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Paleoenvironment of the Late Oligocene from the Kağızman-Tuzluca Basin (northeastern Anatolia) based on the micro- and macrofloras

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Abstract: The Kağızman-Tuzluca Basin in East Anatolia is still poorly documented for its stratigraphy and in particular its paleofloral assemblages. In this study, the microfloras from the Kağızman-Kötek and Kömürlü areas and the macroflora from the Tuzluca area in this basin have been defined to overcome this deficiency. Sedimentary sequences of the Kağızman-Kömürlü area have been deposited in terrestrial conditions different from the sequences of the Kağızman-Kötek and Tuzluca areas, which were deposited in brackish conditions near a shallow marine environment. Paleovegetation in eastern Anatolia is represented by mixed mesophytic and coniferous forests restricted to high and middle altitudes (e.g. *Pinus*, *Ulmus*, Fagaceae, *Engelhardia*, *Sequoia*, *Zelkova*, Lauraceae, *Pterocarya*, and *Quercus*). Open vegetation elements (Asteraceae-Asteroideae, *Tubulifloridites* spp., Poaceae, and Umbelliferae) in East Anatolia are more predominant than in West Anatolia. The presence of some marine dinoflagellates and *Calamus*, Lauraceae, and Arecaceae suggests near-seaside plant distribution in the Kağızman-Kötek and Tuzluca areas. According to micro- and macrofloral records and numerical climatic values calculated by the coexistence approach method, paleoclimatic conditions could have changed between warm temperate and subtropical, and also seasonality was effective in East Anatolia during the Late Oligocene. In addition, the paleoclimate of East Anatolia during the Late Oligocene appears to be colder than in West Anatolia based on the palynological data, and this could be related to the high elevation of East Anatolia as compared to West Anatolia. Moreover, the low precipitation values of East Anatolian indicate a dry period in the paleoclimatic conditions of the Late Oligocene.

Key words: Micro- and macrofloras, Late Oligocene, eastern Anatolia, palaoclimate, paleovegetation

1. Introduction

The Kağızman-Tuzluca Basin is located in northeastern Anatolia, to the east of the intersection point of the major North and East Anatolian faults systems (Allen, 1969; Arpat and Şaroğlu, 1972; Şengör, 1979). This basin extends beyond the borders to Iran and to the southern Caucasian countries (Ketin, 1968). This basin was mainly studied for geological, structural, and some paleontological purposes (e.g., Altınlı, 1966; Allen, 1969; Arpat and Şaroğlu, 1972; Şengör, 1979; Şengör et al., 1985, 2008; Şaroğlu and Yılmaz, 1986; Sancay et al., 2006; Hüsing et al., 2009; Adamia et al., 2011; Şen et al., 2011; Metais et al., 2015; Varol et al., 2016).

The Paleogene floras from Anatolia became rather well known during the last two decades thanks to palynological analyses in several sedimentary basins (e.g., Batı, 1996; Kayseri, 2010; Kayseri-Özer, 2011, 2013, 2017; Kayseri-Özer et al., 2017), and these palynological studies were recorded from West and Central Anatolia. Contrary to this, the Paleogene micro- and macrofloras from East Anatolia and surrounding countries are still poorly documented, mainly due to their occasional occurrences and insufficient interest of the paleobotany community in their records (Sancay et al., 2006). In this study, palynofloral data from the Kağızman-Kötek and Kömürlü areas are given, together with a summary of paleovegetational and paleoclimatic differences between West, Central, and East Anatolia.

Studies on the Paleogene macrofloras from several regions in Central and East Europe demonstrated that their bearing for understanding macrofloral diversity and for paleoenvironmental and paleoclimatic reconstruction is of considerable scientific interest (e.g., Kvaček and

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Walther, 1974, 1995, 2001, 2007; Mai and Walther, 1978, 1991, 2000; Schaarschmidt and Wilde, 1986; Kvaček and Hably, 1991; Wilde and Schaarschmidt, 1993; Mai, 1995; Wilde and Frankenhäuser, 1999; Uhl et al., 2002; Velitzelos et al., 2002; Wilde and Manchester, 2003; Erdei and Wilde, 2004; Kvaček, 2004; Wilde, 2004, 2005; Wilde et al., 2005; Velitzelos et al., 2014). Macrofloral records from the Oligocene of Anatolia are still especially poor, partly due to the rare occurrence of Oligocene deposits preserving macroscopic remains, but also due to insufficient field investigations (Mädler and Steffens, 1979). The Tuzluca macroflora correlated to the Late Oligocene is the first attempt to partly fill this gap in Anatolia. The other aim of the study is to contribute to the understanding of paleovegetation and paleogeographical properties of East Anatolia and the paleoclimatological context of the Kağızman-Tuzluca area during the Late Oligocene according to the Kağızman-Tuzluca macroflora and Kağızman-Kötek and Kömürlü microfloras.

2. Geological setting

The study area is located in the Eastern Turkish High Plateau, which lies east of the intersection point of the North and East Anatolian faults in the Karlıova region (e.g., Şengör et al., 1985, 2008; Şen et al., 2011; Metais et al., 2015; Varol et al., 2016). In this region strike-slip and thrust faults, folds, and large-scale extensional fractures have been developing as a result of continent–continent collision during the neotectonic episode (Şengör and Yılmaz, 1981). The Kağızman-Tuzluca Basin is accompanied by intense volcanism that started during the Late Miocene. According to Şen et al. (2011), Metais et al. (2015), and Varol et al. (2016), this basin has suffered shortening and it is thus most likely to be an intermontane ramp valley basin, and the Holocene volcanic centers (e.g., Mount Ararat) have been controlled by active faults within the pull-apart basin structures (Şaroğlu and Yılmaz, 1986; Yılmaz et al., 1998; Karakhanian et al., 2002; Varol et al., 2009; Şen et al., 2011).

In this study, paleofloras of three areas, namely Tuzluca, Kağızman-Kötek, and Kömürlü, were studied and the geological properties of these areas are summarized below.

2.1. The Tuzluca area

The Kağızman-Tuzluca Basin forms a west-east narrow trough between the town of Kağızman in East Anatolia and Armavir in Armenia. It is crossed west-east by the Aras River. This basin is bordered by the basement rocks derived from the Kağızman Complex (Cretaceous ophiolitic) to the south and mafic volcanic rocks of the Late Miocene-Pliocene in the Kars Plateau to the north and west (Şen et al., 2011; Metais et al., 2015; Varol et al., 2016).

Detailed geological studies of the Cenozoic deposits in the eastern part of the Kağızman-Tuzluca basin (Tuzluca area) allowed the recognition of eight sedimentary units (Varol et al., 2016). The Cenozoic deposits commence with the marine sedimentary rocks of the Kağan Formation interfingering with the terrestrial Alhan Formation, both mapped by Varol et al. (2016) as ?Upper Eocene-Lower Oligocene. The Kağan Formation starts with the red clastic rocks laying unconformably on the ophiolitic basement (Varol et al., 2016). In the middle-upper of the sedimentary sequences of the Kağızman-Tuzluca basin, the Kağan Formation comprises a shallow marine sequence dated to the Early Oligocene on the basis of the occurrence of *Nummulites fichteli* Michelotti, 1841 (Şen et al., 2011). Altınlı (1966) has recorded the following microfossils from the same marine sediments near Hamurkesen village: *Nummulites fabiani passage fichteli*, *Nummulites fichteli*, *Nummulites intermedius*, *Operculina alpina*, *Operculina* cf. *complanata*, and *Operculina* sp. The Alhan Formation consists of deposits of ephemeral rivers, red beds (paleosols), and distal alluvial fan. The Güngören Formation gradually overlies the Alhan Formation, and its lower part is considered as time-equivalent to the marine part of the Kağan Formation. The Güngören Formation displays a complex depositional character with vertical and lateral transitions of fluvial and deltaic deposits. The fluvial deposits occur as channel-fill, flood plain (overbank), and meandering river facies. The deltaic deposits are characterized by remains of a giant rhinoceros *Paraceratherium* sp. (Şen et al., 2011), a primitive ruminant *Iberomeryx* sp., a large carnivoran *Hyaenodon* sp., and a radius fragment of an indeterminate small rhinoceros. The leaf fossils were collected from the limestones deposited in a deltaic environment at the lower part of the Güngören Formations. The age of this leaf flora should be early Chattian based on the marine invertebrates and mammalian fossil records from the Kağan and Güngören Formations, respectively (Figure 1) (Şen et al., 2011; Metais et al., 2015; Varol et al., 2016). The overlying Turabi Formation, which yielded an Early Miocene vertebrate fauna (Şen et al., 2011), is mainly composed of brownish mudstones and thin lignite layers. Near Turabi village, the lower and upper contacts have gradual transition with the underlying Kızılkaya Formation and the overlying Çincavat Formation, which is composed of caliche, ephemeral stream, and flood plain deposits. A layer close to the base of the Çincavat Formation yielded some micromammalian fossils (insectivores, rodents, and lagomorphs) together with terrestrial small gastropods. This fauna is correlated to the late Early-early Middle Miocene (late Burdigalian-Langhian). The last Neogene depositional unit outcrops around Tuzluca town, and it consists of thick evaporites of the Tuzluca Formation, mainly composed of gypsum and

