

The first report of *Lesbosoxylon* Süss & Velitzelos
from the early-middle Miocene of eastern Anatolia

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The first report of *Lesbosoxylon* Süss & Velitzelos from the early-middle Miocene of eastern Anatolia

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ABSTRACT

A new fossil pine species from eastern Turkey is described and its botanical affinities are discussed. The sample was collected from the city of Kemaliye, Erzincan province, Turkey, and derives from the early-middle Miocene Divriği formation. Transverse, tangential and radial sections were taken from the petrified wood, and its palaeoxylotomical features were investigated. Based on its anatomical features including idioblastic cells in rays a new fossil-species of the genus *Lesbosoxylon* Süss & Velitzelos was identified as *Lesbosoxylon kemaliyensis* Akkemik & Mantzouka, sp. nov. Diagnostic features of the new species are: Transition from earlywood to latewood mostly gradual; axial and radial resin canals with thin-walled epithelial cells present; latewood tracheids thin to thick walled; bordered pits on radial walls of tracheids 1-2(-3) seriate; crassulae common; rays heterocellular, uniseriate, partly biseriate; uniseriate rays up to 27 cells high; fusiform rays up to 30 cells high; axial parenchyma occasionally present; ray tracheids 2-3 rows; cell walls of ray tracheids smooth; cross-field pitting pinoid, 1-2(-6) pits per cross-field. Detailed investigation of the botanical affinities of the new fossil wood suggested that the most closely related modern species is *Pinus canariensis* C. Sm in Buch, a relict species from the Canary Islands.

KEY WORDS

Pinaceae,
Miocene,
Sivas Basin,
wood anatomy,
conifer,
biogeography,
new species.

RÉSUMÉ

Le premier rapport d'une espèce de Lesbosoxylon Süss & Velitzelos du Miocène inférieur-moyen de l'Anatolie orientale.

Une nouvelle espèce de pin fossile de l'est de la Turquie est décrite et ses affinités botaniques sont discutées. L'échantillon, a été collecté dans la ville de Kemaliye (province d'Erzincan, en Turquie), et provient de la formation Divriği du Miocène inférieur à moyen. Des sections transversales, tangentielles et radiales ont été prélevées du bois pétrifié et ses caractéristiques paléoxylotomical ont été observées. Basé sur ses caractéristiques anatomiques, notamment des cellules idioblastiques dans les rayons, une nouvelle espèce fossile du genre *Lesbosoxylon* Süss & Velitzelos a été identifiée comme étant *Lesbosoxylon kemaliyensis* Akkemik & Mantzouka, sp. nov. Les caractéristiques diagnostiques de la nouvelle espèce sont les suivantes : transition du bois d'origine au bois final est essentiellement progressive; canaux de résine axiaux et radiaux avec présence de cellules épithéliales à parois minces; trachéides de bois final sont à parois mince à épaisses; fosses bordées sur les parois radiales des trachéides 1-2(-3), sériate, crassulae commun, rayons hétérocellulaires, unisériés, partiellement bisériés; rayons unisériés jusqu'à 27 cellules de haut; rayons fusiformes jusqu'à 30 cellules de haut; parenchyme axial occasionnellement présent; trachéides à rayons de 2-3 rangées; les parois cellulaires des trachéides à rayons sont lisses; ponctuations par champ de croisement pinoïde, 1-2(-6) ponctuations par champ. Une étude détaillée des affinités botaniques du nouveau bois fossile suggère que les espèces les plus modernes est étroitement liée à *Pinus canariensis* C. Sm à Buch, une espèce relictuelle des îles Canaries.

MOTS CLÉS

Pinaceae,
Miocène,
bassin de Sivas,
anatomie du bois,
conifère,
biogéographie,
espèce nouvelle.

INTRODUCTION

Late Oligocene to Pliocene strata in the Eastern Mediterranean region have yielded a particularly rich plant fossil record. This record includes petrified woods (e.g. Sayadi 1973; Selmeier 1990, 2001; Kayacık *et al.* 1995; Akkemik *et al.* 2005, 2009, 2017, 2018; Akkemik & Sakınç 2013; Bayam *et al.* 2018; İamandı *et al.* 2018; Güngör *et al.* 2019), macrofossils (e.g. Kasaplıgil 1977; Denk *et al.* 2017a, b, c; Güner *et al.* 2017) and fossil pollen (e.g., Sancay *et al.* 2006; Yavuz-Işık 2007; Karlıoğlu *et al.* 2009; Akkiraz *et al.* 2011; Bouchal *et al.* 2016, 2017). Recent studies (Bouchal *et al.* 2016, 2017; Denk *et al.* 2017a, b) showed that during the early and early middle Miocene, Turkey was characterized by a forest vegetation dominated by conifers and evergreen and deciduous Fagaceae. Investigations of plant fossil remains (Kayseri Özer *et al.* 2017; Akkemik *et al.* 2018) indicate humid to locally dry climates in the late Oligocene to earliest Miocene and warm temperate climates during the early and middle Miocene in Turkey (Akkiraz *et al.* 2011; Mantzouka *et al.* 2015; Denk *et al.* 2017a, b; Bouchal *et al.* 2016, 2017).

