The middle Miocene palynoflora and palaeoenvironments of Eskihisar (Yatağan Basin, southwestern Anatolia): a combined LM and SEM investigation

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Abstract

Anatolia was a crossroads for mammal migration during the Miocene due to intermittent land connections between Africa and Anatolia and persisting warm conditions. Here, we investigated a palynological section from middle Miocene sediments of Eskihisar (southwestern Anatolia) in order to establish biogeographic links of the palynoflora and to infer the palaeoenvironment. Four algal palynomorphs, nine spore taxa, eight gymnosperms, three monocots, and 67 dicot pollen types were encountered and investigated using the “single grain method” that combines light microscopy and scanning electron microscopy. Two pollen zones reflect different phases of basin development. Zonal vegetation remained fairly stable across the section and reflects heterogeneous environments including broad-leaved deciduous forest, subtropical forest, and sclerophyllous and semi-evergreen oak forest. Conifers were accessory elements in the broad-leaved deciduous forest communities and replaced these at higher elevations. Some herbaceous taxa (Plumbaginaceae) indicate scattered occurrences of sandy and/or rocky soils. Biogeographic affinities are general Northern Hemispheric, North American, and East Asian as also suggested by the macro fossil record. Only two taxa provide potential biogeographic links with the African flora. This suggests that biome shifts of plant taxa between African subtropical /tropical biomes and Anatolian (western Eurasian) temperate forests and shrublands may have been rare in the middle Miocene.
Keywords: basin development; mammal zones; palynostratigraphy; plant fossils; “Pollen Bilder”; radiometric dating; taxonomic resolution

Introduction

The Miocene was the last period in Earth history when particularly warm conditions favoured rich forest vegetation in the Northern Hemisphere including the subarctic region (Denk et al., 2011; Mai, 1995; Zachos et al., 2001). At the same time, exchange of warm temperate plant taxa between North America and Eurasia continued to be possible via the North Atlantic (Denk, Grimsson & Zetter, 2010; Tiffney, 2008) and the Bering land bridges (Tiffney & Manchester, 2001). In addition, collision of the Afro-Arabian plate with Eurasia caused a physical connection between Africa and western Eurasia (Harzhauser & Piller, 2007) that enabled migration of a wide range of large mammals into Europe.

Palaeobotanical investigations of early and middle Miocene fossil bearing strata in western Anatolia predominantly concentrated on pollen stratigraphic correlation (e.g. Akgün & Akyol, 1999; Akgün, Kayseri & Akkiraz, 2007; Benda, 1971a; 1971b) and various aspects of the climatic and palaeoenvironmental development of the region using palynological data (Akgün et al., 2007; Ediger, 1990; Gemici, Akyol & Akgün, 1993; Gemici et al., 1990b, 1991; Kayseri-Özer et al., 2014a; Kayseri-Özer, Sözbilir & Akgün, 2014b; Takahashi & Jux, 1991; Yavuz-Işık, 2007; Yavuz-Işık et al., 2011) and, rarely, evidence from macro fossils (Engelhardt, 1903; Gemici et al., 1990, 1991, 1993; Mädler & Steffens, 1979). All previous studies of dispersed Neogene pollen and spores in Turkey were based on light microscopy. Further, a few taxonomic investigations of macro fossil remains addressed specific biogeographic questions. For example, Erdei, Akgün & Lumaga (2010) described foliage remains of a cycad which they compared to similar Miocene and Oligocene fossils across Europe. These fossils represent an extinct lineage of cycads in southern Europe (western Anatolia, Greece, France to Switzerland) during the Oligocene to the middle Miocene. Güner
Denk (2012) described two species of *Mahonia (Berberis)* based on well-preserved leaf fossils from early-middle Miocene deposits of the Yatağan Basin and Soma, one of which belongs to a lineage today confined to the southern foothills of the Himalayas to Southeast Asia, while the other represents a lineage restricted to North America today. Again different biogeographic relationships were inferred for well-preserved terminal leaf rosettes of *Dracaena*, suggesting links with modern species of East Africa and the Macaronesian islands (Denk, Güner & Grimm, 2014), and for leaves of *Smilax* with affinities to a modern Caribbean to South American lineage (Denk et al., 2015). These patterns illustrate the biogeographic key position of Anatolia during the Miocene both for plants and animals.

The present study is the first part of a series of palaeopalynological investigations the Yatağan Basin (Muğla province, southwestern Turkey). Dispersed spores and pollen recovered from a stratigraphic section of the [Eskihisar lignite mine](#), north-western part of the Yatağan Basin, were investigated using the single grain method (Zetter, 1989; Ferguson et al., 2007). The combined light microscopy (LM) and scanning electron microscopy (SEM) investigation forms the basis for a botanical evaluation of dispersed spores and pollen (cf. Grímsson & Zetter, 2011; Grímsson, Zetter & Baal, 2011; Grímsson et al., 2015a, 2015b, 2016). The present study provides the first palaeopalynological investigation using the single grain method of Miocene sediments in the East Mediterranean region. The aims of this investigation are: To document dispersed pollen and spores from a middle Miocene section in south-western Turkey. The combined LM and SEM investigation allows for detailed comparison with existing palynological studies of modern taxa when determining relationships of fossil pollen and spores. To infer the palaeoenvironment of Eskihisar mine locality during the middle Miocene based on ecological properties of modern representatives of the encountered fossil taxa. To discuss the stratigraphic relevance of generalized pollen assemblages for age inferences. To compare the middle Miocene palynoflora of the Eskihisar lignite mine with published Miocene floras of western Anatolia and to assess the relative contributions of North
American, East Asian, and African biogeographic elements to the Miocene Eskihisar plant assemblage.

**Material and methods**

The Yatağan basin is located in the province of Muğla, southwestern Turkey, south of the Menderes Massif. The basin is a ca 50 km long and 15 km wide south-east trending graben. It is split by a bedrock horst of Menderes Massif metamorphic rock. Up to 600 m thick Neogene sediments filling this basin consist of coarse- to fine-grained siliciclastic alluvial deposits, lignite, lacustrine carbonates and scattered occurrences of volcanic tephra. Two Miocene formations have been designated in the Yatağan basin: the Eskihisar Formation and the Yatağan Formation (Alçiçek, 2010; Atalay, 1980; Becker-Platen, 1970).

The exploited lignite seams of the Eskihisar lignite mine are restricted to the Eskihisar Formation which has been divided into the Turgut Member and Sekköy Member (Alçiçek, 2010; Atalay, 1980). The Turgut Member (Formation) has a thickness of up to 174 m in the main basin and up to 134 m in the Eskihisar mine area south and west of the Ala Dağ (Becker-Platen, 1970). It consists of reddened alluvial-fan deposits (conglomerates alternating with sandstones and mudstones) and sandy fluvial deposits (Alcicek, 2010). These deposits were transported into the subsiding basin from the neighboring mountains comprised of basement rocks. The uppermost part of the Turgut Member is characterized by a thick coal seam (Becker-Platen, 1970; Atalay, 1980) marking the end of the sedimentation of the Turgut layers. According to Becker-Platen (1970), at this time, the mountains surrounding the palaeolake were not much higher than the lake. The Sekköy Member has a thickness of up to 161 m in the main basin and up to 55 m in the Eskihisar mine area (Becker-Platen, 1970). It consists of alternating limestones, clayey limestones, sandstones, and siltstones (Becker-Platen, 1970; see also Fig. 1).
Whereas Becker-Platen (1970) considered the thick coal seam as the uppermost part of the Turgut Member, Atalay (1980) indicated the coal seam and the following 40 meters of sediment as part of the Turgut Member (this boundary was adopted in the scheme of Alcicek, 2010). Querol et al. (1999) appears to place the coal seam at the base of the Sekköy Member (Querol et al., 1999, fig. 2) while stating in the text that the Sekköy Member starts with green to gray-coloured fine-grained sediments overlying the main coal seam.

For the present study, the type profiles of both the Turgut and Sekköy members designated by Becker-Platen (1970, p. 22 ff. and pp. 26-27) were taken as reference points (see Fig. 1). A stratigraphic section of 47 m (hereafter Eskihisar lignite mine section; Fig. 1) located between the hill Ala Dağ to the east and the village Yeşilbağcılar to the west was investigated. Sedimentary samples for pollen analyses were taken at intervals of one meter. In total 56 samples were collected of which 30 were suitable for palynological analysis (detailed sample information is provided in Supporting Information, Appendix 2). The Eskihisar lignite mine section starts with the uppermost part of the Turgut Member. Sediments of weakly compacted, greenish-grey, micaceous, clayey silts are followed by a series of thin lignite seams (0.1–0.9 m in thickness) interbedded with clayey to sandy silt; fragmented leaf remains are common in the clayey layers. Above this series lies the main lignite seam. Within the sampled section the lignite seam reached a thickness of nine meters. The main seam is overlain by the Sekköy Member that starts with a series of dark claystones, rich in organic debris. Plant debris, gastropod shells (mainly Planorbis sp.) and fish fossils are common in the claystones. The following series is comprised of 18–19 m thick greenish-grey limestones interbedded with dark greenish-grey (higher organic content), clayey limestones. Fossil leaves are present in these units but are rare. On top of this is a series, about one meter thick, of finely laminated limestones interbedded with two layers of iron-rich, black sandstones. Further up follows a series of 14–16 m of yellowish-grey limestones interbedded with clayey limestones with low organic content. This section ends in a regolith horizon.
The profile described here closely matches the type profiles and other profiles published for the Turgut and Sekköy members in the Eskihisar area by Becker-Platen (1970). In addition, our palynological section corresponds to the section studied by Benda (1971a) that has been used to define the so-called Eskihisar Pollen Bild (Eskihisar pollen assemblage).

Sickenberg et al. (1975) reported the proboscid *Gomphotherium angustidens* Cuvier, 1817 from the main lignite seam in the Eskihisar lignite mine. The fossil mammal assemblage found in the Sekköy Member of Bağyaka (Muğla, site Çatakbağyaka; Fortelius [coordinator], 2016; Sickenberg et al., 1975) can be assigned to the Mammal Neogene (MN) zones (5-)6–8 (Supporting Information, Appendix S1). Whereas *Gomphotherium angustidens* has a wide stratigraphic range in Turkey (Fortelius [coordinator], 2016) and therefore is inconclusive regarding the age of the main coal seam, the majority of the mammal taxa from Çatakbağyaka have a range from 15.2 to 11.2 Ma (Fortelius [coordinator], 2016). According to Sickenberg et al. (1975), the gomphothere *Choerolophodon* indet. and the mastodon *Zygolophodon tapiroides* Cuvier, 1824 display primitive tooth morphologies. Therefore, an early middle Miocene age (Langhian) possibly extending into the Serravallian is suggested for the investigated Eskihisar lignite mine section. Both the dispersed pollen and spores and the macro fossils of the Eskihisar lignite mine flora also are suggestive of a middle Miocene age rather than a Burdigalian age (see below, Discussion).

Sediment samples were processed following the protocol described in (Grímsson, Denk & Zetter, 2008) and the same pollen grains were investigated using LM and SEM (single grain method, Zetter, 1989).

LM photographs of dispersed fossil pollen were taken with an Olympus BX51 microscope equipped with an Olympus DP71 camera. Specimens were sputter coated with gold and photographed using a Hitachi S-4300 cold field emission scanning electron microscope.

For the pollen diagram 400 grains per sample were counted. Some taxa that were easily distinguished in SEM but not in LM were jointly treated for the LM pollen counts [e.g. five
types of Apiaceae are described using SEM in the systematic part, but only one general Apiaceae pollen type (excluding Saniculoideae) was considered for the LM based pollen counts. The abundance of Botryococcus was assessed qualitatively (x = Botryococcus colonies present, xx = B. colonies frequently encountered). The pollen diagram (Fig. 2) was generated in C2 vers. 1.7.6, maps and sections were drawn in Adobe Illustrator 15.0.0 and photographs were cropped in Adobe Photoshop 12.0. The terminology for pollen morphology followed mostly Punt et al. (2007) and Hesse et al. (2009). Sediment samples, processed samples and SEM stubs are stored at the Swedish Museum of Natural History in Stockholm under accession numbers S153539 to S153593 and S153649.

Ninety-one taxa of algae, ferns and fern allies, gymnosperms and angiosperms were identified. The taxonomic identity of the fossil taxa was determined using palynological reference studies of modern families and genera and of extinct pollen taxa (e.g. Walther & Zetter, 1993, for the extinct genus Trigonobalanopsis, Fagaceae; Praglowski, 1982, 1984; Denk & Grimm, 2009; Denk & Tekleva, 2014, for genera within Fagaceae).

Systematic Palynology

Algae

Division Chlorophyta

Genus Botryococcus Kützing

Botryococcus cf. B. braunii Kützing

(Figs 3A–C)

Remarks: Botryococcus colonies are a common element in all investigated samples of pollen zone 2 of the Eskihisar mine section (Fig. 2) and have been reported from various middle Miocene localities of western Turkey (e.g. Akkiraz, 2011; Akkiraz et al., 2012). The fossil record of Botryococcus spans back to the Mesozoic (Batten & Grenfell, 1996). Extant Botryococcus has a global distribution and is mainly found in freshwater environments.
(swamps, pools, ponds, lakes) but tolerates, to a certain extent, brackish waters (e.g. Baltic Sea; Batten & Grenfell, 1996; Hällfors, 2004).

Family Zygnemataceae Kützning

Zygnemataceae gen. indet. (aff. Spirogyra Link)

(Figs 3D–F)

*Description:* Zygospore or aplanospore, outline elliptic, length of axis parallel to fissure 50–60 µm (LM, SEM), length of axis perpendicular to fissure 35–45 µm (LM, SEM); mesospore ca 1 µm thick (LM); sculpturing psilate (LM, SEM), gap circumfencing zygospore or aplanospore.

*Remarks:* Only present in the lower part of the Eskihisar mine section (Fig. 2), occurring in samples S153539 to S153545 and S153574. Zygnemataceae gen indet. resembles *Ovoidites lanceolatus* Takahashi et Jux, from the Miocene Soma basin, Turkey (Takahashi & Jux, 1991) and *Ovoidites elongatus* (Hunger) Krutzsch (e.g. Worobiec, 2014). The form genus *Ovoidites* has commonly been associated with zygospores/aplanospores of *Spirogyra* (Van Geel & Grenfell, 1996). In palaeoecological studies zygospores/aplanospores of Spirogyra have been used as indicator for clean, oxygen-rich, shallow stagnant, mesotrophic conditons in waterbodies subject to seasonal warming (Van Geel, 2001; Guiry, 2016).

The spore wall of extant Zygnemataceae shows a three-layered structure of which only the middle layer (mesospore) contains sporopollenin and therefore has fossilization potential (Hoshaw & McCourt, 1988). The fossil record of this family extends back to the Carboniferous (Van Geel & Grenfell, 1996).

Algal cyst indet. 1

(Figs 3G–I)
Description: Cyst, spheroidal, outline circular, diameter 20–25 µm (LM, SEM), cyst wall 2–2.5 µm thick (LM); sculpturing psilate (LM), nanoverrucate (SEM); verrucae diameter <0.1 µm.

Algal cyst indet. 2 (Figs 3J–L)

Description: Cyst, spheroidal, outline circular, diameter 25–30 µm (LM, SEM); cyst wall 2–2.5 µm thick (LM); sculpturing echinate (LM), echinate, nanoechinate (SEM); echinus diameter 0.4–0.2 µm, nanoechinus diameter <0.1 µm.

Remarks: Algal cyst indet. 2 resembles Monogemmites pseudosetarius (Takahashi & Jux, 1991). The systematic affinity of Monogemmites pseudosetarius is not known, but it has been associated with eutrophic to mesotrophic open waters (Worobiec, 2014). Algal cyst indet. 1 and 2 have not been discerned for the LM pollen count (Fig. 2) and are the most abundant palynomorph in samples S153570, S153572 S153573, S153575, S153581, and S153591.

Pteridophyta

Family Osmundaceae Bercht. et J.S.Presl

Genus Osmunda L.

Osmunda sp. 1 (Figs 4A–F)

Description: Spore, oblate to spheroidal, amb circular, spore diameter 50–80 µm (LM), 45–65 µm (SEM); exospore (without sculpture elements) up to 1 µm thick (LM); trilete, laesurae ½–⅔ of spore radius; sculpturing baculate, echinate, rugulate (LM, SEM), baculae base width 1–2 µm, baculae length 1–1.5 µm (LM, SEM).

Remarks: Osmunda sp. 1 shows the baculate sculpturing and considerable size range typical of extant and fossil Osmundaceae (Grimsson et al., 2011; Stafford, 2003; Tyron & Lugardon, 1991). The spore depicted in Figs 4A–C corresponds to the form genus Baculatisporites.
major (Raatz) Krutzsch and Figs 4D–F to B. primarius (Wolff) P.W.Thomson et Pflug
(Stuchlik et al., 2001).

*Osmunda* sp. 2
(Figs 4G–I)

*Description*: Spore, oblate to spheroidal, amb circular, spore diameter 45–55 µm (LM), 40–50 µm (SEM); exospore (including sculpture elements) 2–3 µm thick (LM); trilete, laesurae \( \frac{1}{2} - \frac{2}{3} \) of spore radius; sculpturing rugulate, baculate (LM, SEM), rugulae width 1–3 µm; abundance: rare.

*Remarks*: *Osmunda* sp. 2 resembles extant *Osmunda regalis* L. (e.g. Stafford, 2003; Tyron & Lugardon, 1991).

*Osmunda* sp. 3
(Figs 4J–L)

*Description*: Spore, oblate, amb circular, spore diameter 30–40 µm (LM), 30–35 µm (SEM); exospore 2–3.5 µm thick (LM); trilete, laesurae \( \frac{1}{2} - \frac{2}{3} \) of spore radius; sculpturing baculate, echinate, rugulate (LM, SEM), scarcely perforate (SEM), baculae base width 1.5–3 µm, baculae height 1.5–2 µm (LM, SEM).

*Remarks*: *Osmunda* sp. 3 corresponds to *Baculatisporites nanus* (Wolff) Krutzsch (Stuchlik et al., 2001). Osmundaceae spores are a common element in the lower part of the Eskihisar mine section, but are rare to absent in the upper part. Osmundaceae spores are common in European (Grimsson et al., 2011; Stuchlik et al., 2001) and East Mediterranean Miocene localities (Akgün & Akyol, 1999; Akgün et al., 2007; Akkiraz, 2011; Akkiraz et al., 2012; Benda, 1971a; Bozcu et al., 2015; Ediger, 1990; Gemici et al., 1993; Kayseri & Akgün, 2010), but are absent from Soma (Takahashi & Jux, 1991). They are rare in early Miocene deposits and abundant (or at least more common) in middle Miocene deposits (cf. Akgün et
al., 2007; Benda, 1971a). Since extant Osmundaceae spores display a significant size range (cf. Stafford, 2003; Tyron & Lugardon, 1991), it cannot be ruled out that Osmunda sp. 1 to 3 originated from the same biological species.

Family Polypodiaceae Bercht. et J.S.Presl
Polypodiaceae gen. indet.
(Figs 5A–C)
Description: Spore, oblate, amb elliptic to renal shaped, length of polar axis 25–30 µm (LM, SEM), equatorial diameter 35–40 µm (LM, SEM); exospore (including sculpture elements) 2–3 µm thick (LM); monolete, laesurae ⅓–⅓ of polar axis; sculpturing verrucate (LM, SEM), verrucae base width 2.5–3.5 µm (LM, SEM).
Remarks: This spore shows verrucate exospore ornamentation typical of Polypodiaceae (cf. Tyron & Lugardon, 1991). Polypodiaceae spores are rare in Miocene palynofloras of western Anatolia (cf. Akgün et al., 2007; Benda, 1971a; Bozcu et al., 2015). Spores of Polypodiaceae have been encountered in sample S153649.

Family Pteridaceae Reichenbach
Genus Pteris L.
Pteris sp.
(Figs 5D–G)
Description: Spore, oblate, amb convex triangular, length of polar axis 30–35 µm (LM, SEM), equatorial diameter 35–45 µm (LM, SEM); exospore (including sculpture elements) 2–3.5 µm thick (LM); trilete, laesurae ⅔ of radius, cingulum present (LM, SEM); sculpturing rugulate on proximal side, verrucate on distal side, fossulate (LM, SEM); sculpture elements larger on distal spore face; verrucae diameter 4–8 µm on distal side, rugulae width on proximal side 1–3 µm.
Remarks: This spore type corresponds in all morphological characters to extant Pteris spores (Martínez & Morbelli, 2009; Tyron & Lugardon, 1991).

Pteridaceae gen. indet.
(Figs 5H–J)

Description: Spore, spheroidal, amb convex triangular, length of polar axis 30–35 µm (SEM), equatorial diameter 40–50 µm (LM, SEM; exospore (including sculpture elements) 2–3.5 µm thick (LM); trilete, laesurae ⅔ of radius, (equatorial flange) cingulum present (LM, SEM); distal sculpturing rugulate fossulate, proximal sculpturing psilate (LM, SEM); fossulae width 0.5–2 µm, rugulae width 2–4 µm.