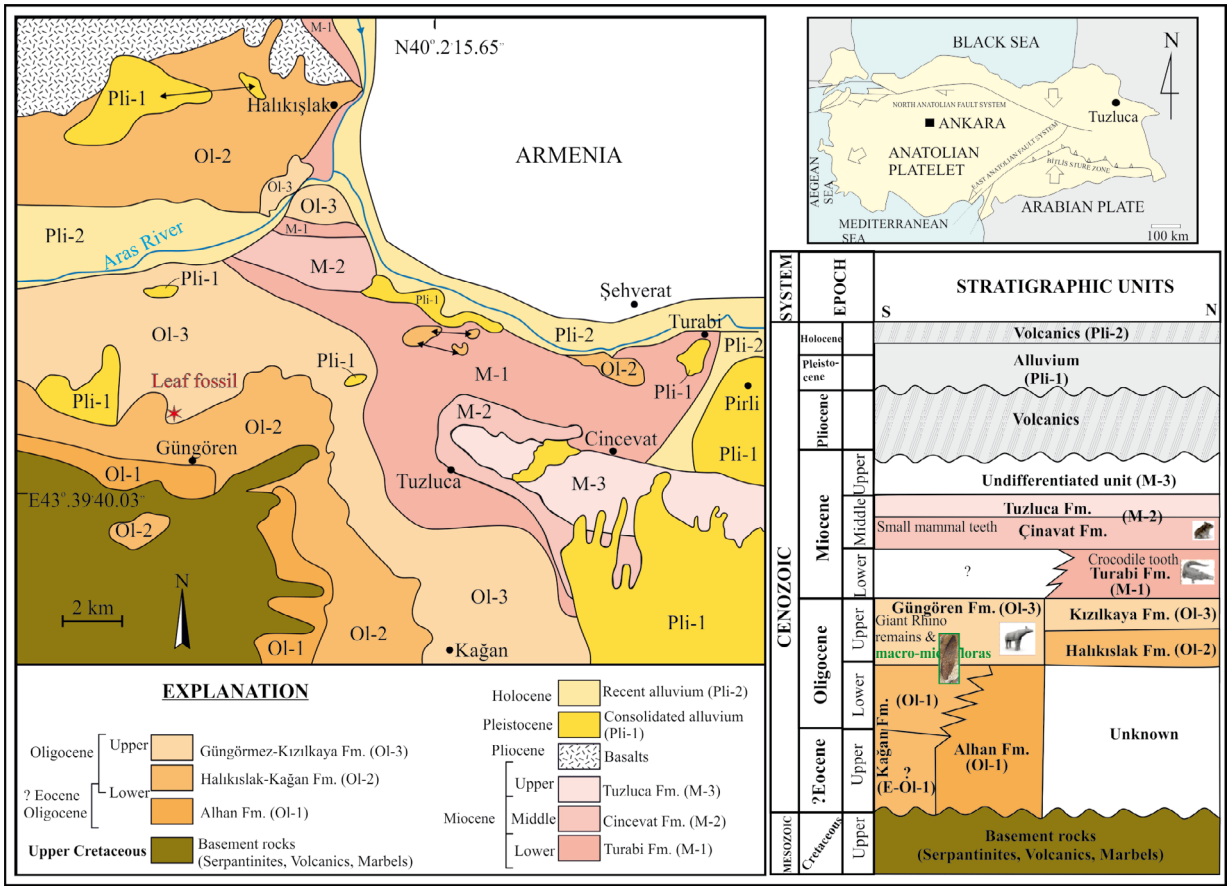


Figure 1. Geological map of the eastern part of the Kağızman-Tuzluca Basin and the location of vertebrate and leaf fossil sites (a), and (b) Cenozoic stratigraphy of the Tuzluca region (Varol et al., 2016).

bedded halite, formed in saline pan and shallow saline lake environments, respectively. Its precise age is not known (Metais et al., 2015; Varol et al., 2016).

2.2. Kağızman-Kötek and Kömürlü areas

In the western part of the Kağızman-Tuzluca Basin (Figure 2), Jurassic-Cretaceous sedimentary rocks and metamorphics form the basement, similar to the nearby Tercan-Aşkale Basin (Şahintürk and Kasar, 1979; Şahintürk et al., 1998; Uğur, 2000). The Penek Formation, from the Late Oligocene to Early-(Middle?) Miocene and deposited in terrestrial conditions, unconformably overlies the basement in the Kömürlü area (Figure 2) (Şahintürk and Kasar, 1979; Uğur, 2000). This formation is mainly composed of reddish and badly sorted clastic lithologies such as conglomerates, sandstones, mudstones, blocks belonging to the basement, and some volcanic inputs such as agglomerates and tuffs. The Penek Formation is gradational to the overlying Oligo-Miocene Kömürlü Formation, which is composed of conglomerates, sandstones, and shale intercalations at the bottom, grading into laminated shales, marls, coal layers, and thin gypsum layers at the top. The Upper Miocene-Pliocene Zırnak Formation and Karakurt Volcanics unconformably overlie the Kömürlü Formation (Şahintürk and Kasar, 1979; Uğur, 2000). The Zırnak Formation, located in the lower part of the Mio-Pliocene sequences, is dominantly composed of clastic lithologies such as conglomerates, sandstones, siltstones, claystones, shales, marls, and coals (Figure 2). The Karakurt Formation (Volcanics) are extensively exposed to the north of the Kağızman-Tuzluca Basin (Figure 2).

The Kötek area is located to the northwest of the town of Kağızman (Figure 2). Limestones of the Upper Cretaceous Orcuk Formation are unconformably overlain by the Kömürlü Formation, which mainly consists of gray to green, moderate to well-sorted, thick-bedded, macrofossiliferous sandstones, black marls, laminated shales, and thin coal layers (Figure 2). Reddish conglomerates and mudstones of the Güllüce Formation unconformably overlie the Kömürlü Formation, different from the Kağızman-Kömürlü area. Tuffs of the Zırnak Formation are seen at the uppermost part of the section

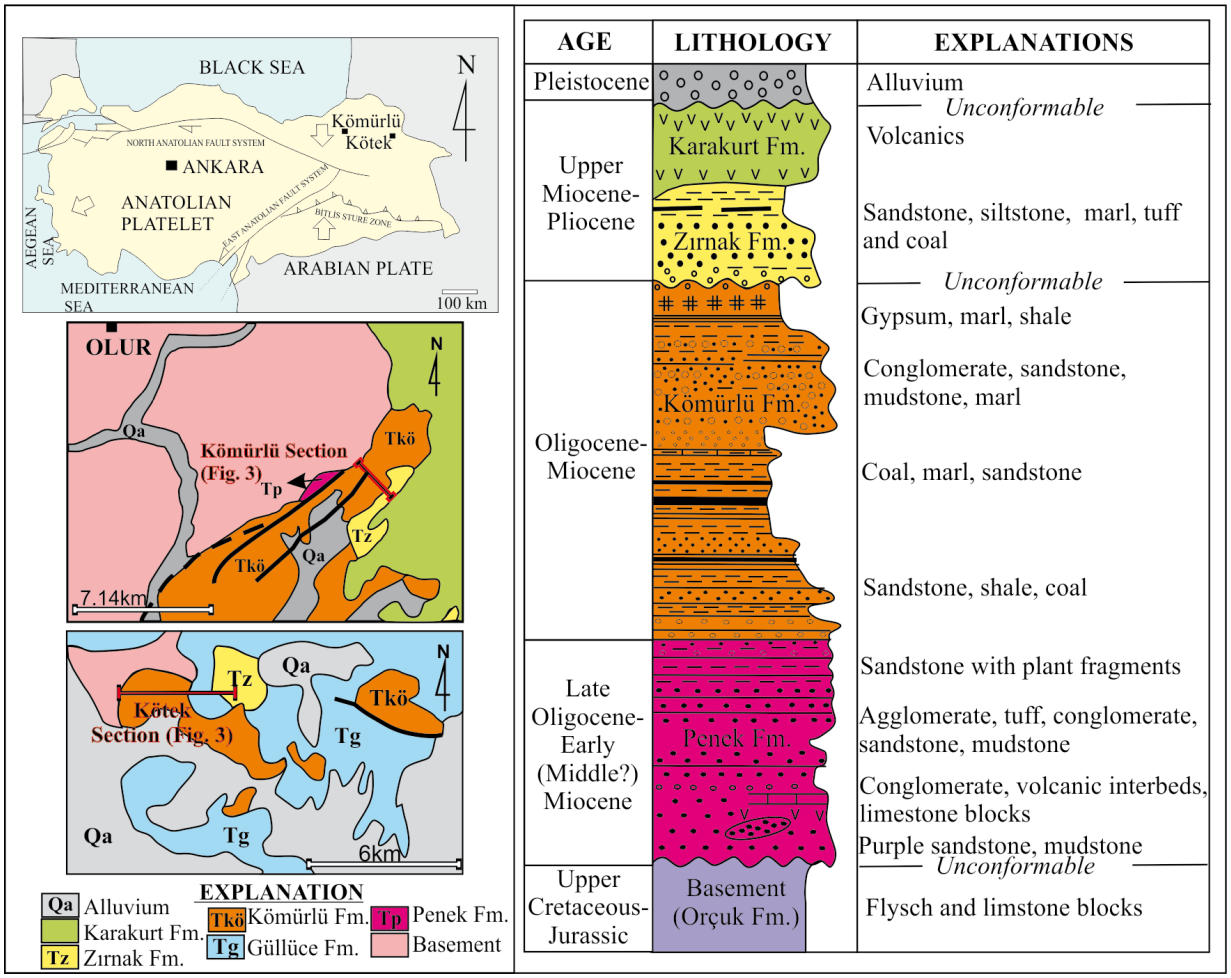


Figure 2. Geological map of the Kağızman-Kötek and Kömürlü areas and general stratigraphic section of these areas (Sancay, 2005).

and unconformably overlie the older units (Figure 2). All palynological samples were collected from coal-bearing sediments of the Kömürlü Formation, which is rich in organic matter.

3. Materials and methods

The macroflora under study comes from a unique location situated in a direct line at about 8 km west of Tuzluca town in the Kağızman-Tuzluca Basin, northeastern Anatolia (Figure 1). The leaf fossil locality is near the bottom of a 15-m-thick sandy limestone, which separates the underlying Alhan Formation from the overlying Güngören Formation. Forty-eight leaf fossil remains were collected from these limestones. This horizon can be followed over 5 km in the landscape. The biostratigraphy of sedimentary deposits in the Kağızman-Tuzluca area is established using invertebrates, pollen, and micro- and macromammalian fossil data (Şen et al., 2011; Métais et al., 2015; Varol et al., 2016). The fossil flora is Late Oligocene in age based on the mammalian fossils and it consists of leaf imprints. Cuticles were not preserved due to taphonomic conditions.

Two stratigraphic sections (Kömürlü and Kötek) were measured by RH Sancay (scope of doctoral study) and sampled during the field study (Figure 2). Palynofloral data were obtained from a total of 57 samples (25 from Kötek and 32 from Kömürlü sections) collected from the coal-bearing sedimentary sequences in the Kötek and Kömürlü areas (Figure 3). Measured sections are mainly composed of clastics (claystones, siltstones, shales, silty marls, marls, sandstones, and conglomerates) and coal beds. All analyzed material is stored in the Palynology Laboratory Archive of the Turkish Petroleum Corporation Research Center, Ankara. Standard palynological processing techniques were used for all samples (Sancay, 2005).

