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# A re-examination of the angiosperm wood record from the early and middle Miocene of Turkey, and new species descriptions

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ABSTRACT. The early and middle Miocene in Turkey was characterised by a warm climate and a diversified and rich vegetation. Many fossil angiosperm genera have been identified from this period. The present study re-examined previously identified genera and identifed new samples of angiosperm wood remains. The studied material included thin sections housed at the Department of Forest Botany, Division of Forest Engineering, Faculty of Forestry, Istanbul University-Cerrahpasa, and also new ones. Twelve new species are described: *Liquidambaroxylon efeae* Akkemik sp. nov., *Eucarpinoxylon kayacikii* Akkemik sp. nov., *Ostryoxylon gokceadaense* Akkemik sp. nov., *Quercoxylon yaltirikii* Akkemik sp. nov., *Cryptocaryoxylon grandoleaceum* Akkemik sp. nov., *Fraxinoxylon beypazariense* Akkemik sp. nov., *Prunoidoxylon prunoides* Akkemik sp. nov., *Populoxylon sebenense* Akkemik sp. nov., *Salicoxylon galatianum* Akkemik sp. nov. *Aceroxylon aceroides* Akkemik sp. nov., *Ulmoxylon kasapligilii* Akkemik sp. nov. and *Zelkovoxylon crystalliferum* Akkemik sp. nov. In addition, four previously described species are documented for the early and middle Miocene: *Pistacioxylon ufukii* Akkemik and I. Poole, *Fagoxylon radiatum* Süss, *Laurinoxylon litseoides* Süss and *Platanoxylon catenatum* Süss and Müller-Stoll. In addition to the species descriptions, identification keys are given for all the genera recognised in this study, including all currently known fossil species of the respective fossil genera. These keys hold important new information, as they place the fossil species from Turkey in a wider taxonomic and biogeographic context. The results show that in the early and early-middle Miocene of Turkey a rich woody flora existed in well-drained upland or lowland and riparian areas. This flora comprised subtropical taxa along with warm-temperate taxa indicative of seasonality of rainfall as well as transitions to xeric conditions in the early Miocene.

KEYWORDS: early Miocene, Galatian Volcanic Province, petrified wood, fossil species, new taxa

## INTRODUCTION

Identification of fossil wood of angiosperms has revealed a great diversity of trees and shrubs in the Miocene of Turkey. In recent years, an increasing number of fossil wood taxa have been assigned to fossil species, but several fossil wood remains have been determined only to genus level. Among fossil angiosperm species, *Laurinoxylon thomasii* Akkemik, 2019, *Mimosoxylon ceratonioides* Akkemik, 2019, *Pterocaryoxylon tuncayii* Akkemik, 2019, *Prunoidoxylon aytugii* Akkemik, 2019 (Akkemik et al., 2019), *Zelkovoxylon yesimae* Akkemik and I. Poole, 2018, and *Pistacioxylon ufukii* Akkemik and I. Poole, 2018 (Akkemik et al., 2018) and *Cercioxylon zeynepae* Akkemik, 2019 (Akkemik, 2019), have been described from Turkey. At genus level, *Acer, Liquidambar, Salix, Populus, Prunus, Ulmus, Zelkova, Fraxinus* and *Quercus* sect. *Ilex* (Akkemik et al., 2016; Acarca Bayam et al., 2018), and *Fagoxylon, Carpinoxylon, Ostryoxylon, Laurinoxylon* and *Platanoxylon* (Güngör et al., 2019) have been identified from Turkey.

The number of studies identifying modern and fossil wood is continuously increasing, generating a wealth of new information; hence the need to re-examine Neogene wood taxa determined to genus level from Turkey. The present study offers species-level descriptions based on a re-examination of numerous thin sections. Newly collected material was investigated as well. The work is intended to reveal the diversity of forest tree species during the early and middle Miocene in Turkey.

Based on macro- and microfossils, Denk et al. (2014, 2015, 2017a, b, 2019), Güner et al. (2017) and Kayseri-Özer (2017) discussed the climate of the early Miocene, and suggested that it was subtropical warm and rainy, with dry transitions during the early Miocene. In respect of early Miocene forests, Denk et al. (2019) suggested that "the data unambiguously showed the presence of riparian and swamp forests and mesic and xeric forest communities on well-drained soils in the early Miocene", and that Laurel Forest Biome was the dominant forest biome. The present study is also intended a contribution to our knowledge of the climate of the early and middle Miocene of Turkey, based on petrified wood species.

## BRIEF GEOLOGICAL SETTINGS

The materials used were taken from two different regions (Fig. 1A): the Galatian Volcanic Province in central Turkey (sites KOZ, HOC, AGU, MEN, KIR, INO, INL) with age of

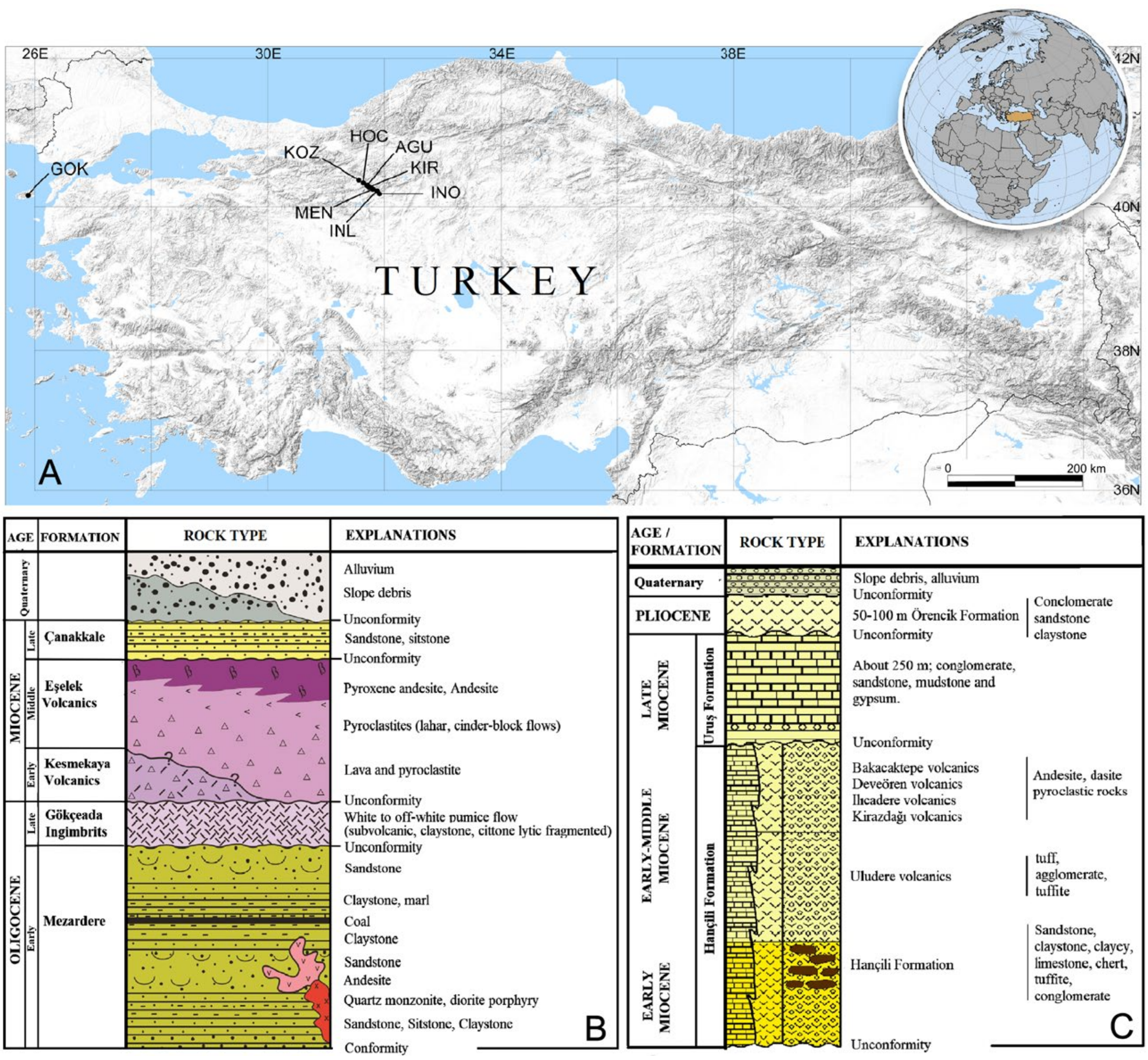


**Fig. 1**. **A**. Fossil localities from which the re-examined and newly investigated specimens derive. HOC is Hoçaş Fossil Site, KOZ is Kozyaka Fossil Site (Akkemik et al., 2016), AGU is Aşağıgüney Village Fossil Site, KIR is Kıraluç Fossil Site, MEN is Mençeler Fossil Site, INL and INO are Inözü Valley Fossil Site (Acarca Bayam et al., 2018), GOK is Gökçeada Fossil Site (Güngör et al., 2019). **B**. Stratigraphic column of Gökçeada (modified from Sarı et al., 2015: fig. 2). **C**. Stratigraphic column of Galatian Volcanic Province (GVP) (modified from Acarca Bayam et al., 2018: fig. 2)

early Miocene, and Gökçeada (Imbros Island) in the Aegean Sea (labelled GOK) with age of middle Miocene. The geological settings of these two different regions are summarized separately below.

### GEOLOGICAL SETTING OF GÖKÇEADA

The fossil wood material used to be assigned to Kesmekaya volcanics of early Miocene age (Güngör et al., 2019) but a more detailed study of the literature (Akartuna, 1950; Sari et al., 2015; Şen et al., 2020) assigns them to Eşelek pyroclastics of middle Miocene age (Fig. 1B). The "Eşelek volcanic rocks" as named and mapped by Sarı et al. (2015) are situated at the east of the island; they consist of of lahars and blocky ash flows (debris flow and pyroclastics) (Sari et al., 2015; Şen et al., 2020). Sari et al. (2015) report also the existence of peat formations in tuffs. The age of Eşelek volcanic deposits is considered middle Miocene because it underlies unconformably the late Miocene Çanakkale formation and it overlies the Mezardere formation, the Gökçeada ignimbrite which has a late Oligocene age and Kesmekaya volcanic rocks.

### BRIEF GEOLOGICAL SETTING OF GALATIAN VOLCANIC PROVINCE

The detailed geological setting of the Galatian Volcanic Province (GVP) was described by Akkemik et al. (2016) and especially Acarca Bayam et al. (2018: 2–4, fig. 2). Briefly, K/Ar dating in the GVP showed that all the sites of the investigated specimens are from the Hançili Formation of early Miocene age (17–23 Ma, Burdigalian) (Keller et al., 1992; Toprak et al., 1996; Wilson et al., 1997; Tankut et al., 1998). The Hançili Formation is composed of sandstone, claystone, clayey limestone, cherty tuffite and conglomerate, and covered by the Uludere, Kirazdağı, Ilıcadere, Deveören and Bakacaktepe volcanics (Fig. 1C). Numerous fossil sites have been discovered in the Hançili Formation (Akkemik et al., 2009, 2016, 2017; Acarca Bayam et al., 2018; Akkemik and Acarca, 2019). Particularly in the western part of the GVP, many fossil sites yield autochthonous fossil stems of *Juniperus* L., *Cedrus* Trew, *Pinus* L., Arecaceae, *Salix* L., *Populus* L., *Quercus* L. and *Liquidambar* L. For that reason, the early Miocene Hançili Formation is a key section for evaluating early Miocene forests in Turkey.

## MATERIAL AND METHODS

Thin sections of fossil woods collected from different parts of Turkey (Akkemik et al., 2016; Acarca Bayam et al., 2018; Güngör et al., 2019) (Fig. 1; Tab. 1) were reexamined here to provide full species descriptions. Thirteen specimens were restudied for that purpose, and three more new specimens (HOC06, HOC567, KIR74) from the Galatian Volcanic Province were also determined to species level (Tab. 1). Some of the wood thin sections in the collections could not be used, due to poor preservation of anatomical details. Thin sections that preserved sufficient anatomical detail (Tab. 1) were restudied, following IAWA hardwood identification terminology (IAWA Committee, 1989), and determined to species level. Many references given in the related sections were used for comparison, and identification keys were prepared for each fossil genus in order to find the exact placement of the identified species and describe its differences from all the identified species within a given genus. All known fossil species of the related genus are included in each identification key. Some doubtful fossil species are not included. The InsideWood database (InsideWood. 2004 onward; Wheeler, 2011) was followed in assessing fossil species. Specimens that show diagnostic characters clearly differing from all existing fossil species are described as new fossil species. For type species, the related references and a generic name index by Andrews (1952) was used.

## RESULTS

The systematic palaeobotany section includes 16 species descriptions: 12 new fossil species are described and 4 additional fossil species are reported for the early Miocene of Turkey (Tab. 1).

Order SAXIFRAGALES
Bercht. et J. Presl, 1820

Family ALTINGIACEAE Horan, 1841

Genus *LIQUIDAMBAROXYLON* Felix, 1884

Type species *Liquidambaroxylon speciosum* Felix, 1884, p. 24, pl. 3, figs 2–4; pl. 4, fig. 4

***Liquidambaroxylon efeae*** Akkemik **sp. nov.**

Pl. 1A–G

Holotype. Three thin sections of specimen HOC37. This species was identified first as *Liquidambar* by Akkemik et al. (2016).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

**Table 1**. Fossil species recognised in the present study, based on angiosperm wood remains. Also provided is information on the fossil localities, previous descriptions, and references

| Family | Fossil species identification in this study | Holotype | Specimen code | Type localities/Localities | Former description | Reference |
|---|---|---|---|---|---|---|
| Altingiaceae | *Liquidambaroxylon efeae* Akkemik sp. nov. | HOC77 | – | Near Hoçaş village, Seben-Bolu | *Liquidambar* | Akkemik et al., 2016 |
| Anacardiaceae | *Pistacioxylon ufukii* Akkemik et I. Poole, 2018 | – | KIR74 | Kıraluç in Nuhhoca village, Beypazarı-Ankara | New specimen | – |
| Betulaceae | *Eucarpinoxylon kayacikii* Akkemik sp. nov. | GOK01 | – | East of Eşelek village, Gökçeada-Çanakkale | *Carpinoxylon* | Güngör et al., 2019 |
| Betulaceae | *Ostryoxylon gokceadaense* Akkemik sp. nov. | GOK02 | – | East of Eşelek village, Gökçeada-Çanakkale | *Ostryoxylon* | Güngör et al., 2019 |
| Fagaceae | *Fagoxylon radiatum* Süss | – | GOK257 | East of Eşelek village, Gökçeada-Çanakkale | *Fagoxylon* | Güngör et al., 2019 |
| Fagaceae | *Quercoxylon yaltirikii* Akkemik sp. nov. | INL09 | – | Inözü Valley near Beypazarı-Ankara | *Quercus* Sec. *Ilex* | Acarca Bayam et al., 2018 |
| Lauraceae | *Cryptocaryoxylon grandoleaceum* Akkemik sp. nov. | GOK05 | – | East of Eşelek village, Gökçeada-Çanakkale | *Lauroxylon* | Güngör et al., 2019 |
| Lauraceae | *Laurinoxylon litseoides* Süss | – | GOK261 | East of Eşelek village, Gökçeada-Çanakkale | *Lauroxylon* | Güngör et al., 2019 |
| Oleaceae | *Fraxinoxylon beypazariense* Akkemik sp. nov. | AGU13 | – | Aşağıgüney village, Beypazarı-Ankara | *Fraxinus* | Acarca Bayam et al., 2018 |
| Platanaceae | *Platanoxylon catenatum* Süss et Müller-Stoll | – | GOK258 | East of Eşelek village, Gökçeada-Çanakkale | *Platanoxylon* | Güngör et al., 2019 |
| Rosaceae | *Prunoidoxylon prunoides* Akkemik sp. nov. | MEN31 | – | Mençeler Plateau, Beypazarı-Ankara | *Prunus* | Acarca Bayam et al., 2018 |
| Salicaceae | *Populoxylon sebenense* Akkemik sp. nov. | HOC567 | – | Near Hoçaş village, Seben-Bolu | New specimen | – |
| Salicaceae | *Salicoxylon galatianum* Akkemik sp. nov. | HOC06 | – | Near Hoçaş village, Seben-Bolu | New specimen | – |
| Sapindaceae | *Aceroxylon aceroides* Akkemik sp. nov. | INL02 | – | Inözü Valley near Beypazarı-Ankara | *Acer* | Acarca Bayam et al., 2018 |
| Ulmaceae | *Ulmoxylon kasapligilii* Akkemik sp. nov. | KOZ16 | – | Kozyaka village, Seben-Bolu | *Ulmus* | Akkemik et al., 2016 |
| Ulmaceae | *Zelkovoxylon crystalliferum* Akkemik sp. nov. | AGU15 | – | Aşağıgüney village, Beypazarı-Ankara | *Zelkova* | Acarca Bayam et al., 2018 |

Plant fossil registry number. PFN002207.

Etymology. The epithet "*efeae*" honours Prof. Dr. Asuman Efe, who was the head of the Forest Botany Department of Faculty of Forestry, Istanbul University-Cerrahpasa before her untimely death in an accident. She worked on the endemic species *Liquidambar orientalis* Mill. for her PhD thesis.

Type locality. Hoçaş Fossil Site of Seben city in Bolu Province.

Age. Early Miocene.

Type horizon. Hançili Formation.

Diagnosis. Growth ring boundaries mostly distinct. Wood diffuse-porous. Vessels exclusively solitary (90% or more), generally angular in outline. Mean vessel tangential diameter 50–100 mm, ~100 vessels per mm$^2$ (Pl. 1A). Axial parenchyma apotracheal and diffuse. Rays of two distinct sizes: narrow uniseriate rays reaching to 0.4 mm high and larger rays commonly 4–6-seriate, some of the rays >1 mm high, 4–12 rays per mm (Pl. 1B, C). 3–4 axial parenchyma cells per strand. Fibre tracheids common. Rays heterocellular with procumbent body ray cells and 1–4 and or more rows of upright and/or square marginal cells (Pl. 1D, G). Intervessel pits opposite, alternate or commonly scalariform (Pl. 1E). Perforation plates scalariform with ~25–30 (20–40) bars (Pl. 1F, G).

Discussion. The combination of these wood features is seen in species of Altingiaceae and Hamamelidaceae. In Altingiaceae, two fossil genera of *Altingioxylon* and *Liquidambaroxylon* were described. As also indicated by Oskolski et al. (2012), in *Altingioxylon rhodoleioides* the wood is rather similar to *Liquidambaroxylon*, with only one difference in having a scalariform perforation plate with up to 20 bars. In contrast, *Liquidambaroxylon* has scalariform perforation plates with up to 40 bars. In *Liquidambaroxylon* the growth ring boundary is indistinct or distinct, the vessels are diffuse-porous, evenly distributed, oval to angular in cross section,

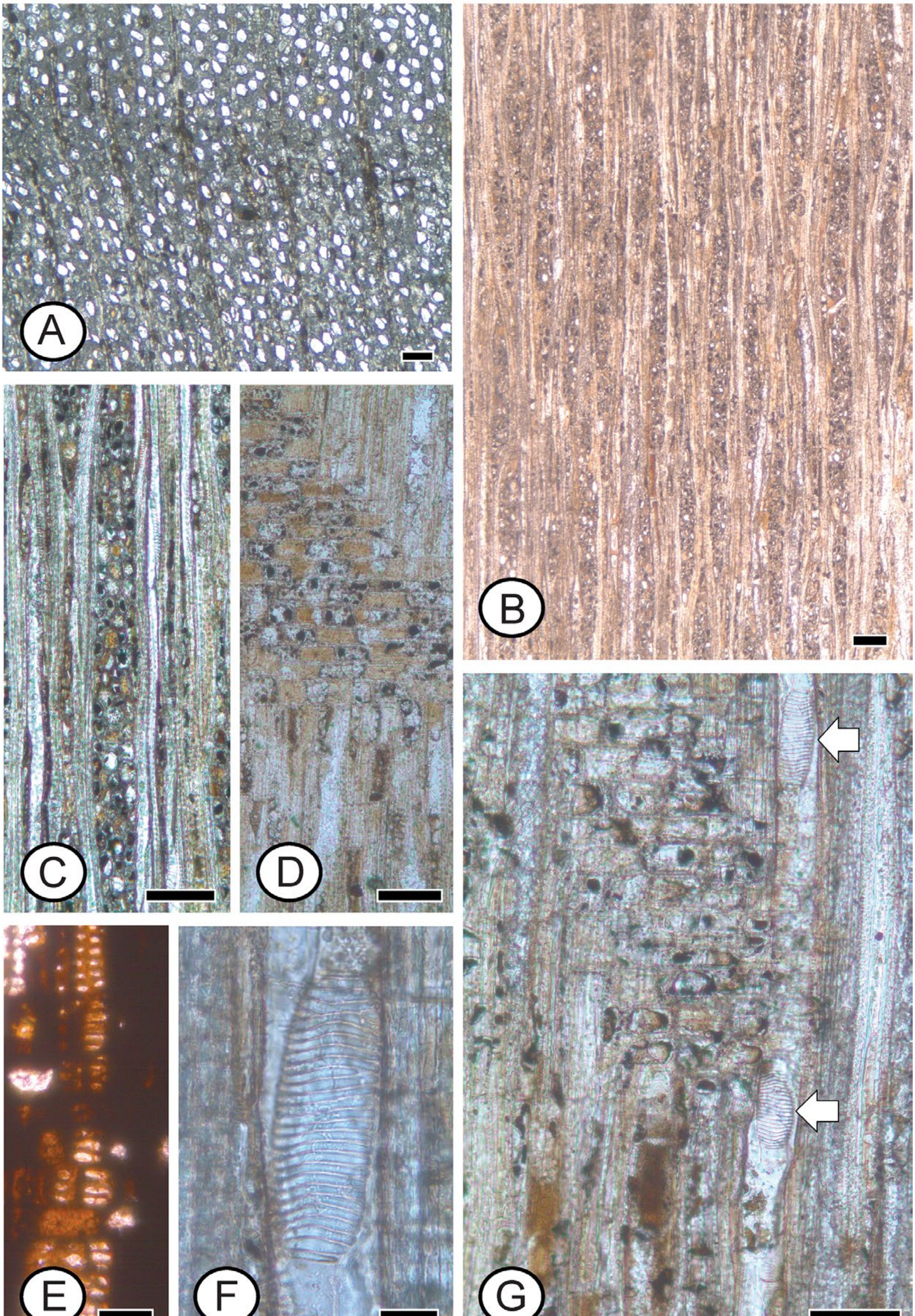


**Plate 1**. Wood anatomical features of *Liquidambaroxylon efeae* Akkemik sp. nov. **A**. Diffuse-porous wood with slightly visible growth ring boundary; **B**, **C**. Two distinct sizes of rays up to 6 cells; **D**. Heterocellular ray; **E**. Opposite and scalariform intervessel pits; **F**. Scalariform perforation plate with 20–30 bars, some bars forked; **G**. Heterocellular rays and scalariform perforation plates (arrows). Scale bars 100 µm in A–D and G, 20 µm in E and F

solitary, in multiples of 2–(3), vessel frequency is around 100 pores per $mm^2$ and more, vessel diameter is less than 100 µm, the perforation plates are scalariform with more than 20 bars, and the intervessel pits are arranged in transverse rows, sometimes opposite, horizontally elongated, orbicular to oval or linear through fusion (Selmeier, 2002; Oskolski et al., 2012). The rays are heterocellular, 1–3-seriate; in some fossil *Liquidambar* species, larger rays are 4–10-seriate (Suzuki and Watari, 1994). Due to having the features of *Liquidambaroxylon*, the present wood was identified as *Liquidambaroxylon*. The fossil genus *Liquidambaroxylon* has five fossil species, fossil *Liquidambar* is known from a single species, and the fossil genus *Altingioxylon* comprises two species. The following identification key was prepared to show the differences between all fossil species of Altingiaceae and to locate the exact position of the present wood on the basis of the following references: Van der Burgh (1964, 1973), Kramer (1974), Suzuki (1982), Gottwald (1992), Suzuki and Watari (1994), Iamandei and Iamandei (2005) and Oskolski et al. (2012):

1. Bar number <20 in scalariform perforation plates (*Altingioxylon, Liquidambaroxylon*) . . . . . . . . . . . . 2
1.* Bar number >20 in scalariform perforation plates (*Liquidambaroxylon*) . . . . . . . . . . . . . . . . . . . . . . . . 4
2. Vessel density 40–45 per $mm^2$; No helical thickening in vessel elements; bars 15–20 in scalariform perforations . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Altingioxylon rhodoleioides* Kramer, 1974
2.* Vessels numerous, >100 vessels per $mm^2$ . . . . . 3
3. Axial parenchyma diffuse and scanty; vessel density 83–127 per $mm^2$; bar 5–18 in scalariform perforations . . . . . . . . . . . . . *Altingioxylon hainanensis* Oskolski, 2012
3.* Axial parenchyma diffuse and terminal . . . . . . . . . . . . . . . *Liquidambaroxylon horvathi* Greguss, 1969
4. Rays 1–3-seriate . . . . . . . . . . . . . . . . . . . . . . . . 5
4.* Larger rays 4–10-seriate; mostly 1–6-seriate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
5. Perforation plates storied . . . . . . . . . . . . . . . . . . . . . . . *Liquidambaroxylon magdefraui* Greguss, 1969
5.* Perforation plates not storied . . . . . . . . . . . . . . . . . 6
6. Vessels diffuse; no vessels exclusively solitary (90% or more); axial parenchyma diffuse and diffuse-in-aggregate; no helical thickening present . . . *Liquidambaroxylon weylandi* Greguss, 1992
6.* Vessels exclusively solitary (90% or more); axial parenchyma diffuse; helical thickening present in vessel elements . . . . . . . . . . . *Liquidambaroxylon speciosum* Felix, 1884
7. Laurocerasus-type secretory cells present and obvious . . . . . . . . . . . . . . *Liquidambaroxylon styraciflua* Greguss, 1959
7.* This feature absent . . . . . . . . . . . . . . . . . . . . . . . . 8
8. Larger ray height ~0.5–1 mm or sometimes more than 1 mm, rays clearly of two distinct sizes, larger rays 4–6-seriate, axial canal not observed, no crystals present . . . . *Liquidambaroxylon efeae* Akkemik sp. nov.
8.* Larger ray height ~0.5 mm or less, rays 1–4-seriate; axial canals normal; crystals in ray cells present . . . . . . . . . . . . . . . . . *Liquidambar hisauchii* (Watari) Suzuki and Watari, 1994

As also seen in the identification key, the new species *Liquidambaroxylon efeae* Akkemik sp. nov. differs from the other species in having larger rays 4–6-seriate, greater ray height (some more than 1 mm), 25–30 (20–40) bars in scalariform perforation plates, and the absence of axial canals and crystals. In the early Miocene of west Anatolia, Güner et al. (2017) identified *Liquidambar europaea* from leaf imprints. Yavuz-Işık (2007, 2008) and Biltekin (2017) identified pollen of *Liquidambar* from the Miocene of western Anatolia and evaluated them as elements of riparian forests. A characteristic azonal riparian forest was recorded from the early Miocene locality Çan, west Anatolia, where *Alnus* and *Liquidambar* were dominating elements in the fossil leaf assemblage (Denk et al., 2019). Also, from the nearby Greek island Lesbos, rich wood records of *Liquidambar* were recorded (see Velitzelos et al., 2014). Hence, *Liquidambar* was an important riparian element in the early Miocene of Turkey.

