology and palaeoclimate. *Courier Forschungsinstitut Senckenberg* 249, 63–69.
- PALAMAREV, E., IVANOV, D. & BOZUKOV, V. 1999. Paläoflorenkomplexe im Zentralbalkanischen Raum und ihre Entwicklungsgeschichte von der Wende Oligozän/Miozän bis ins Villafranchien. *Flora Tertiaria Mediterranea* 6(5), 1–95.
- POPOV, S.V., RÖGL, F., ROZANOV, A.Y., STEININGER, F.F., SHCHERBA, I.G. & KOVAC, M.E. 2004. Lithological-palaeogeographic maps of Paratethys. 10 Maps Late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg* 250, 1–46.
- REIGEL, A., WEHMAYER, D., MEINKE, K., SCHWARZ, G., APSTOLIKAS, A. & VELITZELOS, E. 1989. Succession of depositional environments in the Neogene basin at Aliveri, Evia (Greece). *Palaeogeography, Palaeoclimatology, Palaeoecology* 70, 261–273. DOI 10.1016/0031-0182(89)90095-3
- RÖGL, V.F. 1998. Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Annals of the Natural History Museum Vienna* 99, 279–310.
- SICKENBERG, F., BECKER-PLATEN, J.D., BENDA, L., BERG, D., ENGESSER, B., GAZIRY, W., HEISSIG, K., HUNERMANN, K.A., SONDAAR, P.Y., SCHMIDT-KITTNER, N., STAESCHE, K., STAESCHE, U., STEFFENS, P. & TOBIEN, H. 1975. Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die Internationale Neogen-Stratigraphie. *Geologisches Jahrbuch, Reihe B* 15, 1–167.
- SÖZBİLİR, H., BOZKURT, E., WINCHESTER, J.A. & DENİZ, O. 2005. Ophiolites resting above the Gediz Detachment and their tectonic significance: field and geochemical evidence from Alaşehir area, southwest Turkey. *International Symposium on the Geodynamics of Eastern Mediterranean, Active Tectonics of the Aegean*, p. 70.
- STERNBERG, L., MULKEY, S.S. & WRIGHT, S.J. 1989. Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. *Ecology* 70, 1317–1324. DOI 10.2307/1938191
- STUCHLIK, L., IVANOV, D. & PALAMAREV, E. 1999. Middle and Late Miocene floristic changes in the northern and southern parts of the Central Paratethys. *Acta Palaeobotanica* 2, 91–397.
- SUC, J.-P. & DRIVALIARI, A. 1991. Transport of bisaccate coniferous fossil pollen grains to coastal sediments: an example from the earliest Pliocene Orb Ria (Languedoc, Southern France). *Review of Palaeobotany and Palynology* 70, 247–253. DOI 10.1016/0034-6667(91)90006-O
- SYABRYAJ, S., UTESCHER, T. & MOLCHANOV, S. 2007. Changes of climate and vegetation during the Miocene in the territory of Ukraine. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 153–168. DOI 10.1016/j.palaeo.2007.03.038
- UTESCHER, T., BRUCH, A.A., MICHEELS, A., MOSBRUGGER, V. & POPOVA, S. 2011. Cenozoic climate gradients in Eurasia palaeo-perspective on future climate change? *Palaeogeography, Palaeoclimatology, Palaeoecology* 304, 351–358. DOI 10.1016/j.palaeo.2010.09.031
- UTESCHER, T., ERDEI, B., FRANCOIS, L. & MOSBRUGGER, V. 2007. Studies on diversity of plant functional types in the Miocene of Western Eurasia – spatial distribution patterns in the Langhian, Sarmatian and Tortonian, and their relation to palaeo-vegetation and palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 226–250. DOI 10.1016/j.palaeo.2007.03.041
- WHATELEY, M.K.G. & TUNCALI, E. 1995. Quality variations in the high-sulphur lignite of the Neogene Beypazari Basin, Central Anatolia, Turkey. *International Journal of Coal Geology* 27, 131–151. DOI 10.1016/0166-5162(94)00023-S
- VENGLINSKY, I.V. 1975. *Foraminifery biostratigrafiya miotsenoviykh otlozhennykh Zakarpatskovo progiba*. 262 pp. Naukova dumka, Kiev. [in Russian]

- YAO, Y.F., BRUCH, A.A., MOSBRUGGER, V. & LI, C.S. 2011. Quantitative reconstruction of Miocene climate patterns and evolution in Southern China based on plant fossils. *Paleogeography, Palaeoclimatology, Palaeoecology* 304, 291–307.
DOI 10.1016/j.palaeo.2010.04.012
- YAVUZ-ISIK, N. 2007. Pollen analysis of coal-bearing Miocene sedimentary rocks from the Seyitömer Basin (Kütahya), Western Anatolia. *Geobios* 40, 701–708.
DOI 10.1016/j.geobios.2006.11.006
- YILMAZ, Y., GENÇ, Ş.C., GÜRER, Ö.F., BOZCU, M., YILMAZ, K., KARACIK, Z., ALTUNKAYNAK, Ş. & ELMAS, A. 2000. When did the Western Anatolia grabens begin to develop?, 353–384. In BOZKURT, E., WINCHESTER, J.A. & PIPER, J.D.A. (eds) *Tectonics and Magmatism in Turkey and the Surrounding Area. Geological Society of London, Special Publication* 173.
- YILMAZ, Y. & POLAT, A. 1998. Geology and evolution of the Thrace volcanism, Turkey. *Acta Vulcanologica* 10, 293–303.
- ZACHOS, J.C., DICKENS, G.R. & ZEEBE, R.E. 2008. An early Cenozoic perspective on greenhouse gas warming and carbon-cycle dynamics. *Nature* 451, 279–283.
DOI 10.1038/nature06588
- ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E. & BILLUPS, K. 2001. Trends, rhythms, and aberrations in Global Climate 65 Ma to present. *Science* 292, 686–693.
DOI 10.1126/science.1059412