In the present study, the coexistence approach (Mosbrugger and Utescher, 1997; Mosbrugger, 1999; Utescher et al., 2014) is used for quantitative paleoclimatic analyses for East Anatolia. This method can be applied for quantitative terrestrial climate reconstructions in the Cenozoic using plant fossils (leaves, fruits and seeds, pollen,

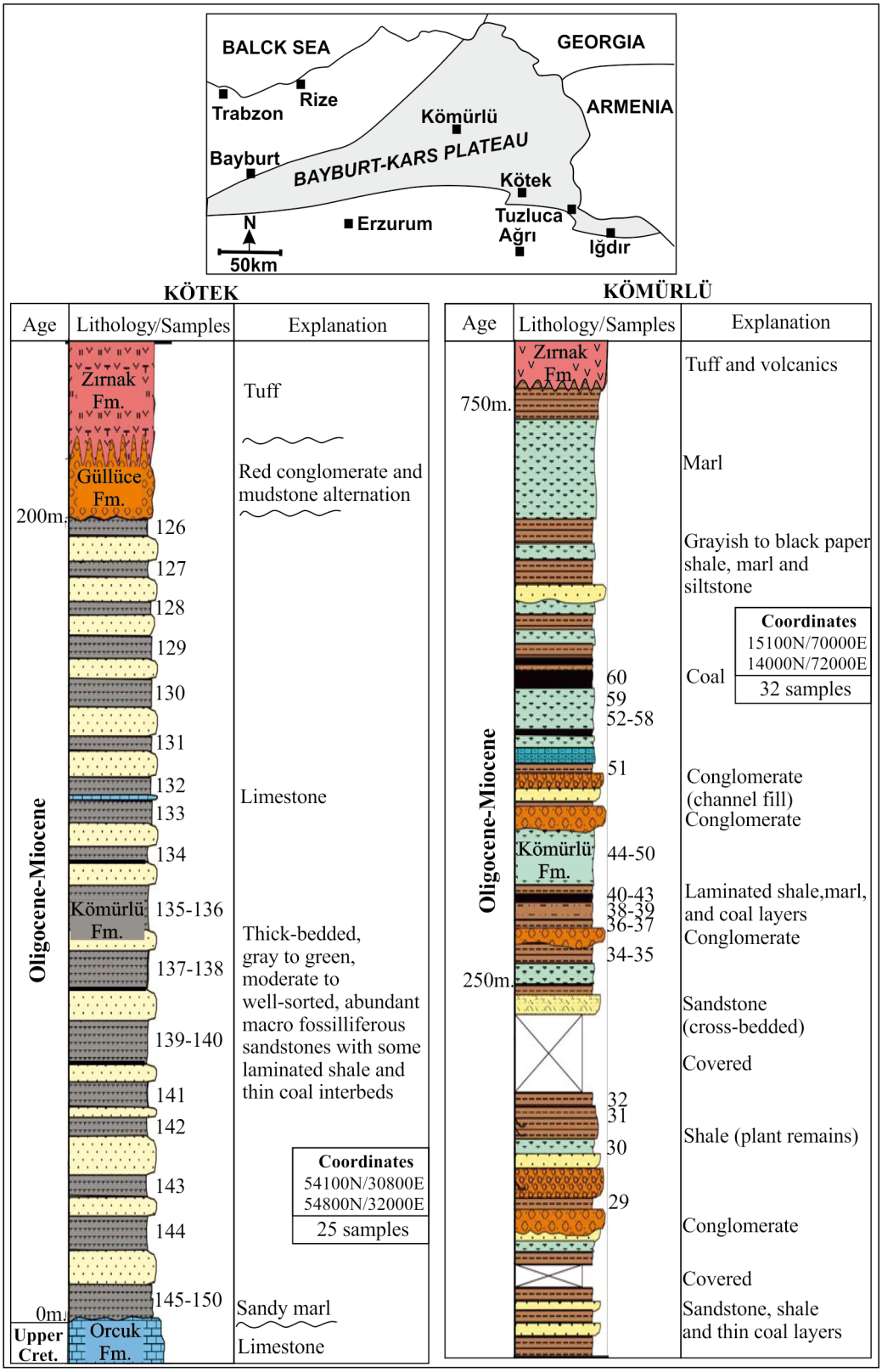


Figure 3. The Kağızman-Kötek and Kömürlü stratigraphic sections and sample locations.

and wood). The purpose of the coexistence approach is to find the climatic ranges of plant associations based on the assumption that the climatic requirements of fossil taxa are similar to those of their nearest living relatives (NLRs) (e.g., Mosbrugger and Utescher, 1997; Mosbrugger, 1999). The coexistence interval is taken as the best estimate of the paleoclimatic conditions under which the fossil flora once lived. The application of the coexistence approach is facilitated by the computer program CLIMSTAT and the Palaeoflora Database at http://www.geologie.unibonn.de/Palaeoflora, which contains NLRs of more than 4800 Cenozoic plant taxa together with climatic requirements of their NLRs. In this study, the paleoclimatic parameters (i.e. mean annual temperature (MAT), mean temperature of the warmest (WMT) and coldest (CMT) months, and mean annual precipitation (MAP)) were calculated using the CLIMSTAT program.

The leaf fossil material is kept in the collections of Dokuz Eylül University in İzmir. Because the plant remains are preserved as impressions only, the descriptions are restricted to leaf morphological features.

4. Results

In this study, the macroflora of Tuzluca and the microfloras of the Kağızman-Kötek and Kömürlü areas have been defined (Appendix).

4.1. Microfloras of Kağızman-Kömürlü and Kötek

In this study, two palynofloras were defined from the Upper Oligocene sediments of the Kömürlü Formation in the Kağızman-Kömürlü and Kötek areas (Eastern Anatolia) (Figures 2 and 3). These palynofloras have been recorded from the 32 coal samples of the Kömürlü Section and are represented by different palynomorphs assemblages such as spores and pollen, organic-walled green algae (*Botryococcus* and *Pediastrum*), and fungal spores. The abundance and the diversity of the spore species increase upwards in the section and they consist of *Cicatricosisporites* sp., *Cingulatisporites macrospeciosus*, *Baculatisporites gemmatus*, *Undulatisporites* sp., *Verrucatosporites alienus*, *Verrucatosporites favus*, *Echinatisporites bifurcus*, *Echinatisporites* sp., *Leiotriletes adriennis*, *Laevigatosporites haardti*, and *Lusatisporites* sp. (Figure 4). Percentages of spore species reached their maximum at the top of the Kömürlü Section. Gymnosperm pollen are only represented by *Pityosporites* spp., *Inaperturopollenites concedipites*, *Inaperturopollenites dubius*, *Sequoiapollenites polyformosus*, and *Inapertisporites* sp., and their abundance is high along the section. The main angiosperm pollen of the Kömürlü palynofloras is *Dicolpopollis kalewensis*, in addition to *Ulmipollenites undulosus*, *Alnipollenites verus*, *Monocolpopollenites tranquillus*, *Monocolpopollenites minus*, *Caryapollenites simplex*, *Momipites* sp., *Tricolporopollenites* spp. (Fagaceae), and *Corsinipollenites oculus noctis*. Herbaceous angiosperm pollens characterized by Asteraceae-Asteroideae, *Tubulifloridites* spp., *Periporopollenites multiporatus*, *Periporopollenites* sp., and *Monoporopollenites gramineoides* are not diverse; however these pollens are abundantly observed in the palynospectra of the Kömürlü Section (Figures 2 and 3). Some algae (*Botryococcus* sp. and *Pediastrum* sp.) are also defined and their abundance is recorded in the middle part of the section. The acme zone of *Botryococcus* sp., which is a freshwater environment element, is between 23 and 393 m, while the abundance of *Pediastrum* sp. is recorded in the lower part of the Kömürlü Section between 23 and 270 m. Fungal spores (*Multicellasporites* sp., *Dicellaesporites* sp., *Anatolinites dongyingensis*, *Biporisporites gunniae*, and *Striadiporites sanctaebarbarae*) are regularly observed along the Kömürlü Section.

The microflora of the Kötek Section is recorded from 25 samples collected in the coal-bearing sediments of the Late Oligocene Kömürlü Formation. Spore species are rich and abundant along the section, and these species consist of *Baculatisporites gemmatus*, *C. macrospecious*, *Laevigatosporites haardti*, *Leiotriletes adriennis/microadriennis*, *Lusatisporites perinatus*, *Magnastriatites howardi*, *Trilites multivallatus*, *Saxosporites* sp., *Reticulatisporites* sp., *Verrucatosporites alienus*, and *Verrucatosporites favus*. The gymnosperm pollens of *Pityosporites* spp. are abundant and regularly recorded in the Kötek palynospectra. The angiosperm pollens, represented by *Inaperturopollenites* sp., *Inaperturopollenites emmaensis*, *Inaperturopollenites concedipites*, *Sparganiapollenites neogenicus*, *Caryapollenites simplex*, *Ulmipollenites undulosus*, *Alnipollenites verus*, *Periporopollenites stigmosus*, *Tricolpopollenites* spp., *Araliaceoipollenites euphorii*, and *Tricolporopollenites* spp. (Fagaceae), are not diverse. Herbaceous species are various and abundant in the palynoflora of Kötek, and these are characterized by *Monoporopollenites gramineoides*, *Periporopollenites multiporatus*, Asteraceae-Asteroideae, *Tubulifloridites* spp., *Ephedripites* sp., and Umbelliferae. Fungal spores (*Dicellaesporites* sp., *Biporisporites* sp., *Anatolinites dongyingensis*), aquatic organisms, and freshwater algae (*Botryococcus braunii*) are rather rare. Marine environment elements include dinoflagellate species (*Cleistosphaeridium* sp., *Spiniferites* sp., *Hystrichokolpoma marigaudiae*, *Lingulodinium machaeophorum*, *Tuberculodinium vancompoae*, *Polysphaeridium* sp., and undifferentiated dinoflagellates) and microforaminiferal linings (Figure 5).

4.2. Macroflora of Tuzluca

The descriptions of the leaf fossils follow the alphabetical order of their genus name for practical reasons. For the description of leaf architectural patterns, the terminology of Dilcher (1974), the Leaf Architecture Working Group (1999), and Ellis et al. (2009) was employed.