Today, *Liquidambar orientalis* is an endemic species for south-western Anatolia and a few Aegean islands. When the fossil and the present species are compared, the growth ring boundary, vessel, fibre tracheids, axial parenchyma and ray features are closely similar (Tab. 2). The similarities between the fossil and extant woods suggest that the fossil species might be the ancestor of the present species.

Order SAPINDALES
Juss. ex Bercht. et J. Presl, 1820

Family ANACARDIACEAE R. Br., 1818

Genus PISTACIOXYLON Dupéron, 1973

Type species *Pistacioxylon muticoides* Dupéron, 1973, p. 317–324, figs 4–6, pls 2, 3

***Pistacioxylon ufukii***
Akkemik et I. Poole, 2018
Pl. 2A–D

Specimen code. KIR74.

**Table 2**. Comparison of the extant *Liquidambar orientalis* Mill. and the fossil species *Liquidambaroxylon efeae* Akkemik sp. nov.

| Features | *Liquidambar orientalis* Mill. (Efe, 1987; Akkemik and Yaman, 2012) | *Liquidambaroxylon efeae* Akkemik sp. nov. |
|---|---|---|
| Growth ring boundary | Distinct | Distinct |
| Vessels | Diffuse; solitary and in radial multiples of 2–3; mostly angular; ~100 vessels per mm$^2$ and 50–100 µm | Diffuse; exclusively solitary and rarely in multiples; mostly angular; ~100 vessels per mm$^2$ and 50–100 µm |
| Fibre tracheids | Present | Present |
| Axial parenchyma | Diffuse | Diffuse |
| Rays | Rays 1–6-seriate, larger rays 4–10-seriate; Procumbent ray cells with 1–4 or more upright or square marginal cells, and square and upright cells mixed throughout the ray | Larger rays 4–6 (–10)-seriate; Procumbent ray cells with 1–4 or more upright or square marginal cells, and some larger rays longer than 1 mm |
| Secretory elements | Intercellular canals of traumatic origin present | Not observed |

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Locality. Kıraluç fossil site near the city of Beypazarı (Ankara).

Age. Early Miocene.

Horizon. Hançili Formation.

Diagnosis. Growth ring boundaries distinct, wood ring-porous. Earlywood vessels 1(–2)-seriate and transition from earlywood to latewood abrupt. Vessel tangential diameter 50–100 µm and 100–200 µm, and radial diameter mostly >100–200 µm in earlywood; <50 (mostly 20–25) µm in latewood. Vessel frequency 5–20 in earlywood and numerous in latewood. Tyloses common in wider vessels. Latewood vessels occur in radial pattern, narrow dendritic pattern and in radially arranged clusters (Pl. 2A). Radial canals common in rays (Pl. 2B, C). Rays 1–4 (–5)-seriate and 6–12 per mm Ray height ~7–36 cells (Pl. 2B–D). Intervessel pits measure 4–7 µm. Rays heterocellular and body ray cells procumbent with mostly 1–4 rows of upright and/or square marginal cells, radial canals also visible in radial section, and perforation plate simple (Pl. 2E, F).

Discussion. The fossil genus *Pistacioxylon* was first described by Dupéron (1973) with the type species *Pistacioxylon muticoides* Dupéron, 1973. Later, four more fossil species were described as *Pistacioxylon holleisii* Selmeier, 2000, from the late Miocene of Bavaria, Germany (Selmeier, 2000), *Pistacioxylon praeterebinthus* Gottwald, 2004, from the Miocene of Baveria, Germany (Gottwald, 2004), *Pistacioxylon leilaoensis* Cheng, Mehrotra, Jin, Yang and Li, 2012, from the Miocene of Leilao, Yuanmou Basin, Yunnan Province, southwest China (Cheng et al., 2012), and *Pistacioxylon ufukii* Akkemik and I. Poole, 2018, from central Anatolia (Akkemik et al., 2018).

The new specimen differs from *Pistacioxylon praeterebinthus* in having earlywood with 1 (–2) rows of vessels, and differs from *P. holleisii* and *P. muticoides* in having relatively wide (3–5-seriate) rays alongside narrow rays (1–3-seriate), and from *P. leilaoensis* in having narrower vessels (50–130 µm). On the other hand, the specimen is rather similar to *Pistacioxylon ufukii* by its vessel and ray characteristics, and therefore it was identified as *P. ufukii*. The collection sites of these two specimens are close to each other and both are of early Miocene age. This present report adds new information on the distribution of this fossil species in the early Miocene of Turkey.

Today, ten species of the genus are known in the world, six of them native to Turkey and the Mediterranean Basin (Yılmaz, 2014). Among the modern species, *Pistacia terebinthus* L. and *P. atlantica* Desf. have features closely similar to the fossil species. They both have earlywood vessels in one row, short or long radial clusters of latewood vessels, rays 3–5-seriate, 10–30 cells high, and horizontal resin canals (Schweingruber, 1990; Akkemik and Yaman, 2012). *Pistacia lentiscus* differs from the fossil wood in having narrower (1–3-seriate) rays. Based on the anatomical similarities, *P. atlantica* and *P. terebinthus* may be evaluated as the closest modern relatives of the fossil species.

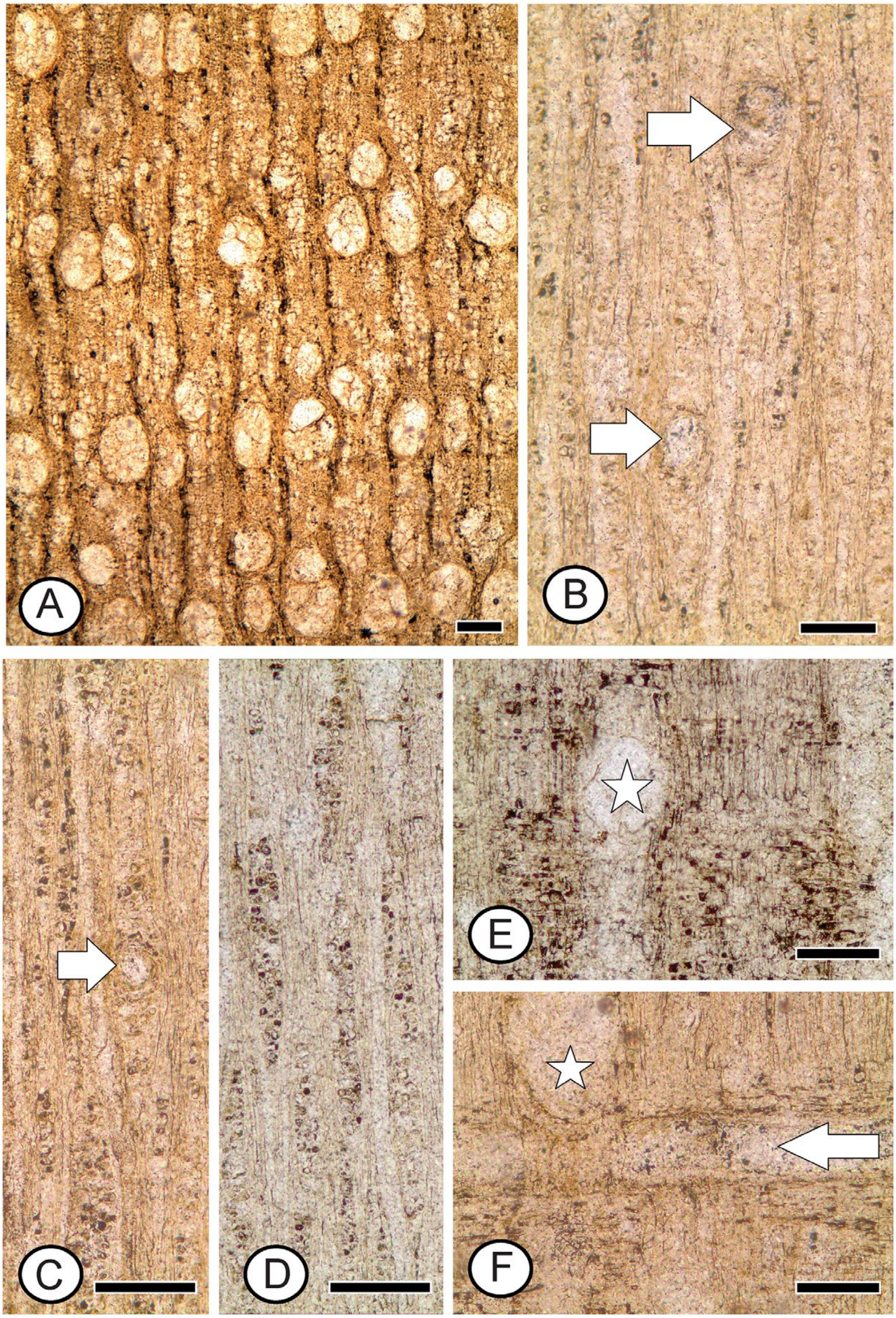


**Plate 2**. Wood anatomical features of *Pistacioxylon ufukii* Akkemik et I. Poole sp. nov. **A**. Transversal section with ring-porous wood, and abrupt transition from earlywood the latewood; **B–D**. Tangential section with rays, which have radial canals (arrows); **E**, **F**. Radial section with simple perforation plate (star) and heterocellular ray with also radial canal (arrow). Scale bars 100 µm

Order FAGALES Engl., 1892

Family BETULACEAE Gray, 1822

Genus EUCARPINOXYLON Müller-Stoll et Mädel, 1959

Type species *Eucarpinoxylon vasculosum* (Felix) Müller-Stoll et Mädel, 1959, p. 183, pl. 8, figs 24–27

***Eucarpinoxylon kayacikii*** Akkemik **sp. nov.**

Pl. 3A–E

Holotype. Three thin sections of specimen GOK2. This specimen was identified as the genus *Carpinoxylon* by Güngör et al. (2019).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number. PFN002208.

Etymology. The epithet "*kayacikii*" honours Prof. Dr. Hayrettin Kayacık, the founder of the Forest Botany Department of the Faculty of Forestry at Istanbul University.

Type locality. East of Eşelek village – Gökçeada, and near coastline.

Age. Middle Miocene.

Type horizon. Kesmekaya Volcanics.

Diagnosis. Growth ring boundaries indistinct. Wood diffuse-porous and vessels arranged in radial multiples, and generally in a dendritic pattern (predominantly flame-like). Radial clusters of vessels very common and solitary vessels rather rare (Pl. 3A, B). Fibres thick-walled. Axial parenchyma commonly apotracheal diffuse and diffuse-in-aggregate, and in narrow and short tangential bands (Pl. 3A). Ray width 1–3-seriate; in some rays, 1–4 rows of square marginal cells present. Aggregate rays occasionally present. Rays per mm ≥12, ray height 1–30 cells (Pl. 3C, D). Rays heterocellular, body ray cells procumbent with one row of square cells. Perforation plates simple (Pl. 3E).

Discussion. Since the wood has a predominantly dendritic (flame-like) pattern of vessels, in radial multiples, with rays 1–3-seriate, apotracheal diffuse and diffuse-in-aggregate axial parenchyma, and exclusively simple perforation plate, it may belong to Betulaceae or Fagaceae. A similar fossil wood, *Fagaceoxylon ostryopsoides* Scott and Wheeler, was described by Wheeler and Manchester (2002), which differs in having distinct growth ring borders marked by radially flattened fibres, marginal parenchyma, and the presence of aggregate rays. The specimen also differs from the other fossil genera of Fagaceae (i.e. *Fagoxylon*, *Quercoxylon*, *Lithocarpoxylon*) in having a flame-like vessel arrangement. The arrangement of vessels is close to that of *Ostryopsis* Decne., but in *Ostryopsis* the perforation plate is scalariform and the rays are heterocellular (Hall, 1952).

The wood is rather similar to *Eucarpinoxylon* with rays 1–3-seriate and diffuse-in-aggregate axial parenchyma. Due to the close similarities between *Fagaceoxylon* and *Eucarpinoxylon*, the following identification key for *Eucarpinoxylon* species and *Fagaceoxylon ostryopsoides* was prepared on the basis of the relevant references (Müller-Stoll and Mädel, 1959; Page, 1970; Wheeler et al., 1977; Suzuki and Hiraya, 1989; Wheeler and Manchester, 2002; Jeong et al., 2009).

A valuable discussion of *Carpinoxylon* was provided by Iamandei et al. (2011), who suggested using *Eucarpinoxylon* for *Carpinus*-type woods. For that reason, the identification key considers *Eucarpinoxylon* species and *Fagaceoxylon ostryopsoides* Scott and Wheeler, 2002, which are very similar in terms of wood anatomy.

1. Ray height more than 1 mm .................. 2
1.* Ray height clearly lower than 1 mm ........... 3
  2. Vessels large, 100–200 µm, 5–20 vessels per per mm² ................. *Eucarpinoxylon gevinii* (Boureau, 1949) Muller-Stoll and Mädel, 1959
  2.* Vessels small, ≤50 µm, ≥100 vessels per mm² ............. *Eucarpinoxylon vasculosum* (Felix) Muller-Stoll and Madel, 1959
3. Vessels predominantly in dendritic pattern (flame-like) and in radial multiples .................. 4
3.* Vessels diffuse and not predominantly in dendritic pattern (not flame-like) ...................... 5
  4. Growth ring boundaries indistinct or absent; rays 1–3-seriate; distinct aggregate rays not observed but indistinct ones present ..................... ..... *Eucarpinoxylon kayacikii* Akkemik sp. nov.
  4.* Growth ring boundaries distinct with marginal axial parenchyma; rays 1–2-seriate; aggregate rays clearly present ......................... *Fagaceoxylon ostryopsoides* Scott and Wheeler, 2002
5. Rays exclusively uniseriate ....... *Eucarpinoxylon hungaricum* (Greguss) Muller-Stoll and Mädel, 1959
5.* Rays 1–3-seriate; banded axial parenchyma in 1–3 rows ....... *Eucarpinoxylon laxum* (Watari, 1952) Muller-Stoll and Madel, 1959

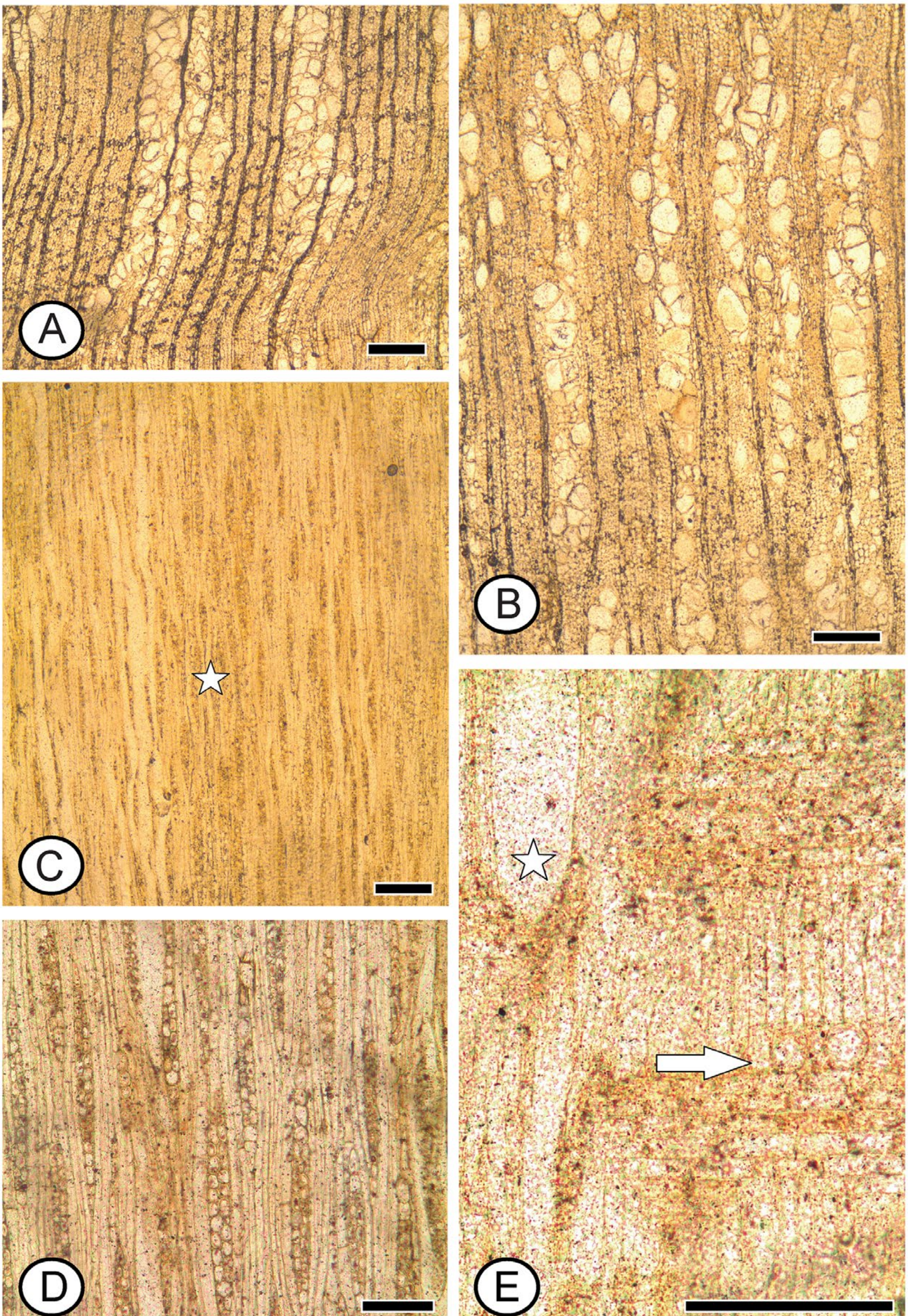


**Plate 3**. Wood anatomical features of *Eucarpinoxylon kayacikii* Akkemik sp. nov. **A**. Flame-like arrangement of vessels, and diffuse-in-aggregate axial parenchyma, growth ring boundary indistinct; **B**. Vessels in radial multiples and vessel clusters; **C**. 1–3-seriate rays and a slightly visible aggregate ray (star); **D**. 1–3-seriate rays; **E**. Simple perforation plate (star) and heterocellular rays (arrow). Scale bars 200 µm in A–C and E, 20 µm in D

Due to having a flame-like pattern of vessels together with radial multiples of vessels, the specimen differed clearly from other fossil species of *Eucarpinoxylon*; although it is similar to *Fagaceoxylon ostryopsis*, *F. ostryopsoides* differs in having indistinct growth ring boundaries and no distinct aggregate rays. Because it possesses features similar to the modern genus *Carpinus* Mill., the fossil wood is assigned to *Eucarpinoxylon*. Leaf imprints of *Fagus* and *Carpinus* were commonly found from the early Miocene of western Anatolia (Denk et al., 2017a, 2019; Güner et al., 2017) and north-western Turkey (Arslan et al., 2013), and their pollen was found by Yavuz-Işık (2007). The micro- and macrofossils showed that *Fagus* and *Carpinus* were common tree species in the early Miocene of Turkey.

Today, two species of *Carpinus* (*C. betulus* L. and *C. orientalis* Mill.) and two species of *Fagus* (*F. orientalis* Lipsky and *F. sylvatica* L.) grow naturally in and around Turkey. The characteristics of the fossil species are closer to the modern *Carpinus* than those of Fagaceae, with a difference based on the absence of distinct aggregate rays in the fossil species. The flame-like arrangement of vessels is the feature closest to modern *Ostryopsis* in Betulacaea, but the perforation plate is scalariform in *Ostryopsis*. Based on the features of the fossil species, it can be suggested that the potential modern analogue of this fossil species may be *Carpinus* species in the Mediterranean Basin, which have a slightly flame-like arrangement of vessels and also simple perforation plates.

Order FAGALES Engl., 1892

Family BETULACEAE Gray, 1822

Genus *OSTRYOXYLON* Akkemik, 2018 emend. Akkemik

Type species ***Ostryoxylon gokceadaense*** Akkemik **sp. nov.**

Pl. 4A–H

Holotype. Three thin sections of specimen GOK02 (2 in Güngör et al., 2019).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number. PFN002209.

Etymology. The epithet “*gokceadaense*” derives from the origin of the sample, Gökçeada (Imbros), an island in the Aegean Sea.

Type locality. East of Eşelek village – Gökçeada, near coastline.

Age. Middle Miocene.

Type horizon. Kesmekaya Volcanics.

Diagnosis. Growth ring boundaries distinct with 1–2 rows of marginal fibre cells. Wood diffuse-porous, and vessels arranged in radial multiples of 2–4 or more (up to 13 vessels). Mean tangential diameter of vessel lumina less than 50 µm. Vessel frequency 50–100 per mm$^2$. Helical thickening on vessels very common. Axial parenchyma present and diffuse (Pl. 4A, B). Ray width 1–4-seriate, aggregate rays not observed. Rays per mm per mm$^2$ $\geq 12$. Maximum ray height up to 71 cells (Pl. 4C). Intervessel pits mostly alternate and opposite, circular in shape (Pl. 4E, F). Perforation plates simple (Pl. 4G). Rays heterocellular; body ray cells procumbent with mostly 1–4 rows of upright and/or square marginal cells (Pl. 4H).

Discussion. Features such as the distinct growth ring boundary, vessels diffuse and in radial multiples, and rays 1–3-seriate match the wood characteristics of Betulaceae. Due to the helical thickening and predominantly simple perforation plate and long and narrower rays, the fossil wood differs from that of extant *Betula* L., *Alnus* Mill., *Corylus* L. and *Carpinus* L. The greatest similarities are with extant wood of *Ostrya* Scop. Only two fossil species of *Ostrya* have been described based on wood: *Ostrya geumgwangensis* Jeong and Kim (Jeong et al., 2009) and *Ostrya monzenensis* Suzuki and Watari (Suzuki and Watari, 1994). Later, in Güngör et al. (2019), the fossil genus name “*Ostryoxylon*” was used. Here I designate the type species *O. gokceadaense* Akkemik sp. nov. The following identification key including the new species was prepared based on the distinctive features of the fossil species (Suzuki and Watari, 1994; Jeong et al., 2009; Güngör et al., 2019).

1. Larger rays commonly 4–10-seriate . . . . . . . *Ostrya geumgwangensis* Jeong and Kim, 2009

1.* Ray width 1–4-seriate . . . . . . . . . . . . . . . . . . . . . . . 2

  2. All rays procumbent . . . . . . . *Ostrya monzenensis* Suzuki and Watari, 1994

  2.* Rays heterocellular. . . . . . . . . . . . . . . *Ostryoxylon gokceadaense* Akkemik sp. nov.

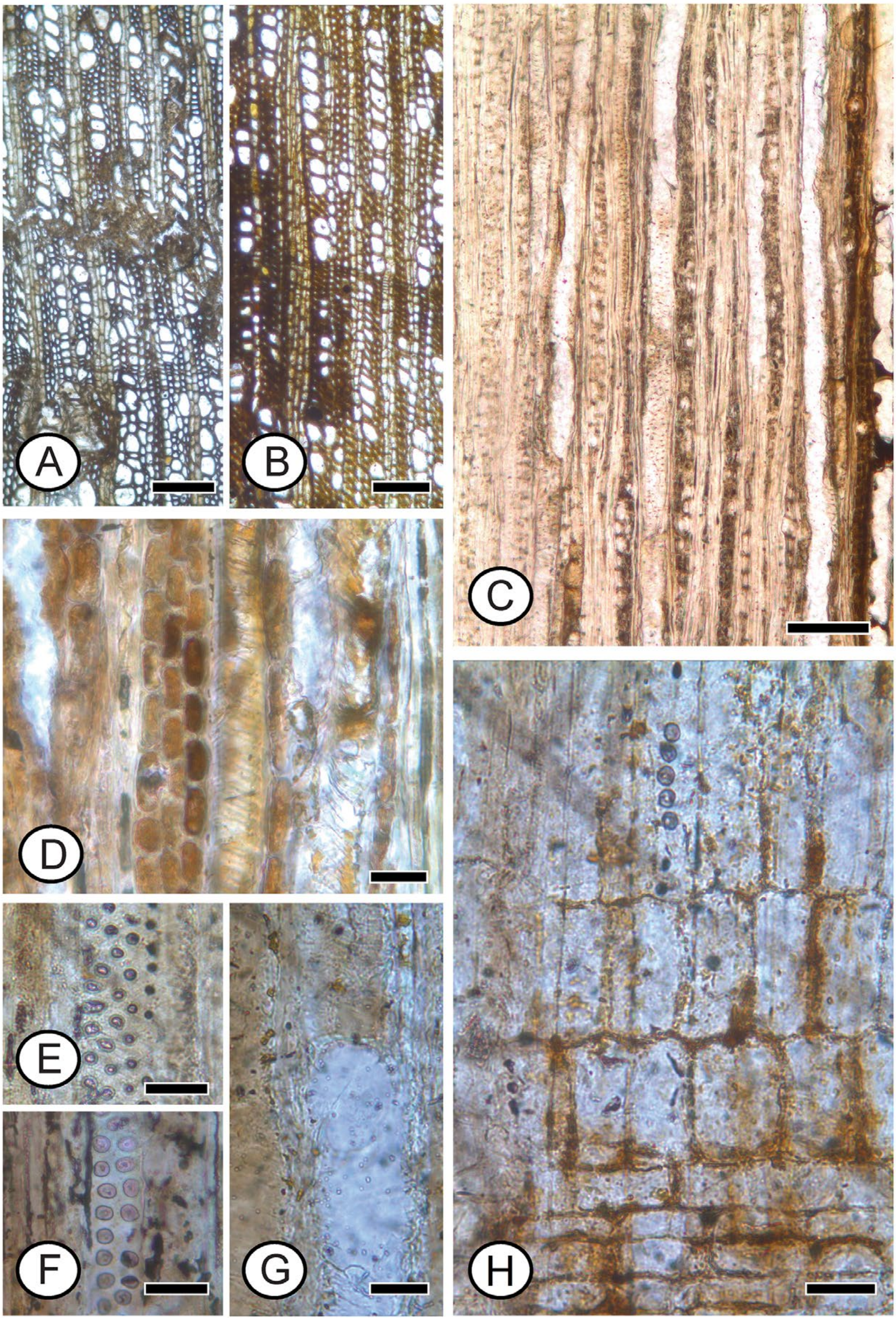


**Plate 4**. Wood anatomical features of *Ostryoxylon gokceadaense* Akkemik sp. nov. **A**, **B**. Diffuse-porous wood with distinct growth ring boundary; **C**, **D**. 1–3 rows of rays in tangential section, and helical thickening in vessels; **E**. Alternate intervessel pits; **F**. Opposite intervessel pits; **G**. Simple perforation plate; **H**. Heterocellular ray, procumbent body ray cells with 3 rows of vertical marginal cells. Scale bars 100 μm in A–C, 20 μm in D–I

In modern species of *Ostrya*, the rays are generally composed of only procumbent cells; in the fossil species, procumbent body ray cells are associated with upright and square marginal cells of 1–4 or more upright and square marginal cells. This feature is more similar to the modern species of *Carpinus*, which have mostly one row of upright or square marginal cells. However, aggregate rays are common in all *Carpinus* species and not common in *Ostrya* species. For that reason, the fossil species looks like an intermediate between *Ostrya* and *Carpinus*. However, in *Ostrya virginiana* (Mill.) K. Koch, a North American species, one row of square marginal cells is present (InsideWood, 2004 onward). In this species, the axial parenchyma is different in having marginal bands up to three cells wide.