Remarks: This spore shows strong affinities to Pteridaceae (Tyron & Lugardon, 1991). Pteridaceae spores are rare in Eskihisar and have only been encountered in samples S153553 and S153649. From the Miocene of western Anatolia Pteridaceae spores (Akkiraz et al., 2012; Bozcu et al., 2015) and at least three form genera with affinities to Pteridaceae have been reported, Cingulatisporites macrospeciosus (R.Potonié et Gelletich) Nakoman (Akgün & Akyol, 1999; Akgün et al., 2007; Gemici et al., 1991), Cicatricosisporites regularis Nakoman (Ediger, 1990), and Verrucingulatisporites cf. V. grandis Nagy (Takahashi & Jux, 1991).

Incertae sedis trilete and monolete spores

Remarks: Trilete spore fam. et gen. indet. 1, 2 and Monolete spore fam. et gen. indet lack the perispore. For Bryophyte or Pteridophyte allocation and determination to family or genus level the perispore is necessary, thus these spores are of uncertain origin. Monolete and trilete spores are encountered in the whole section but are less abundant in the upper part (see Fig. 2).
Trilete spore fam. et gen. indet. 1
(Figs 5K–M)

Description: Spore, oblate to spheroidal, amb circular, equatorial diameter 50–55 µm (LM), 45–50 µm (SEM); exospore 1.5–2 µm thick (LM); trilete, laesurae ½–⅔ of radius; sculpturing verrucate (LM, SEM), verrucae diameter 1–1.5 µm (SEM).

Trilete spore fam. et gen. indet. 2
(Figs 6A–C)

Description: Spore, oblate to spheroidal, amb circular, equatorial diameter 50–55 µm (LM), 48–50 µm (SEM); exospore 1.5–2 µm thick (LM); trilete, laesurae ½–⅔ of radius; sculpturing psilate (LM), microrugulate with a low relief (SEM).

Monolete spore fam. et gen. indet./Laevigatosporites haardti (R.Potonié et Venitz)
P.W.Thomson et Pflug
(Figs 6D–F)

Description: Spore, oblate, amb elliptic, length of polar axis 28–32 µm (LM), 24–28 µm (SEM), equatorial diameter 40–45 µm (LM), 35–40 µm (SEM); exospore 1.5–2 µm thick (LM); monolete, laesurae ½–⅔ of equatorial axis; sculpturing scabrate (LM), perforate, nanorugulate (SEM).

Remarks: Spores of this type fall in the morphological range of Laevigatosporites haardti (R.Potonié et Venitz) P.W.Thomson et Pflug (e.g. Stuchlik et al., 2001). Spores of this type are found in a number of fern families [e.g. Blechnaceae Newman, Polypodiaceae, Gleicheniaceae (R.Br.) Presl] and can only be unambiguously differentiated by their exine stratification using transmission electron microscopy (TEM; cf. Tyron & Lugardon, 1991).

From the Miocene of western Anatolia spores corresponding to this type have been reported
Gymnosperms
Class Coniferopsida
Order Coniferales
Family Cupressaceae Richard ex Bartling (incl. Taxodioideae)
Cupressaceae gen. indet. 1 (non papillate)
(Figs 6J–L)
*Description:* Pollen, spheroidal, outline circular in polar view, equatorial diameter 28–40 µm (LM, SEM); exine 1–1.5 µm thick (LM); leptoma without papilla, leptoma circular (LM, SEM), pollen grain with deep split; sculpturing scabrate (LM), microverrucate (SEM), microverrucae covered with blunt nanoechini, leptoma area nanoverrucate, orbicules covered with blunt nanoechini, orbicule diameter 0.3–0.8 µm (SEM).

Cupressaceae gen. indet. 2 (papillate)
(Figs 6G–I)
*Description:* Pollen, spheroidal, outline circular in polar view, equatorial diameter 28–40 µm (LM, SEM); exine 1–1.5 µm thick (LM); leptoma with papilla, leptoma circular (LM, SEM), papilla length 3–5 µm (LM, SEM), pollen grain with deep split; sculpturing scabrate (LM), microverrucate (SEM), microverrucae covered with blunt nanoechini, leptoma area nanoverrucate, orbicules covered with blunt nanoechini, orbicule diameter 0.3–0.8 µm (SEM).

*Remarks:* Cupressaceae gen. indet. 2 resembles extant Taxodioideae (cf. Kedves, 1985; Li et al., 2010; Miyoshi, Fujiki & Kimura, 2011). Within this subfamily pollen morphology and sculpturing is highly similar and assignment to a genus is not possible or recommended. The
only visible difference between Cupressaceae gen. indet. 1 and Cupressaceae gen. indet. 2 is the presence/absence of a papilla. Extant Taxodioidae pollen may show a papillate or non papillate leptoma (Kedves, 1985). Both pollen types fall in the range of the form genus *Inaperturopollenites* Kremp; closest similarities of the specimen figured in Figs 6G–I are with *I. conceipites* (Wodehouse) Krutzsch and of the specimen figured in Figs 6J–L with *I. dubius* (R.Potonié et Venitz) P.W.Thomson et Pflug (Stuchlik et al., 2002).

Both pollen types are present in all samples, but never in high abundance. Several *Inaperturopollenites [=Taxodiaceaepollenites* (R. Pot.) Kremp] species, Cupressaceae or Taxodioidae are common elements in the Turkish Miocene (Akgün & Akyol, 1999; Akgün et al., 2007; Akkiraz, 2011; Akkiraz et al., 2012; Benda, 1971a; Bozcu et al., 2015; Ediger, 1990; Gemici et al., 1993; Kayseri & Akgün, 2010; Kayseri-Özer et al., 2014b; Takahashi & Jux, 1991; Yavuz-Işık, 2007). In general, cupressaceous macro remains are rare in the Yatağan basin (Güner & Denk, 2014; pers. obs. Johannes M. Bouchal Oct. 2014).

Family Pinaceae Lindl.

Genus *Cathaya* Chun et Kuang

*Cathaya* sp.

(Figs 7A–H)

*Description:* Pollen, monad, bisaccate, shape oblate, corpus rhombic to circular in polar view, sacci half-spherical, attachment area of sacci broad, pollen diameter including sacci 60–80 μm (LM, SEM), corpus width 32–62 μm (LM), sacci width 40–50 μm (LM), sacci height 23–30 μm (LM); leptoma, sacci with alveolate structuring, sculpturing in leptoma area scabrate (LM), microechinate (SEM), cappa rugulate to verrucate, microechinate and perforate to fossulate (SEM), sacci microechinate, perforate (SEM).

*Remarks:* *Cathaya* sp. corresponds to extant *Cathaya* pollen (Li et al., 2010; Stuchlik et al., 2002). In previous palynological studies such grains have been described under different
names. The grain shown in Figs 7A–D corresponds to *Podocarpidites verrucorpus* Wu (Takahashi & Jux, 1991, pl. 7, fig. 4), *Pityosporites* spp. (Ediger, 1990, fig. 4.9), *Podocarpus* (Akkiraz, 2011, fig. 8D) and *Cathayapollis scheuringii* (Sivak) Ziembińska-Tworzydło (Stuchlik et al., 2002); the grain shown in Figs 7E–H corresponds to *Picea*-type (Benda, 1971a, pl. 2, fig. 5), *Cathaya* (Akkiraz, 2011, figs 8A–B; Bozcu et al., 2015; Yavuz-Işık, 2007), *Pityosporites microalatus* (R.Pot.) P.W.Thomson et Pflug (Akyol & Akgün, 1990, pl. 1, fig. 15; Gemici et al., 1993, fig. 3.12), and *Cathayapollis vancampoae* (Sivae) Ziembińska-Tworzydło (Stuchlik et al., 2002).

The monotypic genus *Cathaya* is endemic to south-east China where it occurs in several scattered populations (Farjon, 1990; 2010). The characteristic microechinate pollen sculpturing is only detectable in SEM. In LM strong morphological similarities (e.g. outline, sacci attachment) with *Podocarpus* pollen are present, but *Podocarpus* lacks the microechinate suprasculpturing (cf. Liu & Basinger, 2000).

During the Cenozoic *Cathaya* had a wide Northern Hemispheric distribution; its fossil record (pollen and macrofossils) has been summarized in (Liu, Zetter & Ferguson, 1997) and (Liu & Basinger, 2000). From the Miocene of Turkey *Cathaya* and morphologically similar pollen has been reported (Akgün & Akyol, 1999; Akgün et al., 2007; Akkiraz, 2011; Akkiraz et al., 2012; Akyol & Akgün, 1990; Benda, 1971a; Ediger, 1990; Kayseri & Akgün, 2008). *Cathaya* is a rare element a (<3%), but present in nearly all samples (Fig. 2).

**Genus Cedrus** Trew

*Cedrus* sp.

(Figs 7I–L)

*Description:* Pollen, monad, bisaccate, shape oblate, corpus elliptic, sacci spherical to half-spherical, attachment area of sacci broad, pollen diameter including sacci 60–80 µm (LM, SEM), corpus diameter 45–65 µm (LM), sacci width 40–50 µm (LM), sacci height 20–25 µm
(LM); leptoma; cappa thickened (3–5 µm in LM); sacci with alveolate structuring; sculpturing in leptoma area scabrate (LM), microrugulate (SEM), cappa microrugulate, fossulate to perforate (SEM), sacci perforate to fossulate (SEM).

Remarks: The fossil Cedrus sp. pollen corresponds to extant Cedrus pollen (LM: Beug, 2004; SEM:Fujiki, Zhou & Yasuda, 2003). It shows strong similarities to Cedripites libaniformis (Bolkhovitina ex Krutzsch) Krutzsch (Stuchlik et al., 2002), Pityosporites spp. (Ediger, 1990, fig. 4.8) and Cedrus-type (Benda, 1971a, pl. 3, figs 3–4).

Extant Cedrus comprises three to four species with a disjunct distribution from the Atlas Mountains of Morocco and Algeria, Lebanon, southeast Turkey, Cyprus, and the Himalayas. It occurs from 900 to 3000 m (Farjon, 1990; 2010). Cedrus pollen has previously been reported from various middle Miocene localities of western Turkey (Akgün et al., 2007; Akkiraz, 2011; Akkiraz et al., 2012; Benda, 1971a; Bozcu et al., 2015; Ediger, 1990; Takahashi & Jux, 1991; Yavuz-İşık, 2007). Cedrus sp. is a common element in all samples.

Genus Picea A.Dietr.

Picea sp.

(Figs 7M–P)

Description: Pollen, monad, bisaccate, shape oblate, corpus elliptic in equatorial view, sacci half spherical, sacci attachment area broad, pollen diameter including sacci 95–110 µm (LM), 90–100 (SEM), pollen height including sacci 55–70 µm (LM), 50–60 µm (SEM), corpus length 70–95 µm (LM), 60–77 µm (SEM), corpus height 55–60 µm (LM), sacci width 40–60 µm (LM), 35–45µm (SEM), sacci height 30–40 µm (LM, SEM); leptoma, sacci with alveolate structuring; sculpturing of cappa area scabrate (LM), microrugulate to microverrucate, fossulate perforate (SEM), leptoma psilate (LM), corpus scabrate (LM), microrugulate, fossulate (SEM), sacci perforate, fossulate (SEM), suprasculpturing granulate.
Remarks: This grain corresponds in several morphological characteristics (e.g. small sacci compared to large corpus, wide angle of saccus attachment) to extant and fossil _Picea_ pollen (Erdtman, 1957; Grimsson & Zetter, 2011; Stuchlik _et al._, 2002). Pollen with affinities to extant _Picea_ have commonly been assigned to the form genus _Piceapollis_ Krutzsch (Stuchlik _et al._, 2002). Previous pollen reports from middle Miocene sediments of western Turkey: _Piceapollis_ spp. (Takahashi & Jux, 1991), _Picea_ (Akkiraz, 2011; Akkiraz _et al._, 2012), maybe _Keteleeria_-Typ (Benda, 1971a, pl. 3, figs 1–2). _Picea_ pollen is present in most samples but never abundant (Fig. 2).

Genus *Pinus* L.

Subgenus *Pinus* L. (Diploxylon-pollen-type)

*Pinus* subgenus *Pinus* sp.

(Figs 7Q–T)

Description: Pollen, monad, bisaccate, shape oblate, corpus elliptic in equatorial view, sacci nearly spherical, sacci attachment area narrow, pollen diameter including sacci 75–90 µm (LM), 65–75 µm (SEM), pollen height including sacci 45–55 µm (LM), 40–50 µm (SEM), corpus diameter 45–60 µm (LM), 40–50 µm (SEM), corpus height 35–45 µm (LM), 30–40 µm (SEM), sacci width 35–45 µm (LM), 30–40 µm (SEM), sacci height 25–30 µm (LM), 20–25 µm (SEM); leptoma; sacci with alveolate structuring (LM); sculpturing scabrate in cappa region and psilate in leptoma region (LM), corpus rugulate, verrucate, fossulate (SEM), sacci perforate (SEM), suprasculpturing weakly granulate (nanoverrucate).

Remarks: *Pinus* subgenus *Pinus* (Diploxylon) pollen type is characterized by narrowly attached and nearly spherical sacci (Hesse _et al._, 2009). Similar diploxylon type pollen has previously been reported from various middle Miocene localities of western Turkey: *Pinus silvestris*-Gruppe (=*sylvestris* type) (Benda, 1971a; Bozcu _et al._, 2015; Kayseri-Özer _et al._, 2014b), *Pityosporites* spp. (Ediger, 1990, figs 4.6–7), *P. labacus* [= *Pinus labacus* (R.Potonié)
Subgenus *Strobus* (Lemmon) A.E. Murray (Haploxylon-pollen-type)

*Pinus* subgenus *Strobus* sp.  
(Figs 8A–D)

*Description*: Pollen, monad, bisaccate, shape oblate, corpus elliptic in equatorial view, sacci half spherical, sacci attachment area broad, pollen diameter including sacci 80–100 µm (LM), 65–80 µm (SEM), pollen width including sacci 55–70 µm (LM, SEM), corpus diameter 55–70 µm (LM), 50–65 µm (SEM), corpus width 55–70 µm (LM, SEM), sacci width 50–65 µm (LM), 45–60 µm (SEM), sacci height 30–40 µm (LM), 25–35 µm (SEM); leptoma; sacci with alveolate structuring; sculpturing psilate in leptoma region (LM), corpus weakly rugulate, fossulate (SEM), sacci perforate (SEM), granulae present on leptoma are particles of unknown origin which could not be dissolved during processing of samples and are not sculptural elements, see Figs 8C, D.

*Remarks*: *Pinus* subgenus *Strobus* (Haploxylon) pollen type is characterized by broadly attached half-spherical sacci (Hesse et al., 2009). Similar haploxylon type pollen has previously been reported from various middle Miocene localities of western Turkey: *Pinus* haploxylon type (=haploxylon Gruppe) (Akkiraz, 2011; Akkiraz et al., 2012; Benda, 1971a; Bozcu et al., 2015; Kayseri-Özer et al., 2014b), *Pityosporites microalantus* (R.Potonié) P.W.Thomson et Pflug (Akgün & Akyol, 1999; Akgün et al., 2007; Akyol & Akgün, 1990; Gemici et al., 1991, pl. 1, figs 11–12; Kayseri-Özer et al., 2014a; Takahashi & Jux, 1991). Haploxylon type pollen is present in all samples (Fig. 2).
Order Gnetales

Family Ephedraceae Dumortier

Genus *Ephedra* L.

*Ephedra* sp.

(Figs 8E–G)

**Description:** Pollen, monad, inaperturate, shape oblate, equatorial outline elliptic, length of polar axis 25–35 µm (LM, SEM), equatorial diameter 35–75 µm (LM, SEM); exine ca 1 µm thick, tectate; sculpturing plicate, psilate, fossulate (LM, SEM), 6–9 plicae present, pseudosulci running parallel to plicae, pseudosulci show first and second order branching (LM, SEM).

**Remarks:** *Ephedra* sp. resembles pollen of extant *E. nevadensis* S. Watson and *E. viridis* Coville (Bolinder et al., 2016; Steeves & Barghoorn, 1959). In a recent study on extant *Ephedra* pollen, Bolinder et al. (2016) identified three types of pseudosulci; unbranched (ancestral state), branches of first order present, and branches of first and second order present (most derived state). The grain shown in Figs 8E–G concurs with the most derived state.

Pollen of *Ephedra* is common in the Cenozoic of the Northern Hemisphere (cf. Graham, 1999; Mai, 1995; Stuchlik et al., 2002). Pollen with affinities to extant *Ephedra* have commonly been assigned to the form genera *Ephedripites* Bolkhovitina ex R.Potonié and *Distachyapites* (Krutzsch) Grabowska (Stuchlik et al., 2002).

Today the 35–45 species of *Ephedra* show a Eurasian, North African, South and North American distribution (Kubitzki, 1990). From the Miocene of Turkey *Ephedra* and pollen with affinities to this genus have previously been reported (e.g. Akgün & Akyol, 1999; Akgün et al., 2007; Akkiraz, 2011; Akkiraz et al., 2012; Ediger, 1990; Takahashi & Jux, 1991; Yavuz-Işık, 2007). *Ephedra* sp. is a common element in all investigated samples (Fig. 2).
Class Magnoliopsida

Clade Commelinids

Order Poales Small

Family Poaceae Barnhart

Poaceae gen. indet. 1

(Figs 8H–J)

Description: Pollen, spheroidal, equatorial outline circular to quadrangular, pollen diameter 21–26 µm (LM, SEM); eutectate, exine 1.5–2 µm thick (LM); ulcerate, ulcus diameter 1.4–2 µm (LM, SEM), annulus present (LM, SEM); sculpturing scabrate (LM), nanoechinate, areolate, 3–5 nanoechini per areola, fossulate (SEM).


Poaceae gen. indet. 2

(Figs 8K–M)

Description: Pollen, spheroidal, pollen outline circular, pollen diameter 47–52 µm (LM); eutectate; exine 1.5–2 µm thick (LM); ulcerate, ulcus diameter 2–3 µm (LM, SEM), annulus present (LM, SEM), echinate operculum present (SEM); sculpturing scabrate (LM), nanoechinate (SEM).
Remarks: Poaceae gen. indet. 2 differs from P. gen. indet. 1 by its larger size and absence of fossulae in the sexine sculpturing. Poaceae gen. indet. 2 shows morphological similarities (size, nanoechinate sculpturing, absence of areola) to the *Hordeum*-type (present in e.g. *Hordeum* L., *Bromus* L) of Köhler & Lange (1979), extant Bambusoideae (cf. Li et al., 2010) and to previously depicted fossil pollen from the Miocene of Turkey (Benda, 1971a, Gramineen, pl. 4, figs 18–19). Poaceae pollen is present in nearly all investigated samples, but never abundant (<4%; Fig. 2).

Family Typhaceae Juss.

Genus *Typha* L.

*Typha* sp. (Figs 9A–C)

Description: Pollen, spheroidal, pollen outline circular, pollen diameter 28–35 µm (LM), 26–30 µm (SEM); semitectate, exine 1.5–2 µm thick (LM), nexine thinner than sexine; ulcerate, porus diameter 4–5 µm (LM, SEM); sculpturing reticulate (LM, SEM), muri crested with ridges or smooth, muri often incomplete, lumina of irregular shape.

Remarks: *Typha* sp. falls within the size and morphological range of extant and fossil *Typha* pollen (Beug, 2004; Grimsson et al., 2015a; Hamdi, Assadi & Segarra-Morragues, 2010; Martin & Drew, 1969; Punt, 1975; Stuchlik et al., 2009). This genus consists of 8 to 13 species, is widely distributed on all continents in tropical and temperate regions, and is often forming monospecific stands (important member of the reed belt; Kubitzki, 1998). Macrofossils with strong affinities to Typhaceae from the Yatağan basin (Gemici et al., 1990), Balya, Balıkesir (Engelhardt, 1903), and Soma basin (Gemici et al., 1991); and pollen of Typhaceae (including *Sparganium* L.), ‘Typha-typen’ (Benda, 1971a; Bozcu et al., 2015; Yavuz-Işlık, 2007), *Sparganiaceaepollenites* spp. (Akgün & Akyol, 1999; Akgün et al., 2007),
Sparganiaceae (Akkiraz, 2011; Akkiraz et al., 2012; Kayseri-Özer et al., 2014b), have previously been reported from Turkish middle Miocene localities. *Typha* sp. pollen is present in nearly all investigated samples, but rare (<3%; Fig. 2).

Clade Eudicots

Order Buxales Takht. ex Reveal

Family Buxaceae Dumort

Genus *Buxus* L.

*Buxus* sp.

(Figs 9D–F)

**Description:** Pollen, shape spheroidal, pollen outline circular to elliptic, pollen diameter 30–36 µm (LM); semitectate, exine 1.5–2 µm thick (LM); pantoporate, 18–24 pori (LM), pori diameter 0.8–1.5 µm (SEM); sculpturing scabrate (LM), microreticulate, nanoechinate (SEM), lumina of irregular shape.