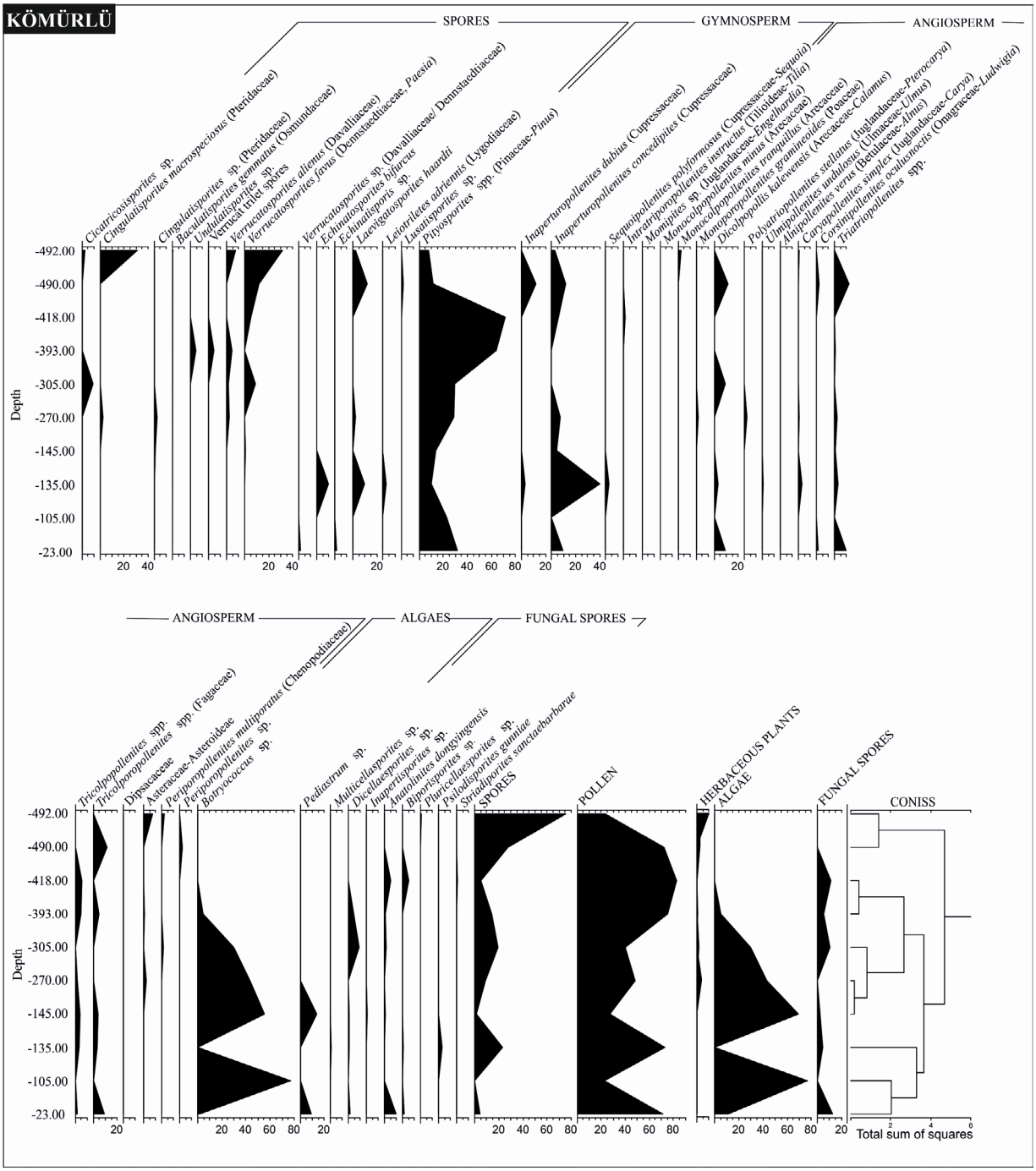


Figure 4. Percentage spore-pollen diagram of the samples collected from the Late Oligocene sediments in the Kağızman-Kömürlü area.

Family: Arecaceae

Arecaceae sp. (Figure 6)

Morphology: Hundreds of leaves from this taxon are seen on the outcrop; the complete leaves reach sizes over 30 cm. We only collected eight fragments of these leaves. The monocotyledonous leaves show parallel venation and these veins are almost of the same thickness. However, the venation becomes thicker on one margin where three veins are significantly thick. This part of the leaf is concave.

Discussion: The gross morphology of these fragments refers clearly to the Arecaceae foliage. However, it is difficult to judge the whole architecture of leaves from the fragments of the studied collection. For this reason, the Tuzluca palm cannot be referred to any morphotaxa (e.g.,

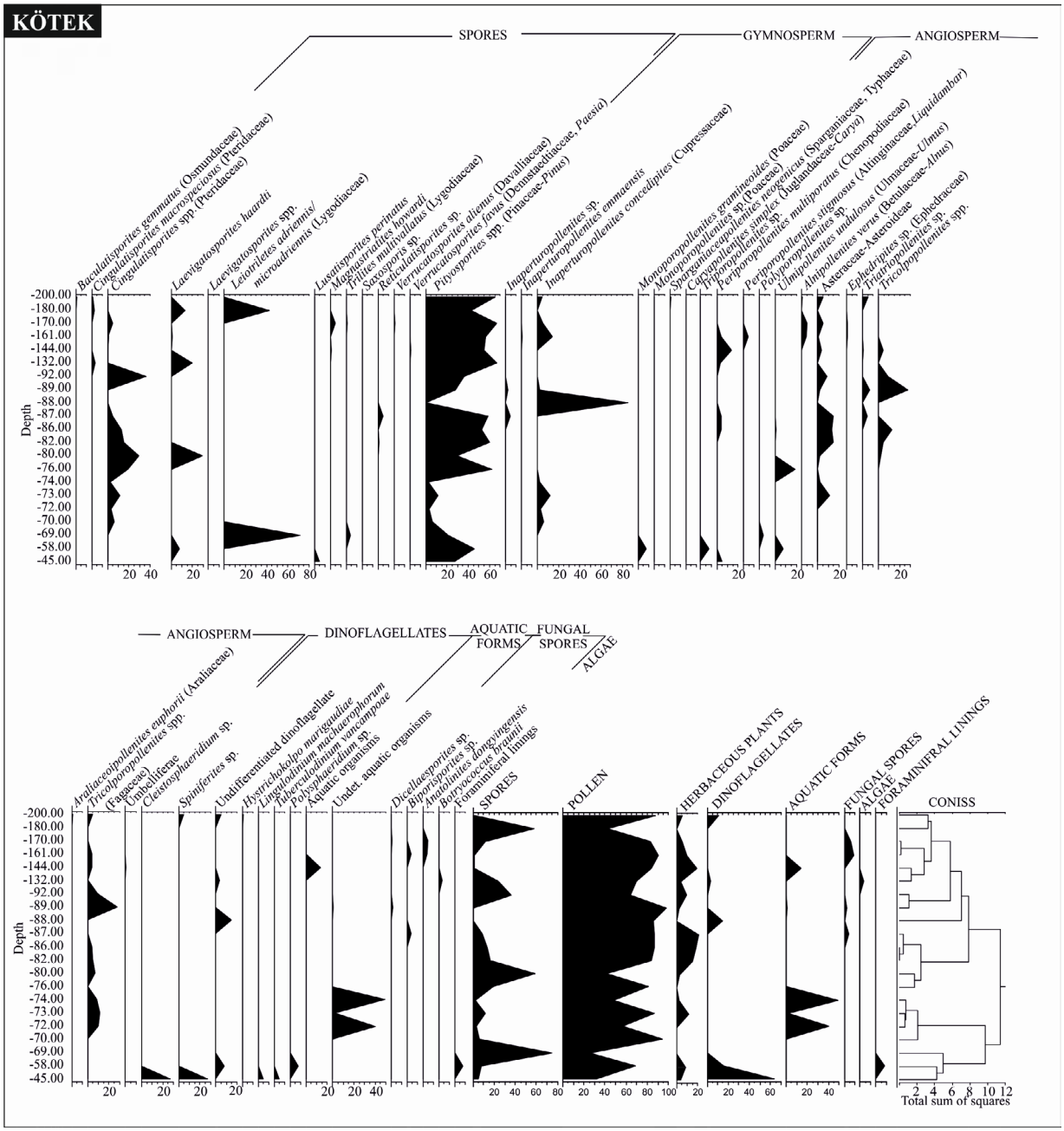


Figure 5. Percentage spore-pollen diagram of the samples collected from the Late Oligocene sediments in the Kağızman-Kötek area.

Sabalites, *Palmacites*). Similar remains of Arecaceae are recorded from the Early Oligocene of the Czech Republic (as Arecaceae gen. et sp. indet., Kvaček and Walther, 2004) and from the Early Oligocene of Flörsheim-SW Germany (as *Monocotyledonea* sp. 2, Kvaček, 2004). Characteristic leaves of sabaloid palms were found at Seifhennersdorf in Germany (Walther, 1996; Walther and Kvaček, 2007) and a fan-like leaf of *Sabal* sp. at Hammerunterwiesenthal in Germany (Walther, 1998). Bozukov et al. (2008) also recorded *Palmophyllum* sp. (Arecaceae) from the Late Oligocene sediments of the Vulche Pole Molasse Formation, SE Bulgaria (Palamarev et al., 2005).

Family Fagaceae

cf. *Eotrigonobalanus furcinervis* (Rossmässler) Kvaček and Walther (1989a) (Figure 7)

1840 - *Phyllites furcinervis* Rossmässler, p. 33, pl. 6, figure 25, pl. 7, figures 32–36, Altsattel (Staré Sedló), northern Bohemia.

1989 - *Eotrigonobalanus furcinervis* (Rossmässler) Walther and Kvaček, p. 581, pls. 33–36, 38–46, pl. 47,

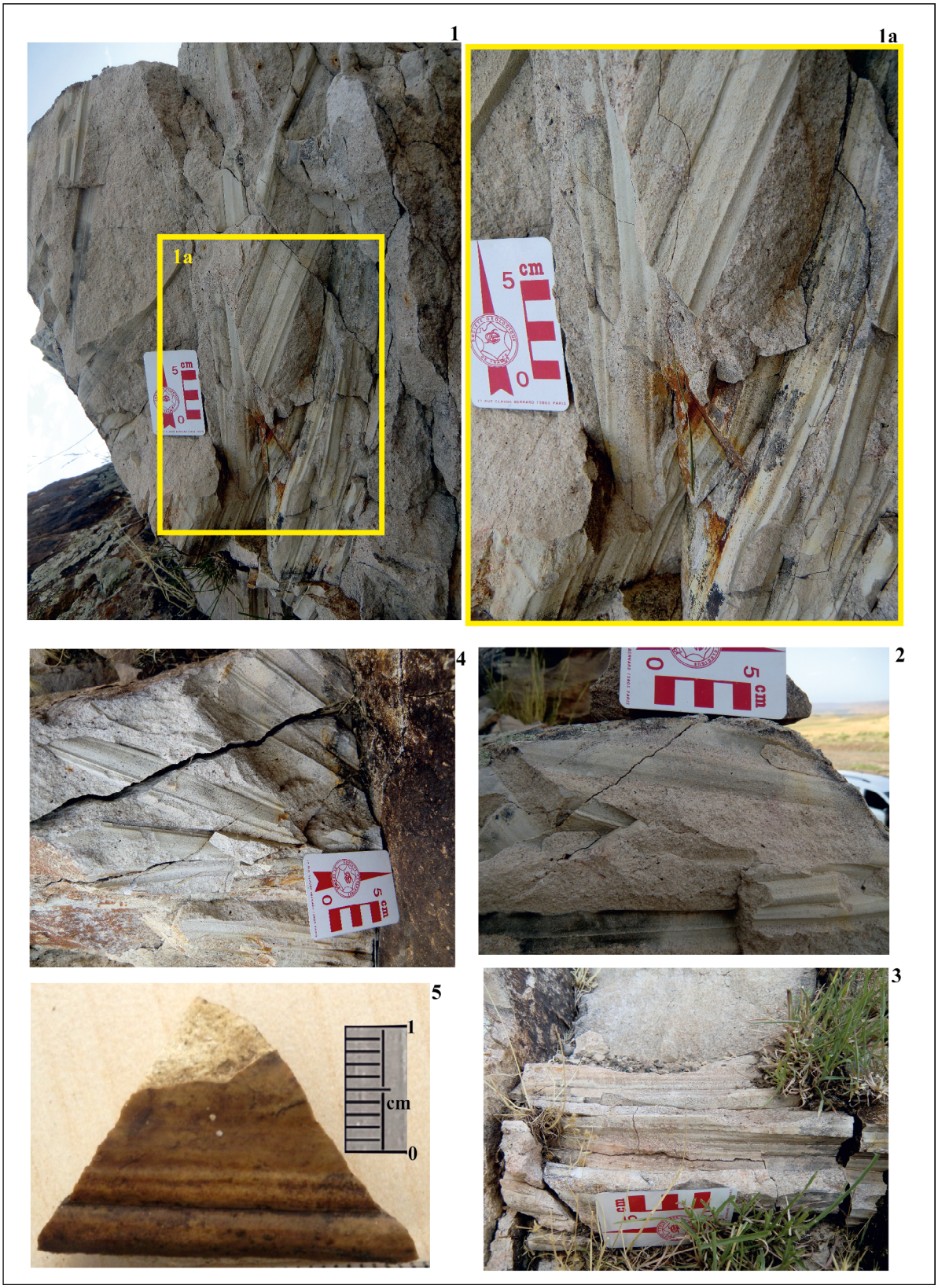


Figure 6. Leaf remains of Arecaceae sp. from Tuzluca locality 5; 1–4: the Arecaceae leaf fossils cropping out in the field at the Güngören Formation in the Tuzluca area; 5: hand sample with leaf imprints.