Because the wood of some species of modern *Carpinus* and *Ostrya* has aggregate rays, with homocellular or heterocellular rays, their wood is closely similar. For that reason, the exact taxonomic affinity of the fossil species cannot be determined at the moment; potential modern analogues of this fossil species are to be found among the modern species of *Ostrya* and *Carpinus*.

Order FAGALES Engl., 1892

Family FAGACEAE Dumort., 1829

Genus *FAGOXYLON* Stopes and Fujli, 1910, emend. Süss, 1986

Type species *Fagoxylon hokkaidense* Stopes and Fuji, 1910, p. 64, pl. 8, figs 50–53; wood

### ***Fagoxylon radiatum*** Süss, 1958

Pl. 5A–D

Specimen code. GOK257 (257 in Güngör et al., 2019).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University, Istanbul, Turkey.

Locality. East of Eşelek village – Gökçeada, near coastline.

Age. Middle Miocene.

Horizon. Kesmekaya Volcanics.

Diagnosis. Growth ring boundary distinct. Towards the end of the latewood zone, vessel number decreases and thick-walled fibres increase. Wood diffuse-porous in general, and slightly semi-ring-porous. Pores frequent and more than 100 per mm$^2$. Vessels solitary and clustered. Axial parenchyma commonly apotracheal diffuse and diffuse-in-aggregate. Mean tangential diameter of vessel lumina ~50 µm (Pl. 5A, B). Rays uniseriate to multiseriate (Pl. 5A–C). Width of multiseriate rays more than 10 cells, all ray cells procumbent, 4–12 rays per mm, height of multiseriate rays more than 1 mm. Perforation plate mostly simple, rarely scalariform. No helical thickening observed. Intervessel pits opposite and scalariform (Pl. 5D).

The identification key prepared by Akkemik et al. (2019) was updated during the present study, using the relevant wood anatomy references (Van der Burgh, 1973; Privé-Gill and Watelet, 1980; Süss and Müller-Stoll, 1984; Süss, 1986; Tereda et al., 2006; Wheeler and Dillhoff, 2009). Takahashi and Suzuki (2003) stated that *Fagoxylon hokkaidense* has radially elongated ray cells (procumbent cells) and therefore may be of the same wood type as *Nishidaxylon*, although *N. jezoense* has much wider rays. For that reason, it is not included in the present key.

1. Banded axial parenchyma present together with diffuse and scanty paratracheal parenchyma . . . . 2
1.* Banded axial parenchyma absent. . . . . . . . . . . . . . 4
   2. Helical thickening present in vessel elements; no tylosed cells; crystals present in ray cells, axial parenchyma cells and enlarged cells. . . . . . . . . . *Fagoxylon caucasicum* (Felix, 1894) Süss, 1986
   2.* No helical thickening in vessel elements; tylosed cells present . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
3. Crystals present in ray cells, and enlarged cells; axial parenchyma diffuse and scanty paratracheal, and banded . . . . . . . . . . . . . . . . *Fagoxylon acerinum* (Windisch, 1886) Süss, 1986
3.* Crystals absent; axial parenchyma diffuse, diffuse-in-aggregate, scanty paratracheal, vasicentric, aliform, confluent and unilateral paratracheal . . . . . . . *Fagoxylon francofurtense* (Mädler, 1939) Süss et Müll.-Stoll, 1984
   4. Only diffuse axial parenchyma present . . . . . . 5
   4.* Axial parenchyma diffuse, diffuse-in-aggregate, vasicentric or scanty paratracheal . . . . . . . . . . 7
5. Scalariform perforation plates; bar number < 10 bars; wood semi-ring-porous or diffuse; axial parenchyma only diffuse . . . . . . . . . . . . . . *Fagus manosii* Wheeler and Dillhoff, 2009
5.* Bar number up to 40 bars in scalariform perforation plates; wood diffuse-porous . . . . . . . . . . . . . . . . . . . 6

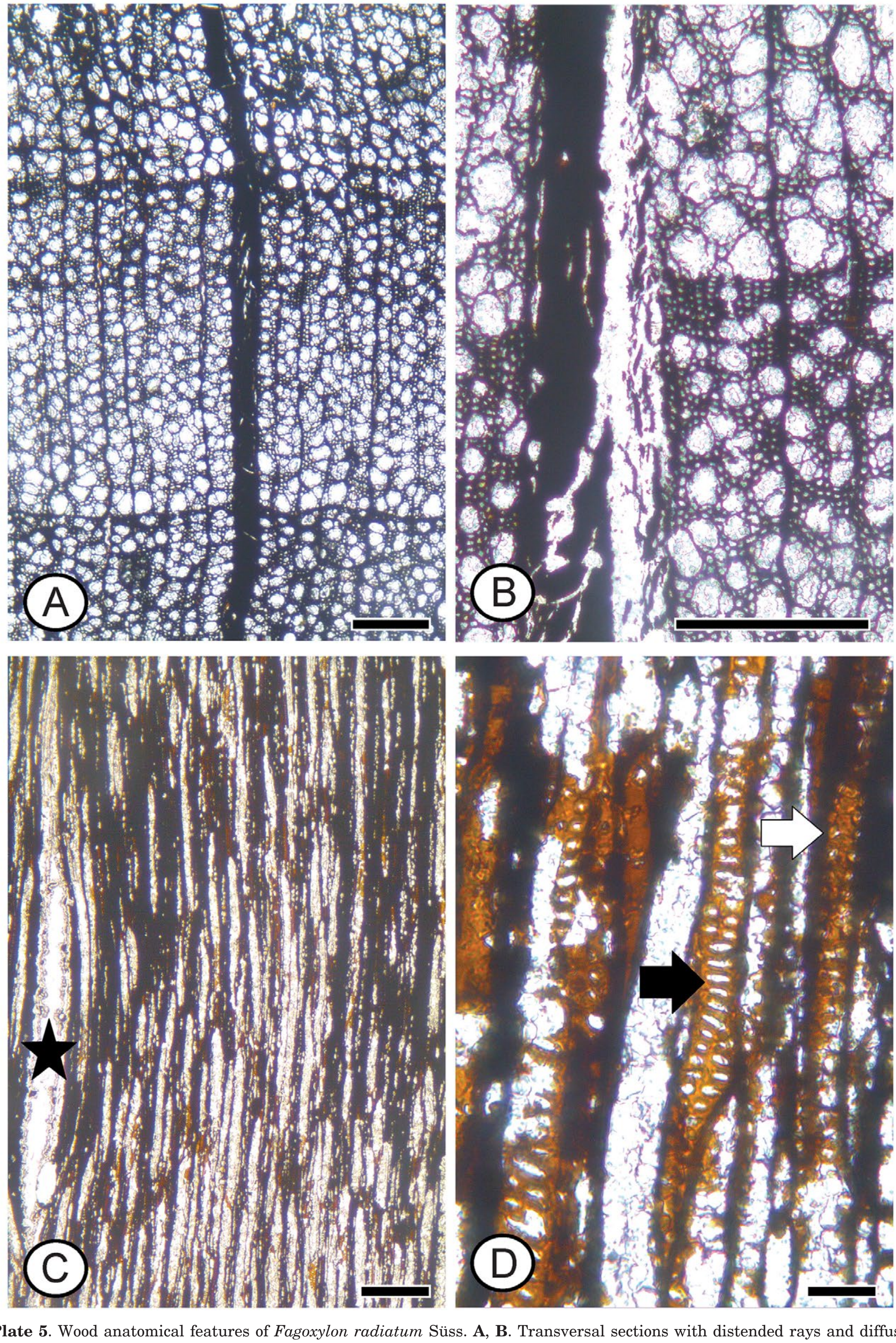


**Plate 5**. Wood anatomical features of *Fagoxylon radiatum* Süss. **A**, **B**. Transversal sections with distended rays and diffuse to slightly semi-ring-porous wood; **C**. Wide (star) and narrow rays; **D**. Scalariform (black arrow) and opposite (white arrow) intervessel pits. Scale bars 200 µm in A–C, 20 µm in D

6. Axial parenchyma diffuse; bar number up to 20 ......... *Fagoxylon subcaucasicum* Privé, 1980
6.* Axial parenchyma diffuse, diffuse-in-aggregate; bar number up to 40...................... ...*Fagoxylon grandiporosum* (Beyer) Süss, 1986
7. Vessels exclusively solitary (90% or more) ......8
7.* Vessels diffuse, not exclusively solitary (90% or more)....................................9
8. Helical thickening present in vessel elements; crystals present in ray cells, axial parenchyma cells and enlarged cells .................... ...........*Fagoxylon mikofalvense* Süss, 1986
8.* No helical thickening in vessel elements; axial parenchyma diffuse, diffuse-in-aggregate and scanty paratracheal ...... *Fagoxylon radiatum* Süss, 1986
9. Prismatic crystals common in ray cells, in upright and/or square ray cells and in enlarged cells; axial parenchyma diffuse, diffuse-in-aggregare, scanty paratracheal, vasicentric, and in narrow bands .... ...*Fagoxylon cristallophorum* Van der Burgh, 1973
9.* Prismatic crystals in idioblast-like cells.......... ........*Fagoxylon hondoense* (Watari) Süss, 1986

According to the features of the specimen (banded axial parenchyma absent, vessels exclusively solitary 90% or more), no helical thickening in vessel elements, axial parenchyma diffuse, diffuse-in-aggregate and scanty paratracheal), the fossil belongs to *Fagoxylon radiatum* Süss, 1958. *Fagoxylon radiatum* Süss, 1958, is a fossil wood of the Eurasian palaeoregion during the Miocene, and was originally described from Bolko, województwo opolskie (Poland) by Süss (1986). Leaf imprints of *Fagus gussonii* A. Massal. 1859 emend. Erw. Knobloch and Velitzelos 1986 (Güner et al., 2017) and *F. cstaneifolia* Unger (Denk et al., 2017a, 2019), and pollen of *Fagus* (Yavuz-Işık, 2007, 2008; Bouchal et al., 2018; Denk et al., 2019) are common in the early and middle Miocene of Turkey.

Akkemik et al. (2019) identified another fossil species from Turkey, *Fagoxylon francofurtense* (Mädler, 1939) Süss et Müll.-Stoll 1984, which has banded axial parenchyma. Today, *Fagus orientalis* Lipsky and *F. sylvatica* L. grow naturally in Turkey; they have features close to both of these fossil species (Tab. 3).

Order FAGALES Engl., 1892

Family FAGACEAE Dumort., 1829

Genus *QUERCOXYLON* Kräusel, 1940, Section *ILEX*

Type species *Quercoxylon retzianum* Kräusel, 1940, Abh. Bayer. Akad. Wiss., Math.-Naturwiss. Abt., Neue Folge, 47: 27. 16 Feb 1940

## ***Quercoxylon yaltirikii*** Akkemik **sp. nov.**

Pl. 6A–G

Holotype. Three thin sections of specimen INL09 (Acarca Bayam et al., 2018).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number. PFN002210.

Etymology. The epithet "*yaltirikii*" honours the late Prof. Dr. Faik Yaltırık, eminent botanist and leading authority on Turkish oak species, who worked in the Department of Forest Botany, Faculty of Forestry, Istanbul University.

Type locality. Beypazarı-Inozu valley (north side).

Age. Early Miocene.

Type horizon. Hançili Formation.

Diagnosis. Growth ring boundaries distinct and semi-ring-porous or almost ring-porous. Vessel tangential diameter 82(22–182) µm,

**Table 3**. Comparison of modern and fossil *Fagus* L. species in Turkey

| Features | *Fagoxylon francofurtense* Mädler (H. Süss and W.R. Müller-Stoll, 1984) | *Fagoxylon radiatum* Süss (Süss, 1986) | *Fagus orientalis*/*F. sylvatica* (Akkemik and Yaman, 2012; Schweingruber, 1988) |
|---|---|---|---|
| Growth ring | Distinct | Distinct | Distinct |
| Vessel | Diffuse | Diffuse to semi-ring-porous | Diffuse, slightly semi-ring-porous |
| Axial parenchyma | Commonly apotracheal diffuse and diffuse-in-aggregate, and banded axial parenchyma present | Commonly apotracheal diffuse and diffuse-in-aggregate | Commonly apotracheal diffuse and diffuse-in-aggregate, and in narrow and short tangential bands and occasionally scanty paratracheal |
| Rays | Uniseriate to >10-seriate | Uniseriate to >10-seriate | Uniseriate to up to 20-seriate |
| Perforation plate | Simple and scalariform | Simple and scalariform | Simple and scalariform |

radial diameter 109 (33–206) µm (Acarca Bayam et al., 2018); vessels exclusively solitary (90% or more) and with thick and circular walls. Tyloses very common in wider vessels (Pl. 6A, B). Large multiseriate rays clearly seen with the naked eye. Well preserved axial parenchyma clearly visible, arranged in short tangential bands in single rows (Pl. 6A, B). Ray number 4–6 per mm of two distinct sizes. Narrow uniseriate and biseriate rays measure 334 (110–805) µm by 14 (4–26) µm in width; large multiseriate rays range from 10 to 25 cells, or 258 (67–411) µm in width by >1 mm in height (Acarca Bayam et al., 2018) (Pl. 6C). Crystals very common in enlarged and not enlarged cells of axial parenchyma and rays, and also found in chambered cells. Some axial parenchyma cells rather enlarged in radial section (Pl. 6D, E). Perforation plates simple (Pl. 6F). All ray cells procumbent and heterocellular, with 1–2 rows of vertical or square marginal cells (Pl. 6D, G).

Discussion. This type of wood, which has diffuse to semi-ring-porous or even ring-porous vessels, very large rays, vessels solitary and arranged in radial direction, and a simple perforation plate, is assigned to *Quercoxylon* sect. *Ilex*. About 12 fossil species within this section have been identified up to now (Webber, 1933; Müller-Stoll and Mädel, 1957; Boureau, 1958; Mädel-Angeliewa, 1968; Petrescu, 1969, 1978; Gevin et al., 1971; Kramer, 1974; Privé, 1975; InsideWood, 2004 onward), and the differences between them are given below:

1. Growth ring boundaries indistinct or absent. . . . . 2
1.* Growth ring boundaries distinct. . . . . . . . . . . . . . . 6
   2. Axial parenchyma banded, unilaterally paratracheal, confluent, aliform together with diffuse, diffuse-in-aggregate, scanty paratracheal, and vasicentric . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
   2.* Axial parenchyma only banded, diffuse-in-aggregate, scanty paratracheal, and vasicentric, no unilaterally paratracheal, confluent, aliform axial parenchyma . . . . . . . . . . . . . . . . . . . . . . . . 4
3. Prismatic crystals present. . . . . . . . . . . . . . . . . . . . . *Quercoxylon viticulosum* (Unger, 1842) Müll.-Stoll et Mädel, 1957
3.* Prismatic crystals absent . . . . . . . . . . . . . . . . . . . . *Quercoxylon helictoxyloides* (Felix, 1884) Müll.-Stoll et Mädel, 1957
   4. All rays procumbent, and body rays procumbent with 1–4 or more rows of upright and/or square marginal cells . . . . . . . *Quercoxylon courpierense* Privé, 1975
   4.* All rays procumbent . . . . . . . . . . . . . . . . . . . . . 5
5. Aggregate rays absent; tyloses common . . . . . . . . . *Quercoxylon cyclobalanopsioides* K. Kramer, 1974
5.* Aggregate rays present. . . . *Quercoxylon caucasicum* (Gajvoronskij) Mädel-Angeliewa, 1968
   6. Perforation plate scalariform and simple . . . . . 7
   6.* Perforation plate simple. . . . . . . . . . . . . . . . . . . 9
7. Body rays procumbent with 1–4 or more rows of upright and/or square marginal cells . . . . . . . . . . . . . . . . . . . . . . . . . . *Quercoxylon gevini* Boureau, 1949
7.* All rays procumbent. . . . . . . . . . . . . . . . . . . . . . . . 8
   8. Prismatic crystals in only chambered axial parenchyma cells . . . . . . *Quercoxylon orepitheci* Mädel-Angeliewa, 1968
   8.* Prismatic crystals in body ray cells, in upright and/or square ray cells, in chambered and non-chambered axial parenchyma cells . . . . . . . . . . . . . . . . . . . *Quercoxylon justiniani* Petrescu, 1969
9. Wood both semi-ring and diffuse-porous or almost ring-porous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10
9.* Wood clearly diffuse-porous. . . . . . . . . . . . . . . . . . 11
   10. Rays heterocellular; larger rays 4–10-seriate; 5–20 vessels per mm$^2$ . . . . *Quercoxylon ogurai* Boureau, 1958
   10.* Wood semi-ring to ring-porous; rays homocellular and heterocellular, larger rays 10–25-seriate, 5–20 and 20–40 vessels per mm$^2$; some axial parenchyma cells including crystals very large, crystals common in axial and ray parenchyma cells. . . . . . . . . . . *Quercoxylon yaltirikii* Akkemik sp. nov.
11. Rays exclusively uniseriate, aggregate rays present; prismatic crystals absent. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Quercus ricardensis* Webber, 1933
11.* Broad rays commonly >10-seriate; aggregate rays present; prismatic crystals present . . . . . . . . . . 12
   12. Axial parenchyma banded up to three cell wide, vasicentric, diffuse-in-aggregate. . . . . . . . . . . . . . . . . . . . . . . . *Quercus mixtum* Petrescu, 1978
   12.* Axial parenchyma diffuse-in-aggregate and scanty paratracheal; prismatic crystals common in ray cells, in upright or square cells, in procumbent cells, in enlarged and chambered cells . . . . . . . . .*Quercoxylon praehelictoxyloides* Petrescu, 1978

A distinct growth ring boundary, predominantly simple perforation plate and semi-ring to almost ring-porous wood are characteristic of *Quercoxylon ogurai*, which is the fossil species most similar to the material described here. In particular, the new species has very large axial parenchyma cells with crystals, wood semi-ring to almost ring-porous, and larger rays 10–25 cells wide; in these features it differs from *Q. ogurai*. Based on these differences, as also indicated in the identification key, the specimen represents a new fossil species. Evergreen oak leaves and pollen are very common in the early and middle Miocene of Turkey; Güner et al. (2017) identified three species of *Quercus* Sect. *Ilex* for the middle Miocene of western Turkey. Today, evergreen oaks belonging to sect. *Ilex* are common in the

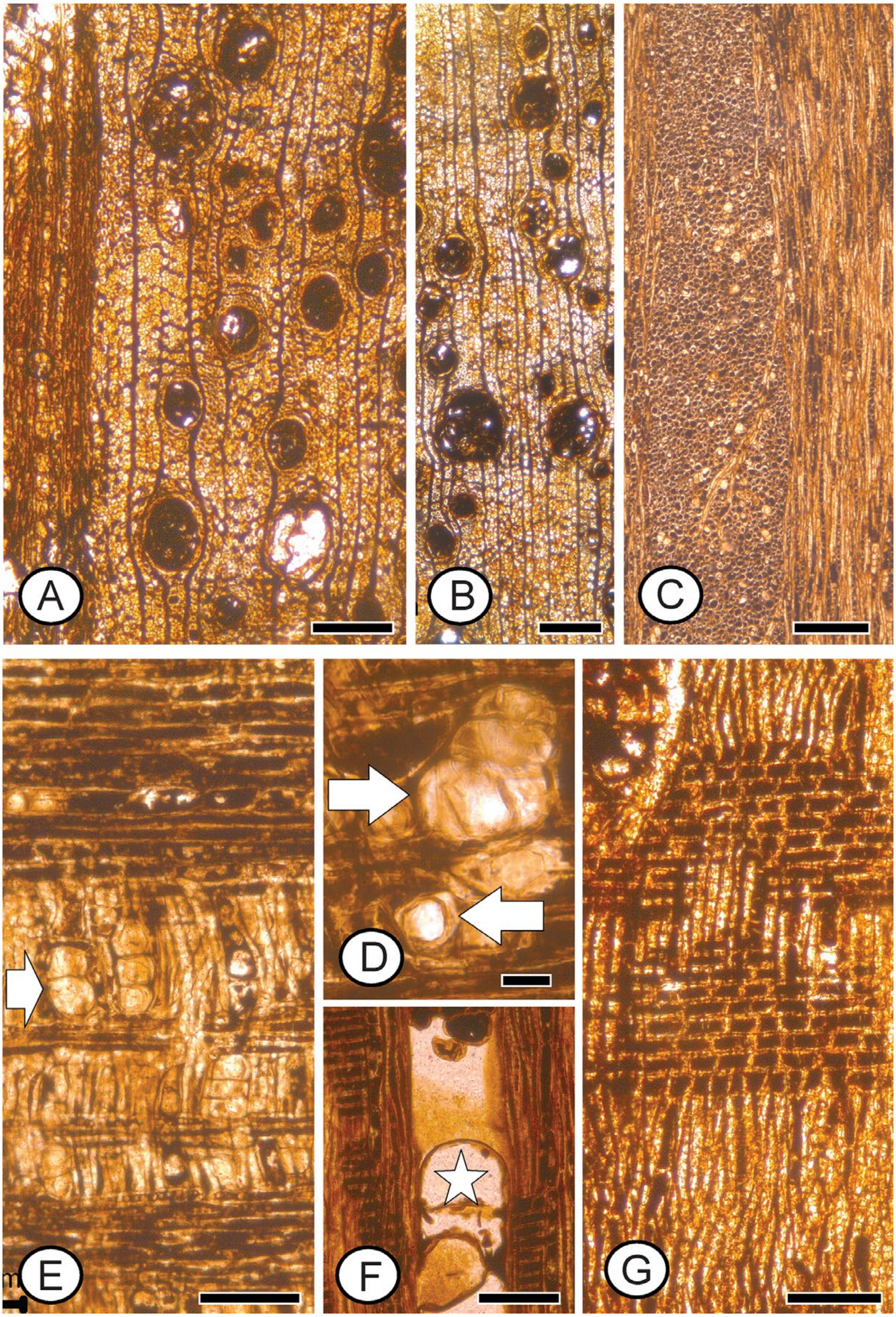


**Plate 6**. Wood anatomical features of *Quercoxylon yaltirikii* Akkemik sp. nov. **A**, **B**. Transversal sections with semi-ring-porous, porous predominantly uniseriate, and tyloses common, diffuse-in-aggregate axial parenchyma common; **C**. Very wide rays (10–20 cells wide) and narrow 1–2-seriate rays; **D**. Crystals in enlarged and chambered ray cells (arrows); **E**. Normal and large axial parenchyma cells with crystals (arrow); **F**. Simple perforation plate (star); **G**. Heterocellular rays, body ray cells procumbent with one row of square marginal cells. Scale bars 200 µm in A–C, 20 µm in D, 100 µm in E–G

Mediterranean Basin, south of Himalaya, and in East Asia and Southeast Asia. Denk et al. (2019) stated that for the early Miocene flora of Güvem "the reconstructed climate parameters suggested warm temperate conditions for mean annual temperature (mean 17.3°C) and coldest month mean temperature (mean 8.9°C) and the duration of the growing season (ca. 9 months). The relatively high growing season precipitation (1000–1900 mm) and the ratio of X3.WET to X3.DRY (ca. 5) further suggest precipitation seasonality but sufficient precipitation during the dry season (Cf climate)". Notably, the flora of Güvem is particularly rich in evergreen *Quercus*. However, other trees such as *Cedrus, Pinus, Juniperus, Cupressus, Salix, Populus, Liquidambar, Acer, Ulmus, Zelkova* and *Pistacia* from the Galatian Volcanic Province (Hançili Formation) showed the effect of well-drained upland or lowland growth site conditions, along with riparian sites exposed to changes in the water table.

Order LAURALES
Juss. ex Bercht. et J. Presl, 1820

Family LAURACEAE Juss., 1789

Genus *CRYPTOCARYOXYLON*
Leisman, 1986

Type species *Cryptocaryoxylon gippslandicum*
Leisman, 1986, figs 1–4

***Cryptocaryoxylon grandoleaceum***
Akkemik **sp. nov.**
Pls 7A–F, 8A–E

Holotype. Three thin sections of specimen GOK05 (5 in Güngör et al., 2019).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number. PFN002211.

Etymology. The epithet "*grandoleaceum*" refers to the characteristics of the wood: very large oil and mucilage cells associated with rays and fibres.

Type locality. East of Eşelek village – Gökçeada, near coastline.

Age. Middle Miocene.

Type horizon. Kesmekaya Volcanics.

Diagnosis. This wood was identified as the fossil genus *Laurinoxylon* by Güngör et al. (2019), and is re-studied here. Growth ring boundaries distinct. Vessel diffuse to semi-ring-porous. Fibres thick-walled at growth ring boundary. Vessels arranged in no specific pattern, solitary, and radial multiples of 2–3 vessels. Mean tangential diameter of vessel lumina 50–100 µm, 20–40 vessels per mm$^2$, vessel frequency decreasing in latewood (Pl. 7A, B). Axial parenchyma scanty paratracheal, diffuse, marginal (Pl. 7C, D), strand length 1–4 cells. Ray width 1–3 cells (Pl. 7E, F), 4–12 rays per mm. In tangential section, width of oil and mucilage cell same as ray width or more (Pl. 7E, F). Oil and mucilage cells associated with rays and among fibres (Pl. 7E, F). Intervessel pits alternate and small (4–7 µm). Perforation plates simple. Shape of alternate pits polygonal or circular (Pl. 8A). All rays procumbent with very large oil and mucilage cells, and body ray cells procumbent with 1 row (rarely 2 rows) of upright and/or square marginal cells and with very large oil and mucilage cells. Height of oil and mucilage cells 70–100 µm (Pls 7E, F, 9B–D). Axial parenchyma common in the wood (Pl. 8E).

Discussion. The determined wood features (e.g. diffuse or semi-ring-porous vessels, simple perforation plate, diffuse, scanty paratracheal and marginal axial parenchyma, presence of oil and/or mucilage cells in rays) suggest that the wood belongs to Lauraceae. Many fossil woods in the family Lauraceae have been described from the early Miocene of the Aegean Islands and west Anatolia (Mantzouka et al., 2016; Akkemik et al., 2019; Güngör et al., 2019).