**Remarks:** This grain resembles extant and fossil pollen of *Buxus* (Beug, 2004; Brückner, 1993; Grimsson et al., 2015a; Köhler, 2004-2005; Li et al., 2010; Miyoshi et al., 2011; Punt & Marks, 1991; Stuchlik et al., 2009). Brückner (1993) investigated pollen of extant Eurasian *Buxus* and identified six different pollen morphotypes. The here depicted pollen falls within the morphological range of Brückner’s *Buxus balearica* type, species within this group are part of the Eurasian clade of *Buxus* (Brückner, 1993; von Balthazar, Endress & Qiu, 2000). From the middle Miocene of Turkey fossil leaves of *Buxus* have been reported from the Yatağan basin (Bouchal et al., 2015; Güner & Denk, 2014) and the Soma basin (Gemici et al., 1991). Previous pollen reports from middle Miocene sediments of western Turkey: *Buxus* (Yavuz-Işık, 2007; Yavuz-Işık et al., 2011). *Buxus* sp. pollen is rare (mostly single encounters; Fig. 2) and present in samples S153579, S153573, S153565, S153559, S153540 and S153649.
Clade Fabids
Order Malpighiales Juss. ex Brecht. et J.Presl
Family Euphorbiaceae Juss.
Subfamily Euphorbioideae
Genus *Euphorbia* L.

*Euphorbia* sp.
(Figs 9G–J)

**Description:** Pollen, prolate, outline elliptic in equatorial view, length of polar axis 35–39 µm (LM), 29–32 µm (SEM), equatorial diameter 28–30 µm (LM), 25–28 µm (SEM); semitectate, exine 2.5–3 µm thick (LM), nexine thickened in aperture area; tricolporate, ectocolpus length ¾ to ⅚ of polar axis (LM, SEM), endoporus circular; sculpturing scabrate (LM), reticulate, fossulate-perforate, margo psilate (SEM).

**Remarks:** El-Ghazaly & Chaudhary (1993) examined the pollen morphology of sixty *Euphorbia* species and distinguished seven pollen types. *Euphorbia* sp. shows strong morphological similarities to *E. akenocarpa* Guss., *E. engleri* (Engl.) Pax, *E. esula* L., *E. monteiroi* Hook.f. (=*E. monteiri* in El-Ghazaly & Chaudhary, 1993), *E. polyantha* Pax, *E. rigida* M. Bieb, and *E. scheffleri* Pax; all of which have been grouped by El-Ghazaly & Chaudhary (1993) into Subtype 1b. - *E. monteiri*. These authors pointed out that these species are not part of a natural group. Among fossil taxa *Euphorbia* sp. shows strong morphological similarities to *Rhoipites pseudocingulum* R.Potonié (Benda, 1971a, only pl. 3, fig. 38; Ediger, 1990, fig. 6.12), *Tricolporopollenites* spp. (Kayseri & Akgün, 2010, figs 5.87–89), *T. helmsteddensis* Pflug in Pflug, and *T. marginatus* Durska (Stuchlik et al., 2014). *Euphorbia* pollen has previously been reported from the early and middle Miocene of Turkey (Yavuz-Işık, 2007; Yavuz-Işık et al., 2011). *Euphorbia* sp. pollen is rare and present in samples S153592 and S153649.
Euphorbiaceae gen. indet. 
(Figs 9K–M)

_Description:_ Pollen, prolate, outline elliptic in equatorial view, lobate in polar view, length of polar axis µm 27–30 (LM), 23–26 µm (SEM), equatorial diameter 18–22 µm (LM), 15–17 µm (SEM); eutectate, exine 1.5–2 µm thick (LM), nexine thickened in aperture area; tricolporate, ectocolpus length ⅖ to nearly entire polar axis (LM, SEM), porus rectangular to weakly elliptic; sculpturing scabrate (LM), microreticulate, perforate, psilate margo present (SEM), microreticulum funnel-shaped.

_Remarks:_ Euphorbiaceae gen. indet. resembles pollen of extant _Cephalocrotonopsis socotrana_ Pax and _Cephalocroton nudus_ Pax et Hoffm. both belonging to subtribe Epiprininae Müll. Arg. (Takahashi et al., 2000; Webster, 2014) with a palaeotropical distribution.

Euphorbiaceae pollen has not been differentiated in the LM pollencount (Fig. 2) and is of rare abundance (<1 %) but present in most investigated samples.

Family Linaceae DC. ex Perleb 
Genus _Linum_ L. 

*Linum* sp. 
(Figs 10A–C)

_Description:_ Pollen, monad, pollen outline circular to elliptic, length of polar axis 50–55 µm, diameter 45–50 µm (LM); atectate, exine 3–4 µm thick (LM), nexine thinner than sexine; tricolporate, ectocolpus length ⅖ to ⅗ of polar axis (LM, SEM); sculpturing, gemmate, clavate (LM, SEM), nexine perforate (SEM), gemma height 1–1.2 µm (SEM), diameter 1.5–2 µm (SEM), outline round to slightly penta- or hexagonal, flat-topped, 3–7 nanoechini present, one in the centre all the remaining towards the margin, several ridges radiating from a central nanoechinus towards margin; clavae height 1–1.2 µm (SEM), thickest part of clavae 0.3–0.6
μm (SEM) in diameter, topped with microechinus, a few ridges radiating from central echinus.

Remarks: This pollen corresponds to extant Linum pollen with closest resemblance to L. austriacum L. (Beug, 2004; Punt & Breejen, 1981). The ca 185 species of Linum show a subcosmopolitan distribution in temperate and subtropical regions (Dressler, Repplinger & Bayer, 2014; McDill & Simpson, 2011). Linum sp. is present in samples S153573 and S153649 (Fig. 2). This is, to our knowledge, the first middle Miocene record of Linum pollen in Anatolia.

Order Fabales Bromhead
Family Fabaceae Lindl.
Genus Podocarpium (A. Braun) Herendeen.

Tricolporopollenites wackersdorfensis Thiele-Pfeiffer/ Podocarpium sp.
(Figs 10D–F)

Description: Pollen, monad, pollen outline circular to irregular, pollen diameter 46–50 μm (SEM); eutectate, exine 1.5–2 μm thick (LM); tricolporate, ectocolpus length ½ to ⅔ of polar axis (SEM); sculpturing scabrate (LM), rugulate, perforate-fossulate (SEM), rugulae segmented, microrugulae width 0.3–0.1 μm (SEM), colpus with segmented margo (SEM).

Remarks: This pollen strongly resembles in situ pollen from fossil flowers of the extinct Fabaceae Podocarpium podocarpum (A. Braun) Herendeen (Liu et al., 2001). In the Miocene fossil record macro-, meso- and micro-fossils of Podocarpium podocarpum and pollen of Tricolporopollenites wackersdorfensis have been reported from localities in Central, East and southeast Europe (Austria, Germany, Switzerland, Italy, Armenia, Georgia, Poland, Hungary, Czech Republic, Serbia, Greece) and China [Grímsson et al., 2015a; Liu et al., 2001; Velizelos, Bouchal & Denk, 2014; Wang, Dilcher & Lott, 2007; as Fupingopollenites wackersdorfensis (Thiele-Pfeiffer) Liu in Liu, 1985; Shatilova & Mchedlishvili, 2009].
According to Wang et al. (2007), the genus was a warm temperate element growing in humid to semi-arid conditions that persisted until the Pleistocene in the eastern Mediterranean. *Tricolporopollenites wackersdorfensis/ Podocarpium* sp. has been encountered in samples S153573 and S153649.

Subfamily Papilionoideae DC.
Genus *Apios* Fabr.

*Apios* sp.

(Figs 10G–I)

Description: Pollen, spheroidal, outline circular in equatorial view, convex triangular in polar view; length of polar axis 30–35 µm (LM), 28–31µm (SEM), equatorial diameter 30–36 µm (LM), 27–30 µm (SEM); eutectate, exine 2.5–4 µm thick (LM), exine thickened around colpus; tricolpate, ectocolpus broad, ectocolpus length ¼ to ⅓ of polar axis (LM, SEM), colpus membrane shows same sculpturing as sexine; sculpturing psilate (LM), microrugulate, perforate, fossulate (SEM), microrugulae segmented (SEM).

Remarks: *Apios* sp. corresponds in most morphological characters (outline, size, apertures, exine thickness) with extant pollen of this genus (Li et al., 2010; Miyoshi et al., 2011; Willard et al., 2004), but differs slightly in sexine suprasculpturing. Extant *Apios fortunei* Maxim. and *A. delavayi* Franch. show smooth nanorugulae (compare Li et al., 2010; Miyoshi et al., 2011) whereas the here depicted pollen comprises segmented nanorugulae. Hence, it is possible that this pollen originated from an extinct species of the genus. Extant *Apios* has a disjunct East Asian and eastern and middle North American distribution (Sa & Gilbert, 2010). *Apios* sp. is present in samples S153539 and S153541.

Order Fagales Engl.
Family Betulaceae Gray
Subfamily Betuloideae Arn.

Genus *Alnus* Mill.

*Alnus* sp. (Figs 10J–L)

*Description*: Pollen, oblate, outline polygonal in polar view, equatorial diameter 24–30 µm (LM, SEM); eutectate, exine in mesocolpium 1–1.5 µm thick (LM), exine in aperture area 2.5–3 µm thick (LM); tetra- to hexaporate, pori diameter 1.5–2 µm, annulus present (LM, SEM), apertures connected by arcus; sculpturing scabrate (LM), nanoechinate, weakly microrugulate (SEM), a few nanoechini on vermiculate microrugulae, microrugulate sculpturing less pronounced on arcus (SEM).

*Remarks*: This pollen resembles extant and fossil *Alnus* pollen (Beug, 2004; Blackmore *et al*., 2003; Li *et al*., 2010; Miyoshi *et al*., 2011; Stuchlik *et al*., 2009). Pollen with affinities to extant *Alnus* has commonly been assigned to the form genera *Allnipollenites* R.Potonié (e.g. Potonié, 1931; Stuchlik *et al*., 2009) and *Polyvestibulopollenites* Pflug (e.g. Pflug, 1953; Stuchlik *et al*., 2009). Similar pollen is common in middle Miocene palynofloras of western Turkey; *Allnipollenites verus* R.Potonié [=*Polyvestibulopollenites verus* (R.Potonié) P.W.Thomson et Pflug (Akgün & Akyol, 1999; Akgün *et al*., 2007; Benda, 1971a; Ediger, 1990; Takahashi & Jux, 1991)]. *Alnus* (Akkiraz, 2011; Akkiraz *et al*., 2012; Bozcu *et al*., 2015; Kayseri-Özer *et al*., 2014b; Yavuz-Işık, 2007; Yavuz-Işık *et al*., 2011). Macrofossils of *Alnus* have previously been reported from Şahmalı, Aydın (Gemici *et al*., 1993) and Eskihisar (Bouchal *et al*., 2015; Güner & Denk, 2014).

*Alnus* sp. is present in nearly all investigated samples with highest abundances in the lower part of the Eskihisar mine section (pollen zone 1, up to 35%; Fig. 2).

Genus *Betula* L.

*Betula* sp.
(Figs 11A–C)

Description: Pollen, oblate, outline circular to convex triangular in polar view, equatorial diameter 20–25 µm (LM, SEM); eutectate, exine 1–1.5 µm thick (LM), nexine thinner than sexine; triporate, pori diameter 1.5–2 µm (LM, SEM), annulus formed by sexine, vestibulum present; sculpturing scabrate (LM), microrugulate, nanoechinate (SEM).

Remarks: This type of pollen resembles extant and fossil Betula pollen (Beug, 2004; Blackmore et al., 2003; Grimsson et al., 2015a; Li et al., 2010; Miyoshi et al., 2011; Stuchlik et al., 2009). Pollen with affinities to extant Betula commonly has been assigned to the form genera Betulapollenites R.Potonié ex R.Potonié and Trivestibulopollenites Pflug in P.W.Thomson et Pflug (Stuchlik et al., 2009) Betula and affiliated pollen have previously been reported from middle Miocene localities of Anatolia: Betulaepollenites bituitus R.Potonié (Benda, 1971a), B. sp., Trivestibulopollenites betuloides Pflug (Takahashi & Jux, 1991), Triatriopollenites bituitus (R.Potonié) P.W.Thomson et Pflug (Akgün & Akyol, 1999; Akgün et al., 2007; Gemici et al., 1991, 1993), Betula (Akkiraz, 2011; Akkiraz et al., 2012; Yavuz-Işık, 2007; Yavuz-Işık et al., 2011). Betula sp. is a common element in nearly all investigated samples, but never with high abundance (<3%; Fig. 2).

Subfamily Coryloideae Hook.f.

Genus Carpinus L.

Carpinus sp.

(Figs 11D–F)

Description: Pollen, oblate to spheroidal, outline circular to quadrangular in polar view, equatorial diameter 30–35 µm (LM); eutectate, exine 1–1.5 µm thick; tri- to tetraporate, pori diameter 2–4 µm (LM, SEM), annulus present; sculpturing scabrate (LM), nanoechinate, microrugulate (SEM).
Remarks: *Carpinus* sp. corresponds with extant and fossil *Carpinus* pollen (Beug, 2004; Blackmore *et al.*, 2003; Li *et al.*, 2010; Miyoshi *et al.*, 2011; Stuchlik *et al.*, 2009).

Pollen with affinities to extant *Carpinus* have commonly been assigned to the form genus *Carpinites* Srivastava (Srivastava, 1966; Stuchlik *et al.*, 2009).


*Carpinus* sp. is present in nearly all samples, with highest abundances in the middle part of the Eskihisar mine section (S153553–S153567, 4–6%; Fig. 2).

Genus *Corylus* L.

*Corylus* sp.

(Figs 11G–I)

*Description*: Pollen, spheroidal to oblate, outline circular to convex triangular in polar view, equatorial diameter 20–25 µm (LM, SEM); eutectate, exine 1–1.5 µm thick (LM), nexine thinner than sexine; triporate, pori diameter 1.5–2 µm (LM, SEM), annulus present; sculpturing scabrate (LM), nanoechinate, microrugulate (SEM).

*Remarks*: *Corylus* sp. resembles extant and fossil *Corylus* (Beug, 2004; Blackmore *et al.*, 2003; Li *et al.*, 2010; Miyoshi *et al.*, 2011; Stuchlik *et al.*, 2009). Pollen with affinities to extant *Corylus* commonly have been assigned to the form species *Triporopollenites coryloides* Pflug in P.W. Thomson et Pflug (Stuchlik *et al.*, 2009; Thomson & Pflug, 1953).

Previous reports from middle Miocene sediments of western Turkey: *Triporopollenites coryloides* (Akgün & Akyol, 1999; Akgün *et al.*, 2007; Benda, 1971a), *Corylus* (Akkiraz,
2011; Akkiraz et al., 2012; Yavuz-Işık, 2007), maybe Engelhardia (Kayseri & Akgün, 2010, figs 5.12, 5.17). Due to high morphological similarities between Corylus, Ostrya and Myricaceae in LM and the suboptimal preservation in most investigated samples these three genera have been combined in the pollen count if their assignment to one of these three genera was not unequivocal (Fig. 2). Only Myrica is known from the macrofossil record of Eskihisar (Bouchal et al., 2015; Güner & Denk, 2014).

Genus Ostrya L. Scop.

Ostrya sp.

(Figs 11J–L)

Description: Pollen, oblate, outline circular in polar view, equatorial diameter 24–30 µm (LM); eutectate, exine 1–1.5 µm thick; tri- to tetraporate, pori diameter 2–4 µm (LM, SEM), annulus present; sculpturing scabrate (LM), nanoechinate, weakly microrugulate (SEM).

Remarks: Ostrya sp. resembles extant and fossil Ostrya pollen (Beug, 2004; Blackmore et al., 2003; Stuchlik et al., 2009). Pollen with affinities to extant Ostrya have commonly been assigned to the form genus Ostryoipollenites R.Potonié ex R.Potonié (Potonié, 1960; Stuchlik et al., 2009). Macrofossils (leaves) of Ostrya have been reported from the Yatağan basin (Gemici et al., 1990), but this macrofossil record is in need of revision. Previous pollen reports from middle Miocene sediments of western Turkey: Ostryoipollenites rhenanus (Thiergart) R.Potonié (Benda, 1971a), Ostrya (Akkiraz, 2011; Akkiraz et al., 2012; Yavuz-Işık, 2007; Yavuz-Işık et al., 2011).

Family Fagaceae Dumontier

Genus Fagus L.

Fagus sp.

(Figs 12A–F)
**Description:** Pollen, spheroidal to prolate, elliptic to circular in equatorial view, circular to slightly lobate in polar view, length of polar axis 33–45 µm (LM, SEM), equatorial diameter 32–42 µm (LM, SEM); eutectate, exine 1.3–1.8 µm thick (LM); tricolporate, ectocolpus length ½ to ⅔ of polar axis (LM, SEM); sculpturing scabrate (LM), rugulate to verrucate-rugulate, fossulate-erforate (SEM), basic sculpturing units are rod-shaped elements, rugulae and verrucae formed by fused rodlets, rodlet length 1–1.5 µm (SEM), rodlet width 0.1–0.3 µm (SEM), relief can be pronounced.

**Remarks:** *Fagus* sp. corresponds to extant and fossil *Fagus* pollen (Beug, 2004; Denk, 2003; Gortemaker, 1986; Grimsson *et al.*, 2016; Miyoshi *et al.*, 2011; Praglowski, 1982; Stuchlik *et al.*, 2014; Van Benthem, Clarke & Punt, 1984). *Fagus* pollen from the Eskihisar mine section displays a marked morphological variability in form, size and ornamentation under LM and SEM. This has also been observed in extant and fossil pollen of this genus (e.g. Denk, 2003; Grimsson *et al.*, 2015b; Praglowski, 1982).

Pollen with affinities to extant *Fagus* commonly have been assigned to the form genus *Faguspollenites* Raatz (Raatz, 1937; Stuchlik *et al.*, 2014). Macrofossils (leaves) of *Fagus* have been reported from Soma (Gemici *et al.*, 1991), Aydın, Şahnalı (Gemici *et al.*, 1993, as *Castanea*), and the Yatağan basin (Bouchal *et al.*, 2015; Gemici *et al.*, 1990). *Fagus* pollen was reported in various middle Miocene localities of western Turkey: *Fagus* (Akkiraz, 2011; Akkiraz *et al.*, 2012; Benda, 1971a; Yavuz-Işık, 2007; Yavuz-Işık *et al.*, 2011).

In addition, a number of pollen types and morphotaxa listed in previous palynological studies under different names show strong resemblance to *Fagus* sp. For example, the pollen illustrated in Figs 12A–C strongly resembles *Nyssa* (Akkiraz, 2011, figs 9.II–JJ), *Nyssapollenites pseudocruciatus* (R.Potonié) Thiergart (Ediger, 1990, fig. 6.4), *Porocolpopollenites vestibulum* (R.Potonié) P.W.Thomson et Pflug (Akgün & Akyol, 1999, figs 9.64, 10.75–76, 11.43–45; *P. vestibuloformis* in Gemici *et al.*, 1993, fig. 3.27); *Tricolporopollenites* sp. (Kayseri & Akgün, 2010, fig 5.96); and the grain shown in Figs
12D–F closely match *Nyssoidites rodderensis* (R.Potonié) Pflug et P.W.Thomson (Benda, 1971a, pl. 4, fig. 2), *Tricolporopollenites kruschi* (R.Potonié) Pflug et P.W.Thomson (Akgün & Akyol, 1999, figs 11.77–79) and *T. edmundi* (R.Potonié) Pflug et P.W.Thomson (Ediger, 1990, fig. 6.14). *Fagus* sp. is present in all samples with fluctuating abundance (<9.25 %; Fig. 2).

Genus *Quercus* L.

*Quercus* sp. 1 (*Quercus* Group Cerris)

(Figs 12G–I)

*Description*: Pollen, prolate, elliptic in equatorial view, circular to lobate in polar view, length of polar axis 29–38 µm (LM), 28–32 µm (SEM), equatorial diameter 21–30 µm (LM), 18–25 µm (SEM); eutectate, exine 1.0–1.5 µm thick (LM); tricolpate to tricolporoidate, ectocolpus length ¾ to ⅚ of polar axis (LM, SEM); sculpturing scabrate (LM), microverrucate, microrugulate, perforate (SEM), basic sculpturing units are rod-shaped, microverrucae formed by fused or conjoined rods, rod length >0.5 µm.