Figure 7. 1–7: *Daphnogene cinnamomifolia* (Brongniart) Unger forma *lanceolata* sensu Kvaček and Walther; 8: *Daphnogene cinnamomifolia* (Brongniart) Unger forma *cinnamomifolia* sensu Kvaček and Walther; 9–13: cf. *Eotrigonobalanus furcinervis* (Rossmässler) Walther and Kvaček.

figures 1–3, text-figs 3–10 (various sites mostly from NW Bohemia and Saxony, the Late Eocene to Oligocene).

Morphology: There are five leaf specimens of this type in the Tuzluca flora. Petiole not preserved. The leaves are simple, incomplete, elongate, up to 87 mm long and 10–25 mm wide. The base and apex are not preserved. The leaf margin is entire. The primary vein is strong and straight. The secondary veins camptodromous to semicraspedodromous and subparallelly arranged. These secondary veins slightly alternate to oppositely positioned, forming angles between 20° and 66° with the primary vein. The tertiary veins are strong.

Discussion and note: *Eotrigonobalanus furcinervis* shows entire to toothed margin, namely lanceolate to ovate forms, camptodromous to semicraspedodromous and craspedodromous venation, and a wide morphological range (Kvaček and Walther, 1989a, 1989b). Entire margined leaves are characteristic of the Oligocene populations of *Eotrigonobalanus furcinervis*. Therefore, they were separated as an independent infraspecific taxon from the typical dentate Late Eocene forms bearing stellate trichomes (Kvaček and Walther, 1989a, 1989b; Walther, 1999). According to several paleobotanical studies (e.g., Mai, 1995; Kvaček and Walther, 1989b, 1998; Mai and Walther, 2000), *Eotrigonobalanus* is the most important forest-forming element of the Paleogene in Europe. The ecological preferences of this taxon changed from the Eocene to Oligocene. In the Late Eocene, *Eotrigonobalanus* characterizes an element of swamp and peat-forming riparian forests, while in the Oligocene, this species is also observed in mixed mesophytic forests (Mai and Walther, 1978, 1991, 2000; Walther, 1999). This species abundantly occurs during the Paleogene (e.g., open cast mine Schleenhein near Borna, Saxony, Late Eocene; Staré Sedlo assemblages, Late Eocene; Haselbach flora, Early Oligocene; drilling at Kleinsaubernitz near Bautzen, Late Oligocene; Kvaček and Walther, 2001, 2003; Kunzmann and Walther, 2007, 2012; Hennig and Kunzmann, 2013). This species was also recorded in the Hochstetten-SW-Germany Oligocene flora (Uhl et al., 2002). Leaf morphology remains constant in specimens from different stratigraphical ages and geographical areas (Velitzelos et al., 1999; Kriegel, 2001). *Eotrigonobalanus* was recorded by Unger (1867) (pl. 4, figure 18 is a misidentification) and Velitzelos et al. (1999) in the Kymi and Evros regions (Greece), and the presence of this species has been used for age determination of the Kymi flora in comparison with the similar Oligocene floras in Europe (Velitzelos et al., 2002). *Eotrigonobalanus furcinervis* was recorded from the Late Oligocene localities at Lagina, Fylakton (Filakto), and Lyra (Lira) in Greece by Velitzelos et al. (2014). Additionally, entire margin leafs were observed from the Early Oligocene leaf floras of Seifhennersdorf (Germany; Walther and Kvaček, 2007) and the Bohemia Massif (Kvaček and Teodoridis, 2007). Leaf imprints of fossil *Lithocarpus* were frequently quoted as *Eotrigonobalanus furcinervis* (Rossmässler) Walther and Kvaček (2007) in the Oligocene from Rhodope and in Trakia, NE Greece (Petrescu et al., 1978; Velitzelos et al., 1999). Similar impressions were also reported from Bulgaria as *Lithocarpus palaeorhodopensis* Palamarev and Mai (1999) (from Dorf Pavelsko, Berzik Smoljan, Central Rhodoppes), as *Castanopsis furcinervis* Palamarev and Petkova (1966) (from Borino), or as *Cyclobalanopsis kryshtofovichii* Palamarev (1964) (from Brezani); subsequently, all these taxa were synonymized with *Eotrigonobalanus furcinervis* (Rossmässler) Walther and Kvaček (Bozukov and Tsenov, 2012; see also Velitzelos et al., 1999). *Eotrigonobalanus furcinervis* is very common in the Early Paleocene-Late Oligocene localities in Europe (Palamarev and Mai, 1998). Although there is a small number of this specimen in the paleoflora, this finding is valuable as the first recording for Anatolia for the Late Oligocene. Furthermore, the entire margin of this species as defined in this study resemble *Eotrigonobalanus furcinervis* recorded from the Seifhennersdorf (Saxony) and Bohemia Massif for the Early Oligocene macrofloras (Uhl et al., 2002; Kvaček and Teodoridis, 2007; Walther and Kvaček, 2007).

Family: Lauraceae

Genus: *Daphnogene* Unger (1850)

***Daphnogene cinnamomifolia* (Brongniart) Unger (1850)**

Morphology: Six fragmentary leaf remains probably belong to *Daphnogene cinnamomifolia* due to the existence of acrodromous venation, but they cannot be assigned to either of the two formae.

Discussion: The leaves of the Lauraceae species *Daphnogene cinnamomifolia* are typical with their acrodromous venation, which is usually imperfectly suprabasal. The leaf epidermal anatomy and macromorphology of *Daphnogene cinnamomifolia* shows differences during the Paleogene (e.g., from the Staré Sedlo Formation and the Zeitz floral-complex: Knobloch et al., 1996; Mai and Walther, 2000; and from Hammerunterwiesenthal: Walther, 1998). Most *Daphnogene cinnamomifolia* leaves are lanceolate and slightly small (forma *lanceolata*), but rarely larger and oval-shaped (forma *cinnamomifolia*) (Kovar-Eder and Berger, 1987; Uhl et al., 2002). This species is characteristic for the Late Oligocene in Central Europe. In Hungary it was found in the Egerian stage at many localities (Kvaček and Hably, 1991; Erdei and Wilde, 2004). Furthermore, the taxon was recorded from the Oligocene flora included in the volcaniclastic sediments in northern Bohemia, from Upper Lusatia and Central Erzgebirge (Eastern Germany), and from other Paleogene localities

in Germany (Haselbach, Thierbach: Uhl et al., 2002). The leaf polymorphism in *Daphnogene cinnamomifolia* was interpreted as being related to the development of distinct sun leaves (forma *lanceolata*) and shade leaves (forma *cinnamomifolia*) (Kvaček and Walther, 1974, 1995; Walther, 1998; Uhl et al., 2002).

***Daphnogene cinnamomifolia* (Brongniart) Unger forma *lanceolata* sensu Kvaček and Walther (1995)** (Figure 7)

1850a - *Daphnogene lanceolata* Unger, p. 424 - Socka, Croatia.

1950 - *Cinnamomophyllum scheuchzeri* (Heer) Kräusel and Weyland, p. 68, pl. 11, figure 7, pl. 6, figures 1–6, pl. 17, figure l, text fig. 25, Thuringia, Germany.

1978 - *Daphnogene lanceolata* Unger; Mai and Walther, p. 40, pl. 2, figures 1–23, pl. 19, figures 1–15, pl. 20, figures l–4, Haselbach in the Weißelster Basin, south of Leipzig, Germany.

1995 - *Daphnogene cinnamomifolia* (Brogniart) Unger forma *lanceolata*, Kvaček and Walther, p. 32, text fig. 4/10, Suletice-Berand near Usti-Außig, Czech Republic.

For a detailed synonymy list, see Mai and Walther (1978).

Morphology: Sixteen leaf remains could be defined as *Daphnogene cinnamomifolia* forma *lanceolata*. The laminae are elongated, lanceolate, or ovate. The leaf margin is entire. The length of the leaves varies between 32 and 117 mm, and the width is between 7 and 22 mm. The apex is long, narrow, and acuminate; the base is acute and the venation is suprabasally acrodromous. The midvein is strong and the basal vein is thinner than the midvein. The basal veins and the secondary veins start from the midvein to form a loop. The angle between the primary vein and the basal secondary veins varies from 5° to 10°.

***Daphnogene cinnamomifolia* (Brongniart) Unger forma *cinnamomifolia* sensu Kvaček and Walther (1995)** (Figure 7)

1822 - *Phyllites cinnamomifolia* Brongniart in Cuvier, p. 359, pl. 11, figure 12. Habichtswald, Hesse, Germany.

1850 - *Daphnogene cinnamomifolia* Unger, p. 168, pl. 39, figures 7–9, Socka, Croatia.

1974 - *Daphnogene cinnamomifolia* (Brongniart in Cuvier) Unger; Kvaček and Walther, p. 199, pl. l, figure 1, 2, pl. 2, figures 1–5, text fig. 3, Seifhennersdorf, Upper Lusatia, Germany.

1995 - *Daphnogene cinnamomifolia* (Brongniart) Unger forma *cinnamomifolia* Kvaček and Walther, p. 32, pl. 2, figure 2m, text fig. 4/19, Suletice-Berand, northern Bohemia.

For further synonyms, see Mai and Walther (1978).

Morphology: Only one leaf remain can be assigned to the forma *cinnamomifolia* of *Daphnogene*. The shape of the lamina is not observed; however the midvein and the basal vein are clearly seen on this leaf. The leaf base and apex are not preserved. The leaf is entire margined, the midvein and basal vein are strong, the tertiary veins are between the midvein and basal vein, and these are parallel.

Note: Despite having very incomplete specimens of *Daphnogene cinnamomifolia* forma *cinnamomifolia* in this study, this remain of *Daphnogene* is bigger than the other specimens of *Daphnogene cinnamomifolia* forma *lanceolata* from Germany (Kovar-Eder and Berger, 1987; Uhl et al., 2002).

Genus: *Laurophyllum* Goeppert (1853)

***Laurophyllum* sp.** (Figure 8)

Morphology: Seven specimens of Lauraceae leaves are recorded. These leaves are characterized by their long, narrow elliptic shape; their width is between 7.5 and 31.2 mm. The base and the apex of leaves are not preserved, the margin is entire, the venation is camptodromous and asymmetrical. Near the margin the veins run almost parallel to the margin, connecting the secondary veins to each other and indicating lobation.