Within the fossil genera of the family Laucraceae, *Cryptocaryoxylon* has distinctive features such as marginal or apparently marginal bands of axial parenchyma, exclusively simple perforation plates, and oil and/or mucilage cells associated with rays and sometimes between fibres (Mantzouka, 2018). Because the present wood has all these features, it is assigned to *Cryptocaryoxylon*. This wood, which was treated as *Laurinoxylon* together with other lauraceous woods by Güngör et al. (2019) was separated from other Lauraceae due to its having marginal or apparently marginal bands of axial parenchyma. The following identification key was prepared for the six fossil species of this fossil genus, based on the relevant

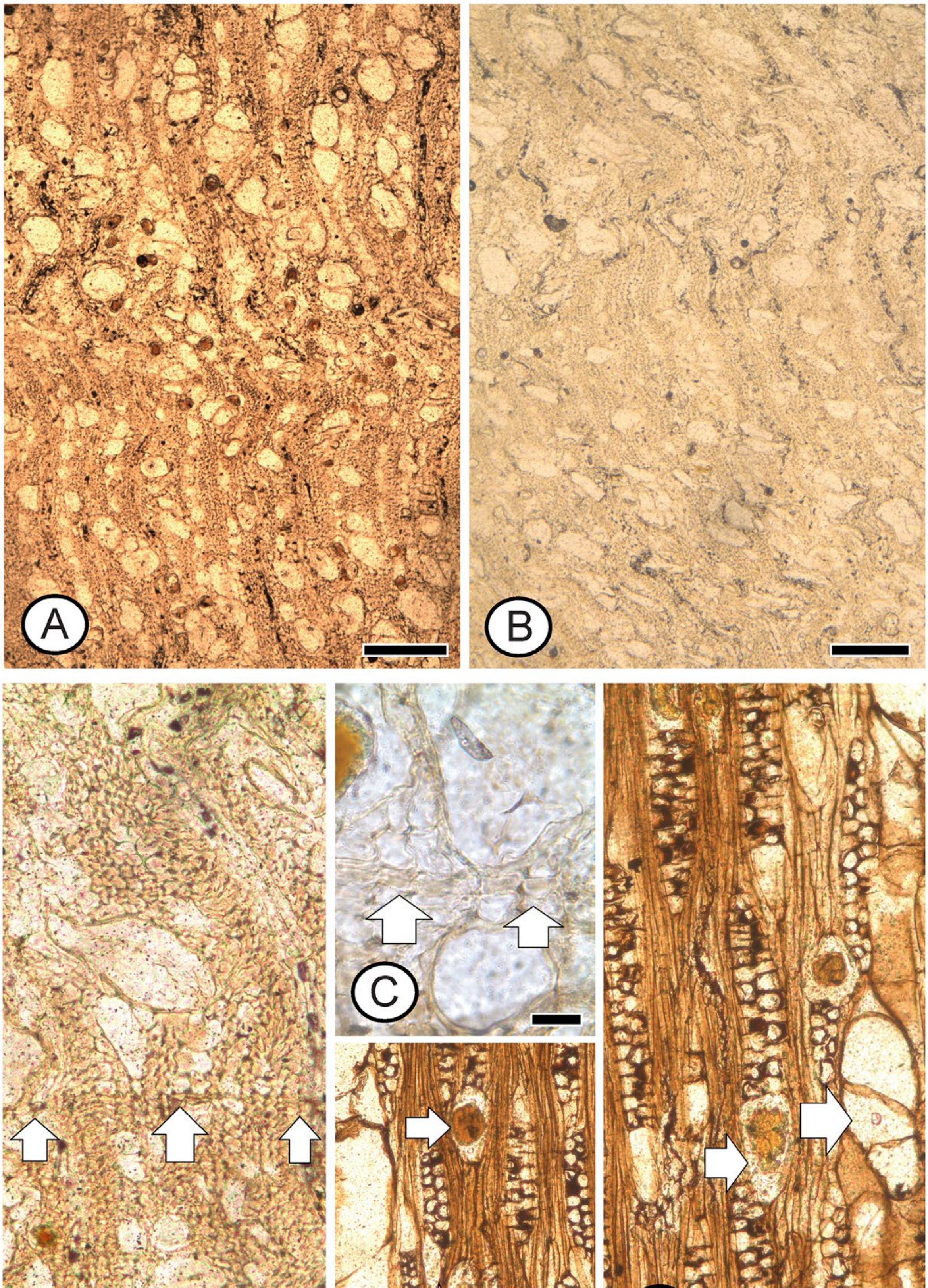


**Plate 7**. Wood anatomical features of *Cryptocaryoxylon grandoleaceum* Akkemik sp. nov. **A**, **B**. Transversal sections with diffuse to semi-ring-porous vessels, and vessels solitary and in radial multiples of 2–3 vessels; **C**, **D**. Marginal axial parenchyma cells (arrows); **E**. Large oil and/or mucilage cells among fibres (arrows) and at tips of rays; **F**. Very large oil and/or mucilage cells among fibres (arrows), and large oil and/or mucilage cells associated with rays. Scale bars 200 µm in A, B, 20 µm in C, 100 µm in D–F

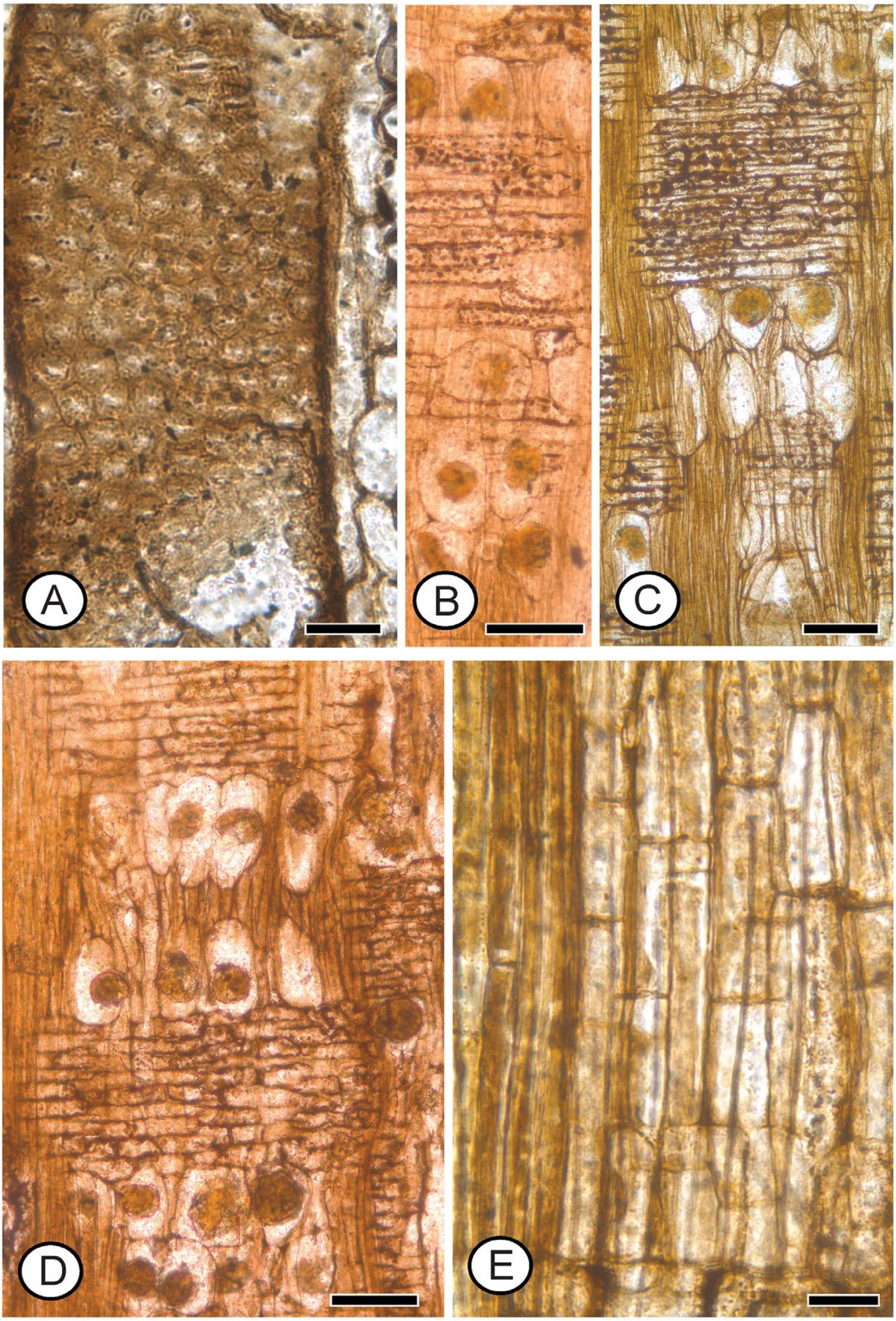


**Plate 8**. Wood anatomical features of *Cryptocaryoxylon grandoleaceum* Akkemik sp. nov. **A**. Small (4–7 µm) intervessel pits; **B**. Very large oil and/or mucilage cells inside and borders of rays; **C**, **D**. Very large oil and mucilage cells in different shapes and associated with rays; **E**. Common axial parenchyma cells in radial section. Scale bars 20 µm in A and E, 100 µm in B–D

references (Leisman, 1986; Wheeler and Manchester, 2002; Mantzouka, 2018):

1. Vessels commonly in radial multiples of 4 or more, clusters present . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

1.* Vessels diffuse and in radial multiples of 2–3 common . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

  2. Axial parenchyma scanty paratracheal, in marginal or apparently marginal bands ray width 1–3 cells; oil and/or mucilage cells associated with ray parenchyma and among fibres . . . . . . . . . . *Cryptocaryoxylon radiporosum* Wheeler and Manchester, 2002

  2.* Marginal or apparently marginal bands of axial parenchyma absent, and parenchyma vasicentric, aliform and confluent; oil and/or mucilage cells associated with ray parenchyma . . . . . . . . . . . . . *Cryptocaryoxylon hancockii* Wheeler and Manchester, 2002

3. Larger rays commonly 4–10-seriate; axial parenchyma vasicentric, aliform or marginal; oil and/or mucilage cells associated with ray parenchyma and among fibres . . . . . . . . . *Cryptocaryoxylon lemnium* Mantzouka, 2018

3.* Rays only 1–3-seriate. . . . . . . . . . . . . . . . . . . . . . . . 4

  4. Oil and/or mucilage cells only among fibres; axial parenchyma banded, bands more than three cells wide, and scanty paratracheal. . . . . . . . . . . . . . . *Cryptocaryoxylon gippslandicum* Leisman, 1986

  4.* Oil and/or mucilage cells not only among fibres but also associated with ray cells, or only associated with ray cells . . . . . . . . . . . . . . . . . . . . . . . 5

5. Rays storied; axial parenchyma scanty paratracheal and vasicentric . . . . . . . . .*Cryptocaryoxylon meeksii* Wheeler and Manchester, 2002

5.* Storied rays absent . . . . . . . . . . . . . . . . . . . . . . . . . 6

  6. Wood semi-ring to diffuse-porous; oil and mucilage cells associated with ray parenchyma and among fibres, and very large . . *Cryptocaryoxylon grandoleaceoum* Akkemik sp. nov.

  6.* Wood diffuse-porous; oil and mucilage cells associated with only ray parenchyma, and not very large. . . . . . . . . . . . . . . .*Cryptocaryoxylon lesbium* Mantzouka, 2018

Due to having rather large and long oil and/or mucilage cells associated with ray parenchyma and among fibres, and semi-ring-porous vessels, the present *Cryptocaryoxylon* specimen is considered to be a new fossil species. In *Cryptocaryoxylon lemnium* Mantzouka, 2018, the oil and mucilage cells are also large and are similar to the new species, but it differs from the new species in having aliform axial parenchyma and larger rays. Another closely similar species is *Cryptocaryoxylon lesbium* Mantzouka, 2018, which differs from the new species in having small oil and mucilage cells, diffuse-porous wood, and axial parenchyma associated only with rays. The epithet "*grandoleaceum*", which refers to the large, long oil and/or mucilage cells, was chosen for this new fossil species.

As also stated by Mantzouka (2018), the nearest modern relative of this genus is *Cryptocarya*, tribe Cryptocaryeae Nee. Species of this genus are distributed mainly in the Southern Hemisphere (Richter, 1981; Rohwer et al., 2014) and grow in tropical and subtropical conditions. The present finding underscores the co-occurrence of tropical and warm-temperate taxa in the early Miocene of western Turkey.

Order LAURALES
Juss. ex Bercht. et J. Presl, 1820

Family LAURACEAE Juss., 1789

Genus *LAURINOXYLON* Felix, 1890

Type species *Laurinoxylon diluviale* (Unger) Felix, 1883a, p. 59, pl. 2, figs 1, 3; pl. 3, fig. 1

### ***Laurinoxylon litseoides*** Süss, 1958

Pl. 9A–G

Specimen code. GOK0261 (261 in Güngör et al., 2019).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Locality. East of Eşelek village – Gökçeada, near coastline.

Age. Middle Miocene.

Horizon. Kesmekaya Volcanics.

Diagnosis. Wood diffuse-porous, growth ring boundaries clearly distinct and marked by thick-walled latewood fibres. In earlywood and latewood, vessel diameter about the same. Vessels diffuse-porous, solitary, and in radial multiples of 2–3 vessels. Mean tangential diameter of vessel lumina 50–100 µm, 20–40 vessels per mm$^2$ (Pl. 9A, B). Axial parenchyma scanty paratracheal. Intervessel pits alternate and small (4–7 µm), their shapes mostly polygonal. Ray width 1–3 cells, body ray cells procumbent with one row of upright and/or square marginal cells; 4–12 rays per mm. Oil cells commonly present, associated only with ray parenchyma (Pl. 9C–F). Septate fibres present (Pl. 9F). Perforation plates simple (Pl. 9G). Strand length of axial parenchyma 1–4 cells.

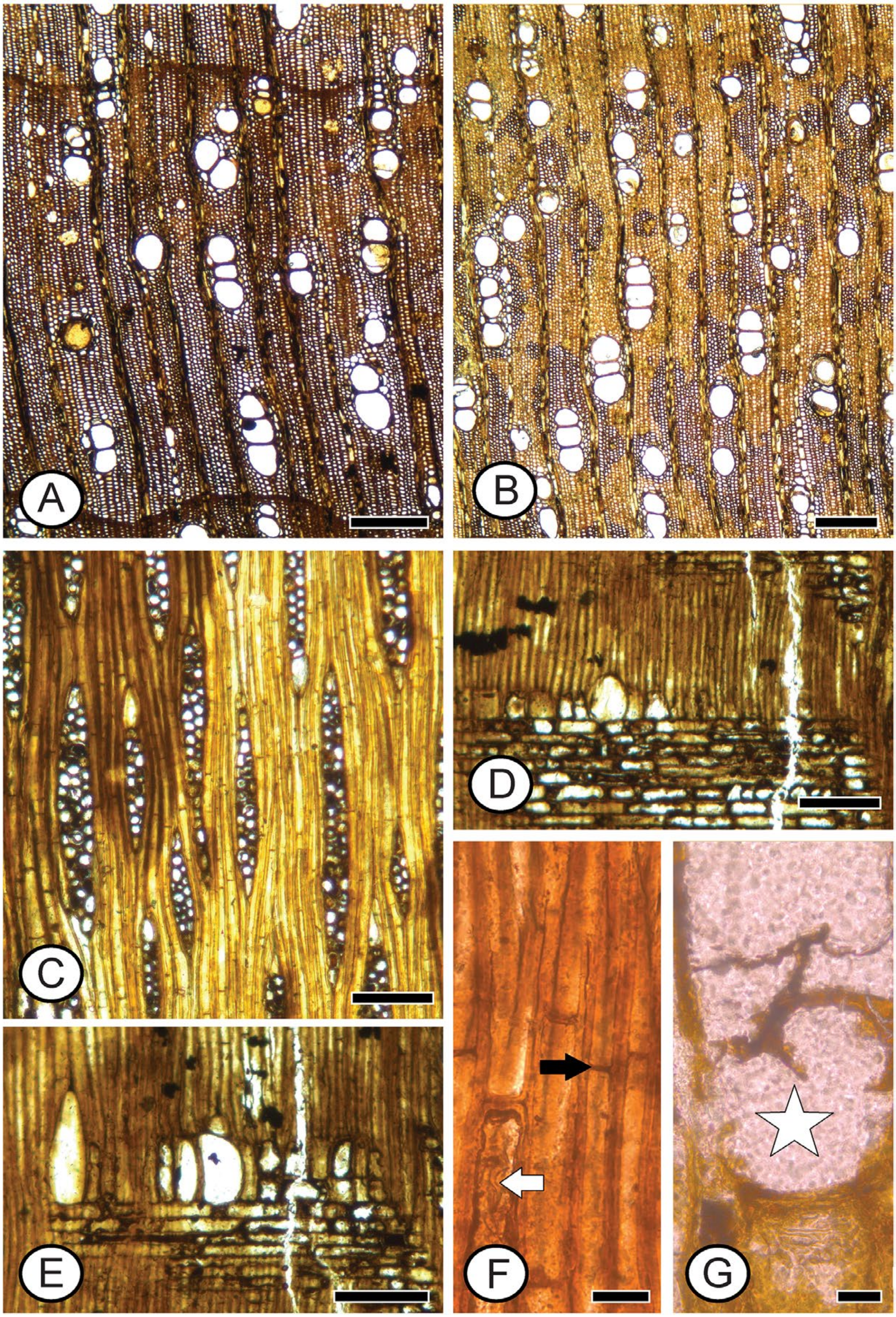


**Plate 9**. Wood anatomical features of *Laurinoxylon litseoides* Süss. **A**, **B**. Transversal section with diffuse-porous wood, growth ring boundary distinct with 1–2 rows of flattened fibres, vessels in radial multiples and solitary; **C**. Rays 1–3-seriate and oil and/or mucilage cells associated only with rays; **D**, **E**. Oil and/or mucilage cells in radial section; **F**. Axial parenchyma cells (white arrow) and septate fibres (black arrow); **G**. Simple perforation plate (star). Scale bars 200 µm in A and B, 100 µm in C–E, 20 µm in E and F

Discussion. The fossil genus *Laurinoxylon* is identified based on characteristics such as diffuse-porous wood, generally distinct growth ring boundaries, no marginal axial parenchyma, the presence of oil and/or mucilage cells, 1–3-seriate ray cells, and the diffuse, scanty paratracheal or vasicentric type of axial parenchyma (Mantzouka et al., 2016). The studied wood has all these characteristics and hence represents *Laurinoxylon*.

Akkemik et al. (2019) identified *Laurinoxylon litseoides* and *L. thomasii* Akkemik, 2019, from the early Miocene of Turkey and prepared an identification key, according to which all features of the present *Laurinoxylon* place it in *L. litseoides*.

Lauraceae leaves are also commonly described in the early Miocene of western and central Turkey (Denk et al., 2017a; Güner et al., 2017; Güner, 2019). Today only one genus and species of Lauraceae, *Laurus nobilis* L., represents the family in Turkey. There are three species in the world [*L. nobilis*, *L. azorica* (Seub.) Franco, *L. novocanariensis* Mart., Lousa, Fern., Prieto, E. Diaz, J.C. Costa and C. Aguiar]. These species grow in warm, humid and semi-humid lowland areas throughout coastal areas. The wood anatomical features of the modern *Laurus nobilis* and the new species are very similar (Tab. 4). Based on this similarity, it may be that *Laurinoxylon litseoides* represents the lineage leading to *Laurus nobilis*. In contrast, according to Süss (1958), *Laurinoxylon litseoides* Süss is similar to modern *Litsea chinensis* L. and *L. citrata* Blume. In *Litsea* species the perforation plates are generally scalariform. *Litsea citrata* has circular scalariform perforation plates (Reinders-Gouwnetak, 1948). For that reason, the fossil species appears to be more closely related to the modern *Laurus nobilis*.

LAMIALES Bromhead, 1838

Family OLEACEAE
Hoffmannsegg et Link, 1809

Genus *FRAXINOXYLON* E. Hofmann, 1952

Type species *Fraxinoxylon prambachense* E. Hofmann, 1952, p. 170, pl. 13, pl. 2

***Fraxinoxylon beypazariense*** Akkemik **sp. nov.**

Pls 10A–E, 11A–D

Holotype. Three thin sections of specimen AGU13.

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number.PFN002212.

Etymology. The epithet "*beypazariense*" refers to the origin of the sample. Beypazarı city has many fossil sites. This fossil genus has not previously been reported from Turkey.

Type locality. Near Aşağıgüney village, Beypazarı, Ankara.

Age. Early Miocene.

**Table 4**. Comparison of modern *Laurus nobilis* L. and its possible ancestor *Laurinoxylon litseoides* Süss

| Features | *Laurus nobilis* L. (Akkemik and Yaman, 2012) | *Laurinoxylon litseoides* Süss (Süss, 1958) |
|---|---|---|
| Growth rings | Growth ring boundaries distinct, marked by thick-walled latewood fibres | Growth ring boundaries distinct, marked by thick-walled latewood fibres |
| Vessels | Wood diffuse-porous. Vessels solitary, and radial multiples of 2–3 vessels. Perforation plates mostly simple and rarely scalariform. Intervessel pits alternate, small (4–7 µm). Shape of alternate pits polygonal. Mean tangential diameter of vessel lumina 50–100 µm, 20–40 vessels per mm$^2$ | Wood diffuse-porous. Vessels solitary, and radial multiples of 2–3 vessels. Perforation plates predominantly simple Intervessel pits alternate, small (4–7 µm). Shape of alternate pits polygonal. Mean tangential diameter of vessel lumina 50–100 µm, 20–40 vessels per mm$^2$ |
| Tracheids and fibres | Fibres mostly non-septate, rarely septate | Fibres sometimes septate |
| Axial parenchyma | Axial parenchyma scanty paratracheal, strand length 1–4 cells | Axial parenchyma scanty paratracheal, strand length 1–4 cells |
| Rays | Ray width 1–4 cells. Body ray cells procumbent with one row of upright and/or square marginal cells. 4–12 rays per mm | Ray width 1–3 cells. Body ray cells procumbent with one row of upright and/or square marginal cells. 4–12 rays per mm |
| Secretory elements and cambial variants | Oil cells present. Oil cells associated with ray parenchyma | Oil cells associated with ray parenchyma |

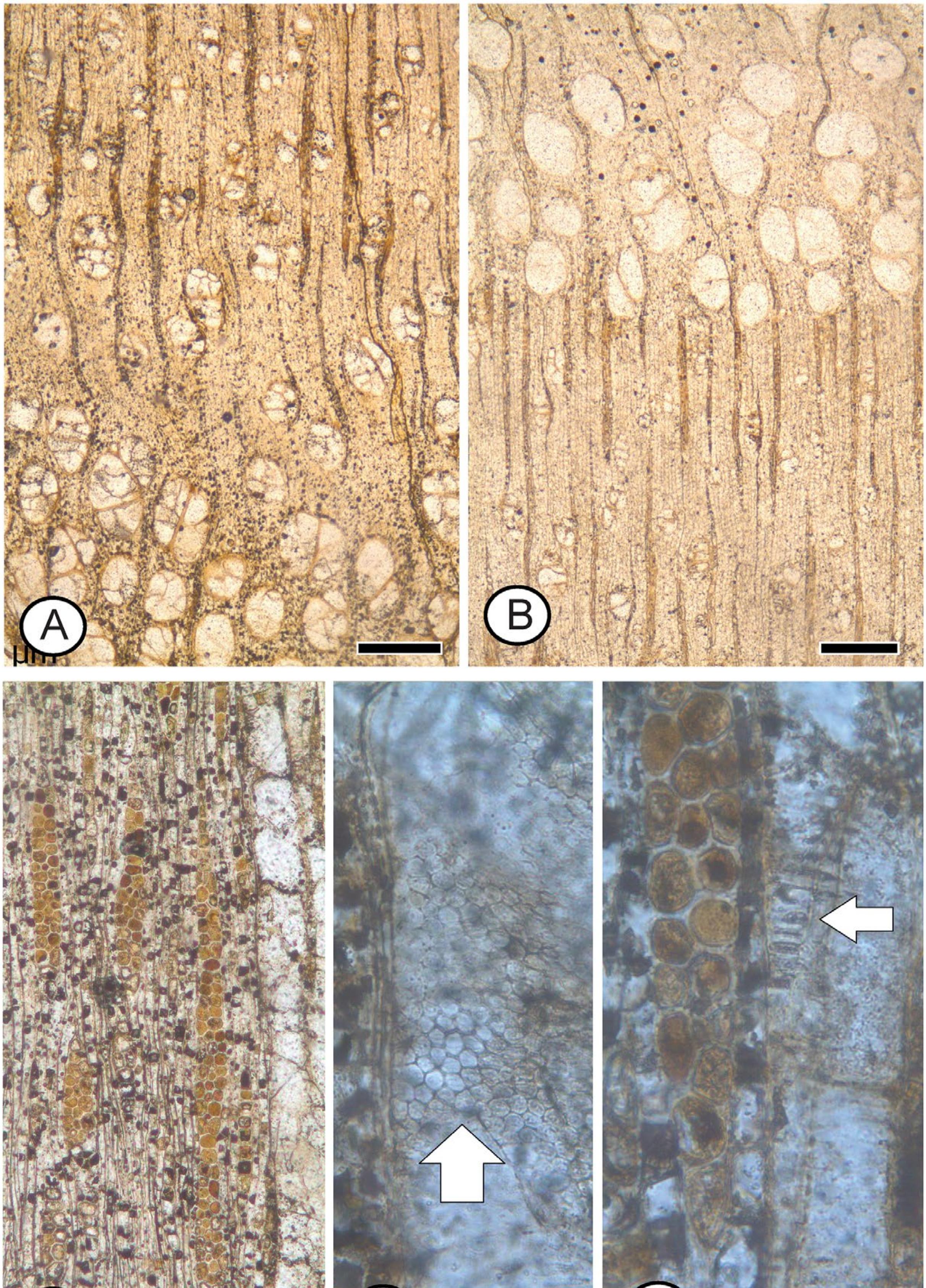


**Plate 10**. Wood anatomical features of *Fraxinoxylon beypazariense* Akkemik sp. nov. **A**, **B**. Transversal sections with ring-porous wood; **C**. Tangential section with 1–3-seriate rays; **D**. Intervessel pits alternate (arrow); **E**. Scalariform pits (arrow). Scale bars 200 µm in A and B, 100 µm in C, and 20 µm in D and E

Type horizon. Hançili Formation.