*Remarks*: This pollen corresponds to extant *Quercus* Group Cerris pollen (Denk & Grimm, 2009; Makino, Hayashi & Takahara, 2009). Fossil pollen with affinities to extant *Quercus* pollen have been assigned to *Quercoidites* R.Potonié, P.W.Thomson et Thiergart ex R.Potonié and *Quercopollenites* Nagy (Stuchlik et al., 2014). Reliable assignment to an infrageneric group for dispersed fossil *Quercus* pollen is only possible using a SEM due to the miniscule defining features. Because of the difficult assignment to infrageneric groups in LM and the poor preservation of the samples, for the pollen count only pollen size was used to designate *Quercus* pollen in the Eskihisar samples (“*Quercus* Large” approximately matching *Quercus* Group Quercus and Group Cerris, and “*Quercus* Small” approximately matching *Quercus* Group Ilex; cf. Fig. 2). Extant oaks of Group Cerris show a distribution from Europe to the Himalayas and East Asia (de Beaulieu et al., 2010; Denk & Grimm, 2010).
Macrofossils (leaves) of *Quercus* have been reported from early/middle Miocene deposits of western Turkey of Balya, Balıkesir (Engelhardt, 1903), Soma (Gemici et al., 1991), Şahinalı, Aydın (Gemici et al., 1993), and the Yatağan basin (Bouchal et al., 2015; Gemici et al., 1990; Güner & Denk, 2014). Previous pollen reports of *Quercus* from middle Miocene sediments of western Turkey: *Intratriporopollenites kettigensis* (R.Potonié) Thiergart (Ediger, 1990), *Quercopollenites asper* (Pflug et P.W.Thomson in P.W.Thomson et Pflug) Kohlman-Adamska et Ziemińska (=*Quercoidites asper* in Akgün et al., 2007; =asper-Gruppe in Benda, 1971a), *Quercoidites henrici* (R.Potonié) R.Potonie (Akgün et al., 2007; Benda, 1971a), *Quercoidites microhenrici* (R.Potonié) R.Potonié, P.W.Thomson et Thiergart ex R.Potonié (Akgün et al., 2007; Benda, 1971a; =Tricolpopollenites microhenrici in Ediger, 1990), *Quercus* (Akkiraz, 2011; Bozcu et al., 2015) *Quercus* evergreen (Akkiraz, 2011; Akkiraz et al., 2012; Yavuz-Işık, 2007; Yavuz-Işık et al., 2011), *Quercus* deciduous (Akkiraz et al., 2012; Yavuz-Işık, 2007; Yavuz-Işık et al., 2011). These reports are difficult to compare to specific taxa of *Quercus*. Roughly, types considered ‘deciduous’ in previous studies correspond to Group Quercus and Group Cerris, while pollen types considered ‘evergreen’ in many cases correspond to *Quercus* Group Ilex. *Quercus* pollen is common in all samples (up to 20%; Fig. 2).

*Quercus* sp. 2 (*Quercus* Group Ilex)

(Figs 12J–L)

*Description*: Pollen, spheroidal to prolate, elliptic to circular in equatorial view, circular to lobate in polar view, length of polar axis 24–28 μm (LM), equatorial diameter 20–24 μm (LM); eutectate, exine 1.0–1.5 μm thick (LM), tricolporate to tricolporoidate, ectocolpus length ¾ to ⅚ of polar axis (LM, SEM); sculpturing scabrate (LM), rugulate, perforate, fossulate (SEM), basic sculpturing units are rod-shaped structures, rugulae formed by fused or conjoined rods, rod length >0.8 μm, pronounced/distinct rod relief (SEM).
Remarks: This pollen type resembles extant *Quercus* Group Ilex with closest resemblance to *Q. baloot* Griff., *Q. baronii* Skan; *Q. coccifera* L., *Q. dilatata* Royle (syn. *Q. floribunda* Lindl. ex A.Camus); *Q. dolicholepis* A.Camus (syn. *Q. spathulata* Seemen); *Q. ilex* L., *Q. lanata* Sm.; *Q. phillryeoides* A.Grey (Denk & Grimm, 2009; Makino *et al.*, 2009).

*Quercus* sp. 3 (*Quercus* Group Quercus)

(Figs 13A–C)

Description: Pollen, prolate, elliptic in equatorial view, apocolpia flat to slightly rounded, length of polar axis 27–31 µm (LM, SEM), equatorial diameter 18–21 µm (LM, SEM); eutectate, exine 1.0–1.5 µm thick (LM), tricolporate, ectocolpus length ⅔ to ¾ of polar axis (LM, SEM); sculpturing scabrate (LM), verrucate, rugulate, fossulate, perforate (SEM), nanoechinate suprasculpture.

Remarks: This pollen type corresponds to extant *Quercus* Group Quercus with close resemblance to e.g. *Q. pyrenaica* L., *Q. pubescens* L., *Q. mongolica* Fisch. ex Turcz. (Chang & Wang, 1986; Denk & Grimm, 2009; Makino *et al.*, 2009; Van Benthem *et al.*, 1984). Pollen of *Quercus* Group Quercus was rarely encountered during this investigation.

Genus *Trigonobalanopsis* Kvaček et Walther

*Trigonobalanopsis* sp.

(Figs 13D–F)

Description: Pollen, prolate, elliptic in equatorial view, length of polar axis 20–22 µm (LM), equatorial diameter 13–15 µm (LM); eutectate, exine 1.0–1.5 µm thick (LM), tricolporate, ectocolpus length ¾ to ⅚ of polar axis (LM, SEM); sculpturing scabrate (LM), rugulate to microrugulate, perforate (SEM), angular pattern formed by three to six microrugulae (SEM), microrugulae distinctly segmented (SEM).
Remarks: The segmented microrugulate sexine sculpturing is the diagnostic characteristic of the extinct genus *Trigonobalanopsis* (Walther & Zetter, 1993). Using only LM it is impossible to distinguish *Trigonobalanopsis* from various other Castaneoideae pollen. Pollen of extant Castaneoideae are difficult if not impossible to distinguish to genus level in LM and even under SEM investigation the pollen morphological variability is overlapping between extant genera (Praglowski, 1984). For the LM pollen count, castaneoid pollen was jointly treated as Castaneoideae. Fossil pollen with affinity to Castaneoideae has commonly been assigned to the form species *Cupuliferoipollenites pusillus* (R.Potonié) R.Potonié ex R.Potonié and *C. oviformis* (R.Potonié) R.Potonié ex R.Potonié (e.g. Stuchlik et al., 2014). All Castaneoideae pollen encountered in LM and cross-checked under SEM showed segmented microrugulate sculpturing, no smoothly microrugulate sculptured pollen as in extant members of Castaneoideae was encountered.


Family Juglandaceae Dumontier DC. ex Preleb

Subfamily Engelhardioideae Iljinsk.

Engelhardioideae gen. indet.

(Figs 13G–L)
**Description:** Pollen, oblate, outline convex triangular in polar view, equatorial diameter 25–30 µm (LM), 22–26 µm (SEM); eutectate, exine 1.0–1.5 µm thick (LM); triporate, pore diameter 1.5–2 µm (LM), ectoporous circular, aperture sunken; sculpturing scabrate (LM), nanoechinate, perforate (SEM).

**Remarks:** Engelhardioideae gen. indet. falls into the morphological range of extant and fossil pollen of this subfamily, with closest resemblance (size range; circular ectoapertures) to *Oremunnea* and *Alfaroa* (Stone & Broome, 1975). The specimens shown in Fig. 13G–L displays light-microscopic affinities to *Platycarya* L. due to the presence of pseudocolpi-like folds. The SEM investigation did not verify the presence of pseudocolpi. Pollen with affinities to extant Engelhardioideae commonly has been assigned to the form genus *Momipites* Wodehouse emend. Nichols and *Plicatopollis* Krutzsch (Manchester, 1987; Stuchlik et al., 2009).


Engelhardioideae gen. indet. is a rare element but present in most of the investigated samples (Fig. 2).

Subfamily Juglandoideae

Genus *Carya* Nutt.
**Carya** sp.

(Figs 14A–C)

*Description*: Pollen, oblate, outline circular in polar view, equatorial diameter 35–48 µm (LM and SEM); eutectate, exine 1.0–1.5 µm thick (LM); triporate, pore diameter 3–4 µm, pores sunken, apertures alignment on equator or slightly shifted to distal face of pollen (LM, SEM); sculpturing scabrate (LM), nanoechinate, perforate (SEM), area between nanoechini made up of fused rodlets (SEM).

*Remarks*: This pollen type resembles extant and fossil *Carya* pollen (Grimsson et al., 2016; Jones et al., 1995; Manchester, 1987; Stone & Broome, 1975; Stuchlik et al., 2009). Pollen with affinities to extant *Carya* commonly has been assigned to the form species *Caryapollenites simplex* (R.Potonié) Raatz ex R.Potonié. Macrofossils of *Carya* have been reported from the Yatağan basin (Bouchal et al., 2015; Gemici et al., 1990; Güner & Denk, 2014), Şahmalı, Aydın (Gemici et al., 1993), and Soma (Gemici et al., 1991). Previous pollen reports from middle Miocene sediments of western Turkey: *Caryapollenites simplex* [=*Subtriopollenites simplex* (R.Potonié) Pflug et Thomson] (Akgün & Akyol, 1999; Benda, 1971a; Ediger, 1990; Gemici et al., 1993; Gemici et al., 1991; Kayseri-Özer et al., 2014a; Takahashi & Jux, 1991), *Carya* (Akkiraz, 2011; Akkiraz et al., 2012; Bozcu et al., 2015; Kayseri & Akgün, 2010; Kayseri-Özer et al., 2014b; Yavuz-Işık, 2007; Yavuz-Işık et al., 2011). *Carya* sp. is a common element in all investigated samples (up to 7%; Fig. 2).

**Genus Juglans** L.

*Juglans* sp.

(Figs 14D–F)

*Description*: Pollen, oblate, pollen outline circular, pollen diameter 39–45 µm (LM, SEM); eutectate, exine 1.0–1.5 µm thick (LM); stephanoporate (9–12) with some pori in both polar
areas, pore diameter 1.5–2 µm (LM), annuli occasionally present, apertures sunken; sculpturing scabrate (LM), nanoechinate, perforate (SEM).

**Remarks:** This pollen resembles extant and fossil *Juglans* pollen (Bos & Punt, 1991; Grimsson *et al.*, 2016; Manchester, 1987; Stone & Broome, 1975; Stuchlik *et al.*, 2009). Pollen with affinities to extant *Juglans* has commonly been assigned to the form genus *Juglanspollenites* Raatz (Manchester, 1987; Stuchlik *et al.*, 2009). Previous pollen reports from middle Miocene sediments of western Turkey: *Juglans*-Typ (Benda, 1971a), *Juglans* (Bozcu *et al.*, 2015; Yavuz-Işık, 2007; Yavuz-Işık *et al.*, 2011). *Juglans* sp. is present in most samples with highest abundances in the lower part of the Eskihisar mine section above the main coal seam (<3%; Fig. 2).

**Genus Pterocarya** Kunth

*Pterocarya* sp.

(Figs 14G–I)

**Description:** Pollen, oblate, pollen outline circular to polygonal in polar view, pollen diameter 38–43 µm (LM, SEM); eutectate, exine 1.0–1.5 µm thick (LM); tetra- to hexaporate, pore diameter 1.5–2 µm (LM), apertures weakly protruding, annulus present; sculpturing scabrate (LM), nanoechinate (SEM).

**Remarks:** This pollen type corresponds to extant and fossil *Pterocarya* pollen (Grimsson *et al.*, 2016; Manchester, 1987; Stone & Broome, 1975). Pollen with affinities to extant *Pterocarya* have commonly been assigned to the form genus *Polyatriopollenites* Pflug (Stuchlik *et al.*, 2009). Fossil leaflets of *Pterocarya* have been reported from Eskihisar (Güner & Denk, 2014). Previous pollen reports from middle Miocene sediments of western Turkey: *Polyatriopollenites stellatus* (R.Potonié) Pflug (Akgün *et al.*, 2007; Benda, 1971a; Gemici *et al.*, 1991; Kayseri-Özer *et al.*, 2014a), *Pterocarya* (Akgün & Akyol, 1999; Akkiraz, 2011; Akkiraz *et al.*, 2012; Bozcu *et al.*, 2015; Yavuz-Işık, 2007; Yavuz-Işık *et al.*, 2011), maybe
Polyporopollenites sp. (Ediger, 1990, fig. 15). Pterocarya sp. is rare (mostly single encounters; Fig. 2) and present in most samples.

Family Myricaceae A.Rich. ex Kunt
Genus Morella Lour. vel. Myrica L.
Morella vel. Myrica sp.
(Figs 14J–L)

Description: Pollen, oblate, outline triangular to triangular convex in polar view, equatorial diameter 26–31 µm (LM), 25–27 µm (SEM); eutectate, exine 1.0–1.5 µm thick (LM), nexine absent in aperture area; triporate, endoaperture wider than ectoaperture, atrium formed by the sexine, ectopore diameter 1.5–2.5 µm (LM, SEM); sculpturing scabrate (LM), nanoechinate (SEM), nanoechini evenly spaced.

Remarks: Myricaceae pollen is very homogeneous; Morella and Myrica show highly similar morphological characters (LM, SEM) and cannot be differentiated; Comptonia L’Hér. can be distinguished by its distinct larger ectopori and Canacomyrica Guillaumin by its distinct larger size and protrusions (Punt, Marks & Hoen, 2002; Sundberg, 1985). Pollen with affinities to extant Myricaceae have commonly been assigned to the form genus Myricipites Wodehouse emend. Grabowska et Ważyńska (Stuchlik et al., 2009). Fossil leaves of Myrica have been reported from the early/middle Miocene of western Anatolia of Balya, Balikesir (Engelhardt, 1903), Soma (Gemici et al., 1991), Şahinalı, Aydın (Gemici et al., 1993) and the Yatağan basin (Bouchal et al., 2015; Güner & Denk, 2014). Previous pollen reports from middle Miocene sediments of western Turkey: Myricipites myricoides (=Triatriopollenites myricoides) (Kremp) Nagy (Akgün & Akyol, 1999; Akgün et al., 2007; Benda, 1971a; Gemici et al., 1991, 1993;), Myricaceae (Kayseri & Akgün, 2010; Kayseri-Özer et al., 2014b), Myrica (Akkiraz, 2011; Bozcu et al., 2015; Yavuz-Işık, 2007; Yavuz-Işık et al., 2011), maybe T. rurensis Pflug et P.W.Thomson (Takahashi & Jux, 1991, pl. 19, figs. 4–7).
In LM pollencounts *Corylus*, *Ostrya* and Myricaceae have been grouped together if no unambiguous determination was possible (Fig. 2). Pollen of this type is present in nearly all samples, but identification to one of the above mentioned genera was rarely possible due to bad preservation.

Order Rosales Bercht. et J.Presl
Family Rosaceae Juss.
Rosaceae gen. indet.
(Figs 15A–C)
*Description*: Pollen, prolate, pollen outline elliptic in equatorial view, length of polar axis 22–24 µm (LM), 20–22 µm (SEM), equatorial diameter 14–18 µm (LM), 12–15 µm (SEM); eutectate, exine 1.2–1.8 µm thick (LM), tricolporate, nexine slightly thickened in equatorial aperture area, ectocolpus length ¾ to ⅚ of polar axis (LM, SEM); sculpturing psilate (LM), striate, perforate (SEM), striae mainly parallel to polar axis in colpus area, in mesocolpium striae can be parallel to equator, striae 0.1–0.2 µm wide (SEM).

*Remarks*: A number of Rosaceae produce pollen with tricolporate apertures and striate perforate exine sculpturing (Hebda et al., 1988a; 1988b; Hebda & Chinnappa, 1990; 1994, table 1). This makes it difficult to assign Rosaceae gen. indet. to genus level. Macrofossils of Rosaceae have only rarely been reported from early and middle Miocene localities in western Anatolia (Bouchal et al., 2015). Previous pollen reports from middle Miocene sediments of western Turkey: Rosaceae (Yavuz-Işık, 2007; Yavuz-Işık et al., 2011). Pollen of this type has been encountered in samples S153649 and S153559.

Family Ulmaceae Juss.
Genus *Cedrelospermum* (Saporta) Manchester
*Cedrelospermum* sp.
Description: Pollen, rarely tetrahedral tetrads (single encounter), tetrad diameter 45–57 µm (LM), 43–52 µm (SEM), aperture arrangement according to Garside’s law; monad, spheroidal to oblate, outline convex triangular to polygonal in polar view, equatorial diameter 32–40 µm (LM), 29–37 µm (SEM), single pollen in tetrad show similar size range; eutectate, exine 1–1.5 µm thick (LM), nexine thinner than sexine, sexine slightly thickend around pori (LM); stephanoporate (3–5), porus sunken, porus diameter 1.5–2 µm (LM); sculpturing verrucate (LM), verrucate, nanoechinate, perforate (SEM), verrucae diameter 1.5–2.5 µm, verrucae circular.

Remarks: Pollen of this type belongs to the extinct ulmaceaeous genus Cedrelospermum (Bouchal, Zetter & Denk, 2016; Grimsson et al., 2016). Paleogene pollen of this type show a slightly smaller size range than pollen encountered in Miocene sediments (compare Bouchal et al., 2016; Grimsson et al., 2016). Cedrelospermum sp. falls within the range of the form genus Ulmipollenites Wolff (Stuchlik et al., 2009). Previous pollen reports of morphological similar to Cedrelospermum sp. from middle Miocene sediments of western Turkey: Ulmipollenites undulosus (Wolff) P.W.Thomson et Pflug (=Polyporopollenites undulosus) (Akgün & Akyol, 1999, only figs 9.43 & 10.57; Benda, 1971a, pl. 4, only fig. 16; Takahashi & Jux, 1991, pl. 21, fig. 15). Pollen of this type is present in most samples but never abundant (Fig. 2).

Genus Ulmus Mirbel

Ulmus sp.

Description: Pollen, oblate, outline circular to polygonal in polar view, equatorial diameter 35–46 µm (LM), 33–41 µm (SEM); eutectate, exine 1–1.5 µm thick (LM), sexine slightly
thickend around pori (LM); stephano(4–6)porate, porus diameter 2–3 μm (LM); sculpturing rugulate (LM), rugulate, nanoechinate, perforate (SEM).

**Remarks:** This pollen resembles extant and fossil *Ulmus* pollen (Grimsson et al., 2016; Stafford, 1995; Stuchlik et al., 2009; Takahashi, 1989; Zavada, 1983). Pollen with affinities to extant *Ulmus* has commonly been assigned to the form genus *Ulmipollenites* Wolff (Stuchlik et al., 2009). Previous pollen reports from middle Miocene sediments of western Turkey: *Ulmipollenites undulosus* (Wolff) P.W.Thomson et Pflug (= *Polyporopollenites undulosus*, Akgün & Akyol, 1999; Akgün et al., 2007; Akyol & Akgün, 1990; Benda, 1971a; Ediger, 1990; Gemici et al., 1991, 1993; Kayseri-Özer et al., 2014a; Takahashi & Jux, 1991), *Ulmus* (Akkiraz, 2011; Akkiraz et al., 2012; Bozcu et al., 2015; Kayseri & Akgün, 2010; Kayseri-Özer et al., 2014b; Yavuz-İşık, 2007; Yavuz-İşık et al., 2011). *Ulmus* sp. is a common element in all investigated samples (<11 % in 171010E34; Fig. 2).

Genus Zelkova Spach

**Zelkova sp.**

(Figs. 16A–C)

**Description:** Pollen, oblate, outline circular to polygonal in polar view, equatorial diameter 28–38 μm (LM, SEM); eutectate, exine 1–1.5 μm thick (LM), nexine thinner than sexine, sexine thickened around pori (LM), exine slightly protruding in aperture area; stephano(4–5)porate, porus diameter 2–3 μm (LM); sculpturing rugulate (LM), rugulate, nanoechinate, perforate (SEM), because of its thickened annuli and protruding apertures folds spanning between adjacent apertures are present, these resemble arci (=pseudoarci).

**Remarks:** Zelkova sp. differs from *Ulmus* sp. in thickened annuli and protruding apertures. This pollen type falls within the morphological range (thickened annuli, “pseudoarci” presence) of the form genus *Zelkovaepollenites* Nagy (Stuchlik et al., 2009). Extant *Zelkova serrata* (Thunb.) Makino shows distinct thickened exine surrounding the protruding apertures.
Macrofossils of Zelkova have been reported from the Yatağan basin (Bouchal et al., 2015; Gemici et al., 1990; Güner & Denk, 2014), and Soma (Gemici et al., 1991). Previous pollen reports from middle Miocene sediments of western Turkey: Zelковаpollenites potoniei Nagy (Takahashi & Jux, 1991; Yavuz Isik et al., 2011), Zelkova (Akkiraz, 2011; Akkiraz et al., 2012; Bozcu et al., 2015; Kayseri & Akgün, 2010; Yavuz-İşık, 2007; Yavuz-İşık et al., 2011). Zelkova sp. is a common element in most samples (Fig. 2).

Malvids

Order Geraniales Juss. ex Bercht. et J.Presl

Family Geraniaceae Juss.

Genus Erodium L’Hér. ex Aiton

Erodium sp.

(Figs 16D–F)

Description: Pollen, oblate, outline circular to elliptic in equatorial view, length of polar axis 57–72 µm (LM), 47–61 µm (SEM), equatorial diameter 52–61 µm (LM), 39–47 (SEM); semitectate, exine 5–7 µm thick (LM), sexine three to five times thicker than nexine, indistinct tricolporate, ectocolpus length ½ to ⅓ of polar axis (LM, SEM); sculpturing striato-reticulate (LM, SEM), muri in two layers, upper layer consisting of winding long and short striae, subjacent layer intertwined and connected with upper layer (SEM), muri width 0.5–0.8 µm, muri surface smooth (SEM).