Discussion: These leaves from Tuzluca could belong to *Laurophyllum* because of their venation pattern. This type of Lauraceae leaf is well known in the Oligocene flora of Sotzka (Slovenia) and in the Egerian floras of Hungary, Bulgaria, and Germany (Mainz Basin). This genus is common in the Oligocene and the Early-Middle Miocene of Central Europe (e.g., Uhl et al., 2002; Erdei and Wilde, 2004; Kvaček, 2004).

Family: Ulmaceae

Genus: *Zelkova* (Spach)

***Zelkova zelkovifolia* (Unger) Bůžek and Kotlaba (1963)** (Figure 8)

1843 - *Zelkova zelkovifolia* Unger, p. 24, figures 9–13, non figure 7 (fructus).

1845 - *Zelkova zelkovifolia* Unger, p. 26, figure 7.

1847 - *Zelkova zelkovifolia* Unger, p. 94.

1963 - *Zelkova zelkovifolia* (Unger) Bůžek and Kotlaba, in Kotlaba p. 59, pl. 3, figures 7 and 6.

Morphology: Only two leaf remains are recorded. They are characterized by the coarse simple-serrate margin of leaves. The shape of the lamina is not observed, although the secondary veins are clearly seen and they reach the tip of the teeth. The leaf base and apex are not preserved. The teeth are extremely coarse, their margin simple and coarsely serrate, and the teeth are slightly convex. The venation is craspedodromous and the midrib is thick. In subcordate leaves the first basal secondary vein bifurcates into two branches. The tertiary veins are not observed.

Discussion: According to Kvaček and Bůžek (1982), *Zelkova zelkovifolia* can be compared with the recent species *Zelkova carpinifolia* (Pal.) K.Koch from the relic deciduous and mesophytic forests of Colchis. In Hungary the species is known to occur sporadically since the Late



Figure 8. 1–4: *Ulmus* sp.; 5–10: *Laurophyllum* sp.; 11, 12. *Zelkova zelkovifolia* (Unger) Bůžek and Kotlaba.

Oligocene (Hably, 1992). It was found as a dominant element in some Sarmatian floristic assemblages (e.g., Erdőbénye: Andreánszky, 1959) and in the Pliocene (Hably and Kvaček, 1997, 1998). This species is also recorded from the Early-Middle Miocene floras of the Milas-Karacaağaç, Ankara, and Çanakkale regions (Anatolia) (Kayseri, 2010).

Genus: *Ulmus* (Linnaeus)

***Ulmus* sp.** (Figure 8)

Morphology: Six fragmentary leaf remains belong to *Ulmus* sp. The shape is lanceolate. Their length is approximately 28–83 mm, their width 10–23 mm. The base and apex are not preserved; the margin is simply dentate with dents small and sharp, basal part slightly concave and apical part concave. The basal side of dents is much longer than the apical one. The venation is craspedodromous; the median vein is straight, slightly thickened at the base; the secondary veins form 10 pairs, opposite, straight or slightly curved, unbranched, with an angle of 30° to the median vein.

Discussion: Unfortunately, the available material does not permit species identification because the apex and the base of leaves are not preserved. On the other hand, these leaves display all characters of the Ulmaceae genus *Ulmus*. Teeth with acute apex as well as the asymmetric lamina of the leaf are much more characteristic of *Ulmus*.

5. Discussion

Based on the paleontological data and paleogeographic conditions, the occurrence of terrestrial and marine environments is evidenced in East Anatolia during the Oligocene. However, paleoclimatic and paleovegetational records are limited due to little evidence of the Oligocene floras in East Anatolia, except the single most exhaustive study by Sancay et al. (2006). Data provided by the present study from the micro- and macropaleoflora record aim to partly fill this gap.

5.1. Paleovegetation and paleoclimate of Kağızman-Kömürlü and Kötek based on the microfloras

The Kağızman-Kömürlü area is located in the northern part of the Kağızman-Tuzluca Basin and the terrestrial condition is widespread in this area during the Late Oligocene based on palynological records. Freshwater swamp vegetation and coniferous forests are the main paleovegetation types in the Kömürlü area and these paleovegetations are represented by an abundance of pteridophytes, gymnosperms, and some angiosperm species (Figure 4). *Pediastrum* and *Botryococcus* are colonial green algae that live in freshwater environments such as lakes and ponds (e.g., Batten and Grenfell, 1996) and the existence of these algae in the lower and middle parts of the Kömürlü Section is supportive of the freshwater paleoenvironment (Figure 4). In the upper part of the section, an abundance of the pteridophytes, which grow in swampy conditions, is observed. According to changes of palynomorph distributions in the Kömürlü palynospectra (Figure 4), the water table of the lake and ponds could have been reduced during the deposition in the Late Oligocene. The mixed mesophytic forest (Fagaceae, *Calamus*, *Tilia*, *Engelhardia*, *Pterocarya*, and Onagraceae) and riparian forest (*Alnus*, *Ulmus*, and *Carya*) communities are defined. The middle and low altitude areas during the Late Oligocene were covered with Pinaceae and these gymnosperms accompanied the mixed mesophytic forest. According to the presence of the herbaceous angiosperm pollen, represented by Asteraceae-Asteroideae and Chenopodiaceae, open vegetation areas existed in the paleovegetation of Kömürlü during the Late Oligocene.

Pollen spectra of the Kömürlü area contain a large amount of subtropical plants such as Davalliaceae, Dennstaedtiaceae, Arecaceae, *Taxodium/Glyptostrobus*, and *Engelhardia*, and warm temperate plants (Fagaceae, *Ulmus*, *Carya*, *Alnus*, *Pterocarya*, and *Tilia*) are also recorded in this section. Data obtained from the collected samples in the area illustrate the dynamics of climatic conditions using the coexistence approach method (Mosbrugger and Utescher, 1997). The MAT of the Kömürlü samples of the Late Oligocene is characterized by 15.6 °C (*Engelhardia* sp.) to 20.8 °C (*Tilia* sp.) (Figure 3; Table 1). The calculated values for the CMT and WMT are between 5 °C (*Engelhardia* sp.) and 13.3 °C (*Carya cordiformis*) and between 24.7 °C (*Engelhardia* sp.) and 28.1 °C (Cupressaceae), respectively. The result of the MAP is 823 mm (*Engelhardia* sp.) to 1520 mm (Taxodiaceae). According to palynological data of the Kömürlü area, paleovegetation during the Late Oligocene broadly corresponds to freshwater swamp plants and mixed mesophytic forests with coniferous forests between subtropical and warm-temperate climatic conditions. The presence of a dry period due to seasonality is also observed (Table).

Paleovegetation of the Kağızman-Kötek area is represented by two types, which are freshwater in terrestrial environments and brackish in the near shallow marine environment. Conifer forests represented by Pinaceae in the terrestrial area are a significant vegetation type in Kötek during the Late Oligocene, and these forests were characterized by high proportions of higher-middle altitude trees (mainly *Pinus*). The wetland forest communities consist of pteridophytes, *Taxodium/Glyptostrobus*, *Alnus*, Sparganiaceae, Araliaceae, and *Carya*. The presence of fungal spores (*Dicellaesporites* sp., *Biporisporites* sp., and *Anatolinites dongyingensis*) and *Botryococcus* also supports the freshwater environment in Kötek during the Late Oligocene (Figure 5). The mixed mesophytic and riparian forests (Fagaceae, *Taxodium/Glyptostrobus*, *Alnus,* Araliaceae, *Carya*, and *Liquidambar*)

Table. Coexistence approach results of this study and published numerical climatic records.

Climatic variables (coexistence approach results)	MAT (°C)	CMT (°C)	WMT (°C)	MAP (mm)	MART (°C)
Kağızman-Tuzluca macroflora, Late Oligocene	13.3 (Palmae) to 16.6 (*Zelkova*)	–0.1 (Palmae) to 7.0 (*Zelkova*)	22.8 (Palmae) to 28.1 (Lauraceae)	619 (*Quercus*) to 1356 (*Zelkova*)	22.00
Kağızman-Kömürlü microflora, Late Oligocene	15.6 (*Engelhardtia*) to 20.8 (*Tilia*)	5 (*Engelhardtia*) to 13.3 (*Carya*)	24.7 (*Engelhardtia*) to 28.1 (Cupressaceae)	823 (*Engelhardtia*) to 1520 (Taxodiaceae)	17.25
Kağızman-Kötek microflora, Late Oligocene	9.4 (*Ephedra*) to 21.3 (*Carya*)	–0.1 (*Ephedra*) to 13.3 (*Carya*)	21.6 (*Lygodium*) to 28.6 (*Carya*)	1122 (*Lygodium*) to 1520 (Taxodiaceae)	19.20
Muş, Erzurum (Kayseri-Özer, 2013), Early Oligocene	13.3–17.4	1.7–8.3	22.8–27.0	1122–1151	19.90
Çankırı-Çorum (Güvendik Formation) (Kayseri-Özer et al., 2016), Late Oligocene	16.4–17.0	7–9.2	24.8–25.5	818–932	17.00
Muğla-Milas-Kultak (Kayseri-Özer, 2013), Late Oligocene	16.1–21.3	5.4–13.3	25.6–28.3	1130–1454	17.50
Denizli-Kale-Tavas (Kayseri-Özer, 2013), Late Oligocene	13.3–21.3	–0.1 to 13.3	22.8–28.1	1122–1520	18.90
Denizli-Çardak-Tokça (Kayseri-Özer, 2013), Late Oligocene	15.6–17.0	4.0–7.7	25.2–26.9	1050–1200.5	20.20
Çanakkale-Tayfur (Akgün et al., 2013) (Danişment Formation), Late Oligocene	16.5–21.3	5.5–13.3	27.3–27.9	887–1623	18.20
İstanbul-Ağaçlı (Kayseri-Özer, 2013), Late Oligocene	16.5–21.3	9.6–13.3	26.0–27.9	629–1520	15.50

are accompanied by coniferous forests in the middle and low altitude areas of terrestrial paleoenvironment. Herbaceous plants (20%) are represented by Poaceae, Apiaceae, Ephedraceae, Asteraceae-Asteroideae, and Chenopodiaceae in the Kötek pollen spectra, and the existence of these herb species indicates the grassland area in the paleovegetation of the Kötek area during the Late Oligocene, as in the Kağızman-Kömürlü area (Figure 5). The other paleoenvironment is the brackish condition in the near shallow marine environment, represented by sporomorphs (e.g., Arecaceae, Palmae, *Calamus*) and dinoflagellate species (*Cleistosphaeridium* sp., *Spiniferites* sp., *Hystrichokolpo marigaudiae*, *Lingulodinium machaerophorum*, *Tuberculodinium vancompoae*, *Polysphaeridium* sp., and undifferentiated dinoflagellates) and foraminiferal linings (Sancay, 2005).