Diagnosis. Growth ring boundaries distinct, wood ring-porous. Earlywood vessels wide, tyloses common. Vessels in latewood narrower. Vessels solitary and in radial multiples of up to three vessels in earlywood, vessel clusters common in latewood (Pl. 10A, B). Earlywood vessels sometimes in dendritic pattern. Tangential and radial diameter of vessel lumina 69 (26–116) µm and 90 (33–130) µm in earlywood, 27 (13–46) 50 µm and 24 (11–52) µm in latewood. Vessel density 83 (67–104) per mm$^2$, with 26 (23–32) vessels per mm$^2$ in earlywood and 57 (44–72) vessels per mm$^2$ in latewood (Acarca Bayam et al., 2018). Paratracheal axial parenchyma almost lozenge-aliform, especially in latewood. 1–4 rows of marginal banded axial parenchyma present (Pl. 10A, B). Rays 1–2 (–3)-seriate, ≥12 per mm. Ray height 8–25 (–52) cells (Pls 10C, 11A). Intervessel pits alternate, small (4–7 µm), sometimes scalariform (Pl. 10D, E). Axial parenchyma in longitudinal section common, fibres thin- to thick-walled (Pl. 11B). Perforation plates simple (Pl. 11C). Rays mainly heterocellular, body ray cells procumbent with 1–4 rows of upright and square marginal cells, sometimes homocellular with only procumbent body ray cells (Pl. 11D).

Discussion. Due to its ring-porous wood, wide earlywood vessels and narrow latewood vessels in clusters, simple perforation plate, rays 1–2(–3)-seriate, and the presence of paratracheal axial parenchyma almost lozenge-aliform, this wood can be placed within *Fraxinoxylon*. Süss (2005) used *Ornoxylon* for this type of wood and described two fossil species, but *Fraxinoxylon* has been used more commonly (Iamandei et al., 2011; Wheeler and Dillhof, 2009; Koutecký et al., 2019). The following identification key including the new species was prepared based on the distinctive features of the fossil species of both *Ornoxylon* and *Fraxinoxylon* described by Andreanszky (1952), Müller-Stoll (1954), Prakash and Barghoorn (1961), Suzuki (1982), Suzuki and Watari (1994), Süss (2005), Iamandei and Iamandei (2008), Iamandei et al. (2011), Wheeler and Dillhof (2009) and Koutecký et al. (2019):

1. Body ray cells procumbent with 1–4 rows of square marginal cells (rays heterocellular) . . . . . . . . . . . 2
1.* All rays procumbent (rays homocellular) . . . . . . . . 7
2. Oil and mucilage cells present . . . . . . . . . . . . . . *Fraxinoxylon* cf. *americana* Andreánszky, 1951
2.* Oil and mucilage cells absent . . . . . . . . . . . . . . 3
3. Perforation plate simple . . . . . . . . . . . . . . . . . . . . . 4
3.* Perforation plate scalariform; terminal banded axial parenchyma up to 8 cells . . . . . . . . . . . . . . . . . . . . *Fraxinoxylon aff. F. komlosense* Greguss, 1969
4. Larger rays 4–10-seriate . . . . . . . . . . . *Ornoxylon grandiporosum* Süss, 2005
4.* Rays 1–3-seriate . . . . . . . . . . . . . . . . . . . . . . . . . 5
5. Vessel diffuse or semi-ring-porous; rays storied; marginal axial parenchyma absent . . . . . . . . . . . . . *Fraxinus washingtoniana* (Prakash and Barghoorn, 1961) Wheeler and Dillhoff, 2009
5.* Wood ring-porous; rays not storied; one or 2–3 rows of marginal banded cells of axial parenchyma present . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
6. Vessels large, mainly solitary, radial/tangential diameter 120–300/170–390 µm (unknown in original description); one row of marginal banded axial parenchyma present (banded axial parenchyma unknown in original description); rays slightly heterocellular, one row of marginal square cells present . . . . . . . . . . . . . . . . . . . . . . . *Fraxinoxylon prambachense* Hofmann, 1952
6.* Vessels small, mainly in groups, radial/tangential diameter 26–116/33–130 µm; vessel frequency 20–40 cells per mm$^2$ in earlywood; 1–4 rows of marginal banded axial parenchyma present, axial parenchyma diffuse, vasicentric and lozenge-aliform; rays clearly heterocellular, 1–4 rows of marginal square cells present . . . . . . . . . . . *Fraxinoxylon beypazariense* Akkemik sp. nov.
7. Aliform axial parenchyma present . . . . . . . . . . . . . . . . . . . . . . . *Fraxinoxylon gothani* Müller-Stoll, 1954
7.* Aliform axial parenchyma absent. . . . . . . . . . . . . . 8
8. Marginal axial parenchyma present. . . . . . . . . . . . . . . . . . . . . *Fraxinus oligocenica* Suzuki, 1982
8.* Marginal axial parenchyma absent. . . . . . . . . . 9
9. Confluent axial parenchyma present . . . . . . . . . . . . . . . . . *Fraxinus notoensis* Suzuki and Watari, 1994
9.* Confluent axial parenchyma absent . . . . . . . . . . . 10
10. Axial parenchyma scanty paratracheal and vasicentric; tyloses common . . . . . . . . *Fraxinus macropunctatum* Wheeler and Dillhoff, 2009
10.* Axial parenchyma vasicentric . . . . . . . . . . . 11
11. Vessel diameter 100–200 µm . . . . . . . . . . . . . . . . *Fraxinoxylon crisii* Iamandei and Iamandei, 2008
11.* Vessel diameter >200 µm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ornoxylon mikófalvense* Süss, 2005

The present wood differs from all other similar fossil species, due to its combination of smaller vessels, heterocellular rays, simple perforation plates, 1–2(–3)-seriate rays, lozenge-aliform axial parenchyma cells and 1–4 rows of marginal banded axial parenchyma. Therefore, the present *Fraxinoxylon* specimen is described as a new fossil species, *Fraxinoxylon beypazariense* Akkemik sp. nov.; this is the first record of *Fraxinoxylon* for Turkey.

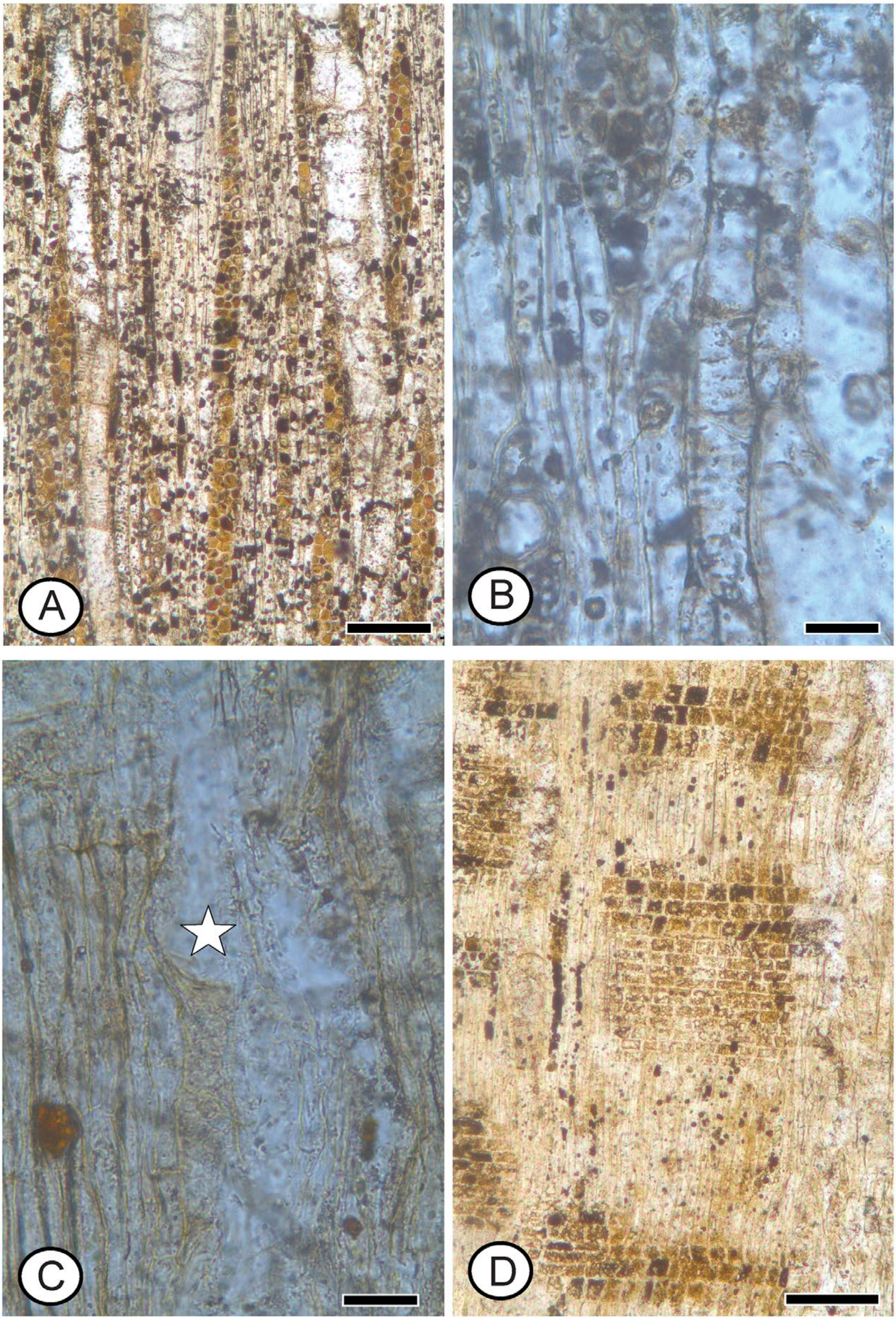


**Plate 11**. Wood anatomical features of *Fraxinoxylon beypazariense* Akkemik sp. nov. **A**. Tangential section with 1–3-seriate rays; **B**. Axial parenchyma cells; **C**. Simple perforation plate (star); **D**. Radial section with heterocellular rays. Scale bars 100 µm in A and D, 20 µm in B and C

Today there are 43 species of *Fraxinus* L. in the world (Wallander, 2008), and four of them grow in Turkey. Erşen Bak and Merev (2016) suggested that the wood anatomical features of those four species (*Fraxinus angustifolia* Vahl.*, F. excelsior* L.*, F. ornus* L., *F. palliasii* Willmott) are very similar; they treated the wood anatomical features together. Schweingruber (1990) also showed that the wood anatomical features of the three modern species in Europe and around the Mediterranean are highly similar. Moreover, Iamandei et al. (2005) stated that modern *Fraxinus excelsior* and *F. ornus* are rather similar and that distinguishing them based on wood anatomy is difficult. Comparing fossil and modern species in Europe and Turkey showed that the main characteristics (ring porosity, presence of confluent, diffuse and vasicentric axial parenchyma, 1–3 rows of rays) are highly consistent, but that ray height is greater and that heterocellular rays are more common in the fossil species.

PROTEALES
Juss. ex Bercht.
et Jan Svatopluk Presl, 1820

Family PLATANACEAE T. Lestib., 1826

Genus *PLATANOXYLON* E. Hofmann, 1952

Type species *Platanoxylon* sp.
E. Hofmann, 1952, p. 137, text fig. 3

***Platanoxylon catenatum***
Süss et Müller-Stoll, 1977
Pl. 12A–F

Specimen code. GOK0258 (258 in Güngör et al., 2019).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Locality. East of Eşelek village – Gökçeada, near coastline.

Age. Middle Miocene.

Horizon. Kesmekaya Volcanics.

Diagnosis. Growth ring boundary distinct, marked by distended rays and by thick-walled and radially flattened latewood fibres. Wood diffuse-porous, vessels arranged in no specific pattern, generally solitary and rarely in radial multiples. Shape of solitary vessel outline angular. Vessel diameter 50–100 µm. Vessel frequency 40–100 per mm$^2$. Axial parenchyma diffuse-in-aggregate and scanty paratracheal (Pl. 12A). Rays distended at growth ring boundaries (Pl. 12A), mostly multiseriate, larger rays commonly both 4–10-seriate and >10-seriate. Ray height generally more than 1 mm. Prismatic crystals common in procumbent ray cells (Pl. 12B). All ray cells procumbent (homocellular) (Pl. 12C). Perforation plates both simple and scalariform. Scalariform perforation plates mostly with 10–30 bars (Pl. 12D, E). Intervessel pits opposite and scalariform (Pl. 12F).

Discussion. According to the identification key of Akkemik et al. (2019), the features of this specimen place it within *Platanoxylon cetanatum* Süss and Müller-Stoll, 1977. The characteristics [e.g. vessels exclusively solitary (90% or more) or vessel cluster common, intervessel pits scalariform and opposite; axial parenchyma diffuse and diffuse-in-aggregate] are typical descriptive features of *P. cetanatum*. Today, *Platanus orientalis* L., one of the typical elements of riparian vegetation, has a wide distribution, occurring in Southeastern Europe and across the Middle East and Western Asia. The present assessment shows that this fossil species is closely similar to the modern species *Platanus orientalis* except for one difference: bar number is up to 20 in the extant species but up to 30 in the fossil species (Tab. 5). This similarity suggests that *Platanoxylon cetanatum* may represent the lineage leading to the modern *Platanus orientalis*. *Platanoxylon cetanatum* has been reported from different regions (Süss and Müller-Stoll, 1977; Iamandei and Iamandei, 1999; Akkemik et al., 2019) and had a wide distribution area during the Miocene.

Order ROSALES Bercht.
et J. Presl, 1820

Family ROSACEAE Jussieu, 1789

Genus *PRUNOIDOXYLON* Dupéron, 1975

Type species *Prunoidoxylon multiporosum*
Dupéron, 1975S, p. 67–75, Abb. 19–21, Taf. 9,
Figs 1–4, Taf. 10, Figs 1–4

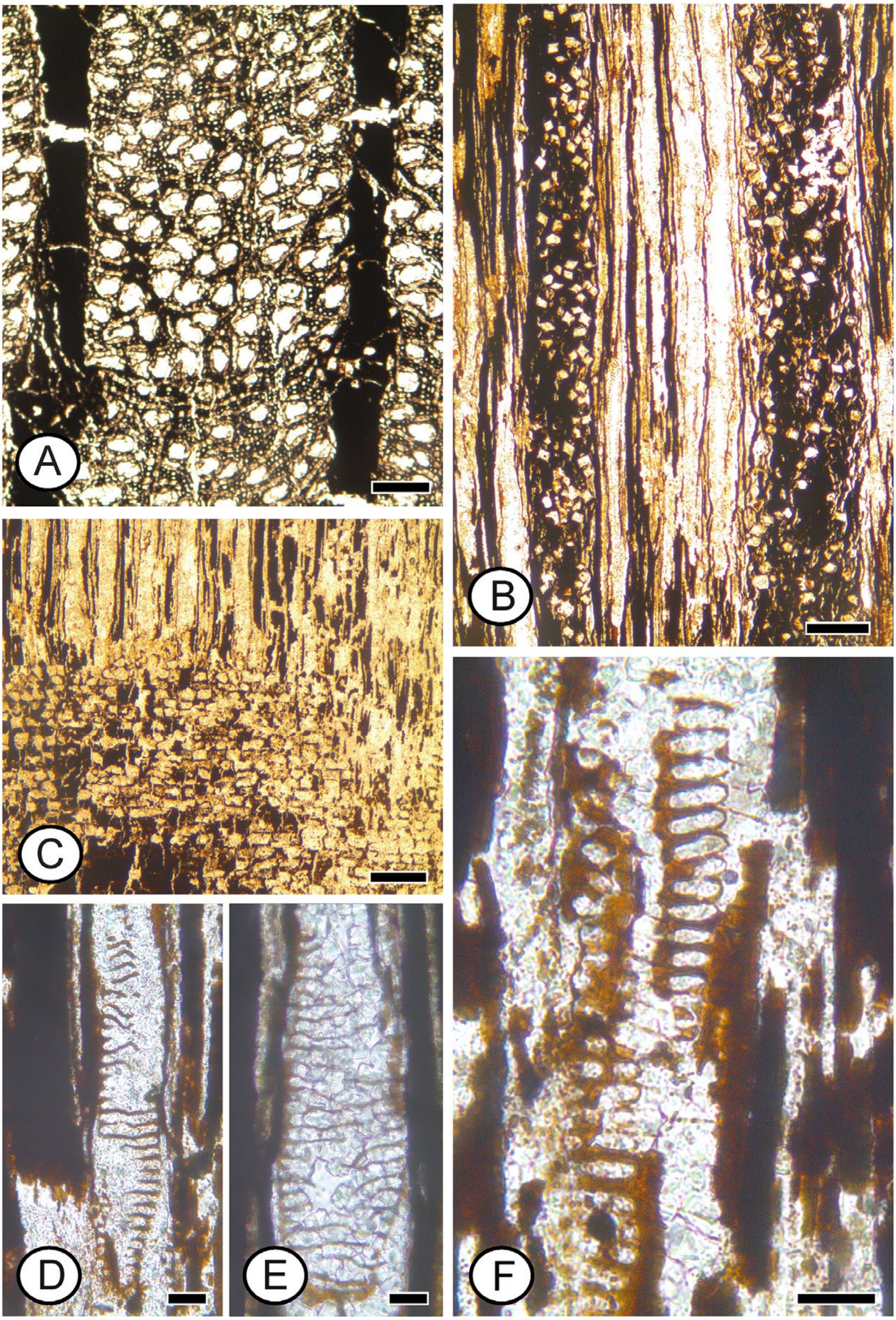


**Plate 12**. Wood anatomical features of *Platanoxylon cetanatum* Süss et Müller-Stoll. **A**. Transversal section with large and distended rays and diffuse-porous wood, growth ring boundary distinct; **B**. Large and long rays in tangential section; **C**. Radial section with homocellular rays; **D**, **E**. Scalariform perforation plates; **F**. Scalariform intervessel pits. Scale bars 200 µm in A–C, 20 µm in D–F

**Table 5**. Comparison of modern *Platanus orientalis* L. and its possible ancestor *Platanoxylon cetanatum* Süss et Müller-Stoll

| Features | *Platanus orientalis* L. (Akkemik and Yaman, 2012; Schweingruber, 1990) | *Platanoxylon catenatum* Süss et Müller-Stoll (Iamandei and Iamandei, 1999) |
|---|---|---|
| Growth rings | Growth rings distinct, marked by distended rays and by thick-walled and radially flattened latewood fibres at the boundary | This feature is the same as in modern species |
| Vessels | Wood diffuse-porous. Vessels solitary, in tangential or radial multiples, or in clusters of 2–7. Shape of solitary vessel outline angular. Perforation plates both simple and scalariform in oblique end walls. Scalariform perforation plates both with ≤10 bars and with 10–20 bars. Intervessel pits opposite and small, 4–7 µm. Vessel-ray pits with distinct borders; similar to intervessel pits in size and shape throughout the ray cell. Vessel diameter 50–100 µm. Vessel frequency 40–100 | Bar number 10–20 (–30). Other vessel features are similar |
| Axial parenchyma | Axial parenchyma diffuse-in-aggregate and scanty paratracheal. 2–5 cells per parenchyma strand | Axial parenchyma diffuse-in-aggregate and scanty paratracheal |
| Rays | All ray cells procumbent (homocellular). Rays distended at growth ring boundaries. Rays mostly multiseriate, larger rays commonly both 4–10-seriate and >10-seriate. Rays 4–12/mm. Ray height >1 mm | This feature is the same as in modern species |
| Prismatic crystals | Present | Present |

***Prunoidoxylon prunoides*** Akkemik **sp. nov.**

Pls 13A–E, 14A–E

Holotype. Three thin sections of specimen MEN31. This fossil wood was identified as *Prunus* L. by Acarca Bayam et al. (2018).

Repository. Department of Forest Botany, Faculty of Forestry-Cerrahpasa, Istanbul University, Istanbul, Turkey.

Plant fossil registry number. PFN002213.

Etymology. The epithet "*prunoides*" refers to the wood of the holotype, which has typical features of the genus *Prunus* L.

Type locality. Mençeler Plateau, Beypazarı city, Ankara Province.

Age. Early Miocene.

Type horizon. Hançili Formation.

Diagnosis. Wood ring-porous with distinct growth ring boundaries. Tangential and radial diameter of vessels 55 (32–75) µm and 82 (33–136) µm in earlywood, 22 (8–43) µm and 30 (15–50) µm in latewood (Acarca Bayam et al., 2018). Vessels generally solitary, rarely in groups of 2–3 cells. Vessel frequency 40–100 per mm$^2$ (Pl. 13A, B). Axial parenchyma present, scanty paratracheal, in marginal or apparently marginal bands (Pl. 13C). Rays of two distinct sizes, as 1–2 rows and 4–10 rows. Larger rays generally wide, 7 (5–8) cells wide, longer rays more than 1 mm high, narrow rays uniseriate (very rarely biseriate). Number of rays 4–12 per mm (Acarca Bayam et al., 2018) (Pl. 13D, E). Rays heterocellular with procumbent body ray cells and one or more rows of upright and/or square marginal cells (Pl. 14A, C, E). Perforation plates simple (Pl. 14B). Prismatic crystals present in rays (Pl. 14C). Intervessel pits alternate (Pl. 14D) or rarely slightly opposite.

Discussion. The characteristics [e.g. semi-ring-porous, wider rays (up to 8 cells), heterocellular rays, simple perforation plate, more than 1 mm of longer rays] are typical features of *Prunoidoxlon*. Based on these features, this wood is assigned to *Prunoidoxylon.* Recently Akkemik et al. (2019) described a new fossil species of *Prunoidoxylon* and prepared an identification key (see Akkemik et al., 2019). This identification key is updated as follows:

1. Vessels exclusively solitary (90% or more). . . . . . . 2

1.* Vessels not exclusively solitary (not 90% or more); vessels solitary or in radial multiples of 2–3 and 4 or more . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

 2. Prismatic crystals present; axial parenchyma diffuse. . . . . . . . . . . . . . . . . . . . . . *Prunus iwatense* Takahashi et Suzuki, 1988

 2.* Prismatic crystals absent; axial parenchyma diffuse and diffuse-in-aggregate . . . . *Prunoidoxylon eocenicum* Wheeler et London, 1992

3. Axial parenchyma present, scanty paratracheal, in marginal or in apparently marginal bands . . . . . . 4

3.* Axial parenchyma absent or extremely rare; if present diffuse . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

 4. Body ray cells procumbent with one row of upright and/or square marginal cells; vessels in radial multiples of 4 or more common. . . . . . . . . . . . *Prunus rodgersae* Wheeler and Dillhoff, 2009

 4.* Body ray cells mostly procumbent with 1–4 or more rows of upright and/or square marginal cells; ray cells mostly irregular in shape; vessels mostly solitary or in radial multiples of 2–3, rarely to 4 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

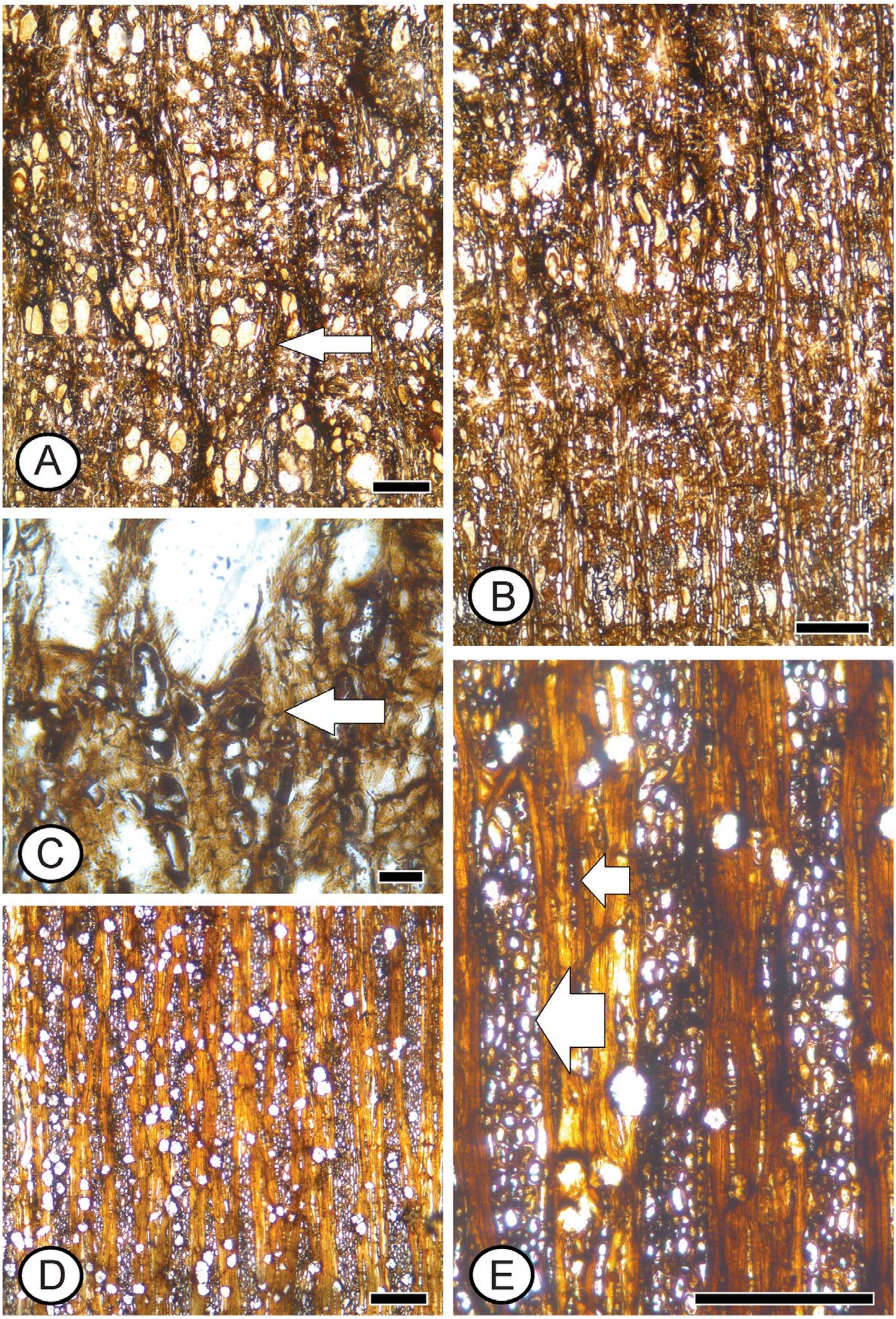


**Plate 13**. Wood anatomical features of *Prunoidoxylon prunoides* Akkemik sp. nov. **A**, **B**. Transversal sections with ring-porous wood, and distinct growth ring (arrow); **C**. Marginal axial parenchyma in annual ring boundary (arrow); **D**. Large and long rays; **E**. Two distinct sizes of rays, narrow (small arrow) and wider ones (big arrow). Scale bars 200 μm in A, B, D and E, 20 μm in C

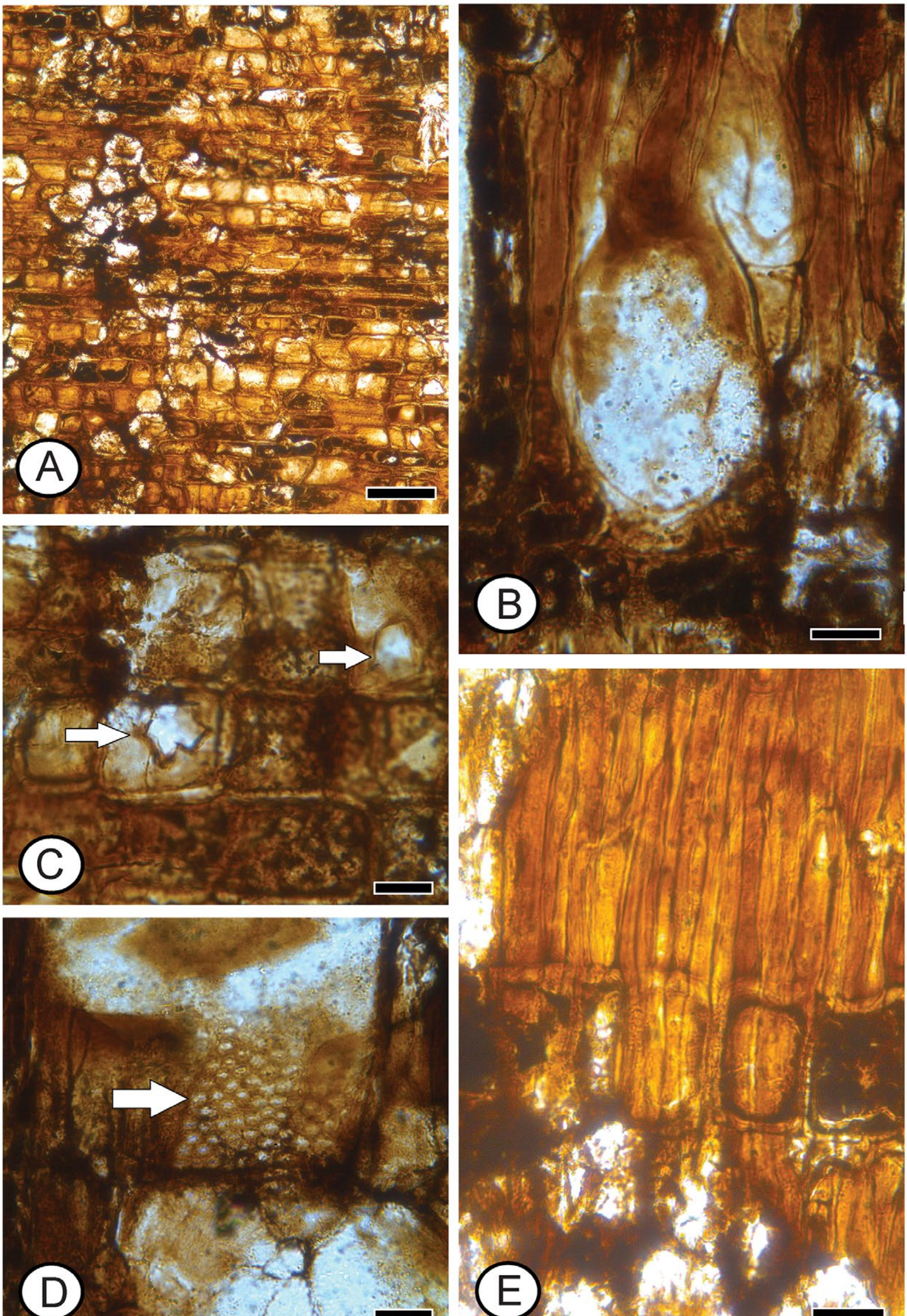


**Plate 14**. Wood anatomical features of *Prunoidoxylon prunoides* Akkemik sp. nov. **A**. Heterocellular ray; **B**. Simple perforation plate; **C**. Crystals in ray cell (arrows); **D**. Alternate intervessel pits (arrow); **E**. Heterocellular rays. Scale bars 100 μm in A, 20 μm in B–E

5. Wood diffuse to semi-ring-porous; rays narrower (4–5 cells wide) and shorter in general (sometimes longer than 1 mm) . . . . . . . . *Prunoidoxylon aytugii* Akkemik, 2019

5.* Wood clearly ring-porous; rays wider (generally 6–7 cells wide and much longer (all larger rays longer than 1 mm) and clearly of two distinct sizes. . . . . . . . . . . . *Prunoidoxylon prunoides* Akkemik sp. nov.