Remarks: Erodium sp. corresponds in its morphological characteristics (size range, thick sexine, complex reticum) to Stafford & Blackmore (1991) Erodium cicutarium type, a common pollen type of the extant Eurasian Erodium species, e.g. E. cicutarium (L.) L’Hér., E. laciniatum (Cav.) Willd. (El-Ghazaly, 1991; Perveen & Qaiser, 1999). Extant Erodium consists of ca 80 species, shows a fairly cosmopolitan distribution and a high concentration in
Mediterranean climate regions (Albers & Van der Walt, 2007). *Erodium* pollen has been reported from the Pliocene sediments of the western Turkey (Yavuz Isik et al., 2011).

*Erodium* sp. is present in a single sample from the coal seam and more regularly occurring in the upper part of the Eskihisar mine section (Fig. 2).

Order Myrtales Juss. ex Bercht. et J.Presl
Family Lythraceae J.St.-Hil.
Genus *Decodon* J.F.Gmel.

*Decodon* sp.
(Figs 16G–I)

*Description*: Pollen, prolate, elliptic in equatorial view, length of polar axis 16–18 µm (LM), 14–16 µm (SEM), equatorial diameter 10–12 µm (LM), 9–11 µm (SEM); eutectate, exine 1.5–2 µm thick (LM); tricolporate, ectocolpus with bridge, ectocolpus length ¾ to ⅚ of polar axis (LM, SEM), nexine surrounding endoporus thickened (LM); sculpturing psilate (LM), perforate, fossulate, rugulate (SEM), few perforations present in apocolpium and central mesocolpium, ornamentation increasing towards colpus area, strongest rugulation in equatorial area.

*Remarks*: *Decodon* sp. resembles extant and fossil *Decodon* pollen (Grímsson, Ferguson & Zetter, 2012a). Grímsson *et al* (2012a) investigated pollen morphological trends within fossil *Decodon* and identified six morphotypes. *Decodon* from Eskihisar. is most similar to morphotype 6 only differing by its smaller size. This morphotype has been reported from the late Miocene of Iceland, Austria, and Northeast China and from the Pliocene of Germany. Pollen with affinities to extant *Decodon* commonly have been assigned to the form species *Lythraceae pollenites decodonensis* Stuchlik (Stuchlik *et al*., 2014; Ziembińska-Tworzydlo *et al*., 1994).
Extant *Decodon verticillatus* (L.) Elliott shows an eastern North American distribution, thriving in wetland habitats (Graham, 2007). This genus was more species rich and had a more extensive Northern Hemispheric distribution in the Oligocene and Neogene (Kvaček & Sakala, 1999). Previous reports of pollen with morphological similarities to *Decodon* sp. from middle Miocene sediments of western Turkey: *Cupuliferoipollenites oviformis* R.Potonié (Benda, 1971a), *C. pusillus* (R.Potonié) R.Potonié ex R.Potonié (Takahashi & Jux, 1991, pl. 16, only fig. 17), *Decodon* sp. is common in samples from the coal seam and in the upper part of the Eskihisar mine section, but absent in the middle of the section (Fig. 2).

Family Onagraceae Juss.

Genus *Ludwigia* L.

*Ludwigia* sp.

(Figs 16J–M)

*Description*: Pollen, oblate, convex triangular in equatorial view, equatorial diameter 43–50 µm (LM), 40–48 µm (SEM); eutectate, exine 2–2.5 µm thick (LM); triporate, atrium present (SEM); sculpturing psilate to scabrate (LM), micorugulate, fossulate (SEM), rugula length <1 µm, rugulae width 0.2–0.4 µm, smooth viscin threads present.

*Remarks*: The morphological characteristics (size, microrugulate sculpturing, smooth viscin threads) of this grain correspond to extant and fossil *Ludwigia* pollen (Grímsson, Zetter & Leng, 2012b; Praglowski *et al.*, 1994). Pollen with affinities to extant Onagraceae have commonly been assigned to the form genus *Corsinipollenites* Nakoman (Stuchlik *et al.*, 2009). From the middle and late Miocene of western Turkey Onagraceae pollen has previously been reported; *Corsinipollenites occlusanoctis* (Thiergart) Nakoman (Akgün & Akyol, 1999; Kayseri-Özer *et al.*, 2014b), Onagraceae (Akkiraz *et al.*, 2012), Oenotheraceae
Ludwigia sp. has been encountered in a single sample (S153582) of the Eskihisar mine section (Fig. 2).

Order Malvales Juss. ex Bercht. et J.Presl
Family Malvaceae Juss.
Subfamily Malvoideae Burnett
Malvoideae gen. indet.
(Figs 17A–C)

*Description*: Pollen, spheroidal, outline circular equatorial view, equatorial diameter without echini 65–72 µm (LM, SEM); eutectate, exine 2.5–4 µm thick (LM), sexine thinner than nexine, columellae ca 1 µm high (SEM); pantoaperturate (80+ pores), porus diameter 1.5–2.5 µm (SEM), operculum present; sculpturing echinate (LM), echinate, perforate (SEM), echinus base diameter 1.5–2.7 µm (SEM), short (1.5–3.5 µm) and long (5–7 µm) echini present (SEM).

*Remarks*: Malvoideae gen. indet. falls in the morphological range of extant Malvoideae with particular morphological similarities (pollen size, number of pores, echini size) to *Malva* L. pollen (Christensen, 1986) and *Malva sylvestris* type of Culhane & Blackmore (1988), but differing by the absence of microgranulae as supratectal elements. Pollen with affinities to extant *Malvaceae* has commonly been assigned to the form genera *Malvacipollis* Harris emend. Krutzsch and *Malvacearumpollis* Nagy emend Krutzsch (Krutzsch, 1966; Stuchlik *et al.*, 2009). A single grain of Malvoideae gen. indet. was encountered in sample S153541 (Fig. 2).

Subfamily Tilioideae Arnott
Genus *Tilia* L.
*Tilia* sp.
Description: Pollen, oblate, outline circular to convex triangular in polar view, equatorial diameter 28–35 µm (LM), 25–30 µm (SEM); semitectate, exine 1.5–2 µm thick (LM), nexine slightly thinner than sexine, nexine thickened in aperture areas (3–4 µm in LM); tricolporate, ectoapertures brevicolpate; sculpturing reticulate (LM), “microreticulate”, perforate (SEM), “lumina” (funnel-shaped concavities) irregularly shaped, base of concavities perforate (SEM).

Remarks: This pollen type corresponds to extant and fossil Tilia pollen, with strongest morphological similarities (“lumina” size and form) to extant T. platyphyllos Scop. (Beug, 2004; Chambers & Godwin, 1971; Christensen & Blackmore, 1988; Perveen, Grafström & El-Ghazaly, 2004; Stuchlik et al., 2014; Yu-Long & Yan-Sheng, 1984).

Tilia consists of ca 23 tree species, with a temperate to subtropical Northern Hemispheric distribution (Bayer & Kubitzki, 2003). Pollen with affinities to extant Tilia has commonly been assigned to the form species Intratriporopollenites instructus (R.Potonié) P.W.Thomson et Pflug (Stuchlik et al., 2014; Thomson & Pflug, 1953). Fossil inflorescence bracts of Tilia have been reported from Eskihisar (Bouchal et al., 2015). Previous pollen reports from middle Miocene sediments of western Turkey: Intratriporopollenites instructus (=Tiliaepollenites instructus R.Potonié ex R.Potonié et Venitz) (Akgün & Akyol, 1999; Akgün et al., 2007; Benda, 1971a; Gemici et al., 1993; Gemici et al., 1991; Takahashi & Jux, 1991), I. indubitabilis (R.Potonié) P.W.Thomson et Pflug (Akgün et al., 2007), Tilia (Akkiraz, 2011; Kayseri-Özer et al., 2014b; Yavuz-Işık, 2007; Yavuz-Işık et al., 2011).

In the Eshkihisar section Tilia sp. occurs sporadically and only single encounters per sample were observed.

Order Sapindales Juss. ex Bercht. et J.Presl
Family Anacardiaceae R.Br./Simaroubaceae DC./Rutaceae Juss.
**Remarks:** Anacardiaceae, Simaroubaceae and Rutaceae produce prolate, striate to striatoreticulate pollen with a distinct costa (e.g. Barento et al., 1987; Beug, 2004; Erdtman, 1952). Using LM, assignment of dispersed pollen belonging to these three families is difficult because of overlapping pollen morphology. Therefore, pollen showing a prolate, striate to striatoreticulate morphology with a distinct costa has been combined for the LM pollen count within the category Anacardiaceae/Simaroubaceae/Rutaceae (ASR)-type (Fig. 2.). Previous reports of pollen corresponding to ASR-type-pollen from middle Miocene sediments of western Turkey: *Tricolporopollenites* spp. (Akyol & Akgün, 1990, pl. 1, fig. 53; Kayseri & Akgün, 2010, figs 5.87–95), *T. dolium* (R.Potonié) P.W.Thomson et Pflug (Akgün & Akyol, 1999), *T. helmsteddensis* Pflug in P.W.Thomson et Pflug (Akgün & Akyol, 1999), *T. pseudocingulum* (R.Potonie) P.W.Thomson et Pflug (=*Rhoipites pseudocingulum*) (Akgün & Akyol, 1999; Akgün et al., 2007; Benda, 1971a; Kayseri-Özer et al., 2014b), *Rohipites retiformis* Rocknall et Mildenhall (Takahashi & Jux, 1991), *Striatocolporites* sp. a (Takahashi & Jux, 1991), Anacardiaceae (Yavuz-İşık et al., 2011).

In the lower part of the Eshkhisar (S153539–S153555) section ASR-type-pollen is common; in the upper part only sporadic occurrences were observed.

**Anacardiaceae/Simaroubaceae/Rutaceae (=ASR-type-pollen) gen. indet. 1**

(Figs 17G–I)

**Description:** Pollen, prolate, elliptic in equatorial view, length of polar axis 32–38 µm (LM), 31–35 µm (SEM), equatorial diameter 30–35 µm (LM), 28–32 µm (SEM); semitectate, exine 2–2.5 µm thick in polar area, sexine thicker than nexine, costae present, costae not reaching polar colpus endings (LM); tricolporate, ectocolpus length ¾ to ⅞ of polar axis (LM, SEM), endoporous circular, framed by circular costa (LM); sculpturing striate (LM), striato-reticulate (SEM), muri (striae) width 0.3–0.6 µm (SEM).
Remarks: ASR-type-pollen gen. indet. 1 shows a more irregular shaped striato- reticulum and lacks the perpendicular links connecting striae (compare ASR-type-pollen gen. indet. 2).

ASR-type-pollen gen. indet. 2 (aff. *Ailanthus* Desf.)
(Figs 17J–L)

Description: Pollen, prolate, elliptic in equatorial view, length of polar axis 32–36 µm (LM), 30–34 µm (SEM), equatorial diameter 26–30 µm (LM), 24–28 µm (SEM); semitectate, exine 2–2.5 µm thick in polar area, sexine thicker than nexine, costae present, costae nearly reaching polar colpus endings (LM); tricolporate, ectocolpus length ⅔ to ¾ of polar axis (LM, SEM), endopori circular, framed by quadrangular costa (LM); sculpturing striate (LM), striato-reticulate (SEM), muri (striae) width 0.3–0.6 µm (SEM), striae on sub level connected by perpendicular links forming a reticulum in the grooves (SEM).

Remarks: ASR-type-pollen gen. indet. 2 differs from ASR-type-pollen gen. indet. 1 by distinct striato-reticulate exine sculpturing (striae connected by perpendicular links forming a reticulum in the grooves), and by longer and more rectangular costae. Pollen of extant *Ailanthus altissima* (Mill.) Swingle shows similar morphological features (compare Beug, 2004; Li et al., 2010; Diethart, 2005). Pollen of this type has been encountered in sample S153546.

ASR-type-pollen gen. indet. 3 (aff. Anacardiaceae)
(Figs 18A–C)

Description: Pollen, prolate, elliptic in equatorial view, length of polar axis 40–45 µm (LM), 34–38 µm (SEM), equatorial diameter 25–28 µm (LM), 22–26 µm (SEM); semitectate, exine 2.5–3.5 µm thick in polar area, exine thickened in polar area, sexine thicker than nexine, costae present, costae nearly reaching polar colpus endings (LM); tricolporate, ectocolpus length ⅖ to nearly whole length of polar axis (LM, SEM), endopori circular, framed by
elliptic costa (LM); sculpturing striate (LM, SEM), muri (striae) width 0.4–0.6 μm (SEM), striae densely packed (SEM).

**Remarks:** ASR-type-pollen gen. indet. 3 differs from the two other types by a more elongated shape, thickened exine in polar areas, larger size and more tightly packed striae. This pollen type strongly resembles (size, thickened polar areas and apertures) *Tricolporopollenites turcianus* Takahashi et Jux (Takahashi & Jux, 1991, pl. 16, figs 26–29) and *Cupuliferopollenites villensis* P.W.Thomson (Benda, 1971a). ASR-type-pollen gen. indet. 3 has only been encountered in sample S153567.

Family Sapindaceae

Genus *Acer* L.

*Acer* sp.

(Figs 18D–F)

**Description:** Pollen, prolate, elliptic in equatorial view, lobate to circular in polar view, length of polar axis 30–40 μm (LM, SEM), equatorial diameter 23–30 μm (LM, SEM); eutectate, exine 1.0–1.5 μm thick (LM); tricolpate; sculpturing striate (LM, SEM), striae running parallel to colpus in mesocolpium area (LM, SEM), striae 0.25–0.35 μm wide (SEM), nexine perforate.

**Remarks:** This pollen corresponds to extant and fossil *Acer* pollen (Biesboer, 1975; Clarke & Jones, 1978; Fürstl, 2002; Li et al., 2010; Miyoshi et al., 2011; Stuchlik et al., 2014; Tian et al., 2001). *Acer* consists of 126 species and shows a Northern Hemispheric distribution (Acevedo-Rodríguez et al., 2010). Pollen with affinities to extant *Acer* commonly have been assigned to the form genus *Aceripollenites* Nagy (Stuchlik et al., 2014).

Macrofossils have been reported from early/middle Miocene deposits of western Turkey from Balya, Balıkesir (samaras: Engelhardt, 1903), Soma (leaves: Gemici et al., 1991), Şahnahı, Aydın (leaves: Gemici et al., 1993), and the Yatağan basin (samaras and leaves: Bouchal et
Previous reports from middle Miocene sediments of western Turkey: *Aceripollenites striatus* (Pflug) Thiele-Pfeiffer (Akgün *et al.*, 2007; Kayseri-Özer *et al.*, 2014a), *Acer* (Akkiraz, 2011; Kayseri & Akgün, 2010; Kayseri-Özer *et al.*, 2014b; Yavuz-İşık, 2007; Yavuz-İşık *et al.*, 2011). *Acer* sp. is present in most samples but never abundant (Fig. 2).

Order Caryophyllales Juss. ex Bercht. et J.Presl

Family Amaranthaceae Juss.

Amaranthaceae gen. indet. 1 (aff. Chenopodioideae)

(Figs 18G–I)

*Description*: Pollen, spheroidal, pollen outline circular, pollen diameter 20–25 µm (LM, SEM); eutectate, exine 0.8–1.2 µm thick (LM), nexine thinner than sexine; pantoporate, pori diameter 0.7–1 µm (SEM), pori sunken, pori operculate, operculum ornamented with 2–6 nanoechini; sculpturing scabrate (LM), nanoechinate, perforate (SEM).

Remarks: Several studies on subfamilies of Amaranthaceae (Dehghani & Akhani, 2009; Hamdi *et al.*, 2009; Müller & Borsch, 2005; Olvera, Fuentes-Soriano & Hernandéz, 2006; Toderich *et al.*, 2010) have shown that within a genus pollen characters can be a useful diagnostic tool to distinguish species. However, pollen characters are not informative at subfamily level because of substantial overlap in morphological variability.

Amaranthaceae gen. indet. 2 (aff. Chenopodioideae)

(Figs. 18J–L)

*Description*: Pollen, spheroidal, pollen outline circular, pollen diameter 28–33 µm (LM, SEM); eutectate, exine 1–1.5 µm thick (LM), nexine thinner than sexine; pantoporate, pori diameter 1.5–2 µm (SEM), pori sunken, pori operculate, operculum ornamented with 9–12 nanoechini; sculpturing scabrate (LM), nanoechinate, perforate (SEM).
Remarks: Amaranthaceae gen. indet. 2 differs from A. gen. indet. 1 by its larger pollen size, pore diameter, and higher number of echini on the operculi. Pollen with affinities to extant Chenopodioideae commonly has been assigned to the form genera *Periporopollenites* Pflug et P.W.Thomson in P.W.Thomson et Pflug and *Chenopodipollis* Krutzsch (Krutzsch, 1966; Stuchlik *et al.*, 2009). Previous reports from middle Miocene sediments of western Turkey: Chenopodiaceae (=Chenopodiaceae-Amaranthaceae) (Akkiraz, 2011; Akkiraz *et al.*, 2012; Benda, 1971a; Yavuz-Işık, 2007; Yavuz-Işık *et al.*, 2011), *Chenopodipollis multiplex* (Weyland et Pflug) Krutzsch (Takahashi & Jux, 1991), *Periporopollenites* spp. (Akgün & Akyol, 1999; Akgün *et al.*, 2007; Gemici *et al.*, 1991; Kayseri-Özer *et al.*, 2014a; Kayseri-Özer *et al.*, 2014b),. In the LM pollen counts, both Amaranthaceae types were combined. Amaranthaceae gen. indet. type pollen is a common element throughout the section with highest abundances (up to ca 20%) in the upper part of the Eskihisar mine section (Fig. 2).

Family Caryophyllaceae Juss.

Caryophyllaceae gen. indet. 1

(Figs 19A–C)

*Description:* Pollen, spheroidal, pollen outline circular to slightly polygonal, pollen diameter 26–31 µm (LM), 21–27 µm (SEM); eutectate, exine 3–4 µm thick (LM); pantoporate, pori diameter 1.6–2.5 µm (SEM), number of pori 18-21, pori sunken, pori operculate, operculum ornamented with 4–9 nanoechini (SEM); sculpturing scabrate (LM), nanoechinate, perforate (SEM), nanoechini evenly spaced.

*Remarks:* Caryophyllaceae gen. indet. 1 corresponds to the *Arenaria serpyllifolia* type, differing slightly by the smaller pollen size and pore diameter (Punt & Hoen, 1995).

Caryophyllaceae gen. indet. 1 and 2 have not been separated in the LM pollen count (Fig. 2).

Caryophyllaceae gen. indet. 2
Description: Pollen, spheroidal, pollen outline circular, pollen diameter 34–40 µm (LM), 28–34 µm (SEM); eutectate, exine 3–4 µm thick (LM); pantoporate, pori diameter 1.6–2.5 µm (SEM), number of pori 12–18, pori sunken, pori operculate, operculum ornamented with 4–9 microechini (SEM); sculpturing scabrate (LM), nanoechinate, perforate (SEM), nanoechini absent around pori.

Remarks: Caryophyllaceae gen. indet. 2 differs from C. gen. indet. 1 by its larger pollen size and pore diameter, and absence of microechini around the pores. Caryophyllaceae gen. indet. 2 corresponds to the *Cerastium fontanum* type (Punt & Hoen, 1995). Recent phylogenetic studies showed that several Caryophyllaceae taxa are polyphyletic and hence assignment to subfamily or generic level is not advisable (Harbaugh et al., 2010). Pollen with affinities to extant Caryophyllaceae commonly have been assigned to the form genus *Caryophyllidites* Couper (Stuchlik et al., 2009). Previous reports from middle Miocene sediments of western Turkey: Caryophyllaceae (Akkiraz et al., 2012; Benda, 1971a; Yavuz-İşik, 2007; Yavuz-İşik et al., 2011). Caryophyllaceae are present in most samples of Eskihisar but with low abundance (<1.5 %; Fig. 2).

Family Plumbaginaceae Juss.

Subfamily Staticoideae Kusn.

Staticoideae gen. indet. 1 (coarse reticulate)

(Figs. 19G–I)

Description: Pollen, monad, pollen outline circular, pollen diameter 43–46 µm (LM, SEM); semitectate, exine 6–8 µm thick (LM), nexine thinner than sexine, columellae 4–5 µm high, columellae width 0.8–1.2 µm (SEM); tricolpate; sculpturing reticulate, (LM, SEM), muri 0.5–1 µm wide (SEM), muri crested with a single row of microechini (LM, SEM), lumina polygonal, lumen psilate (SEM).
Staticoideae gen. indet. 2 (fine reticulate)

(Figs. 19J–L)

**Description:** Pollen, monad, pollen outline circular, equatorial diameter 34–38 µm (LM), 32–35 µm (SEM); semitectate, exine 3–4 µm thick (LM), nexine thinner than sexine; tricolpate, ectocolpus length ⅔ to ¾ of polar axis (LM, SEM); sculpturing reticulate (LM), microreticulate-perforate, lumina size increases gradually towards equator, muri 0.5–1 µm wide (SEM), muri form a hexa- to pentagonal reticulum, muri intersection points crested with microechini, lumina rimmed with microruglate sculpturing perpendicular to muri.