The palynoflora of the Kağızman-Kötek area consists of subtropical (Davalliaceae, Dennstaedtiaceae, and *Taxodium/Glyptostrobus*) and warm-temperate (Fagaceae, *Ulmus*, *Carya*, *Alnus*, *Liquidambar*, and Araliaceae) plants. Numerical climatic values are obtained using the coexistence approach method. Climatic intervals of the Late Oligocene in Kötek are the MAT of 9.4 °C (*Ephedra* sp.) to 21.3 °C (*Carya cordiformis*), CMT of –0.1 °C (*Ephedra* sp.) to 13.3 °C (*Carya cordiformis*), WMT of 21.6 °C (*Lygodium* sp.) to 28.6 °C (*Carya cordiformis*), and MAP of 1122 mm (*Lygodium* sp.) to 1520 mm (Taxodiaceae). According to palynofloral data and numerical climatic values, the paleovegetation of Kötek during the Late Oligocene grew under warm-temperate and subtropical climatic conditions. Seasonality could have existed due to the abundance of the herb species, which characterize a dry period in the humid climatic conditions (Figure 5; Table).

5.2. Paleovegetation and paleoclimate of Kağızman-Tuzluca based on the macroflora

In this study, the leaf remains of Lauraceae species are observed predominantly in the Tuzluca leaf flora. This flora also includes *Daphnogene cinnamomifolia* forma *cinnamomifolia*, *Daphnogene cinnamomifolia*, cf. *Eotrigonobalanus furcinervis*, *Laurophyllum acutimontanum, Laurophyllum* sp., *Zelkova zelkovifolia*, *Ulmus* sp., and some leaf remains of Arecaceae. Sporomorphs represented by Osmundaceae, Pinaceae, Asteraceae-Tubuliflorae, Umbelliferae, Poaceae, *Carya*, *Ulmus*, and Sparganiaceae of the Kağızman-Tuzluca area

were also defined by Şen et al. (2011). Thus, it is possible to approach a paleovegetational reconstruction.

The species of Lauraceae are common in the Oligocene macrofloras of Europe (e.g., Spain, Hungary, Bulgaria, and Germany) (e.g., Hably, 1989; Uhl et al., 2002; Erdei and Wilde, 2004). In the Tuzluca macroflora, *Daphnogene cinnamomifolia* forma *cinnamomifolia*, *Daphnogene cinnamomifolia* forma *lanceolata*, *Laurophyllum acutimontanum*, and *Laurophyllum* sp. belong to this family. In the Paleogene flora of Hochstetten-Dhaun (SW Germany), *Daphnogene cinnamomifolia* forma *cinnamomifolia* is observed in the riparian vegetation together with *Eotrigonobalanus furcinervis* (Fagaceae) (Uhl et al., 2002). Furthermore, *Trigonobalanopsis rhamnoides*, *Eotrigonobalanus furcinervis*, *Daphnogene cinnamomifolia* forma *cinnamomifolia*, and *Daphnogene cinnamomifolia* forma *lanceolata* may also be interpreted as elements of evergreen mesophytic or mesophytic lowland forests, which may also include *Laurophyllum* sp. (Erdei and Wilde, 2004). These Lauraceae were growing well under humid subtropical and tropical paleoclimatic conditions (Hably 1989; Erdei and Wilde, 2004).

Eotrigonobalanus furcinervis is a typical member of evergreen Paleogene forests of Greece, Germany, Czech Republic, Hungary, Romania, and Bulgaria in Central and East Europe (Kvaček and Walther, 1989a, 1989b; Wilde, 1989; Knobloch et al., 1996; Hably and Fernandez-Marron, 1998). In the Early Oligocene flora of Fürfeld (Rhenany, Germany), *Daphnogene cinnamomifolia* and *Eotrigonobalanus furcinervis* are also the dominant dicotyledonous elements (Uhl et al., 2002), as well as *Pinus*. According to Uhl et al. (2002), there existed two distinct tree levels in the forest of the Fürfeld region (SW Germany). *Eotrigonobalanus* may represent an element of an upper tree level up to 20 m, which is comparable to that of modern laurel forests (Walther and Stuchlik, 1982), whereas *Daphnogene* may have been a constituent of a second level in the forest beneath *Eotrigonobalanus*, at levels approximately 3 to 10 m high (Uhl et al., 2002). This species is the most characteristic element of the Oligocene Evros flora in northeastern Greece (Velitzelos et al., 1999). cf. *Eotrigonobalanus furcinervis* is less abundantly recorded from the Tuzluca macroflora of the Late Oligocene, while *Pinus* species are observed in the palynoflora from the Kağızman-Tuzluca area. The presence of both species in the Tuzluca flora during the Late Oligocene could indicate two tree levels, as in the Fürfeld region in Germany (Uhl et al., 2002).

At present, the palm family Arecaceae (=Palmae) is a monophyletic group including 183 genera and 2364 species (Govaerts and Dransfield, 2005; Dransfield et al., 2008). Most palms are distributed in the tropics with a few species reaching subtropical areas (Henderson et al., 1995). Fossil records from the tropics are less common, however, than those from middle latitudes (Harley and Morley, 1995; Dransfield et al., 2008; Gomez-Navarro et al., 2009). Leaf fossils of Arecaceae are frequently recorded in Europe (Staré Sedlo Formation, Kučlín, Tard Clay, and Haselbach) (Mai and Walter, 1978; Knobloch et al., 1996; Palamarev and Mai, 1998; Kvaček and Walther, 2004). Up to now, the species of Arecaceae were recorded by palynological studies in the Eocene-Oligocene sediments deposited under brackish conditions in Anatolia (e.g., Sancay et al., 2006; Kayseri, 2010; Kayseri-Özer, 2011, 2013). In particular, Arecaceae, *Calamus*, and *Acrostichum aureum* together with marine dinoflagellate species and nannoplankton were recorded in the brackish sediments of Erzurum-Kötek in East Anatolia (Sancay et al., 2006). Arecaceae is not only observed along the seaside; it can be found in mainland forests in tropical areas. However, the presence of this family in the Kağızman-Tuzluca area could indicate a brackish environment close to the fossil locality and this evidence is coherent with the Oligocene paleogeography of East Anatolia (Popov et al., 2004).

Juglandaceae (*Carya*) and Ulmaceae (*Ulmus* and *Zelkova*) are broad-leaved elements and they are well represented in the macro- and microfloras of several regions in Europe and Anatolia during the Eocene-Miocene time interval. The species of these families also exist in the Tuzluca micro- and macrofloras. These species indicate lowland and middle-altitude areas.

Freshwater swamp environments are represented by *Magnastriatites howardi* (Parkeriaceae), *Baculatisporites* sp. (Osmundaceae), Sparganiaceae, and fungal spores (*Inapertisporites* sp., *Dicellaesporites* sp., and *Anatolinites dongyingensis*) and these are recorded in the microflora of the Kağızman-Tuzluca area (Şen et al., 2011). The presence of freshwater and brackish elements indicates that the locality where the macroflora is recorded could be at the confluence of fluvial and marine environments.

The herb species of the Tuzluca palynoflora are represented by Asteraceae-Asteroideae, *Tubulifloridites* spp., Umbelliferae, and Poaceae; they could be distributed in lowland areas rather open and/or scarcely wooded (Şen et al., 2011). The presence of these open vegetation elements could be interpreted as indicative of seasonality during the Late Oligocene in the Kağızman-Tuzluca area.

In the paleovegetation of the Late Oligocene, based on the palynological and paleobotanical data of the Kağızman-Tuzluca area, two different aquatic conditions, which are the freshwater swamp of the fluvial and the brackish area of the near shallow marine environment, could have existed in the area. The paleovegetation of the freshwater swamp is characterized by Parkeriaceae, Osmundaceae, Sparganiaceae, and fungal spores (*Inapertisporites* sp., *Dicellaesporites* sp., and *Anatolinites dongyingensis*), and

the other environment is represented by the Arecaceae. The evergreen mixed mesophytic and broad-leaved mixed mesophytic forests represented by Fagaceae (cf. *Eotrigonobalanus furcinervis*, *Quercus* sp.), *Ulmus*, *Zelkova* (*Zelkova zelkovifolia*, *Ulmus* sp.), and *Carya* usually occupy lowland and middle-altitude areas in the Kağızman-Tuzluca area (East Anatolia). The presence of *Pinus* may indicate the high altitude area around the deposition area. Herb species (Asteraceae-Asteroideae, *Tubulifloridites* spp., Umbelliferae, and Poaceae) could grow in the open areas during the Late Oligocene.

The paleoclimate in the Kağızman-Tuzluca area in the Late Oligocene could be humid and subtropical, as indicated by existence of Arecaceae and the abundance of the species of Lauraceae (*Daphnogene* and *Laurophyllum*). Additionally, cf. *Eotrigonobalanus furcinervis* (Fagaceae), *Ulmus*, *Carya*, Asteraceae-Asteroideae, *Tubulifloridites* spp., Umbelliferae, and Poaceae, which are represented dry and warm-temperate climatic conditions, could have existed in the Kağızman-Tuzluca area (Tamás and Hably, 2009). The combination of humid subtropical and xeric warm temperate plants may be associated with changes in rainfall due to seasonality during the Late Oligocene. Numerical climatic values calculated by the coexistence approach based on the macroflora are 13.3 °C (Palmae) to 16.6 °C (*Zelkova carpinifolia*) for the MAT, –0.1) °C (Palmae) to 7.0 °C (*Zelkova carpinifolia*) for the CMT, 22.8 °C (Palmae) to 28.1 °C (Lauraceae) for the WMT, and 619 mm (*Quercus*) to 1356 mm (*Zelkova carpinifolia*) for the MAP. According to the coexistence intervals of MAT, CMT, and MAP, seasonality could be effective in the Kağızman-Tuzluca area.

6. Conclusions

The paleoecological reconstructions of the Kağızman-Kötek, Kömürlü, and Tuzluca areas are quite consistent with the paleoclimatological reconstructions of CLIMSTAT, which also suggest warm temperate to subtropical conditions for the Late Oligocene based on terrestrial spores and pollen. As far as terrestrial sporomorphs are concerned, the following ecological groups may be distinguished: mixed mesophytic forests, restricted to the high and middle altitude areas (e.g., *Pinus*, *Ulmus*, Fagaceae, *Engelhardia*, *Sequoia*, *Zelkova*, Lauraceae, *Pterocarya*, *Quercus*, and Sapotaceae) (Figure 9). Among these, *Pinus* grains are always overrepresented in all of the studied samples related to their windblown nature. They can be transported long distances in large quantities by means of their air sacs. They mainly represent mountainous backgrounds with those plants surrounding the depositional environments (Figure 9). The lowland-riparian paleovegetation (e.g., Arecaceae, *Calamus*, Taxodioidea-*Glyptostrobus*, Myricaceae, *Alnus*) and brackish water elements (e.g., Arecaceae, *Calamus*, Schizaceae, Lygodiaceae, and dinoflagellate species) mainly represent forest associations in moisturized open areas. The freshwater elements (e.g., Osmundaceae, Sparganiaceae, Davalliaceae, Polypodiaceae, *Pediastrum*, *Botryococcus*, and fungal spores) represent the fluvial activity and freshwater swamps in the near vicinity. Finally, the existence of some marine dinoflagellates and the terrestrial palynomorph-dominated assemblage of the Kötek and Tuzluca micro- and macrofloras suggests shallow marine depositional conditions during the Late Oligocene in the Kağızman-Kötek and Tuzluca areas.