6. Normal axial canals present . . . . . . . . . . . . . . . 7

6.* Axial canals absent. . . . . . . . . . . . . . . . . . . . . . . 8

7. Growth ring boundaries distinct; wood diffuse-porous . . . . . . . . . . . . . . *Prunus gummosa* Wheeler, Scott et Barghoorn, 1978

7.* Growth ring boundaries indistinct or absent; vessels in diagonal and/or radial pattern . . . . .*Prunus wadiai* Guleria, Thankar, Virdi et R.N.Lakh., 1983

8. Rays homocellular with all ray cells procumbent . . . . . .*Prunus barneti* Wheeler et Dillhoff, 2009

8.* Rays heterocellular; body ray cells procumbent with one or more upright or square ray cells . . 9

9. Prismatic crystals present in ray cells . . . . . . . . . . . . . . . . . . . *Prunus ascendentiporulosa* Suzuki, 1984

9.* Prismatic crystals absent . . . . . . . . . . . . . . . . . . . .10

10. Wood semi-ring-porous or diffuse-porous . . 11

10.* Wood diffuse-porous; vessels in radial multiples of 4 or more common . . . . . . . . . . . . . 12

11. Vascular and vasicentric tracheids present. . . . . . . . . . *Prunoidoxylon multiporosum* Dupéron, 1976

11.* Vascular and vasicentric tracheids absent . . . . . . . . . . . . . . . *Prunus palaeozippeliana* Suzuki, 1984

12. Tylosis absent . . . . . . . . . *Prunus polyporulosa* Suzuki, 1984

12.* Tylosis common. . . . . . . . . *Prunus uviporulosa* Suzuki, 1984

Based on the differences given in the identification key, this wood is designated as a new species, *Prunoidoxylon prunoides* Akkemik sp. nov. The new fossil species is similar to *Prunus rodgersae* and *Prunoidoxylon aytugii*. *Prunus rodgersae* differs from the new fossil species in having body ray cells procumbent with only one row of upright and/or square marginal cells, and vessels in radial multiples of 4 or more common. *Prunoidoxylon aytugii* differs from the new fossil species in having diffuse to semi-ring- or ring-porous wood, narrower and shorter rays. Schweingruber (1990) and Akkemik and Yaman (2012) investigated the wood anatomical characteristics of some modern *Prunus* species and showed that the wood has a distinct growth ring boundary, the wood is semi-ring to ring-porous, vessels are solitary and in radial multiples of 2–3 or more, with a simple perforation plate, and the rays are 1–7 cells wide, heterocellular, and longer than 1 mm. All these features are typical of the modern subfamily Prunoidae in the Rosaceae (Schweingruber, 1990; Akkemik and Yaman, 2012); therefore, the epithet "*prunoides*" was preferred for the new species.

Order MALPIGHIALES C. Martius, 1835

Family SALICACEAE Mirb., 1815

Genus *POPULOXYLON* Mädel-Angeliewa, 1968

Type species *Populoxylon priscum* Mädel-Angeliewa, 1968, Geol. Jahrb., 86: 454

### ***Populoxylon sebenense*** Akkemik **sp. nov.**

Pl. 15A–I

Holotype. Three thin sections of specimen HOC567.

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number. PFN002214.

Etymology. The epithet "*sebenense*" refers to the city of Seben, the type locality of the new fossil species.

Type locality. Fossil site in Hoçaş village, Seben city, Bolu.

Age. Early Miocene.

Type horizon. Hançili Formation.

Diagnosis. Growth ring boundaries distinct, with 1 (–2) rows of flattened axial parenchyma cells. Wood diffuse-porous, vessels mostly in short radial multiples of 2–4 (–6) cells, and solitary. Solitary vessels circular in general, vessel cells in radial multiples, tangentially flattened, some vessel cells triangular at tips of radial multiples. Mean vessel tangential diameter 50–100 µm, vessel frequency 40–100 per mm$^2$ (Pl. 15A, B). Axial parenchyma diffuse, in 1 (–2) rows of marginal bands (Pl. 15B, C). Rays exclusively uniseriate, 5–20 (–35) cells high. 4–12 rays per mm (Pl. 15D, E); 2–4 cells per parenchyma strand (Pl. 15E). Perforation plates simple (Pl. 15F). Vessel-ray pits simple, large, slightly honeycomb-like (Pl. 15G). Vascular and vasicentric tracheids absent, septate fibres present, axial parenchyma common (Pl. 15H). Rays homocellular; all ray cells procumbent (Pl. 15I).

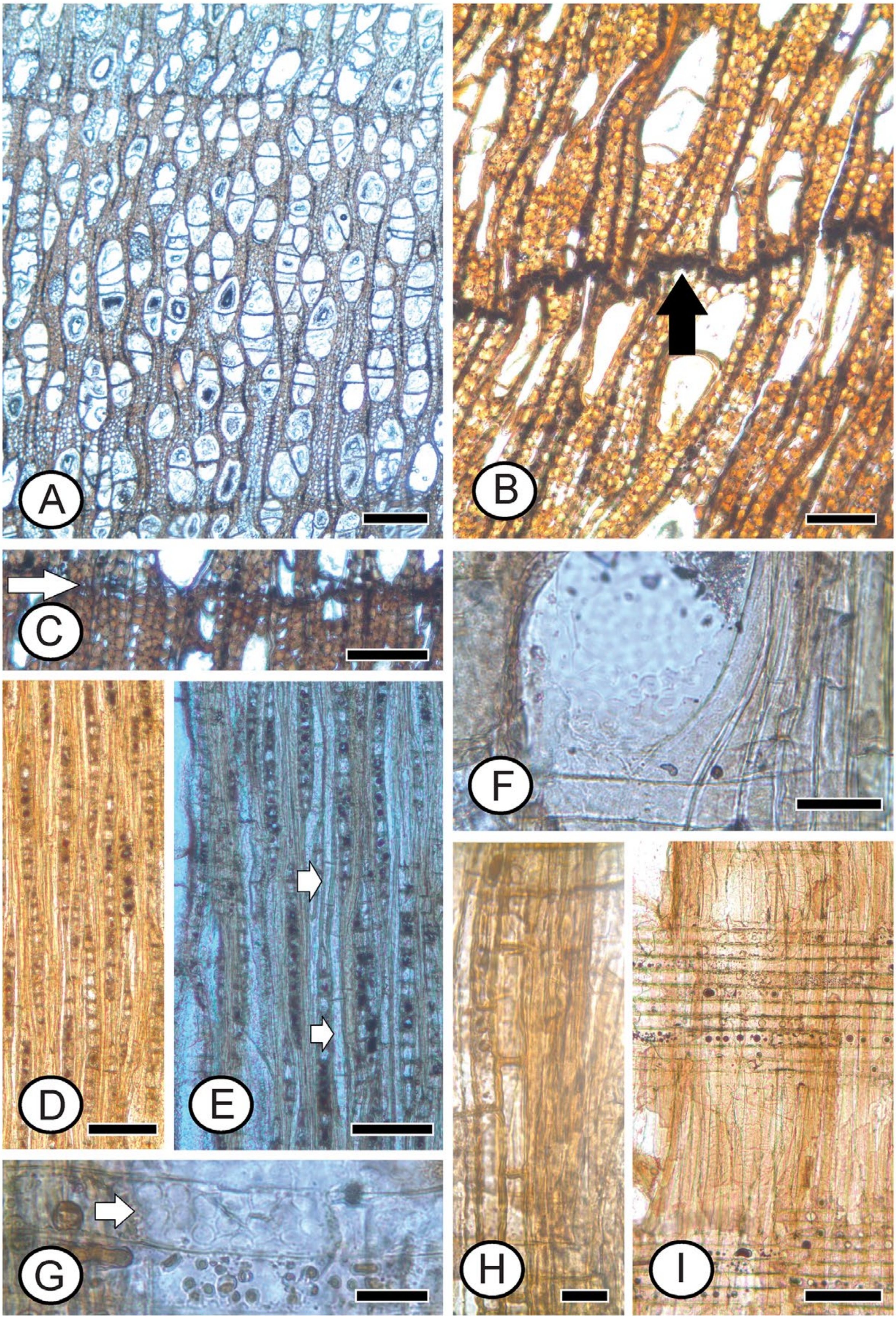


**Plate 15**. Wood anatomical features of *Populoxylon sebenense* Akkemik sp. nov. **A**. Transversal section with diffuse-porous wood, growth ring boundary distinct, vessels predominantly in radial multiples; **B**, **C**. One row of marginal axial parenchyma common in growth ring boundary (arrow); **D**, **E**. Rays predominantly uniseriate, and axial parenchyma strands (arrows); **F**. Simple perforation plate; **G**. Honeycomb-like vessel-ray pits (arrow); **H**. Axial parenchyma cells; **I**. Homocellular rays. Scale bars 200 µm in A and B, 100 µm in C–F and I, 20 µm in G and H

Discussion. The characteristics (distinct growth ring boundary, diffuse-porous wood, vessels predominantly in radial multiples of 2–3, vessel diameter 50–100 µm, 40–100 vessels per mm$^2$, uniseriate and homocellular rays) are typical features of *Populoxylon*. Several species of the fossil genus have been identified: *Populoxylon priamurensis* Blokhiana and Snezhkova, 2003 (Blokhiana and Snezhkova, 2003), *Populuxylon priscum* Mädel-Angeliewa, 1968 (Mädel-Angeliewa, 1968), *Populoxylon* (cf. *Populus alba* L.) (Iamandei et al., 2005), *Populoxylon tremuloides* Iamandei and Iamandei (Iamandei and Iamandei, 2005) and *Populus soyaensis* Terada and Suzuki, 2010 (Choi et al., 2010). An identification key was prepared for all these species and the new specimen:

1. Scanty paratracheal parenchyma present together with diffuse and marginal axial parenchyma; marginal axial parenchyma common, growth ring delineated by 1 (–2) layer(s) of marginal axial parenchyma at end of growth rings ..... *Populoxylon sebenense* Akkemik sp. nov.

1.* Scanty paratraheal parenchyma absent, axial parenchyma extremely rare .................. 2

2. Marginal axial parenchyma present, not common ................................ 3

2.* Marginal axial parenchyma absent; axial parenchyma absent or extremely rare ............ 5

3. Growth ring delineated by 5–6 layers of radially flattened fibres at end of growth rings, vessel radial diameter more than 100 µm; vessel density 60–70 pores per mm$^2$, ray height 5–9 (4–18) cells, partly biseriate rays present ...........*Populoxylon* sp. cf. *Populus alba* L.

3.* Growth ring delineated by 1–2 rows of flattened fibres ..................................... 4

4. Triangular vessels absent; rays exclusively uniseriate .................... *Populus soyaensis* Terada and Suzuki, 2010

4.* Vessels present in clusters, and end vessels in clusters are triangular in shape; rays uniseriate, rarely biseriate ....... *Populoxylon tremuloides* Iamandei and Iamandei, 2005

5. Vessel density lower, 20–100 vessels per mm$^2$ in general, sometimes more...................... *Populoxylon priamurensis* Blokhiana and Snezhkova, 2003

5.* Vessel density higher, more than 100 vessels per mm$^2$ .................... *Populoxylon priscum* Mädel-Angeliewa, 1968

According to the identification key, axial parenchyma is one of the most important distinctive features. Due to having common marginal and diffuse axial parenchyma and sometimes scanty axial parenchyma, the present wood differs from all previously described species. For this reason, it is described as a new species. In macro- and microfossil studies, leaf imprints (Güner et al., 2017) and pollen (Yavuz-Işık, 2008) of *Populus* have been commonly identified. These were probably some of the commonest trees in lowland humid and riparian forests of the early Miocene of Turkey. Akkemik et al. (2016) identified many in-situ fossil stems as *Populus*/*Salix* from the Seben-Hoçaş fossil site. Arslan et al. (2013) reported both *Salix* and *Populus* leaves from the same fossil site.

Five *Populus* species (*Populus alba* L., *P. nigra* L., *P. tremula* L., *P. euphratica* Oliver, *P.* × *canascens* (Aiton) Sm.) grow naturally in Turkey and Europe today. Schweingruber (1990) stated that their woods are closely similar and that these species cannot be distinguished from each other on the basis of their wood anatomy. The characteristics of the new species are very similar to the wood anatomical characteristics given by Schweingruber (1990) and Akkemik and Yaman (2012). There is only one small difference: the rays are higher in the fossil species, and marginal axial parenchyma is more common in the new fossil species.

Order MALPIGHIALES C. Martius, 1835

Family SALICACEAE Mirb., 1815

Genus SALICOXYLON Mädel-Angeliewa, 1968

Type species *Salicoxylon messinianum* (Pamp.) Mädel-Angeliewa, 1968, Geol. Jahrb., 86: 454.

***Salicoxylon galatianum***
Akkemik **sp. nov.**

Pl. 16A–I

Holotype. Three thin sections of specimen HOC06.

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number.PFN002215.

Etymology. The epithet "*galatianum*" refers to the Galatian Volcanic Province, which is the Miocene area of the specimens.

Type locality. Fossil site in Hoçaş village, Seben city, Bolu.

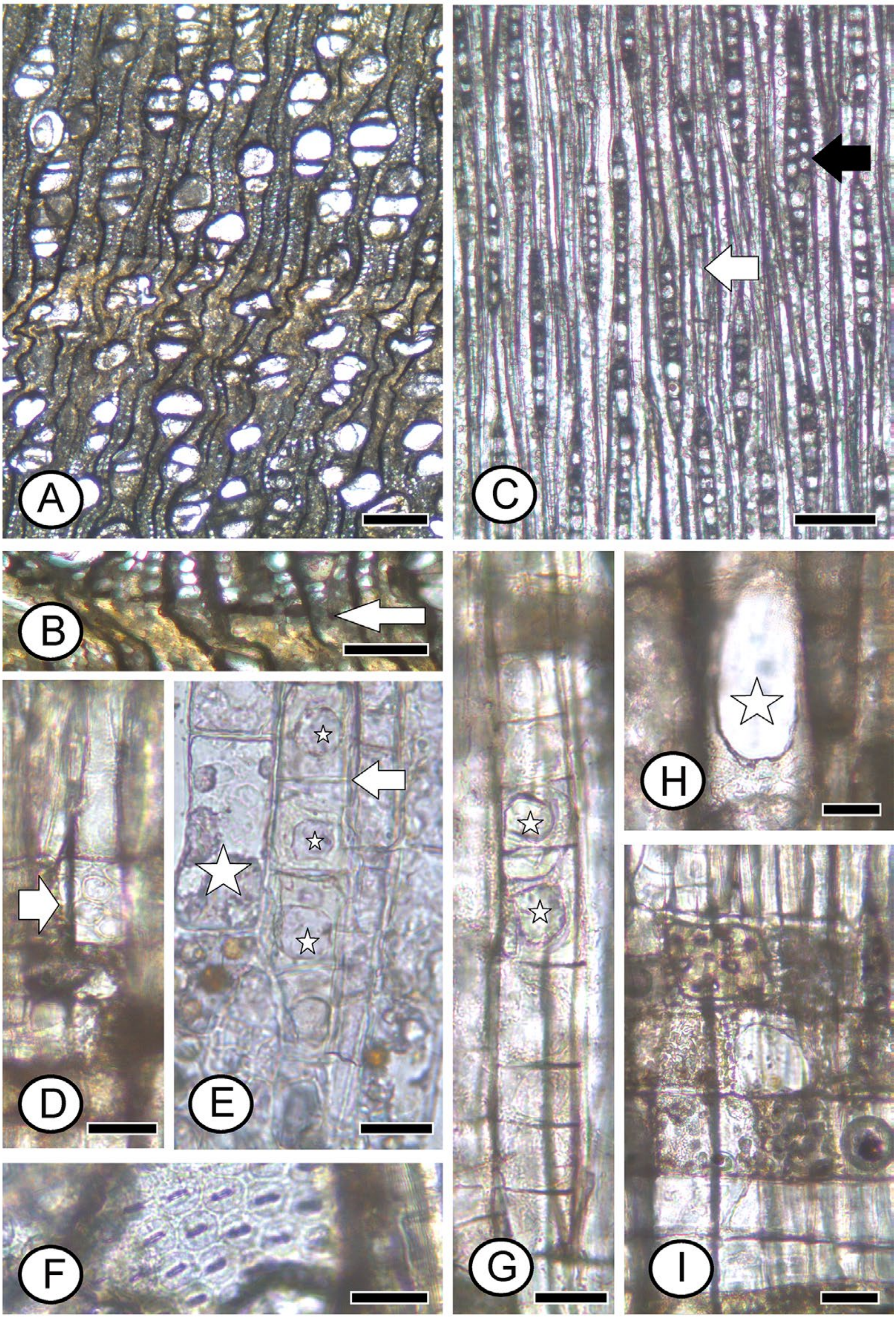


**Plate 16**. Wood anatomical features of *Salicoxylon galatianum* Akkemik sp. nov. **A**. Transversal section with diffuse-porous wood, pores solitary and commonly in radial multiples; **B**. One row of marginal axial parenchyma cells in growth ring boundary (arrow); **C**. Uniseriate and partly biseriate rays (black arrow), and axial parenchyma strand (white arrow); **D**. Slightly honeycomb-like vessel-ray pits (arrow); **E**. Axial parenchyma cell (star) and septate fibres (white arrow) with crystals (small stars); **F**. Alternate pits on vessel wall; **G**. Crystals (stars) in septate fibres; **H**. Simple perforation plate (star); **I**. Heterocellular rays. Scale bars 200 µm in A, 100 µm in B and C, 20 µm in D–I

Age. Early Miocene.

Type horizon. Hançili Formation.

Diagnosis. Wood diffuse-porous, vessels mostly in short radial multiples of 2–4(–6) cells, solitary. Growth ring boundaries distinct, with 1 (rarely 2) rows of axial parenchyma cells (Pl. 16A, B). Solitary vessels circular in general, vessel cells in radial multiples tangentially flattened. Mean vessel tangential diameter 50–100 µm, vessel frequency 40–100 per mm$^2$ (Pl. 16A, B). Rays mostly uniseriate, sometimes partly biseriate, 5–20(–27) cells high. 4–12 rays per mm (Pl. 16C). Axial parenchyma diffuse, in marginal bands. Septate fibres common (Pl. 16D, E). Intervessel pits alternate (Pl. 16F). Prismatic crystals present in septate fibres (Pl. 16E–G). Vessel-ray pits simple, large, slightly honeycomb-like; 2–4 and 5–8 cells per parenchyma strand. Perforation plates exclusively simple (Pl. 16H). Rays heterocellular, body ray cells procumbent with one to three rows of square marginal cells (Pl. 16I). Some rays composed of only procumbent cells. Vascular and vasicentric tracheids absent.

Discussion. The wood is very similar to *Populoxylon sebenense* Akkemik sp. nov., but heterocellular and partly biseriate rays are typical characteristics of *Salicoxylon*. Due to these features the present wood belongs to *Salicoxylon*. Two species of this type of wood were described as *Salix pawneenesis* Wheeler and Matten, 1977 (Wheeler and Matten, 1977) and *Salicoxylon basillicum* Iamandei and Iamandei, 2005. An identification key was prepared for the fossil species:

1. Marginal axial parenchyma common, growth ring boundary distinctly visible due to the 1(–2) row(s) of marginal axial parenchyma, diffuse and sometimes scanty paratracheal axial parenchyma present. . . . . . . . . . . . .*Salicoxylon galatianum* Akkemik sp. nov.

1.* Axial parenchyma extremely rare . . . . . . . . . . . . . 2

   2. More than 100 vessels per mm$^2$; rays 1(–2)-seriate . . . . . . .*Salicoxylon basilicum* Iamandei and Iamandei, 2005

   2.* Less than 50 vessels per mm$^2$; rays exclusively uniseriate. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Salix pawneenesis* Wheeler and Matten

According to the identification key, axial parenchyma is one of the most important distinctive features of this early Miocene willow in Turkey. Due to having common marginal and diffuse axial parenchyma and sometimes scanty axial parenchyma, the present wood differs from all former species. Therefore it is described as a new species. In macrofossil studies (Güner et al., 2017), leaf imprints of *Salix* are common. These were probably some of the commonest trees in lowland humid and riparian forests of the early Miocene of Turkey. Akkemik et al. (2016) identified many in-situ fossil stems as *Populus*/*Salix* from the Seben-Hoçaş fossil site. Arslan et al. (2013) reported both *Salix* and *Populus* leaves from the same fossil site. Thirty-four willow species grow in Turkey today; some of them (e.g. *Salix alba* L., *S. fragilis* L., *S. triandra* L.) are trees and others are shrubs. Woods of tree-like *Salix* species are closely similar, and it is almost impossible to separate them based on wood anatomy (Schweingruber, 1990). Comparison of the fossil species with modern representatives of the genus *Salix* shows similar features.

Order SAPINDALES
Juss. ex Bercht. et J. Presl, 1820

Family SAPINDACEAE Jussieu, 1789

Genus *ACEROXYLON* E. Hofmann, 1939

Type species *Aceroxylon campestre*
E. Hofmann, Tisia, 3: 261, 265. 1939

***Aceroxylon aceroides*** Akkemik **sp. nov.**

Pls 17A–D, 18A–E

Holotype. Three thin sections of specimen INL02. This fossil wood was identified as *Acer* L. by Acarca Bayam et al. (2018).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number. PFN002216.

Etymology. The epithet "*aceroides*" refers to the modern genus *Acer*.

Type locality. Inözü Valley of Beypazarı (north side), Ankara.

Age. Early Miocene.

Type horizon. Hançili Formation.

Diagnosis. Growth ring boundaries distinct and marked by 1–2 rows of marginal axial parenchyma cells. Wood diffuse-porous. Vessels circular or angular, solitary or mainly in radial multiples of 2–3 or rarely 4 or more vessels. Mean vessel tangential diameter ≤ 50 µm, 40–100 vessels per mm$^2$. Axial parenchyma both apotracheal diffuse and marginal. Some vessels filled with dark deposits (Pl. 17A–C). Rays of two distinct sizes, generally uniseriate, sometimes biseriate and multiseriate, with wider rays commonly 4–5-seriate (Pl. 17D). Average height 213.5 (50.7–471.5) µm (max. 46 cells) (Acarca Bayam et al., 2018). Helical thickenings common (Pl. 18A, D, E). Fibres generally thin-walled, septate fibres common. Prismatic crystals present in chambered cells (Pl. 18B). Rays homocellular, composed of procumbent ray cells. Intervessel pits alternate (Pl. 18C, D). Perforation plates simple (Pl. 18E).