**Remarks:** Within extant Plumbaginaceae two main pollen types, *Plumbago* type (clavate sculpturing, all Plumbaginoideae, but not exclusively) and *Armeria* type (reticulate sculpturing, Staticoideae *pro parte*) have been identified by (Nowicke & Skvarla, 1977). In genera with *Armeria* type pollen a distinct pollen dimorphism, including coarse- and fine-reticulate pollen grains, has been documented (El-Ghazaly, 1991; Erdtman & Dunbar, 1966; Nowicke & Skvarla, 1977; Turner & Blackmore, 1984). Staticoideae gen. indet. 1 (coarse reticulate) and S. gen. indet. 2 (fine reticulate) fall within this morphological range of *Armeria* type pollen and could possibly have originated from the same species. Nowicke & Skvarla (1977) observed in LM a superficial similarity between Polygonaceae and *Armeria* type pollen. Extant Plumbaginaceae show a global distribution, with preferences for cold and arid and for saline, coastal habitats (Kubitzki, 1993). Both types of Staticoideae gen. indet. have been encountered in samples S153572 and S153649 (Fig. 2).

Family Polygonaceae Juss.

Genus *Rumex* L.

*Rumex* sp.

(Figs 20A–C)
Description: Pollen, monad, pollen outline circular, pollen diameter 23–33 µm (LM, SEM); eutectate, exine 0.8–1.2 µm thick (LM); tricolporate to tricolporoidate, ectocolpus length ¼ to ⅔ of polar axis (LM, SEM); sculpturing scabrate (LM), rugulate, nanoechinate, perforate-fossulate (SEM).

Remarks: Rumex sp. corresponds to extant Rumex pollen (Nowicke & Skvarla, 1977; Van Leeuwen, Punt & Hoen, 1988). Rumex has previously been reported in palynological studies of middle Miocene sediments of western Turkey (Yavuz-Işık, 2007; Yavuz-Işık et al., 2011). Rumex sp. is present in samples S153649, S153539, S153540, S153546, S153555, S153572, S153574, S153575 and commonly rare (<1%; Fig. 2).

Subfamily Polygonoideae Eaton

Genus Polygonum L.

Polygonum sp.
(Figs 20D–F)

Description: Pollen, prolate, pollen outline elliptic in equatorial view, length of polar axis 29–32 µm (LM), 27–29 (SEM), equatorial diameter 22–26 µm (LM), 19–22 µm (SEM); tectate, exine 1–1.5 µm thick (LM), nexine thinner than sexine; tricolporate, ectocolpus length ⅔ to ¾ of polar axis (LM, SEM), endoporus elongated; sculpturing psilate to scabrate (LM), nanoechinate, perforate (SEM), number of nanoechini decreasing gradually towards polar areas, nanoechinus diameter 0.2–0.3 µm (SEM).

Remarks: Van Leeuwen et al. (1988) distinguished five pollen types for northwestern European Polygonum, P. aviculare type, P. bistorta type, P. convolvulus type, P. persicaria type, and P. polystachyum type. The pollen encountered in the Eskihisar samples corresponds to Polygonum aviculare type, with resemblance to the extant P. aviculare L., P. bistorta L., P. maritimum L., and P. patulum M.Bieb., (Hong, Oh & Ronse de Craene, 2005; Nowicke & Skvarla, 1977; Van Leeuwen et al., 1988). Pollen of Polygonum has previously been reported
from the early Miocene of Turkey (Yavuz-Işık et al., 2011). Polygonum sp. is present in a single sample (S153541) with a single encounter.

Asterids
Order Ericales Bercht. et J.Presl
Family Ericaceae Juss.
Genus Erica L.

*Erica* sp.
(Figs 20G–I)

*Description*: Pollen, tetrahedral tetrad, heteropolar, triangular in polar view, tetrad diameter 22–28 µm (LM), 20–24 µm (SEM); single pollen length of polar axis 12–14 µm (LM), single pollen equatorial diameter 14–18 µm (LM, SEM); euticate, exine 1.0–1.5 µm thick (LM); tricolporate to tricolporoidate apertures arranged according to Fischer’s law; sculpturing scabrate (LM); rugulate, nanoverrucate, fossulate, perforate (SEM).

*Remarks*: This grain resembles pollen of extant *Erica*, with strongest morphological affinities to *E. tetralix* L. and *E. arborea* L. (Halbritter & Buchner, 2012; Sarwar & Takahashi, 2014).

Ericaceae gen. indet.
(Figs 20J–L)

*Description*: Pollen, tetrahedral tetrad, heteropolar, triangular in polar view, tetrad diameter 35–39 µm (LM), 32–35 (SEM), single pollen length of polar axis 17–19 µm (LM), single pollen equatorial diameter 20–24 µm (LM, SEM); euticate, exine 1.3–1.8 µm thick (LM); tricolporate to tricolporoidate, apertures arranged according to Fischer’s law; sculpturing scabrate (LM), rugulate, microrugulate, fossulate, perforate (SEM), rugulae show microrugulate suprasculpture.
Remarks: Rugulae with microrugulate suprasculpturing are not restricted to a single genus or subfamily and occur for instance in Cassiopoideae Kron et Judd, Ericoideae Link, and Vaccinioideae Arn. (Sarwar, 2007; Sarwar & Takahashi, 2009; 2014).

Pollen with affinities to extant Ericaceae commonly have been assigned to the form genus *Ericipites* Wodehouse (Stuchlik *et al.*, 2014; Wodehouse, 1933). Previous reports from middle Miocene sediments of western Turkey: Ericaceae (Akkiraz, 2011; Akkiraz *et al.*, 2012), Ericales (Benda, 1971a), *Tetradopollenites ericus* (R.Potonié) P.W.Thomson et Pflug (Akgün & Akyol, 1999; Ediger, 1990; Gemici *et al.*, 1991, 1993). Ericaceae pollen has not been differentiatd in the LM pollencount and is present in samples S153539, S153541, S153546, S153547, and S153649 as single encounters (Fig. 2).

Order Solanales Juss. ex Bercht. et J.Presl

Family Convolvulaceae Juss.

Genus *Convolvulus* L.

*Convolvulus* sp.

(Figs 21A–C)

*Description*: Pollen, prolate, outline elliptic in equatorial view, length of polar axis 48–53 µm (LM), equatorial diameter 38–43 µm (LM); eutectate, exine 3–4 µm thick (LM), nexine thinner than sexine; tricolpate, ectocolpus length ¾ to ⅚ of polar axis (LM, SEM), at polar ends of colpi echinate sculpturing of colpus membrane visible (SEM); sculpturing scabrate (LM), microechinate, perforate (SEM), microechinus diameter 0.4–0.6 µm (SEM), microechinus length 0.4–0.6 µm (SEM).

*Remarks*: This pollen corresponds in a number of morphological characteristics (pollen wall architecture, colpate aperture, echinate perforate exine sculpturing) to extant *Convolvulus* (= *C. arvensis* type in Cronk & Clarke, 1981; Sengupta, 1972). Previous reports of morphologically similar pollen from middle Miocene sediments of western Turkey:

Convolvulus sp. is present in three samples (S153541, S153542, S153649; Fig. 2).

Lamiids

Order Garryales Lindl.

Family Eucommiaceae Engl.

Genus Eucommia Oliv. in Hooker

Eucommia sp.

(Figs 21D–F)

Description: Pollen, prolate, elliptic in equatorial view, length of polar axis 33–36 µm (LM), 31–34 µm (SEM), equatorial diameter 26–30 µm (LM), 24–27 µm (SEM); eutectate, exine 1.5–2 µm thick (LM), sexine thicker than nexine; tricolporate to tricolporoidate, ectocolpus length ½ to ⅔ of polar axis (LM, SEM); sculpturing psilate (LM), nanoechinulate, perforate (SEM).

Remarks: This pollen corresponds in size, shape, aperture and exine sculpturing to extant and fossil Eucommia (Li et al., 2010; Stuchlik et al., 2014; Yu-Long, Fu-Hsiung & Nan-Feng, 1988). Pollen with affinities to extant Eucommia has commonly been assigned to the form genus Eucommiapollis Menke or the form species Tricolpopollenites parmarius (R.Potonié) P.W.Thomson et Pflug (Stuchlik et al., 2014; Thomson & Pflug, 1953). The Cenozoic fossil record of Eucommia shows a wide Northern Hemispheric distribution (Ferguson, Liu & Zetter, 1997; Manchester et al., 2009). Today the monotypic family Eucommiaceae, with its extant species Eucommia ulmoides Oliv., is restricted to Central China (Zhang & Turland, 1999). Previous reports from middle Miocene sediments of western Turkey:

Tricolpopollenites parmarius (=T. anatolicus Takahashi et Jux) (Akgün & Akyol, 1999; Akgün et al., 2007; Benda, 1971a; Takahashi & Jux, 1991), maybe T. liblarensis
Eucommia sp. is present in most samples but is rare (<1.5 %; Fig. 2).

Order Lamiales Bromhead

Family Oleaceae Hoffmans. et Link

Oleaceae gen. indet. 1 (aff. Fraxinus)

(Figs 21G–I)

Description: Pollen, spheroidal to prolate, outline circular to weakly lobate in polar view, equatorial diameter 22–25 µm (LM), 20–23 µm (SEM); semitectate, exine 1.5–2 µm thick (LM), nexine thinner than sexine; tricolporate, ectocolpus length ⅔ to ¾ of polar axis (LM, SEM), endoaperture indistinct; sculpturing microreticulate (LM, SEM), muri width 0.4–0.7 µm (SEM), muri crested with weak ridges, ridges perpendicular to muri, lumina narrow and of irregular shape, lumina decreasing in size towards the colpi, nexine psilate (SEM).

Remarks: Oleaceae type 1 to 4 correspond in size, aperture, and microreticulate to reticulate exine sculpturing to extant and fossil Oleaceae pollen (Nilsson, 1988; Punt, Bos & Hoen, 1991; Renault-Miskovsky, Girard & Trouin, 1976; Sachse, 2001). The degree of morphological variability in pollen of Oleaceae differs greatly between genera and pollen morphology is not necessarily genus-diagnostic, making a precise identification of dispersed Oleaceae pollen difficult [e.g. Olea L., (Nilsson, 1988); Fraxinus L., (compare Li et al., 2010; Miyoshi et al., 2011; Punt et al., 1991)]. Closest morphological similarities (microreticulum, weak perpendicular ridges) are with extant Fraxinus ornus L. (Punt et al., 1991, pl. 5, fig. 6; Renault-Miskovsky et al., 1976, pl. 4, fig. 6).

Pollen with affinities to extant Oleaceae has commonly been assigned to the form genus Oleoidearumpollenites Nagy (Stuchlik et al., 2014). Previous reports from middle Miocene sediments of western Turkey: Tricolpopollenites retiformis (P.W.Thomson) P.W.Thomson et Pflug (Akgün & Akyol, 1999, figs 11.51–53), T. margaritatus (R.Potonié) P.W.Thomson et
Oleaceae pollen has not been differentiated in LM pollen counts and is present in most samples of the Eskihisar mine section but never abundant (<3%; Fig. 2).

Oleaceae gen. indet. 2
(Figs 21J–L)

Description: Pollen, spheroidal to weakly prolate, outline elliptic in equatorial view, circular to weakly lobate in polar view, length of polar axis 23–26 µm (LM), equatorial diameter 19–26 µm (LM), 19–23 µm (SEM); semitectate, exine 1.5–2 µm thick (LM), nexine thinner than sexine; tricolporate; sculpturing reticulate (LM, SEM), muri width 0.3–0.5 µm (SEM), muri crested with sharp edged ridges, ridges perpendicular to muri, lumina wide and of irregular shape, nexine psilate (SEM).

Remarks: Pollen with similar sharp edged perpendicular ridges is present in Phillyrea angustifolia L. (Renault-Miskovsky et al., 1976; Sachse, 2001), Linociera obtusifolia (Lam.) H.Perrier and Noronhia linocerioides H.Perrier (Cerceau-Larrivall, Straka & Friedrich, 1984). Similar pollen has been reported from late Miocene of Northern Italy (Sachse, 2001).

Oleaceae gen. indet. 3
(Figs 22A–C)

Description: Pollen, spheroidal, outline circular in equatorial view, circular in polar view, length of polar axis 23–26 µm (LM), equatorial diameter 22–26 µm (LM), 20–24 µm (SEM);
semitectate, exine 1.5–2 µm thick (LM), nexine thinner than sexine; tricolporate, ectocolpus length ⅓ to ¾ of polar axis (LM, SEM), endoaperture indistinct; sculpturing reticulate to microreticulate (LM, SEM), muri width 0.4–0.7 µm (SEM), muri crested with ridges and microechini, ridges perpendicular to muri, lumina of irregular shape and size, nexine psilate (SEM).

Remarks: Reticulum with irregular lumen size, perpendicular ridges and microechinate suprasculpturing is present in pollen of *Olea* L. (Nilsson, 1988; Punt *et al.*, 1991; Renault-Miskovsky *et al.*, 1976) and *Osmanthus* Lour. (Miyoshi *et al.*, 2011; Xu, Hao & Hu, 2005). Similar pollen has been reported from late Miocene of Northern Italy (Sachse, 2001).

Oleaceae gen. indet. 4

(Figs 22D–F)

Description: Pollen, spheroidal, outline circular in equatorial view, circular in polar view, length of polar axis 23–26 µm (LM), 20–24 µm (SEM), equatorial diameter 22–26 µm (LM), 20–24 µm (SEM); semitectate, exine 1.5–2 µm thick (LM), nexine thinner than sexine; tricolpate, ectocolpus length ⅓ to ¾ of polar axis (LM, SEM), endoaperture indistinct; sculpturing reticulate to microreticulate (LM, SEM), muri width 0.6–0.8 µm (SEM), muri crested with microechini, lumina of irregular shape and size, nexine psilate (SEM).


Campanulids

Order Asterales Link

Family Asteraceae Bercht. et J.Presl

Subfamily Asteroideae (Cass.) Lindl.
Asteroideae type 1
(Figs 22G–I)

*Description*: Pollen, spheroidal, outline circular in equatorial view, circular to slightly lobate in polar view, equatorial diameter 32–34 µm (LM) 30–33 µm (SEM); exine including echini 3–7 µm thick (LM), sexine thicker than nexine; tricolporate, colpus membrane covered with granular ornamentation; sculpturing echinate, perforate (LM, SEM), echinus base diameter 4–5 µm (SEM), echini blunt, echinus height 2–3 µm (SEM), perforations up to the upper half to upper third of the echini.

*Remarks*: Asteroideae type 1 to 4 fall in the morphological range of extant Asteroideae (e.g. Punt & Hoen, 2009), further allocation to genus level is not possible due to their deformed preservation. Separation in the here used four types is superficial and only based on morphological characters (length of polar axis, echinus height) discernible in LM. Pollen with blunt echini and a polar axis length of 20–35 µm (LM) has been grouped in Asteroideae type 1. Pollen with affinities to extant Asteroideae has commonly been assigned to the form genus *Tubulifloridites* Cookson ex Potonié (Stuchlik et al., 2014). Previous reports from middle Miocene sediments of western Turkey: *Tricolporopollenites* spp. tubuliflorae type (=Compositae tubuliflorae type) (Akgün & Akyol, 1999; Akgün et al., 2007; Akyol & Akgün, 1990; Benda, 1971a; Kayseri-Özer et al., 2014a; Kayseri-Özer et al., 2014b), Asteraceae Asteroideae (Akkiraz et al., 2012; Yavuz-Işık et al., 2011).

Asteraceae pollen has not been differentiated in LM pollen counts and is present in most samples of the Eskihisar mine section but never abundant (<1.5 %; Fig. 2).

Asteroideae type 2
(Figs 22J–L)

*Description*: Pollen, spheroidal, outline circular in equatorial view, circular to slightly lobate in polar view, length of polar axis 48–54 µm (LM) 45–50 µm (SEM), equatorial diameter 48–
54 μm (LM), 43–49 μm (SEM); exine including echini 8–10 μm thick (LM), sexine thicker than nexine; tricolporate; sculpturing echinate, perforate (LM, SEM), echini blunt, echinus base diameter 6–9 μm (SEM), echinus height 3–5 μm (SEM), perforations up to the upper third to upper quarter of the echini.

Remarks: Pollen with blunt echini and a polar axis length of 35–55 μm (LM) has been grouped in Asteroideae type 2.

Asteroideae type 3
(Figs 23D–F)

Description: Pollen, spheroidal, outline circular in equatorial view, length of polar axis 56–60 μm (LM), 53–58 μm (SEM), equatorial diameter 54–59 μm (LM), 51–55 μm (SEM); exine including echini 4–8 μm thick (LM), sexine thicker than nexine; tricolporate; sculpturing echinate (LM), echinate, perforate (SEM), blunt and pointy echini present, echinus base diameter 3–5 μm (SEM), echinus height 3–6 μm (SEM), perforations up to the lower third to lower half of the echini.

Remarks: Pollen with blunt echini and a polar axis length of 55–75 μm (LM) has been grouped in Asteroideae type 3.

Asteroideae type 4
(Figs 23A–C)

Description: Pollen, spheroidal, outline circular in equatorial view, circular to slightly lobate in polar view, length of polar axis 57–62 μm (LM), 51–56 μm (SEM), equatorial diameter 50–54 μm (LM), 47–51 μm (SEM); exine including echini 4–10 μm thick (LM), sexine thicker than nexine; tricolporate; sculpturing echinate, perforate (LM, SEM), echini acute, echinus base diameter 8–11 μm (SEM), echinus height 5–6 μm (SEM), perforations up to the lower third to half of the echini.
*Remarks:* Pollen with acute echini and a polar axis length of 55–75 µm (LM) has been grouped in Asteroideae type 4.

Subfamily Cichorioideae (Juss.) Chevall.
Cichorioideae gen. indet.
(Figs 23G–I)

*Description:* Pollen, spheroidal, pollen outline polygonal, pollen diameter 27–34 µm (LM), 25–29 µm (SEM); lophate, exine including lophae and echini 3–5 µm thick (LM), tricolporate, sculpturing lophate, echinate (LM), lophate, echinate, perforate (SEM), echinus base diameter 2–3 µm (SEM and LM), echinus height 1.5–2.5 µm (SEM), perforations up to the lower third of echini, echini present only on lophae, lophae perforate.

*Remarks:* Extant Cichorioideae produce lophate lacunate pollen (Blackmore, 1984). Pollen with affinities to extant Cichorioideae commonly has been assigned to the form genus *Cichoraecidites* Sah (Stuchlik et al., 2014). Previous reports from middle Miocene sediments of western Turkey: *Tricolporopollenites* spp. liguliflorae type (=Compositae liguliflorae type) (Akgün & Akyol, 1999; Akgün et al., 2007; Akyol & Akgün, 1990; Benda, 1971a; Ediger, 1990; Kayseri-Özer et al., 2014a), Asteraceae Cichorioideae (Akkiraz et al., 2012; Yavuz-Işık et al., 2011)

Cichorioideae pollen is present in samples S153545, S153573, S153581, S153582, S153590, S153592, and S153649 of the Eskihisar mine section, mostly as single encounters (Fig. 2).

Order Dipsacales
Family Caprifoliaceae Juss.
Genus *Lonicera* L.

*Lonicera* sp. 1
(Figs 23J–L)
**Description:** Pollen, oblate, outline circular to convex triangular in polar view, equatorial diameter 61–65 µm (LM), 57–61 µm (SEM); eutectate, exine without echini 3–4 µm thick, thickened in polar area (LM), nexine thinner than sexine; brevicolporate (3), apertures weakly protruding, colpi short with obtuse ends; sculpturing echinate (LM), echinate, perforate (SEM), perforations irregular distributed, echinus base diameter 1.4–1.8 µm (SEM), echinus height 1.5–2.2 µm (SEM), echini acute.

**Remarks:** Lonicera sp. 1 shows strong morphological similarities to extant Lonicera alpigena type (Punt, Reitsma & Reuvers, 1974). Pollen with affinities to extant Lonicera commonly have been assigned to the form genus Lonicerapollis Krutzsch (Stuchlik et al., 2014).

Lonicera and Linnaeoideae pollen have been combined in the LM pollen count. Previous pollen reports of Caprifoliaceae from middle Miocene sediments of western Turkey: Lonicerapollis gallwitzi Krutzsch (Akgün et al., 2007), Caprifoliaceae (Yavuz-Işık, 2007).

Caprifoliaceae, excluding Dipsacoideae, pollen is very rare in the Eskihisar mine section and present in samples S153545, S153554, S153555, S153565, S153570, S153572, S153573, S153649.

**Lonicera sp. 2**

(Figs 24A–C)

**Description:** Pollen, oblate, outline circular to convex triangular in polar view, equatorial diameter 72–78 µm (LM), 69–74 µm (SEM); eutectate, exine 3–5 µm thick (LM), exine thinned in aperture area, 4–6 µm thick (LM), nexine thinner than sexine; brevicolporate (3); sculpturing echinate (LM), echinate, perforate (SEM), perforations regularly distributed, echinus base diameter 1–1.5 µm (SEM), echinus height 1–1.5 µm (SEM).