Subtropical climatic conditions were observed during the Oligocene in Anatolia based on the palynofloral records (e.g., Batı, 1996; Kayseri, 2010; Kayseri-Özer, 2011, 2013, 2017). According to the numerical climatic variables obtained from the microfloral records of East Anatolia using the coexistence approach (Mosbrugger and Utescher, 1997), the lowest coldest month temperature values were recorded from the Kağızman area in the Early-Late Oligocene due to continental conditions (Ararat, Taurus highs, and Eastern Pontides (Popov et al., 2004; Kayseri-Özer, 2013)). The high mean annual temperature range (MART = warmest month – coldest month temperatures; between 17.25 and 22 °C) and the low mean annual precipitation of East Anatolia (MAP: 619–1356 mm) support remarkable drought and terrestrial conditions in the Oligocene (Table). However, the presence of high precipitation values (MAP: 1122–1520 mm) also indicates humidity during this time due to seasonality (Table). Paleoclimatic conditions of the Kağızman-Tuzluca area resemble the conditions of the Kağızman-Kötek area during the Late Oligocene. However, the lower and upper boundaries of the MAP values from Tuzluca (619–1356 mm) are lower. Higher numerical climatic values are calculated from the Kağızman-Kömürlü area, which is farthest from the edge of the sea (Table).

Most of the taxa recorded in the studies mentioned above have also been identified in the East Anatolian Oligocene sediments, but in different quantities. For instance, *Calamus*, *Engelhardia*, *Fagaceae*, *Alnus*, and *Quercus* are seen in relatively low abundances whereas Asteraceae-Asteroideae, *Tubulifloridites* spp., Poaceae, and Umbelliferae are recorded in high abundances in the palynofloras of East Anatolia. With the coexistence values of the Late Oligocene in other regions of Anatolia, this shift in the terrestrial palynomorph assemblages might be related to paleoclimatological and/or paleotopographic conditions. In addition, East Anatolia experienced relatively colder and drier conditions than the western part of Anatolia during the Late Oligocene based on numerical climatic values recorded from the macro- and microfloras (Table).

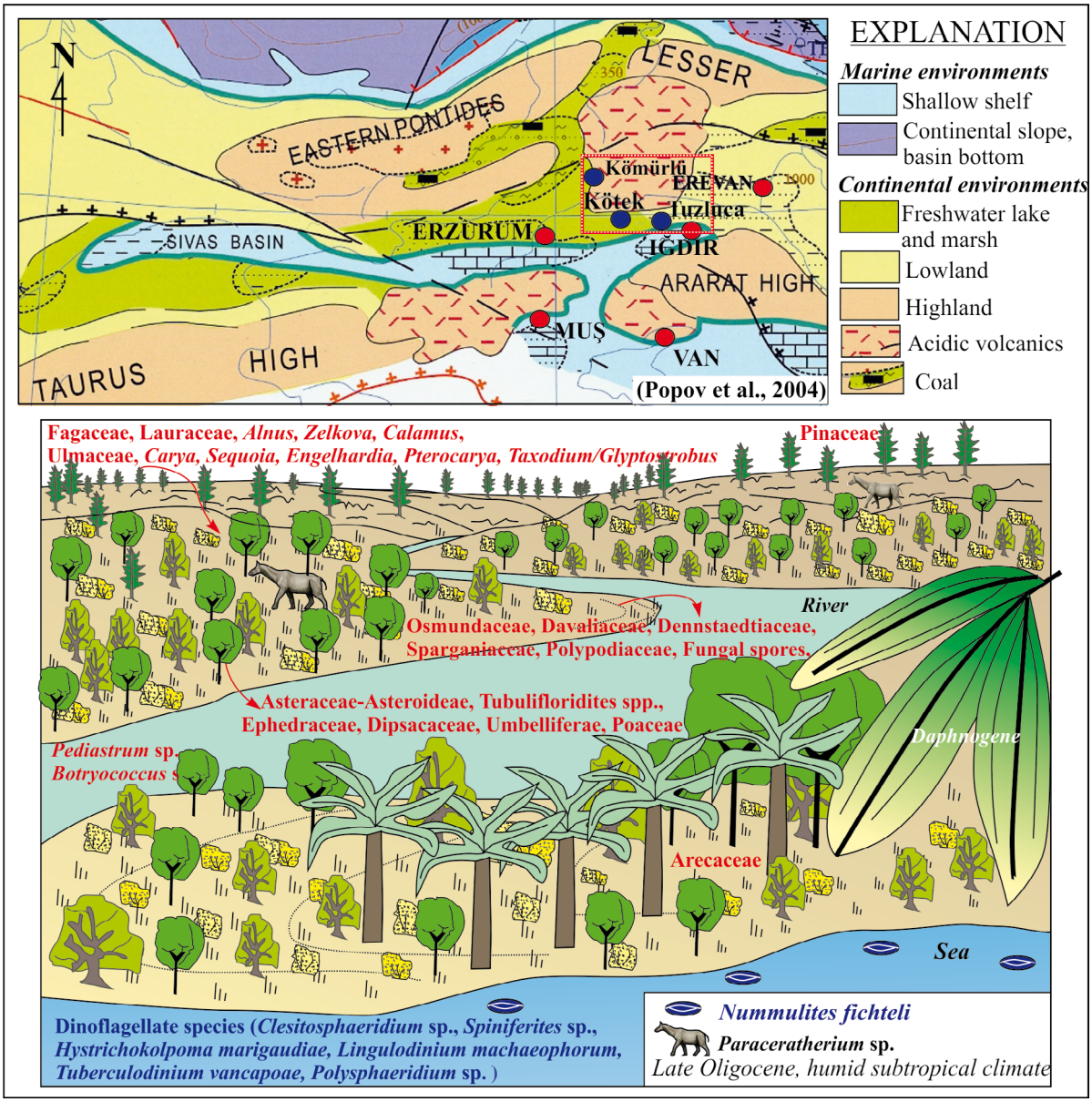


Figure 9. Paleoenvironmental reconstruction of the Tuzluca, Kötek, and Kömürlü areas during the Late Oligocene based on the micro- and macrofloral data.

In the Kağızman-Tuzluca, Kömürlü, and Kötek areas, macro- and microfloras are represented by the herbaceous angiosperms and spore species in general. Woody angiosperms characterized by *Ulmus*, *Zelkova*, *Alnus*, *Quercus*, *Calamus*, *Taxodium/Glyptostrobus*, and *Pterocarya* are not diverse and abundant, while gymnosperm pollen species (Pinaceae) are very abundant in the floras. According to these floral compositions, the reason for the nonrich leaf floras in the Tuzluca area could be related to taphonomy because herbaceous and spore species that are commonly observed in East Anatolia during the Oligocene would not be fossilized. Abundance of the gymnosperm pollen could be explained by transportation by air from the high lands near the deposition area.

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Appendix.

List of the Tuzluca macroflora (alphabetical order).
Arecaceae sp. (Arecaceae)
cf. *Eotrigonobalanus furcinervis* (Fagaceae)
Daphnogene cinnamomifolia cinnamomifolia (Lauraceae, *Daphnogene*)
Daphnogene cinnamomifolia lanceolata (Lauraceae, *Daphnogene*)
Laurophyllum sp. (Lauraceae, *Laurophyllum*)
Ulmus sp. (Ulmaceae, *Ulmus*)
Zelkova zelkovifolia (Ulmaceae, *Zelkova*)

List of the Kömürlü and Kötek Microfloras (alphabetical order).
Spores
Baculatisporites gemmatus (Osmundaceae)
Cicatricosisporites sp.
Cingulatisporites macrospeciosus (Pteridaceae)
Cingulatisporites sp. (Pteridaceae)
Echinatisporis sp.
Echinatosporites bifurcus
Laevigatosporites haardti
Laevigatosporites spp.
Leiotriletes adriennis (Lygodiaceae)
Leiotriletes microadriennis (Lygodiaceae)
Lusatisporites perinatus
Lusatisporites sp.
Magnastriatites howardi
Reticulatisporites sp.
Saxosporis sp.
Trilites multivallatus (Lygodiaceae)
*Undulatisporite*s sp.
Verrucatosporites alienus (Davalliaceae)
Verrucatosporites favus (Dennstaedtiaceae, *Paesia*)
Verrucatosporites sp. (Davalliaceae/ Dennstaedtiaceae)
Verrucat trilet spores
Gymnosperm pollen
Inaperturopollenites concedipites (Cupressaceae)
Inaperturopollenites dubius (Cupressaceae)
Inaperturopollenites emmaensis
Inaperturopollenites sp.
Pityosporites spp. (Pinaceae-*Pinus*)
Sequoipollenites polyformosus (Cupressaceae-*Sequoia*)
Angiosperm pollen
Alnipollenites verus (Betulaceae-*Alnus*)
Araliaceoipollenites euphorii (Araliaceae)
Asteraceae-Asteroideae
Caryapollenites simplex (Juglandaceae-*Carya*)
Corsinipollenites oculus noctis (Onagraceae-*Ludwigia*)
Dicolpopollis kalewensis (Arecaceae-*Calamus*)
Dipsacaceae
Ephedripites sp. (Ephedraceae)
Intratriporopollenites instructus (Tilioideae-*Tilia*)
Momipites sp. (Juglandaceae-*Engelhardia*)
Monocolpopollenites minus (Arecaceae)
Monocolpopollenites tranquillus (Arecaceae)
Monoporopollenites gramineoides (Poaceae)
Monoporopollenites sp. (Poaceae)
Periporopollenites sp.
Periporopollenites multiporatus (Chenopodiaceae)
Periporopollenites stigmosus (Altinginaceae, *Liquidambar*)
Polyatriopollenites stellatus (Juglandaceae-*Pterocarya*)
Polyporopollenites sp.
Sparganiaceapollenites neogenicus (Sparganiaceae, Typhaceae)
Triatriopollenites spp.
Tricolpopollenites spp.
*Tricolporopollenite*s spp. (Fagaceae)
Triporopollenites sp.
Ulmipollenites undulosus (Ulmaceae-*Ulmus*)
Umbelliferae
Dinoflagellates
Cleistosphaeridium sp.
Hystrichokolpo marigaudiae
Lingulodinium machaerophorum
*Polysphaeridiu*m sp.
Spiniferites sp.
Tuberculodinium vancompoae
Undifferentiated dinoflagellate
Aquatic forms
Aquatic organisms
Undetermined aquatic organisms
Fungal spores
Multicellasporites sp.
Dicellaesporites sp.
Inapertisporites sp.
Anatolinites dongyingensis
Biporisporites sp.
Pluricellaesporites sp.
Psilodisporites gunniae
Striadiporites sanctaebarbarae
Algae
Botryococcus sp.
Pediastrum sp.
Foraminiferal linings