Discussion. Ten fossil species of *Aceroxylon* have been identified up to now. Their identification key is based on the relevant references (Watari, 1952; Prakash and Barghoorn, 1961; Parakash, 1968; Suzuki, 1982; Takahashi and Suzuki, 1988; Wheeler and Manchester, 2002; Jeong et al., 2009; Iamandei and Iamandei, 2017). In the key, the identified fossil species was separated into two main groups based on ray width: rays 1–3-seriate and larger rays 4–10-seriate. Then the axial parenchyma features were used as the main diagnostic characters:

1. Rays 1–3 (rarely 4)-seriate .................. 2

1.* Larger rays 4–10-seriate .................... 6

2. Wood semi-ring-porous; rays obviously dilated at ring boundary and darker at limit of annual rings .................. *Aceroxylon pravalense* Iamandei and Iamandei, 2017

2.* Wood diffuse-porous; rays not obviously dilated at ring boundary ......................... 3

3. Axial parenchyma present in marginal or apparently marginal bands ...................... 4

3.* Axial parenchyma diffuse and scanty paratracheal ................... *Acer minokamoensis* Jeong, Kim et Suzuki, 2009

4. Prismatic crystals present in axial parenchyma; axial parenchyma very rare.... *Acer beckianum* Prakash and Barghoorn, 1961

4.* No or rare prismatic crystals; axial parenchyma not very rare ........................... 5

5. Axial parenchyma as wider (3–4-seriate) marginal bands, diffuse and scanty paratracheal; septate fibres absent and fibres with crystals........... *Aceroxylon zarandense* Iamandei and Iamandei, 2017

5.* Axial parenchyma as narrow marginal or apparently marginal bands and scanty paratracheal........... *Acer berkhoffii* Wheeler and Dillhoff, 2009

6. Rays distinctly in two sizes ................ 7

6.* Rays not distinctly in two sizes............. 9

7. Ray height never more than 1 mm, longest ray lower than 500 µm; narrow rays 1–2-seriate, wider ones 3–6-seriate; helical thickening thin; septate fibres common............. *Aceroxylon aceroides* Akkemik sp. nov.

7.* Ray height more than 1 mm .................. 8

8. Rays homocellular and heterocellular with one row of marginal square cells ................ *Aceroxylon palaeosaccharinum* Greguss, 1943, emend. Iamandei and Iamandei, 2017

8.* Rays exclusively homocellular and all rays procumbent....... *Acer* cf. *amoenum* Watari, 1952

9. No axial parenchyma in marginal or apparently marginal bands .......................... 10

9.* Axial parenchyma present in marginal or apparently marginal bands ...................... 11

10. Axial parenchyma diffuse................. *Acer integrifolioxylon* Wheeler and Manchester

10.* Axial parenchyma diffuse and scanty paratracheal ... *Acer pohangensis* Jeong et Kim, 2009

11. Axial parenchyma absent or extremely rare ... 12

11.* Axial parenchyma present and not extremely rare .................................... 13

12. No prismatic crystal record..... *Acer olearyi* Prakash and Barghoorn, 1961

12.* Prismatic crystals present in axial parenchyma ................................ *Acer puratanum* Prakash and Barghoorn, 1961

13. Septate fibres present......... *Acer watarianum* Takahashi and Suzuki, 1988

13.* No record of septate fibres .... *Acer palmatoxylum* Suzuki, 1982

The fossil *Aceroxylon* wood has larger rays and two distinct sizes of rays, together with *Acer* cf. *amoenum*, which is the most similar species. In *Acer* cf. *amoenum*, the larger rays are more than 1 mm long and are wider, and septate fibres are absent. In contrast, in the new fossil species, ray width maximum is 4 cells, ray height never exceeds 0.5 mm, and septate fibres are present. Based on these differences, it is here considered a new fossil species.

Eleven extant *Acer* species grow naturally in Turkey. Their wood anatomical features were studied by Yaltırık (1971) and Akkemik and Yaman (2012). Later, Akkemik et al. (2018) compared the modern *Acer* woods with the fossil woods in Turkey. Among these species, the nearest extant species is *Acer monspessulanum* L. (Tab. 6). As stated by Akkemik et al. (2018) the fossil species and *Acer monspessulanum* showed similar and high xeromorphy ratios, which indicates exposure to dry conditions. All these similarities (see Tab. 4) suggest that the fossil *Aceroxylon aceroides* Akkemik sp. nov. may be the potential ancestor of *Acer monspessulanum* L. and similar modern species in the Mediterranean Basin.

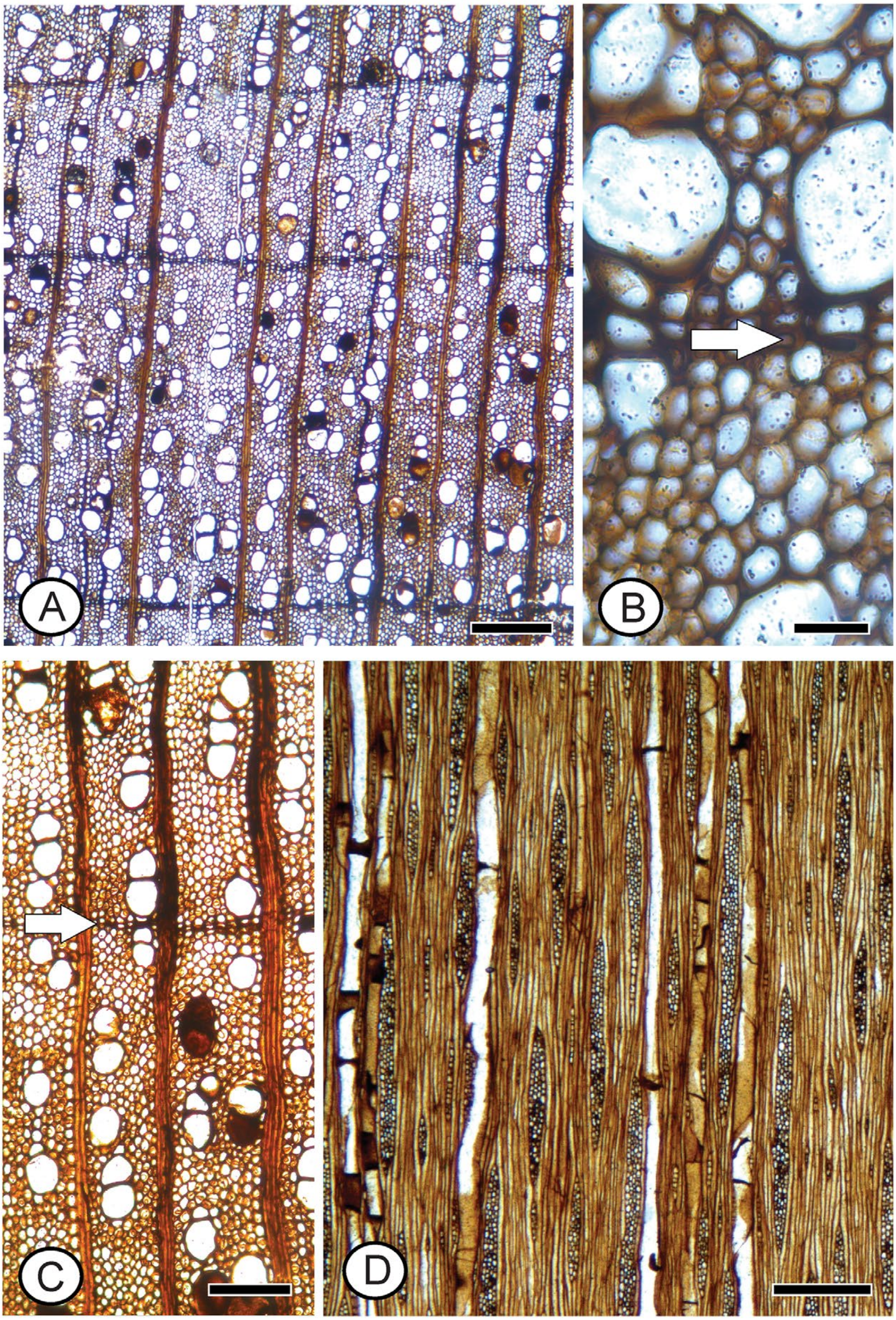


**Plate 17**. Wood anatomical features of *Aceroxylon aceroides* Akkemik sp. nov. **A**. Transversal section with diffuse-porous wood, distinct growth ring boundary, and vessels filled with dark content; **B**, **C**. Marginal axial parenchyma in growth ring boundary (arrow); **D**. Tangential section with 1–6-seriate rays. Scale bars 200 µm in A and D, 20 µm in B, 100 µm in C

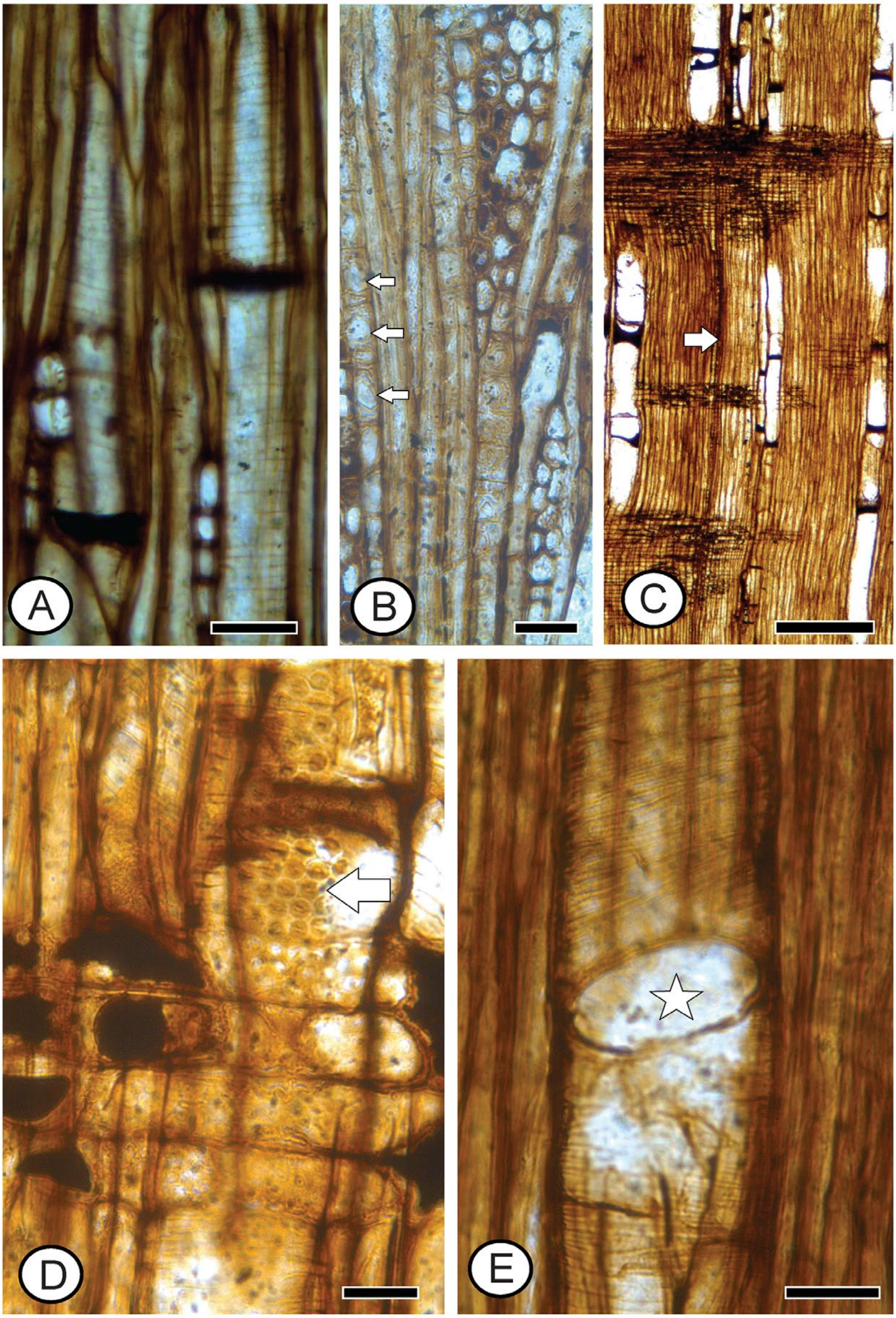


**Plate 18**. Wood anatomical features of *Aceroxylon aceroides* Akkemik sp. nov. **A**. Helical thickening in vessels; **B**. Axial parenchyma with crystals (arrows); **C**. Homocellular rays and axial parenchyma in the boundary of annual rings (arrow); **D**. Alternate intervessel pits (arrow); **E**. Simple perforation plate (star) and helical thickening in vessels. Scale bars 100 μm in A, 20 μm in B, D and E, 200 μm in C

**Table 6**. Comparison of the fossil *Aceroxylon aceroides* Akkemik sp. nov. with the extant *Acer monspessulanum* L.

| Features | *Acer monspessulanum* L. (Akkemik and Yaman, 2012) | *Aceroxylon aceroides* Akkemik sp. nov. |
|---|---|---|
| Growth ring | Growth ring boundaries mostly distinct with 1–2 rows of marginal axial parenchyma cells | The same |
| Vessels | Diffuse-porous, vessels solitary and arranged in radial multiples of 4 or more, and rounded. Perforation plates simple. Intervessel pits alternate and medium (7–10 µm). Mean tangential diameter of vessel lumina ≤50 µm. 40–100 vessels per $mm^2$. Helical thickening common. Most of the vessels filled with coloured material | The same |
| Tracheids and fibres | Vascular/vasicentric tracheids absent. Fibres with simple to minutely bordered pits. Fibres non-septate, thin- to thick-walled | Fibres non-septate, thin- to thick-walled |
| Axial parenchyma | Axial parenchyma diffuse and scanty paratracheal, marginal. 2–4 cells per parenchyma strands | Axial parenchyma diffuse and scanty paratracheal, marginal |
| Rays | Rays of two distinct sizes. Rays generally uniseriate and multiseriate, sometimes biseriate. All rays procumbent. Larger rays commonly 4–5-seriate. Rays 4–12 per mm. Maximum ray height up to 45 cells | The features are about the same. Maximum ray height up to 46 cells |

Order ROSALES Bercht. et J. Presl, 1820

Family ULMACEAE Mirbel, 1815

Genus *ULMOXYLON* Kaiser, 1879

Type species *Ulmoxylon lapiduriorum* (Unger) Kaiser, 1879, p. 100; Unger, 1842b, p. 176. See also Unger, 1854, p. 182, pl. 7, figs 1–3

***Ulmoxylon kasapligilii*** Akkemik **sp. nov.**

Pls 19A–D, 20A–D

Holotype. Three thin sections of specimen KOZ16. This fossil wood was identified as *Ulmus* L. by Akkemik et al. (2016).

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number. PFN002217.

Etymology. The epithet "*kasapligilii*" honours the late Prof. Dr. Baki Kasaplıgil, one of the pioneers of palaeobotany in Turkey.

Type locality. Kozyaka village, Seben city, Bolu Province.

Age. Early Miocene.

Type horizon. Hançili Formation.

Diagnosis. Growth ring boundaries distinct. Wood ring-porous with 2–3 rows of vessels in earlywood. Earlywood vessels solitary or in radial multiples; latewood vessels arranged in tangential bands. Mean vessel tangential diameter 100–200 µm, ≥200 µm in earlywood, ≤50 µm in latewood. Axial parenchyma diffuse, vasicentric, banded, confluent (Pl. 19A, B). Rays in two distinct sizes, generally larger rays 4–8-seriate, rarely 1–2-seriate rays present. Ray width up to 8 cells, height up to 61 cells (Pl. 19C). Storied structure common in axial parenchyma (Pls 19D, 20A). Intervessel pits alternate, perforation plates simple (Pl. 20B). All rays procumbent, body ray cells procumbent with one row of upright and/or square marginal cells (Pl. 20C, D). Helical thickening common in latewood vessels (Pl. 20D).

Discussion. Fossil *Ulmus*-type woods were named *Ulminium* Unger 1842, *Ulmoxylon* Hofmann 1939 and *Ulmus* L., 1753. Because the fossil genus *Ulminium* was moved into Lauraceae (Wheeler et al., 1977), *Ulminium* is not used for *Ulmus*-type wood anymore. *Ulmus* and *Ulmoxylon* are commonly used (e.g. Greguss, 1969; Wheeler and Manchester, 2007). Here I prefer to use the fossil genus name *Ulmoxylon*. The following identification key was prepared based on the 11 fossil species of *Ulmus* and *Ulmoxylon* (Platen, 1908; Watari, 1652; Prakash and Barghoorn, 1961; Greguss, 1969; Insidewood, 2004 onward; Privé-Gill et al., 2008; Wheeler and Dillhoff, 2009; Klusek, 2012; Koutecký and Sakala, 2015; Koutecky et al., 2019).

1. Axial parenchyma storied .................... 2
1.* Axial parenchyma not storied ................ 5
   2. Axial parenchyma absent in marginal or apparently marginal bands ........... *Ulmus woodi* Wheeler and Manchester
   2.* Axial parenchyma present in marginal or apparently marginal bands together with vasicentric and confluent axial parenchyma ............ 3

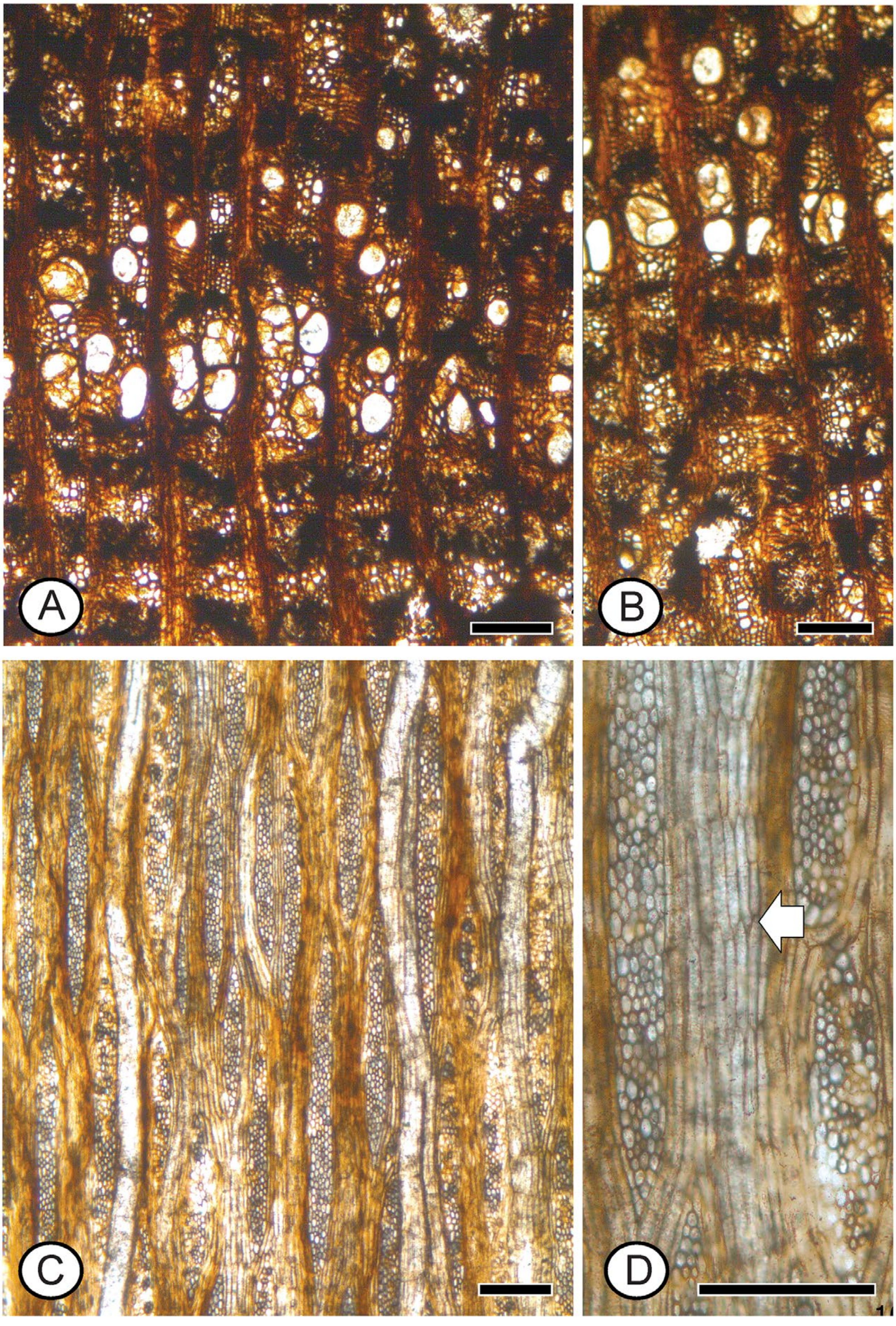


**Plate 19**. Wood anatomical features of *Ulmoxylon kasapligilii* Akkemik sp. nov. **A**, **B**. Transversal sections with ring-porous wood, and diagonal and tangential bands of latewood vessels; **C**. Tangential section with wide rays; **D**. Storied axial parenchyma cells (arrow). Scale bars 200 µm

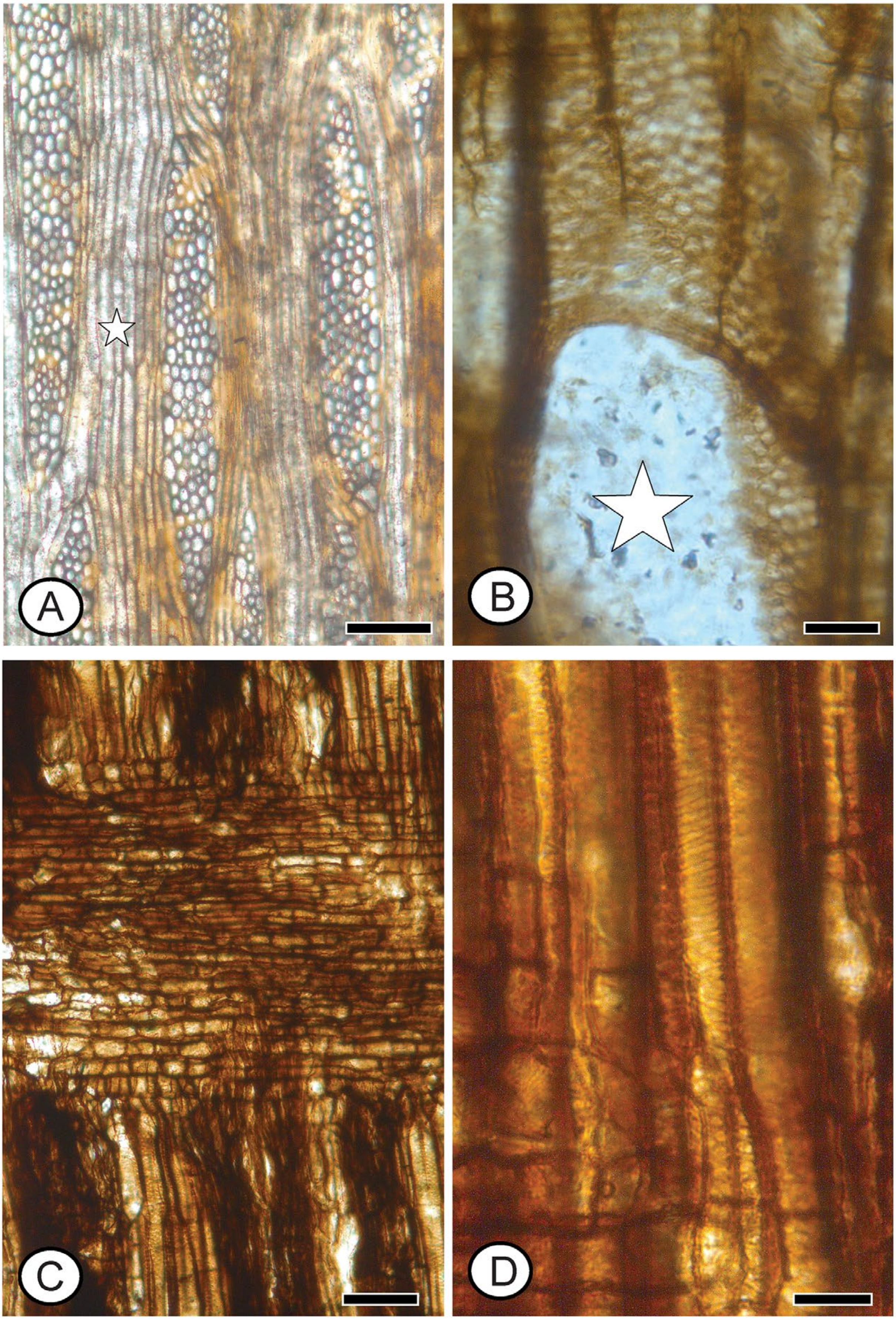


**Plate 20**. Wood anatomical features of *Ulmoxylon kasapligilii* Akkemik sp. nov. **A**. Storied axial parenchyma cells (star) and wide rays; **B**. Simple perforation plate (star); **C**. Heterocellular ray; **D**. Helical thickening in latewood vessels. Scale bars 100 µm in A and C, and 20 µm in B and D

3. Ray height up to 30 cells . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ulmoxylon scabroides* Greguss, 1969
3.* Ray height up to 80 cells . . . . . . . . . . . . . . . . . . . . . 4
   4. Prismatic crystals absent; rays both homocellular and heterocellular; axial parenchyma clearly storied . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ulmoxylon kasapligilii* Akkemik sp. nov.
   4.* All rays procumbent; prismatic crystals in axial parenchyma and in chambered cells common, storied structure slightly . . . . . . . . . . . . . . . . . . . . . . . . *Ulmoxylon* cf. *carpinifolia* Greguss, 1969
5. Rays heterocellular . . . . . . . . . . . . . . . . . . . . . . . . . 6
5.* All rays procumbent. . . . . . . . . . . . . . . . . . . . . . . . . 7
   6. Earlywood vessels in one row; prismatic crystals in both axial parenchyma and ray cells; procumbent ray cells associated with 1–4 upright and square cells. . . .*Ulmoxylon simrothi* Platen, 1908
   6.* Vessel 2–3 rows in earlywood; prismatic crystals only in axial parenchyma cells; procumbent ray cells associated with one row of upright and square cells . . . . . *Ulmoxylon marchesonii* Biondi
7. Wood semi-ring and diffuse-porous . . . . . . . . . . . . 8
7.* Wood ring-porous . . . . . . . . . . . . . . . . . . . . . . . . . . 10
   8. No record of prismatic crystals and helical thickening . . . . . . . . . . . . . . . . . . . . . . . *Ulmus pacifica* Prakash and Barghoorn, 1961
   8.* Helical thickening present. . . . . . . . . . . . . . . . . 9
9. Prismatic crystals present. . . . . . . . *Ulmus danielii* Wheeler and Manchester, 2007
9.* Prismatic crystals not present . . . . . *Ulmoxylon* cf. *kersonianum* Starostin and Trelea, 1969
   10. Ray height more than 1 mm . . . . . . . . . . . . . . *Ulmus baileyana* Prakash and Barghoorn, 1961
   10.* Ray height less than 1 mm . . . . . . . . . . . . . 11
11. Axial parenchyma vasicentric and confluent. . . . . *Ulmus miocenica* Prakash and Barghoorn, 1961
11.* Axial parenchyma vasicentric. . . . . . . . . . . . . . . 12
   12. No record of tyloses; diffuse axial parenchyma present. . . . . . . . . . . . . . . *Ulmus crystallophora* (Watari) Watari, 1952
   12.* Tyloses common; only vasicentric axial parenchyma present. . . . . . *Ulmoxylon lapidariorum* (Unger) Felix, 1883

According to the identification key, the present fossil wood differs from many fossil *Ulmoxylon* species in having storied axial parenchyma. The nearest fossil species are *Ulmus woodi, Ulmoxylon scabroides* and *Ulmoxylon* cf. *Ulmus carpinifolia*. The present wood differs from *Ulmus woodi* in having marginal and/or apparently marginal axial parenchyma bands. In cf. *Ulmus carpinifolia*, prismatic crystals are common and all rays are procumbent. In *Ulmoxylon scabroides*, ray height is less than 30 cells, and prismatic crystals are present in axial parenchyma and in chambered axial parenchyma cells. Due to the clear differences from its most similar fossil species, the here-described *Ulmoxylon* is considered a new fossil species.