**Remarks:** The pollen has strong morphological similarities to extant Lonicera caprifolium type and Lonicera periclymeum type (Punt et al., 1974) and to the form genus Lonicerapollis grandis Grabowska (Stuchlik et al., 2014).
Subfamily Linnaeoidae Rafinesque

Linnaeoidae gen. indet.

(Figs 24D–F)

*Description*: Pollen, prolate, outline elliptic in equatorial view, length of polar axis 59–63 µm long (LM), 56–60 µm (SEM), equatorial diameter 54–58 µm (LM), 50–54 (SEM); eutectate, exine 3–5 µm thick (LM), nexine thinner than sexine; tricolpate, ectocolpus length ½ to ⅔ of polar axis (LM, SEM); sculpturing echinate (LM), echinate, perforate (SEM), echinus base diameter 1–1.8 µm (SEM), microechinus height 0.5–2 µm (SEM), perforations connected by shallow furrows.

*Remarks*: Morphologically similar pollen is found in Linnaeoidae (Chia-Chi & Chao-Xin, 1988; Li *et al.*, 2010; Maciejewska, 1997; Miyoshi *et al.*, 2011).

Subfamily Dipsacoideae Eaton

Genus *Succisa* Haller

*Succisa* sp.

(Figs 24G–I)

*Description*: Pollen, spheroidal, outline circular in equatorial view, length of polar axis 84–89 µm (LM, SEM), equatorial diameter 81–86 µm (LM); eutectate, exine 7.5–10 µm thick (LM), nexine thinner than sexine; tricolpate, ectocolpus length ½ to ½ of polar axis (LM, SEM); sculpturing echinate (LM), echinate, microechinate, perforate (SEM), echinus base diameter 1.6–2 µm (SEM), echinus height 2.5–3 µm (SEM), microechinus base diameter 0.7–1.1 µm (SEM), microechinus height 0.6–1 µm (SEM).

*Remarks*: This grain corresponds in aperture, exine structure and sculpturing to extant *Succisa* (Beug, 2004; Clarke & Jones, 1981). Pollen of *Succisa* is present in sample S153649. In the
LM pollen count pollen of Dipsacoideae has not been further differentiated (Fig. 2), we do not rule out a higher diversity for this subfamily in the Eskihisar mine section.

Order Apiales Nakai
Family Apiaceae Lindl.
Apiaceae gen. indet. 1
(Figs 24J–M)

Description: Pollen, prolate, outline slightly bone-shaped in equatorial view, length of polar axis 24–31 µm (LM), 22–28 µm (SEM), equatorial diameter including protruding apertures 14–17 µm (LM, SEM); eutectate, exine 1.5 µm thick in polar area (LM), outer contour straight, slightly apiculate, inner contour straight to slightly convex; tricolporate, slit-like colpus with protruding sexine in porus area (LM, SEM), ectocolpus length ⅔ to ¾ of polar axis, pori circular; sculpturing scabrate (LM), microrugulate, fossulate, perforate (SEM), sculpture elements elongated (0.5–3 µm long) in polar area, short in colporus area (SEM), rugulae densely packed in colporus and polar area, loosely packed in mesocolpium area (SEM).

Remarks: For Apiaceae pollen morphology, in particular the description of outer and inner contours, the nomenclature of Punt (1984) was used. Determination of extant genera uses several morphological characteristics only discernable in three-dimensional preserved grains. Apiaceae gen. indet. 1 shows morphological similarities in aperture, protruding bridge and outline to e.g. Daucus Typ (Beug, 2004), Bifora radians type and Chaerophyllum hirsutum type (Punt, 1984).

Pollen with affinities to extant Apiaceae commonly has been assigned to the form genus Umbelliferaepollenites Venkatachla et Kar emended Nagy (Stuchlik et al., 2014)

Previous pollen reports of Apiaceae from middle Miocene sediments of western Turkey: Umbelliferaepollenites sp. (Akgün et al., 2007), Apiaceae (=Umbelliferen) (Benda, 1971a;
Yavuz-Işık, 2007; Yavuz-Işık et al., 2011). Apiaceae are present in all samples of the Eskihisar mine section (Fig. 2).

Apiaceae gen. indet. 2
(Figs 25A–D)

Description: Pollen, prolate, outline bone-shaped in equatorial view, length of polar axis 19–22 µm (LM), 17–19 µm (SEM), diameter including protruding apertures 8–11 µm (LM, SEM); eutectate, exine thickened in polar area (up to 2.2 µm LM), outer contour straight, slightly apiculate, inner contour slightly convex; tricolporate, slit-like colpus with protruding sexine in porus area (LM, SEM), ectocolpus length ½ to ⅔ of polar axis, pori circular; sculpturing scabrate (LM), microrugulate, fossulate, perforate (SEM), in polar area perforate with fused sculpture elements, in mesocolpium and colporus area fossulate short rugulate sculpture elements (SEM), rugulae densely packed around colporus, loosely packed in other parts of the mesocolpium (SEM).

Remarks: Apiaceae gen. indet. 2 differs from Apiaceae gen. indet. 1 in smaller size and shorter colpi. Apiaceae gen. indet. 2 shows morphological similarities in size, aperture, protruding bridge, thickened polar areas, and outline to Anthriscus cerefolium (Beug, 2004) and Anthriscus cerefolium type (Punt, 1984).

Apiaceae gen. indet. 3
(Figs 25E–H)

Description: Pollen, prolate, outline elliptic in equatorial view, length of polar axis 18–21 µm (LM), 17–19 µm (SEM), equatorial diameter 10–13 µm (LM), 9–11 µm (SEM); eutectate, exine 2–2.3 µm thick in polar area (LM), outer and inner contour straight; tricolporate, ectocolpus length ½ to ⅔ of polar axis, pori circular; sculpturing scabrate (LM), microrugulate, fossulate, perforate (SEM), in polar area perforate and microrugulae indistinct,
in mesocolpium area fossulate, perforate and microrugulae distinct, around apertures microrugulae fused (SEM).

Remarks: Apiaceae gen. indet. 3 differs from Apiaceae gen. indet. 1 and 2 by the lack of a protruding aperture.

Apiaceae gen. indet. 4
(Figs 25I–L)

_Description_: Pollen, prolate, outline elliptic in equatorial view, length of polar axis 19–23 µm (LM), 17–19 µm (SEM), equatorial diameter 13–16 µm (LM), 11–14 µm (SEM); eutectate, exine 1.5–2 µm thick in polar area (LM), outer contour convex weakly apiculate, inner contour weakly convex; tricolporate, ectocolpus length ¾ to ⅚ of polar axis, pori rectangular, sexine protruding in porus area (SEM), costae indistinct; sculpturing scabrate (LM), microrugulate, perforate, fossulate (SEM), in polar and aperture area perforate microrugulae fused and indistinct, mesocolpium fossulate with loosely packed microrugulae (SEM).

Remarks: Apiaceae gen. indet. 4 differs from Apiaceae gen indet. 1, 2, and 3 by its convex inner and outer contour. Closest morphological similarities are with _Pleurospermum austriacum_ type (Beug, 2004; Punt, 1984).

Apiaceae gen. indet. 5
(Figs 25M–P)

_Description_: Pollen, prolate, outline elliptic to weakly rhombic in equatorial view, length of polar axis 22–26 µm (LM, SEM), equatorial diameter 17–20 µm (LM), 16–18 µm (SEM); eutectate, exine ca 2 µm thick (LM), outer contour convex apiculate, inner contour convex; tricolporate, ectocolpus length ≥5% of polar axis, pori circular, sexine protruding in porus area (LM, SEM), costae indistinct (LM); sculpturing scabrate (LM), microrugulate,
microverrucate, fossulate, perforate (SEM), rugulae in aperture area fused, microverrucae and loosely packed microrugulae present only in equatorial mesocolpium (SEM).

Remarks: Closest morphological similarities are with Bupleureum type and Molopospermum type pollen (Beug, 2004; Punt, 1984).

Subfamily Saniculoideae Thome ex P.Royen
Saniculoideae gen. indet.
(Figs 26A–D)

Description: Pollen, prolate, weakly constricted in equator area, length of polar axis 40–50 µm long (LM), 35–45 µm (SEM), equatorial diameter 15–18 µm (LM), 13–16 µm (SEM); eutectate, exine 2–2.3µm thick in polar area, 1.5–2 µm in mesocolpium (LM), outer contour weakly concave, inner contour concave; tricolporate, ectocolpus length ≥ ⅚ of polar axis length, pori rectangular, pori diameter 4–6 µm (LM), band like costae around the equator (endocingulum); sculpturing scabrate (LM), microrugulae fused in mesocolpium, polar area and around the equator (SEM), rugulae loosely packed in colpus area (SEM).

Remarks: Saniculoideae gen. indet. resembles Astrantia (major) type pollen (Beug, 2004; Cerceau-Larrivall et al., 1984; Punt, 1984).

Incertae sedis
Pollen type 1
(Figs 26E–H)

Description: Pollen, monad, outline circular in polar view, equatorial diameter 20–23 µm (LM), 18–21 µm (SEM); semitectate, exine 1.5–2 µm thick, nexine thinner than sexine (LM); tricolporate, colpus membrane rugulate-perforate, pori circular, pori diameter 1.5–2 µm (LM, SEM); sculpturing reticulate (LM, SEM), lumina decreasing in size in polar area (SEM).
Remarks: Morphological similarities are with Rubiaceae pollen with closest similarities to *Mastixiodendron* Melch. and *Molopanthera* Turcz. (Huysmans et al., 1999). Pollen type 1 has been encountered in sample S153541 in low abundance (1.5 %).

Pollen type 2
(Figs 26I–K)

Description: Pollen, prolate, outline elliptic to rhombic in polar view, length of polar axis 15–18 µm (LM), 14–16 µm (SEM), equatorial diameter 10–12 µm (LM, SEM); semitectate, exine 1–1.5 µm thick, nexine thinner than sexine (LM); tricolporate, ectocolpus length ⅔ to ¾ of polar axis, pori circular, pori diameter 1–1.5 µm (LM), costa present (LM); sculpturing scabrate (LM), microreticulate, perforate (SEM), lumina size decreasing in aperture area and polar area (SEM).

Remarks: Morphological similarities are with Araliaceae, e.g. “Schefflera Hoi-type” pollen (Tseng & Shoup, 1978). Pollen of this type falls within the morphological range of the form genus *Edmundipollis* Konzalová, Słodkowska et Ziemińska-Tworydlo (Stuchlik et al., 2014). Morphologically similar pollen from the middle Miocene of Turkey: *Tricolporopollenites cingulum* (R.Potonié) P.W.Thomson et Pflug (Akgün & Akyol, 1999, figs 9.55–56, 10.77–78, 11.61–63). Pollen type 2 has been encountered in samples S153542 and S153543 in low abundance (1.5–2.75 %).

Discussion

**SEM investigation of dispersed pollen and taxonomic resolution**

The present study is the first combined LM/SEM study of dispersed spores and pollen in the East Mediterranean region. A main reason to complement conventional LM observations with detailed SEM investigations is the need for more accurate identifications of dispersed pollen grains (Ferguson, Zetter & Paudayal, 2007). High taxonomic resolution is the prerequisite for
meaningful inferences of palaeoenvironments and palaeoclimate. A few examples may serve
to illustrate this: (1) The Pinaceae *Cathaya* has commonly been identified as *Podocarpus*
(Akkiraz, 2011; Takahashi & Jux, 1991) or *Picea* (Benda, 1971a). (2) *Cedrus* has not been
considered in a number of previous LM studies because it was included within a general
Pinaceae type (e.g. Akgün & Akyol, 1999). (3) *Fagus* pollen has sometimes been referred to
as *Nyssa* (e.g. Akkiraz, 2011; Benda, 1971a).

More importantly, a number of taxa are potentially highly informative for inferring
palaeoenvironments, palaeoecology, and palaeobiogeographic patterns. Investigations based
solely on LM either are not able to capture all the information or are prone to
misinterpretations.

One of the best examples to illustrate the significance of accurate high taxonomic resolution
identification of pollen is within the Fagaceae. Fagaceae are among the most diverse families
in the Eskihisar mine section in terms of number of genera and most abundant among woody
angiosperms in terms of encountered pollen grains.

It has previously been shown that the six infrageneric (monophyletic) groups of *Quercus*
can be distinguished based on pollen sculpturing (Bouchal *et al.*, 2014; Denk & Grimm, 2009;
Denk & Tekleva, 2014; Grimsson *et al.*, 2016; Grimsson *et al.*, 2015b). Today *Quercus*
Group Cyclobalanopsis (cycle cup oaks), *Quercus* Group Cerris, and *Quercus* Group Ilex are
strictly Eurasian, and *Quercus* Group Lobatae (red oaks) and *Quercus* Group Protobalanus
(golden cup oaks) are strictly American. *Quercus* Group Quercus (white oaks) have a general
Northern Hemispheric distribution (Denk & Grimm, 2009). In this study, *Quercus* Group
Cerris, *Quercus* Group Ilex, and *Quercus* Group Quercus were encountered. In previous LM
studies of dispersed pollen and spores in western Anatolia (Table 1) *Quercus* has either been
treated at the genus level or has been subdivided in *Quercus* *ilex/coccifera* (sclerophyllous
evergreen) type (small) versus *Quercus* deciduous type (large) based on the size of pollen
grains. Without further taxonomic differentiation, the presence of “deciduous *Quercus*” in the
East Mediterranean Neogene does provide but limited ecological and environmental information. Members of *Quercus* Group Quercus and Group Cerris generally produce large pollen. Members of *Quercus* Group Quercus (white oaks) comprise riparian, mesic and xeric species, whereas Group Cerris (Cerris oaks) are either mesic or xeric. Among macrofossils from Eskihisar, *Q. kubinyii* (Kováts ex Ettingshausen) Czeczott strongly resembles *Q. castaneifolia* C.A.Mey., *Q. acutissima* Carruth., and *Q. variabilis* Blume (see Supporting Information, Appendix S3). These extant species thrive in humid temperate forests (Menitsky, 2005). A large fraction of the “*Quercus* deciduous type” (*Quercus* L in Fig. 2) belongs to *Quercus* Group Cerris, while only a small part belongs to *Quercus* Group Quercus. The distinction between Group Quercus and Group Cerris can only be made using SEM. For castanoids (*Castanea, Castanopsis, Lithocarpus, Notholithocarpus, Chrysolepis*) that have a highly conservative pollen (Denk & Tekleva, 2014; Praglowski, 1984), SEM investigation enables distinguishing *Trigonobalanopsis*, an extinct member of this group (Walther & Zetter, 1993). This pollen type has not previously been reported for the East Mediterranean Cenozoic and commonly has been referred to as *Castanea* or *Castanea/Castanopsis* type.

Another family where pollen microstructure is potentially important for palaeoclimate interpretation are Oleaceae. This family is a large and ecologically diverse family with some taxa characteristic of the modern Mediterranean vegetation (*Phillyrea, Olea europaea* L.). In several LM studies of Neogene dispersed pollen and spores *Olea* and *Phillyrea* have been identified and sometimes been taken as evidence for a summer dry Mediterranean type climate (e.g Akkiraz, 2011; Akkiraz et al., 2012; Jiménez-Moreno *et al.*, 2009; Jiménez-Moreno *et al.*, 2008; Yavuz-İşık, 2007). Based on a thorough comparison of extant members of Oleaceae (published accounts and own observations) and fossil dispersed pollen, we are unable to unequivocally assign dispersed pollen to a particular modern genus.
At the same time, the morphological variability in Oleaceae pollen grains encountered by us includes morphotypes found in eastern Madagascan taxa (*Linociera* Schreb., *Noronhia* Stadm.). Also Euphorbiaceae gen. et spec. indet. shows similarities with species in tropical East Africa (*Cephalocrotonopsis* Pax, *Cephalocroton* Hochst.). The pollen form species *Tricolporopollenites wackersdorfensis* can unambiguously be linked with the extinct genus *Podocarpium* (Fabaceae) based on identical pollen grains found *in situ* in flowers (Liu *et al.*, 2001). In addition, another Fabaceae, the North American-East Asian disjunct woody vine *Apios*, is recorded.

**Pollen zones and inferred palaeoenvironment**

General trends of spore and pollen composition and abundance across the stratigraphic section are illustrated in the pollen diagram for Eskihisar (Fig. 2). Two pollen zones can be distinguished. Pollen zone 1 is derived from the lignite seam and a single sample of the underlying clayey siltstones indicating a swamp environment. High percentages of *Alnus* and *Decodon* pollen and of Osmundaceae spores suggest the presence of an *Alnus-Decodon-Osmunda* swamp forest for this pollen zone. Pollen zone 2 is derived from lacustrine sediments above the lignite seam and is characterized by the presence of *Botryococcus* and transient peaks of algal cysts. This may reflect more alkaline conditions of a lake. Apart from this, the two pollen zones are fairly similar in composition. A few taxa are strictly azonal (riparian, temporally flooded environments). These are Typhaceae, *Alnus*, *Pterocarya*, *Decodon*, and (possibly) *Cedrelospermum*. A large number of other taxa are not confined to either well-drained or flooded environments but can occur in both of them. This is true for most of the herbaceous taxa recorded, and for Cupressaceae, *Pinus*, *Quercus* Group Quercus (white oaks), *Carya*, *Juglans*, *Acer*, *Ulmus*, and *Zelkova*. These taxa may have occurred in different vegetation types including closed and more open vegetation.
Major vegetation types outside the wetland and riparian zone connected to the depositional area are best characterized by strictly zonal taxa (climax vegetation of well-drained areas). For the Eskihisar mine section, members of Fagaceae are the dominant elements of the pollen assemblages. *Fagus* occurs throughout the section but is more abundant (to 10%) in pollen zone 2 (Fig. 2). This genus indicates the presence of humid temperate forest in the hinterland of the depositional area (Ellenberg, 1996; Peters, 1997). Taxa most likely associated with these forests were *Cathaya* among the gymnosperms and *Eucommia* among angiosperms. Pollen of Castaneoideae mainly belongs to the extinct genus *Trigonobalanopsis* which occurred in western Eurasia from the Paleogene to the Miocene, with a peak in the early Miocene subtropical “*Mastixioideenfloren*” (see Kvaček & Walter, 1988). This warmth-loving element possibly constituted broad-leaved evergreen forests below the *Fagus* belt. Also Bambusoideae might have occurred in association with this forest type.

A further genus of Fagaceae, *Quercus*, is represented by three infrageneric groups, *Quercus* Group Ilex, *Q.* Group Cerris, and *Q.* Group Quercus. The first two groups exclusively occur on well-drained soils, whereas the third one (white oaks) occur both in riparian and well-drained vegetation types. White oaks constitute only a small portion among the encountered oak pollen. Evergreen oaks of *Quercus* Group Ilex have a distribution from the Mediterranean region to the southern foothills of the Himalayas and to East Asia. Most extant species occur in humid warm temperate climates (fully humid or winter dry) with the exception of four Mediterranean species growing under distinct summer dry climate. One of the Mediterranean species, *Quercus ilex* occurs both in summer dry and fully humid climates (Denk, 1998; Menitsky, 2005). The Himalayan species of *Quercus* Group Ilex constitute forests (*Q.* *dilatata* communities) that occur in areas with high summer rainfall and mean annual precipitation between 800 and 1200 mm (Freitag, 1971). *Quercus dilatata* co-occurs with *Quercus baloot*, *Q. semecarpifolia* (all *Quercus* Group Ilex), *Juglans, Acer, Pinus* spp., *Picea*, and *Cedrus*. 
This forest type may serve as a modern analogue for communities with sclerophyllous evergreen oaks of Group Ilex in the middle Miocene Yatağan basin.

A transition from a broad-leaved deciduous (Fagus) forest to mixed broad-leaved deciduous and conifer forest may have occurred at the upper limit of beech forest where Picea and Cedrus first co-occur with Fagus and then form pure conifer forests. Similar conditions are found today in northern Turkey (Erbaa, Çatalan; Akkemik, 2003) where Cedrus co-occurs with evergreen and deciduous (Quercus Group Cerris) oaks, Fagus, Acer spp., Carpinus, Tilia, Phillyrea, Olea, Pinus etc., and in south central Turkey (Kahramanmaraş-Andırın district and Amanos Mountains; Ayasligil, 2014; Mayer & Aksoy, 1986).

Other woody angiosperms are not confined to particular forest types. For example, Buxus may occur as understorey in Fagus forests, but also in light oak forests composed of members of Quercus Group Ilex and Group Cerris. Acer and Ulmus either may be part of riparian vegetation or accessory trees and shrubs in well-drained zonal forests.

Among the herbaceous taxa, Armeria, Erodium, and Linum commonly grow on dry and sandy soils or in dry grasslands and rocky outcrops on calcareous substrates. These environments likely occurred scattered around the river/lake and in the hinterland.

**Age of the Eskihisar lignite mine palynoflora**

The here accepted age for the investigated plant-bearing sediments of the upper part of the Turgut Member and lower part of the Sekköy Member (Eskihisar Formation) is Langhian (early middle Miocene, ca 16-13.8 Ma) and possibly extending into the Serravallian. This is based on the rich vertebrate fauna of Çatakbağyaka (Bağyaka, Muğla) recovered from lower layers of the Sekköy Member, which is considered middle Miocene in age (Fortelius [coordinator], 2016; **Supporting Information, Appendix S1**). Gomphotherium angustidens has been recovered from the main coal seam, uppermost Turgut layers, in Eskihisar (Sickenberg, 1975). The main coal seam (Turgut Member) is palynologically very similar to
the overlying sediments of the Sekköy Member suggesting they were deposited at fairly similar times. Macro fossils in the lower Sekköy Member also point to a middle Miocene age. For example, abundant Fagus foliage recovered from the Eskihisar lignite mine does not correspond to the early Miocene F. castaneifolia Unger typical of the early Burdigalian Güvem flora (MN3; Fortelius [coordinator], 2013) and the late Burdigalian Kimi-Aliveri flora of Euboea (Greece, MN4; Velitzelos et al., 2014). Further, ongoing investigations of the macrofloras of Kimi, Güvem, and Eskihisar have also shown that evergreen oaks (Q. drymeja Unger) found at these localities differ significantly. While an archaic leaf type is most abundant in Güvem and Kimi, this type is absent in Eskihisar and middle Miocene floras of the Parathetys (e.g. Parschlug, Austria). Hence, we suggest a Langhian (–Serravallian) age for the Eskihisar lignite mine palynoflora.

There has been considerable disagreement about the age of the Neogene coal basins of western Anatolia. Benda (1971a, 1971b) and Becker-Platen, Benda & Steffens (1977) proposed a biostratigraphic subdivision of the Turkish Neogene based on palynofloras. Based on similarity (taxonomic composition and abundance) Benda recognized various “Pollen Bilder” (pollen assemblages, PA) and assigned them to different stratigraphic levels. Seyitoglu, Benda & Scott (1994) and Seyitoglu & Scott (1994) established the lower boundary of the Eskihisar PA using radiometric dates of volcanic rocks in the Gördes Basin and suggested an age of 21.1 to 18.4 Ma for the lower boundary. Seyitoglu & Benda (1998) placed the upper limit of the Eskihisar PA at 14.8 Ma using radiometric ages of volcanic rocks in the Selendi and Uşak-Güre Basins. Thus, these authors suggested a stratigraphic range of ca 20 to 14.8 Ma for the Eskihisar PA. The Langhian age inferred for the Eskihisar lignite mine palynoflora in the present study roughly corresponds to this time frame. However, numerous pollen assemblages of western Anatolia falling into this time frame do not correspond to the Eskihisar PA as defined by Benda (1971a, b; see following section).
Akgün & Akyol (1999) investigated palynofloras of the Büyük Menderes area in western Anatolia included within the Eskihisar PA by Benda (1971a) and considered the floras to be of Langhian to earliest Tortonian age (ca 16 to 11 Ma). Akgün & Akyol (1999) and Akyol & Akgün (2001) questioned the results of radiometric dates for sites they considered to be markedly younger based on palynological evidence than suggested by the radiometric ages. Notably, Akyol & Akgün (2001) pointed out that radiometric dates for the Turgut and Sekköy members provided by Becker-Platen et al. (1977) are in need of revision as they suggested a much younger age for the stratigraphically older Turgut member. Also, the Langhian age inferred by Akgün & Akyol (1999) for the Kulloğullari pollen assemblage based on dispersed spores and pollen appears to be more reliable than the dating of the tuffites at this locality to 21 Ma by Becker-Platen et al. (1977). More recently, the reliability of radiometric dates has improved substantially and in some cases radiometric dates may aid in revising age estimates for palynofloras. For example, the palynological assemblage from Akhisar-Çıtak (Gördes Basin, Manisa) considered by Akgün & Akyol (1987) and Akgün et al. (2007) as early-middle Serravallian may be older as suggested by radiometric dates from the central Gördes volcanics (Seyitoglu & Sen, 1999).

Based on published palynofloras from western Anatolia it appears that Benda’s Pollen Assemblages may be less stratigraphically controlled than assumed by Benda and co-workers and Seyitoğlu and co-workers. This is reflected in age assessments for Benda’s Kale Pollen Assemblage that is supposed to be stratigraphically older than the Eskihisar PA. The Kale PA has been correlated with Burdigalian (20.4–16 Ma) marine microfossil zones (Benda et al., 1977) while at the same time Seyitoglu & Benda (1998) considered the Eskihisar PA to range from 20–14.8 Ma. Also Takahashi & Jux (1991), when investigating the palynological content of the Soma profile, stated that there was no qualitative difference between the Kale and the Eskihisar PA of Benda (1971a, 1971b). Likewise, Yavuz-Işık (2008) described a palynoflora from Güvem, the age of which is well-constrained by radiometric dates of
bracketing basalts as 19.7 to 17.9 Ma (Burdigalian). However, the entire pollen flora has a strongly mixed signal, suggesting affinities to the Kale PA (abundant Engelhardioidae), Eskihisar PA (dominating evergreen and deciduous *Quercus*; evergreen more abundant than deciduous), and Yeni Eskihisar PA (high percentage of *Ulmus*, moderate presence of *Fagus*).

Noteworthy, according to Benda’s scheme, the first occurrence of *Fagus* pollen is in the Yeni Eskihisar PA, some twenty million years after the actual first occurrence of *Fagus* in the pollen and macro fossil record of the East Mediterranean (see Velitzelos et al., 2014). This discrepancy may be explained by the fact that some of the pollen grains treated by Benda (1971a) as *Nyssa* do belong to *Fagus* (see above, Systematic Palynology, *Fagus*). This suggests that Benda’s Pollen Assemblages may be in need of revision and that they ought not to be generally linked with radiometric ages obtained from different sites.

Ideally, when inferring the age for different sedimentary basins using dispersed pollen and spores additional evidence from mammal data (e.g. Akkiraz et al., 2012; Yavuz-Işık, 2007; present study), radiometric data (e.g. Kayseri-Özer et al., 2014b), or both (e.g. Yavuz-Işık, 2008), should be considered.

**Comparison with other early-middle Miocene western Anatolian palynofloras**

Previous palynological studies in western Anatolia are listed in Table 1. In view of the difficulties to constrain the exact age of early to middle Miocene plant-bearing deposits in western Anatolia it is difficult to decide whether similarities among different palynofloras are due to convergent vegetation development or contemporaneous deposition.

The Burdigalian Güvem flora (Ankara) has a well-constrained age (radiometric age of bracketing basalts, 19.7-17.9 Ma); it is clearly older than the Eskihisar flora, and may serve as a starting point for comparison. A total of 50 taxa could be identified in the Güvem section (Yavuz-Işık, 2008). As in the Eskihisar mine section, Fagaceae is the most dominant angiosperm group, followed by *Ulmus/Zelkova*. In terms of taxonomic composition, there is
an almost 100% congruence between the Güvem palynoflora and the Eskihisar flora.

However, “Engelhardia” (Engelhardioideae) is much more abundant in the Güvem section (up to 15%) and Fagus is less common (Fagus is also much less common in the macrofossil record of Güvem; T. Denk, unpublished data). Since neither Myrica (Myricaceae) nor Corylus (Betulaceae) is recognized in the pollen record, some of the Engelhardioideae pollen may actually belong to these genera. Myrica is a very common element in the macroflora of Güvem (Kasapligil, 1977; T. Denk, unpublished data).

A further difference between the Güvem and the Eskihisar palynofloras is the slightly higher abundance of “evergreen Quercus” as compared to “deciduous Quercus” in the Güvem assemblage. However, the distinction between these two categories is difficult when established in LM. Denk et al. (2010) listed pollen size ranges for all infrageneric groups of Quercus and found a considerable amount of overlap between the main groups.

Possibly of similar age is the Hacıbekir group in the Uşak-Güre Basin (Seyitoglu, 1997). A palynoflora described from here (Akkiraz et al., 2015) has more abundant evergreen oaks than deciduous oaks, 5% to >5% pollen of castanoids, and up to 10% Engelhardioideae, plus less than 5% Fagus pollen. In addition, Alnus is very abundant in the Hacıbekir group (to >20%). Apart from this Alnus peak, the palynoflora is similar to the Güvem flora. Yavuz-Işik (2007) investigated sediments of the Seyitömer Basin and recognized two pollen zones (55 taxa). The transition between the two pollen zones at ca 16 Ma is, according to Yavuz-Işik (2007), represented by the increase in Quercus, Ulmus, and Poaceae pollen. Noteworthy, Fagus is quite abundant (5-15%) in the (older) pollen zone 1 and rare in pollen zone 2. Yavuz-Işik (2007) reported high amounts of both evergreen and deciduous Quercus in pollen zone 2. Overall, pollen zone 2 of Yavuz-Işik (2007) is very similar in composition and abundance of major pollen groups to the Eskihisar lignite mine section (Langhian; Table 1).

This similarity includes high abundance of Alnus and Ulmus, low abundance of Taxodioidae, and regular occurrence of Oleaceae, among others. In contrast, Akkiraz et al. (2012)
investigating the same layers in the Seyitömer Basin recognized 53 spore and pollen taxa and interpreted dispersed *Quercus* pollen grains in a different way, recognizing up to 40% evergreen *Quercus* and less than 5% deciduous *Quercus*. This discrepancy may be explained by the somewhat arbitrary boundary between these two categories (see above).

Similarities with the Eskihisar palynoflora are also seen in the Vişneler Formation (Kocaçay Basin, Menderes; Kayseri-Özer et al., 2014b) that might be ca 14 Ma based on radiometric dates of volcanic rocks and mammal fossils (Table 1). Unfortunately, *Cedrus* has not been distinguished from other Pinaceae in this study; *Fagus* appears to be absent from the palynoflora. A further palynoflora from the Ankara region (Peltiçik Basin) that was deposited between 18 and 11 Ma (Yavuz-İşık & Demirci, 2009), shows remarkable similarities with the Eskihisar flora in the upper half of the stratigraphic sequence. Differences are due to a *Salix* peak in the basal part of pollen zone 2 in the Peltiçik Basin as compared to an *Alnus* peak in the Eskihisar mine section. Furthermore Taxodiaceae/ Cupressaceae are fairly abundant in the upper part of pollen zone 2 in the Peltiçik Basin, along with Polypodiaceae and *Sparganium*. Overall, differences between the two palynofloras are restricted to the azonal vegetation.

The floras reported from the Büyük Menderes graben (Akgün & Akyol, 1999; Akgün et al., 2007) are considered to be of middle Miocene age based on pollen and spores. Some of these floras are fairly similar to the Eskihisar flora. Highest similarity is between the Langhian Kulloğulları pollen assemblage and the roughly coeval Eskihisar lignite mine assemblage. Also the palynoflora from Aydın/Şahınalı (Akkiraz, 2011) is very similar in general composition, but differs by abundant Cupressaceae in the upper part of the section. In addition, *Fagus* is very rare in the macrofossil record of Şahınalı, while abundant in Eskihisar (T. Denk, personal observation).

In general, closest similarities of the Eskihisar palynoflora are with the middle Miocene floras recovered from the Seyitömer Basin, Peltiçik Basin, and Büyük Menderes graben (Kulloğullari, Şahınalı). Burdigalian floras are distinguished from younger ones by generally
higher amounts of Engelhardioideae and less Fagus pollen. The amount of Quercus pollen may be high in Burdigalian as well as in Langhian floras. Middle Miocene palynofloras commonly have higher abundance of Fagus pollen. Supposedly upper Miocene sediments differ by low abundance of Engelhardioideae and increased values of various herbaceous taxa, most of which were present since the Burdigalian.

The (weak) trends seen in the Miocene of Anatolia cannot be straightforwardly correlated with trends seen in the Paratethys. For example, from a latest early-middle Miocene core from the Pannonian Basin (Hungary) spanning a period from ca 16 Ma to ca 12 Ma, Jiménez-Moreno et al. (2005) reported high abundance of Engelhardioideae during the Langhian and Serravallian. At the same time, evergreen oaks did not play a significant role during this time interval. Deciduous oaks were moderately abundant during the Langhian and increased during the Serravallian. Similarly, Jiménez-Moreno et al. (2008) reported high values, to >20% of Engelhardioideae pollen for the Langhian of southeast Croatia. Levels of deciduous and evergreen Quercus were around 5%, Fagus was not present at all, whereas Rubiaceae and Sapotaceae were fairly abundant. Sapotaceae are rare in Turkish early and middle Miocene floras. For the Miocene of the Forecarpathian Basin (Bulgaria), Ivanov et al. (2002) reported ca 10% of Engelhardioideae pollen for the time period ca 13 Ma to ca 12 Ma, and up to 15% at ca 14 Ma. Also here, Fagus was rare throughout the middle Miocene.

Conclusions

In the present study 91 palynomorph taxa are described from the middle Miocene Eskihisar lignite mine palynoflora in southwestern Anatolia. Two pollen zones are recognized. Pollen zone 1 is characterized by high amounts of Alnus, Decodon, and Osmunda reflecting a swamp forest that developed prior to and during the formation of the main lignite seam. Pollen zone 2 is derived from lacustrine sediments above the lignite seam and is characterized by the presence of Botryococcus and algal cysts. Besides, the two pollen zones are fairly similar and
reflect heterogeneous environments including broad-leaved deciduous (*Fagus*) forest, subtropical *Trigonobalanopsis* forest, and sclerophyllous and semi-evergreen oak (*Quercus*) forest. Conifers such as *Cathaya*, *Cedrus*, and *Picea* may have been accessory elements in the *Fagus* and *Quercus* forest communities and replaced these at higher elevations. Among the herbaceous taxa, some indicate the presence of sandy and/or rocky soils that occurred scattered around the area of deposition and in the hinterland. The two pollen zones are interpreted as two stages of basin development reflecting the change from swamp to lacustrine conditions and the drowning of the coal swamp due to basin subsidence. They do not appear to reflect regional or large scale climatic changes.

A review of published palynological accounts of western Anatolia suggests that generalized pollen assemblages alone cannot resolve stages of the late early and middle Miocene as has previously been claimed. This has implications for using traditional “*Pollen Bilder*” to infer ages of plant-bearing sediments and for correlating radiometric dates with more than one sedimentary basin.

The biogeographic information in the encountered spores and pollen indicates general Northern Hemispheric affinities (*Acer, Juglans, Ulmus*), North American affinities (*Decodon*), and East Asian affinities (*Cathaya, Eucommia*) as also suggested by macro fossils (*e.g. Mahonia*). Only two taxa provide potential biogeographic links with the African flora: Euphorbiaceae gen. indet. with affinities to *Cephalocrotanonopsis* and *Cephalocroton* (tropical East Africa) and Oleaceae gen. indet. 2 with affinities to *Noronhia*. This suggests that biome shifts of plant taxa between African subtropical /tropical biomes and Anatolian (western Eurasian) temperate forests and shrublands may have been rare in the Miocene.

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References


Figure 1. (A–D) Geographic and regional geologic setting of the Eskihisar lignite mine section, Yatağan basin. A. Map showing the geographical position of the Yatağan basin (B) and other Miocene palynofloras: squares – early Miocene localities: 1–Peltiçik, 2–Güvem; circles – middle Miocene localities: 3–Aydın, Şahnali, 4–Cumaovası and Kocaçay, 5–Soma, 6–Seyitömer, 7–Çan, 8–Balya, Balikesir. B. Regional geological map of the Yatağan basin (map based on Becker Platen, 1970, and Atalay, 1980). C. Lithostratigraphic units of the Eskihisar Formation from which sediment samples were taken. The sampled section includes the uppermost part of the Turgut Member and the lower part of the Sekköy Member, both of which are here considered to be middle Miocene in age. D. Photograph of the sampled Eskihisar lignite mine section.

Figure 2. LM pollen count diagram of the Eskihisar mine section showing percentages of taxa.
+ rare (<2.5 %); x = Botryococcus colonies present, xx = B. colonies frequently encountered; * taxon comprises several genera or infrageneric groups discernible in SEM but not in LM. Hence these genera are not considered in the pollen diagram. ASR = Anacardiaceae/Simaroubaceae/Rutaceae. N = 400 pollen per sample. Sample numbers are indicated next to the simplified stratigraphic section.


Figure 4. LM overview (A, D, G, J), SEM overview (B, E, H, K) and SEM detail (C, F, I, L) micrographs of dispersed, fossil Osmundaceae spores. A–F. Osmunda sp. 1 (S153581). G–I. Osmunda sp. 2 (S153581), polar view. J–L. Osmunda sp. 3 (S153575), polar view. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1µm (C, F, I, L).


**Figure 8.** LM overview (A, D, G, J), SEM overview (B, F, I, L) and SEM detail (C, D, G, J, M) micrographs of dispersed Pinaceae, Ephedraceae and Poaceae pollen. A–C. Pinus subgenus Strobus sp. (S153565), (A, B) polar view, (C) leptoma and (D) saccus detail. D–F. Ephedra sp. (S153567), equatorial view. G–J. Poaceae gen. indet. 1 (S153539), polar view; (I) annulus. K–L. Poaceae gen. indet. 2 (S153548), polar view; (L) annulus with operculum. Scale bars – 10 µm (A, B, E, F, H, I, K, L), 1 µm (C, D, G, H, K, L, O, P, S, T).


**Figure 10.** LM overview (A, D, G, J), SEM overview (B, E, H, K) and SEM detail (C, F, I, L) micrographs of dispersed Linaceae, Fabaceae and Betulaceae pollen. A–C. Linum sp. (S153573), equatorial view. D–F. Tricolporopollenites wackersdorfensis / Podocarpium sp. (S153573), polar view. G–I. Apios sp., (G top) equatorial view (S153539), (G bottom, H, I) polar view (S153541). J–L. Alnus sp., (J top) pentporate pollen grain (S153546), polar view, (J bottom, K, L) hexaporate pollen grain (S153546), polar view. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

Figure 12. LM overview (A, D, G, J), SEM overview (B, E, H, K) and SEM detail (C, F, I, L) micrographs of dispersed Fagaceae pollen. A–F. *Fagus* sp., (A–C) (S153572) polar view; (D–F) (S153572) equatorial view. G–I. *Quercus* sp. 1 (*Quercus* Group *Cerris*) (S153541), polar view. J–L. *Quercus* sp. 2 (*Quercus* Group *Ilex*) (S153542), equatorial view. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1µm (C, F, I, L).


Figure 16. LM overview (A, D, G, J), SEM overview (B, E, H, K) and SEM detail (C, F, I, L, M) micrographs of dispersed Ulmaceae, Geraniaceae, Lythraceae and Onagraceae pollen. A–C. *Zelkova* sp. (S153572), polar view. D–F. *Erodium* sp. (S153590), equarorial view. G–I.


Table 1. Previous palynological investigations in western Turkey. Abundance of key taxa and age control.
Fig. 16
Fig. 24
Fig. 26
<table>
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<th>Locality/Taxon</th>
<th>Pinus diploxylon</th>
<th>Pinus haploxylon</th>
<th>Quercus decidua</th>
<th>Quercus coccifera</th>
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⁴Akkiraz 2011; Akgün & Akyol, 1999; ⁵Akgün & Akyol, 1999; Akgün et al., 2007; ⁶Kayseri et al., 2014b; ⁷Akkiraz et al., 2015; Takahashi & Jux, 1991; Seyitoğlu, 1997; ⁸Yavuz-Işık, 2007; ⁹Akkiraz et al., 2012; ¹Ediger, 1990; Bozcu et al., 2015; ²Yavuz-Işık & Demirci, 2009; ³Yavuz-Işık, 2008.

*= absent; • = to 1%; + = to 5%; ++ = to 10%; +++ = to 30%+
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<th>Stratigraphic range in Turkey</th>
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<td><strong>18 - 9.5 Ma</strong> 18 - 17 Ma (Akcahisar 1) 11.2 - 9.5 Ma (Araplı, Igdebaglar) 15.2 - 12.5 Ma (Inönü 1, Sinap 24A) 12.5 - 11.2 Ma (Saricay)</td>
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Data from Fortelius (coordinator), 2016; Sarac, 2003; Sickenberg et al., 1975

Supporting Information: Appendix S1 (1)
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Data from Fortelius (coordinator), 2016; Sarac, 2003; Sickenberg et al., 1975

Supporting Information: Appendix S1 (2)
Turkey

*Gomphotherium angustidens*, the only mammal encountered in the Ezhikher gallery, main lignitic seam, Turkgut Member (Sickenberg et al., 1975), in Turkey and stratigraphic ranges of mammals encountered in the Catakbaygaya fauna (Fortelius et al., 1996; Sickenberg et al., 1975), in comparison to Neogene Mammal Zones and standard stages (Harzhauser & Filler, 2007).
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<th>colour</th>
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Supporting Information, Appendix S3

*Quercus kubinyii* (Kováts ex Ettingshausen) Czeczott from marls above the main coal seam of the Eskihisar mine collected during field work in 2010 and 2013.