Today, four *Ulmus* species (*Ulmus minor* Mill., *U. glabra* Huds., *U. laevis* Pall., *U. canascens* Melville) grow naturally in Turkey. Akkemik (1995) stated that modern *Ulmus* species have no storied axial parenchyma; the fossil wood differs from all extant native species. Storied axial parenchyma is a common feature in North American species such as *U. alata* Michx., *U. crassifolia* Nutt., *U. rubra* Muhl., *U. serotina* Sarg. and *U. thomasii* Sarg., and in *U. castaneifolia* Hemsl. from Europe and temperate Asia (Insidewood, 2004 onward). The most similar modern species are the North American *Ulmus* species, particularly *Ulmus serotina* and *U. thomasii.*

Order ROSALES Bercht. et J. Presl, 1820

Family ULMACEAE Mirbel, 1815

Genus *ZELKOVOXYLON* P. Greguss, 1969

Type species *Zelkovoxylon yatsenko-khmelevskyi* P. Greguss, 1969, pl. 2, fig. 11

### ***Zelkovoxylon crystalliferum*** Akkemik **sp. nov.**

Pls 21A–D, 22A–D

Holotype. AGU15.

Repository. Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpasa, Istanbul, Turkey.

Plant fossil registry number. PFN002218.

Etymology. The epithet “*crystalliferum*” refers to the presence of very dense crystals in rays and axial parenchyma cells.

Type locality. Near Aşağıgüney village, Beypazarı city, Ankara Province.

Age. Early Miocene.

Type horizon. Hançili Formation.

Diagnosis. Wood ring-porous, growth ring boundaries distinct, with abrupt transition from earlywood to latewood. Earlywood vessels in 1–2 rows; vessel clusters and diagonals common in latewood. Vessel tangential and radial diameter both measure 50–100 µm and 100–200 µm in earlywood and >50 µm in latewood (Pl. 21A, B). Axial parenchyma paratracheal, mainly in vessel clusters of latewood. Rays

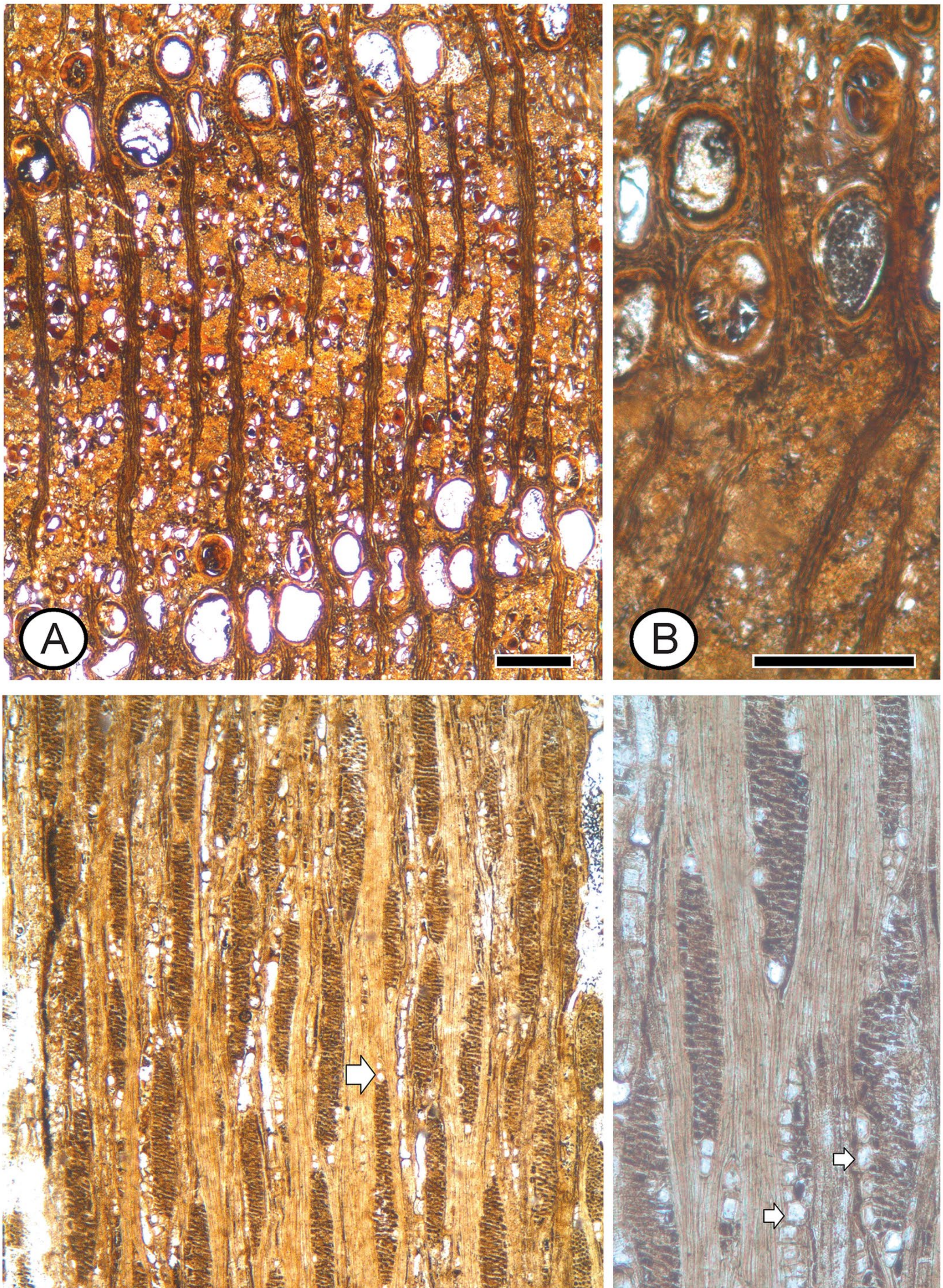


**Plate 21**. Wood anatomical features of *Zelkovoxylon crystalliferum* Akkemik sp. nov. **A**. Transversal sections with ring-porous wood and growth ring boundary distinct, transition from earlywood to latewood abrupt, latewood vessels in tangential bands; **B**. Circular vessels with thick walls; tyloses common; **C**, **D**. Rays wide, prismatic crystals common in rays and axial parenchyma (arrows). Scale bars 200 µm

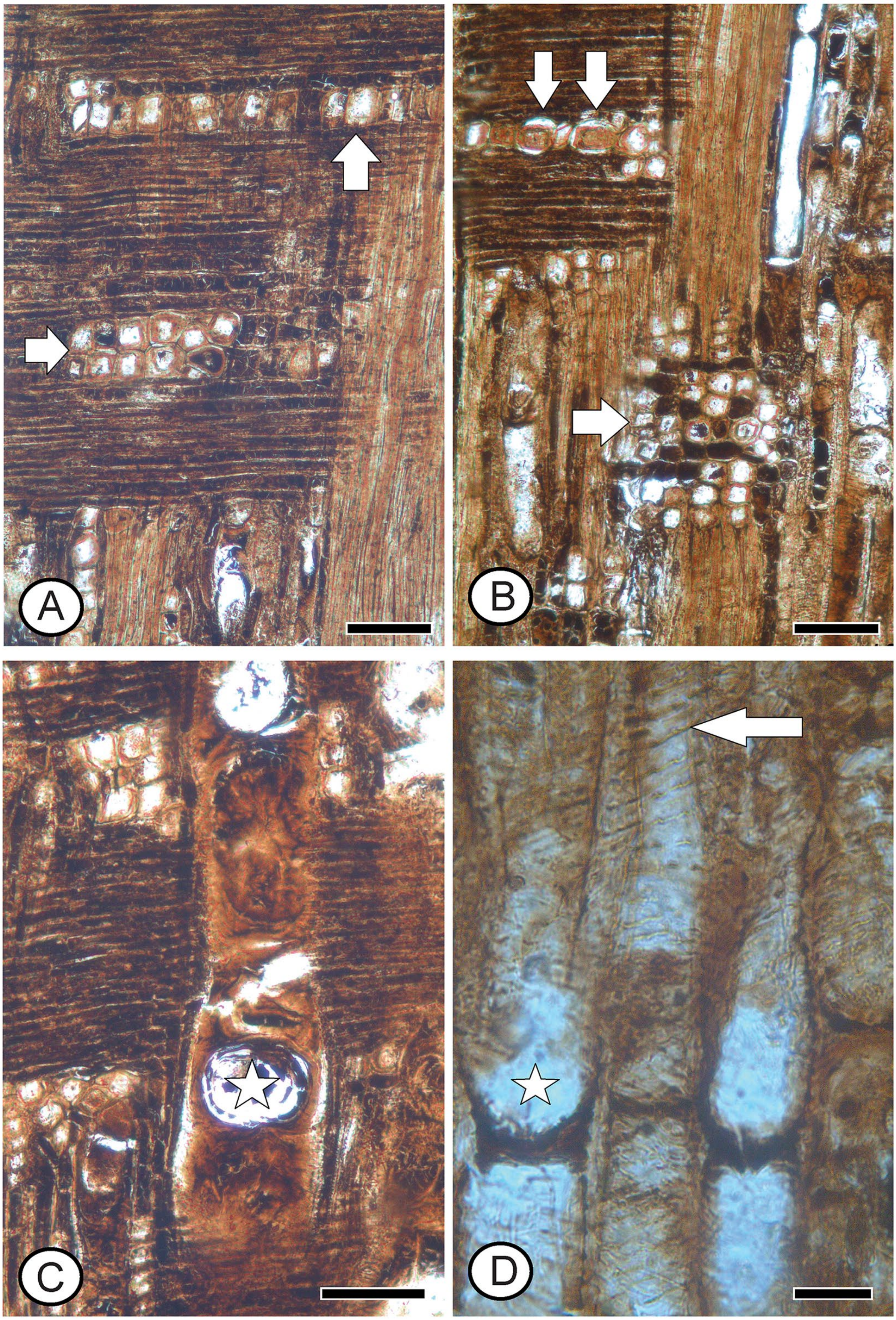


**Plate 22**. Wood anatomical features of *Zelkovoxylon crystalliferum* Akkemik sp. nov. **A–C**. Heterocellular rays, and very common prismatic crystals in enlarged and chambered rays and axial parenchyma cells (arrows); **C**, **D**. Simple perforation plate (stars); **D**. Helical thickening in latewood vessels (arrow). Scale bars 100 µm in A–C, 20 µm in D

1–6-seriate, in two distinct sizes. Wider rays 4 (3–6)-seriate, generally 25–35 (–51) cells high; narrow rays (1–2-seriate) and generally 11–23 cells high (Pl. 21C, D). Rays homocellular with entirely procumbent ray cells and heterocellular with mostly procumbent body ray cells and 1–4 rows of upright and/or square marginal cells. Axial parenchyma in strands of 2–4 cells. Prismatic crystals extremely dense in axial parenchyma and in enlarged axial parenchyma cells, and in procumbent and upright cells of rays (Pl. 22A–C). Crystals appear as clusters in some rays (Pl. 22B). Perforation plates simple (Pl. 22C, D). Helical thickening common in latewood vessels and vascular/vasicentric tracheids (Pl. 22D).

Discussion. So far, nine species of *Zelkovoxylon* have been described, four of which are known from Europe (Watari, 1952; Greguss, 1969; Petrescu, 1971; Wheeler et al., 1978; Gottwald, 1981; Suzuki and Hiraya, 1989; Wheeler and Landon, 1992; Wheeler, 2001; Cheng et al., 2018) and one from Turkey.

1. Wood semi-ring-porous, transition from earlywood to latewood gradual; ray cells with crystals inflated; rays heterocellular; vessels in radial multiples present . . . . . . . . . . . . . . . . . . . *Zelkovoxylon occidentale* Wheeler, Scott and Barghoorn, 1978, *Zelkovoxylon dacicum* Petrescu, 1971

1.* Wood clearly ring-porous; transition from earlywood to latewood abrupt . . . . . . . . . . . . . . . . . . . . . 2

2. Rays 1–2 cells wide. . . . . . *Zelkovoxylon yesimae* Akkemik, 2018

2.* Larger rays commonly 4–10-seriate . . . . . . . . . 3

3. All rays procumbent. . . . . . . . . . . . . . . . . . . . . . . . 4

3.* Rays heterocellular . . . . . . . . . . . . . . . . . . . . . . . . 5

4. Vessels in earlywood large, up to 400 µm; aliform axial parenchyma present . . . . . . . . . . . . . . . . . . . . . . . . . . *Zelkovoxylon strausii* Gottwald, 1981

4.* Vessels in earlywood not large; aliform axial parenchyma absent. . . . . . . . . . . . . *Zelkovoxylon yatsenko-khmelevskyi* Greguss, 1969

5. No banded axial parenchyma . . . . . . . . . . . . . . . . . 6

5.* Banded axial parenchyma present . . . . . . . . . . . . 7

6. Axial parenchyma vasicentric and confluent, sometimes inflated; crystals present in axial parenchyma cells and in square marginal ray cells; earlywood vessels generally in one row . . . . . . . . . . . . . . . . . . . . . *Zelkova wakimizui* Watari, 1952

6.* Axial parenchyma vasicentric and confluent but not inflated; crystals extremely dense in axial parenchyma, in square marginal ray cells and in procumbent cells; earlywood vessels thick-walled and generally in 2 rows. . . . . . . . . . . . . . . . . . . . . . . . *Zelkovoxylon crystalliferum* Akkemik sp. nov.

7. Axial parenchyma vasicentric, in marginal or apparently marginal bands; prismatic crystals only in rays . . . . . . . *Zelkova zelkowiforme* Watari, 1952

7.* Axial parenchyma vasicentric; not in marginal or apparently marginal bands; vessels in tangential bands . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

8. Axial parenchyma vasicentric and confluent; vessels not much smaller . . . . . . . . . . . . . . . . . . . . . . . . . *Zelkovoxylon chadronensis* Wheeler, 2001

8.* Diagonal or radial pattern and vessel clusters common; vessels much smaller . . . . . . . . . . . . . . . *Zelkova microporosum* Wheeler and Landon, 1992

According to the identification key, the fossil *Zelkova* wood differs from *Zelkovoxylon occidentale* and *Z. dacicum* in having distinctly ring-porous wood. *Zelkovoxylon yesimae* from Turkey has only 1–2-seriate rays.

The fossil *Zelkova* wood differs from *Zelkovoxylon strausii* and *Z. yatsenko-khmelevskyi* in having heterocellular rays, and from *Z. zelkowiforme, Z. chadronensis* and *Z. microporosum* by the absence of banded parenchyma. In *Z. microporosum* the vessels are narrower.

The most similar fossil species is *Zelkova wakimizui*, which shares most features with *Z. crystalliferum* except for the presence of dense crystals. The presence of prismatic crystals is a typical character for the newly described wood taxon. Six *Zelkova* species grow in the world; one of them, *Zelkova carpinifolia*, is native to Turkey. Generally the fossil species shows similarities to all modern species of *Zelkova*, but it is more similar to *Zelkova sinica* C.K.Schneid. from China; that modern species commonly has prismatic crystals, as also encountered in the fossil *Z. crystalliferum*.

## DISCUSSION

The early and middle Miocene in Turkey is the period richest in number of fossil woody plants. Identified fossil wood (e.g. Akkemik et al. 2009, 2016, 2017, 2018, 2019; Acarca Bayam et al., 2018; Güngör et al., 2019), macrofossils (e.g. Kasaplıgil, 1977; Erdei et al. 2010; Güner and Denk, 2012; Denk et al., 2014, 2015, 2017a, b, 2019; Güner et al., 2017; Güner, 2019) and microfossils (e.g. Akgün et al., 2007; Akkiraz et al., 2012; Bouchal et al., 2018) show the great diversity of woody plants for this period. Today more than 600 woody species grow naturally in Turkey (Akkemik, 2018), and the palaeobotanical record shows that there was a rich woody flora in the early and middle Miocene as well.

Despite the great abundance of fossil wood in the early and middle Miocene palaeobotanical record of Turkey, the number of papers examining these records is still low. In view of the richness of the woody flora of Turkey in the Miocene and in present times, there is a great potential for detection of new fossil species. The present documentation of 16 fossil species based on wood is an important step towards understanding the forest composition, local and regional site conditions and climate during the early and middle Miocene of Turkey.

Based on macrofossils and dispersed pollen grains, Denk et al. (2017a) and Güner et al. (2017) classified the site conditions for woody plant growth. The conditions of growth sites were divided into seven vegetation units ranging from swamp and riparian to dry hinterland. The 16 fossil angiosperm species identified in the present paper were evaluated with respect to these vegetation units (Tab. 7). In general, aquatic, riparian, subtropical and well-drained lowland and upland forest conditions were determined. Well-drained upland and lowland forests and riparian areas also had conifer species.

Denk et al. (2017a, 2019) and Güner et al. (2017) suggested that the climate during the early and middle Miocene was warmer and rainier than at present, and Denk et al. (2019) stated that the macrofossil data from 33 sites unambiguously show the continuous presence of forest vegetation across western and central Turkey. Denk et al. (2019) also used a wide fossil dataset of pollen and spores, leaves, and woods to assess the biomes and associated climate of the early Miocene of Turkey. The data showed the presence of riparian and swamp forests and mesic and xeric forest communities on well-drained soils in the early and middle Miocene. The climate was subtropical and warm, and the taxonomic composition suggested that the predominating forest biome was the Laurel Forest Biome. However, in that study they indicated periods of transition to dry conditions, based on the pollen, macrofossil and wood data. The presence of *Cedrus, Pinus* (as *Lesbosoxylon* in the wood record of the early Miocene), *Pistacia* and particular species of *Acer* may indicate drier climate and open forests during these transition periods, together with swamp and riparian conditions. The swamp and riparian conifers in the wood record, such as *Glyptostroboxylon rudolphii* and *Taxodioxylon gypsaceum* from the early and middle Miocene of Turkey (Akkemik et al., 2016, 2017; Acarca Bayam et al., 2018; Akkemik, 2020), are the commonest trees. *Salix, Populus* and *Liquidambar*-type woods are further evidence for riparian conditions.

The presence of Lauraceae woods [*Laurinoxylon thomasii* Akkemik (Akkemik et al., 2019), *Laurinoxylon litseoides* Süss, *Cryptocaryoxylon grandoleaceoum* Akkemik sp. nov.] suggest tropical and subtropical conditions.

All these findings from wood anatomical study support the results from other materials examined by Denk et al. (2019), but I suggest that within the early Miocene there was a period with xeric conditions. More pronounced seasonality is also suggested by findings of particular fossil species from early Miocene localities of Turkey, and in particular an extinct cycad (Erdei et al., 2010) of *Dracaena*, which is closely similar to the modern *D. draco* (L.) L. from the Canary Islands, Cape Verde and western Morocco (Denk et al., 2014), and *Smilax* related to modern species in the Caribbean region (Denk et al., 2015); these would all suggest seasonality of precipitation, although the distinction between summer-dry and winter-dry climates is difficult to make. For evergreen oaks present in the early Miocene of Turkey, Denk et al. (2017b) suggested that ecologically they were more similar to their extant Himalayan than to their extant Mediterranean relatives. This would suggest that morphologically similar fossil species had ecologies different from the modern Mediterranean species, and that the possibility of niche shifts should be considered when evaluating fossil species. According to Bouchal et al. (2018) and Denk et al. (2018), the shift to modern steppe and Mediterranean conditions in Turkey occurred during and after the middle Miocene, but modern conditions were established in large parts of Turkey during the late Miocene. This shift to modern conditions happened earlier than in adjacent areas (e.g. northern Greece), where humid conditions of the early Miocene persisted into the late Miocene (Denk et al., 2018; Bouchal et al., 2020).

Biltekin (2018) observed a trend from warm and humid climate to cooler and drier conditions during the Aquitanian in pollen zones dominated by Pinaceae. Denk et al. (2019) also discussed the possibility that more xeric conditions characterized *Cedrus*-dominated forest communities. Climate inferences from Köppen signatures also suggest an ecotone between tropical and warm temperate (subtropical) forest biomes. This illustrates the point that climatic trends as

**Table 7**. Fossil species recognized in the present study, also their potential modern relatives and modern vegetation units in which modern relatives typically occur.
* – Vegetation Units: VU0 – subtropical, moist or dry light forest; VU1 – aquatic; VU2 – bogs, wet meadows; VU3 – swamp forest; VU4 – riparian forest; VU5 – well-drained lowland forest (edaphically and aspect-wise dry forest); VU6 – well-drained upland forest; VU7 – well-drained (lowland and) upland conifer forest including hummocks (Denk et al., 2017; Güner et al., 2017)

| Fossil species identified | Potential modern representatives | Distribution areas of the modern representatives | Vegetation unit* |
|---|---|---|---|
| *Liquidambaroxylon efeae* Akkemik sp. nov. | *Liquidambar orientalis* Mill. | South-west Anatolia and a few Aegean islands | VU1, VU4 |
| *Pistacioxylon ufukii* Akkemik, 2018 | *Pistacia terebinthus* L., *P. atlantica* Desf. | Mediterranean Basin, Europe, Asia | VU5 |
| *Eucarpinoxylon kayacikii* Akkemik sp. nov. | *Carpinus* L. sp. | Mediterranean Basin, Europe, Asia | VU5, VU6 |
| *Ostryoxylon gokceadaense* Akkemik sp. nov. | *Carpinus* L. sp. / *Ostroxylon* Scop. sp. | Mediterranean Basin, Europe, Asia | VU5, VU6 |
| *Fagoxylon radiatum* Süss | *Fagus orientalis* Lipsky<br>*Fagus sylvatica* L. | Throughout Europe, Turkey, Iran, Caucasia | VU5, VU6 |
| *Quercoxylon yaltirikii* Akkemik sp. nov. | *Quercus* L. Section *Ilex* | Mediterranean Basin, subtropical Asia | VU5 |
| *Cryptocaryoxylon grandoleaceum* Akkemik sp. nov. | *Cryptocarya* R. Br. sp. | Tropical and subtropical South America, Mauritius, India, China, Java, to New Guinea, and Africa in Southern Hemisphere | VU0 |
| *Laurinoxylon litseoides* Süss | *Laurus nobilis* L. | Mediterranean Basin | VU4, VU5, VU6 |
| *Fraxinoxylon beypazariense* Akkemik sp. nov. | *Fraxinus angustifolia* Vahl., *F. excelsior* L., *F. ornus* L. and *F. pallisae* Wilmott | Mediterranean Basin, Europe, Asia | VU4 |
| *Platanoxylon catenatum* Süss et Müller-Stoll | *Platanus orientalis* L. | Mediterranean Basin, Europe, Turkey, Asia | VU4 |
| *Prunoidoxylon prunoides* Akkemik sp. nov. | Subfamily of Prunoidae | Mediterranean Basin, Europe, Turkey, Asia | VU5, VU6 |
| *Populoxylon sebenense* Akkemik sp. nov. | *Populus alba* L., *P. nigra* L., *P. tremula* L., *P. euphratica* Oliver and P. × *canascens* (Aiton) Sm. | Mediterranean Basin, Europe, Turkey, Asia | VU4, VU7 |
| *Salicoxylon galatianum* Akkemik sp. nov. | *Salix alba* L., *S. cinerea* L., *S. purpurea* L., *S. viminalis* L., *S. babylonica* L., *S. caprea* L., *S. daphneoides* Vill., *S. fragilis* L., *S. pentandra* L., *S. triandra* L. | Mediterranean Basin, Europe to Asia | VU4 |
| *Aceroxylon aceroides* Akkemik sp. nov. | *Acer monspessulanum* L. | Mediterranean Basin | VU5, VU6 |
| *Ulmoxylon kasapligilii* Akkemik sp. nov. | *Ulmus alata* Michx., U. *crassifolia* Nutt., *U. rubra* Muhl., *U. serotina* Sarg., *U. thomasii* Sarg.<br><br>*U. castaineifolia* Hemsl. | North America<br><br><br>Europe and temperate Asia | VU5, VU6<br><br><br>VU5, VU6 |
| *Zelkovoxylon crystalliferum* Akkemik sp. nov. | *Zelkova sinica* C.K. Schneid. | China | VU4, VU5 |

seen in globally averaged climate curves (cooler Burdigalian, warmer Langhian) are not necessarily seen in local floras. Thus, tropical plant groups may have gone through bottlenecks prior to mid-Miocene warming. The wood anatomical properties of the trees described in the present study also support the occurrence of transitions to xeric conditions.

The angiosperm genera show a high degree of similarity between early and middle Miocene and extant woody genera. As presented in Table 7, the closest modern relatives of some fossil species are found among modern representatives from the Mediterranean Basin.

## CONCLUSIONS

The fossil wood specimens identified from early and middle Miocene sites in Turkey have revealed a rich woody flora. Today as well, the woody plant flora of Turkey shows an outstandingly high degree of diversity. In this study, twelve new fossil angiosperm species were described and four additional angiosperm species were identified. In comparing the species composition and diversity in the early and middle Miocene with today's species, an important correlation is seen. The wood anatomical features of the fossil species are very similar to their present-day relatives; only small differences were found. The wood characteristics of species such as *Aceroxylon acerinum, Fagoxylon radium, Fraxinoxylon beypazariense, Laurinoxylon litseoides*, *Liquidambaroxylon efeae*, *Pistacioxylon ufukii*, *Platanoxylon cetanatum*, *Populoxylon sebenesis, Prunoidoxylon prunoides*, *Quercoxylon yaltirikii* and *Salicoxylon galatianum* are almost identical to their present-day relatives from the Mediterranean Basin. However, the modern relatives of *Zelkovoxylon crystalliferum*, *Ulmoxylon kasapligilii, Eucarpinoxylon gokceadaense, Ostroyoxylon kayacikii* and *Cryptocaryoxylon grandoleaceoum* are not particular species but rather are higher taxa (e.g. subgenera, genera), and their possible modern analogues are likely not from the Mediterranean Basin. The taxonomic composition of fossil wood species from the early and middle Miocene of Turkey suggests xeric conditions, but the presence of tropical/subtropical species shows that the period was warmer, humid and rainy. This means that within the early-middle Miocene of Turkey there was a transitional period from subtropical conditions to Mediterranean or otherwise seasonal conditions, and the identified woody flora reflects this transitional condition.

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