The petrified wood record in the Aegean Basin and Anatolia is remarkably rich and includes many fossil-species from the Neogene such as *Sequoioxylon egemenii* Özgüven-Ertan (Özgüven-Ertan 1971), *Cupressinoxylon akdiki* Özgüven-Ertan (Özgüven-Ertan 1977), *Lesbosoxylon paradoxum* Süss & Velitzelos, *L. pseudoparadoxum* Süss & Velitzelos (Süss & Velitzelos 2010), *Taxaceoxylon biseriatum* Süss & Velitzelos (Süss & Velitzelos 1994a), *Taxodioxylon megalonissum* Süss & Velitzelos and *Glyptostroboxylon microtracheidale* Süss & Velitzelos (Süss & Velitzelos 1997), *Tetraclinoxylon velizelosi* Süss (Süss 1997), *Thujoxylon antissum* Süss & Velitzelos (Süss & Velitzelos 1998), *Chimairoidoxylon lesboense* Süss & Velitzelos (Süss & Velitzelos 1999), *Podocarboxylon articula-*

tum Süss & Velitzelos and *P. graciliradiatum* Süss & Velitzelos (Süss & Velitzelos 2000), *Chimairoidoxylon conspicuum* Süss & Velitzelos (Süss & Velitzelos 2001), *Ginkgoxylon lesboense* Süss & Velitzelos and *G. diversicellulatum* Süss (Süss 2003), *Lesbosoxylon diversiradiatum* Süss & Velitzelos and *L. graciliradiatum* Süss & Velitzelos and *L. ventricosur-radiatum* Süss & Velitzelos (Süss & Velitzelos 2010), *Cryptocaryoxylon lesbium* Mantzouka and *C. lemnium* Mantzouka (Mantzouka 2018), *Pinuxylon alonissianum* Mantzouka & Sakala (Mantzouka *et al.* 2019), *Pistacioxylon ufukii* Akkemik and *Zelkovoxyylon yesimae* Akkemik (Akkemik *et al.* 2018), *Laurinoxylon thomasii* Akkemik, *Mimosoxylon ceratonioides* Akkemik, *Pterocaryoxylon tuncayi* Akkemik, *Prunoidoxylon aytugii* Akkemik (Akkemik *et al.* 2019), *Cupressinoxylon pliocenica* Akkemik and *Cercioxylon zeynepae* Akkemik (Akkemik 2019).

Among these petrified wood taxa, pine was found to be one of the most common woods and various species of pine woods were identified. Within pine wood, two major types corresponding to two subgenera can be referred to as haploxylon and diploxylon types (Mantzouka *et al.* 2019). Furthermore, another diagnostic feature was the presence of axial parenchyma. Together, these features provide reliable information for assessing botanical affinities of fossil wood remains (Wang *et al.* 2017; Mantzouka *et al.* 2019). The aim of the present study is to describe a new fossil pine species from east-central Turkey and to discuss its botanical and biogeographic affinities.

GEOLOGICAL SETTING

The study area is located in the southeast of Divriği, Sivas province, east-central Turkey (Fig. 1). Since the Late Cre-



FIG. 1. — The location of the site, in the Erzurum province, east-central Turkey.

taceous, the Middle East region, Eurasia and Africa-Arabia were involved in the formation of the Alpine belt resulting from plate convergence (Poisson *et al.* 1995). The corresponding N-S shortening caused the closure of the North-Neotethys ocean basins and finally the collision between the Eurasian plate, the Anatolian block and the Arabian plate (Poisson *et al.* 1995).

The convergence of Arabian and Eurasian plates since the mid-Miocene has resulted in the Tibetan-type crustal thickening of the Anatolian Block with the development of the right lateral strike-slip North Anatolian Fault Zone (Şengör & Kidd 1979) and the left lateral strike-slip East Anatolian Fault Zone (Dewey *et al.* 1986). Between these two major faults, the Anatolian Block continues to move westward to accommodate the constant convergence between the Arabian and Eurasian plates (Şengör & Yılmaz 1981; Cater *et al.* 1991).

The formation of sedimentary basins on the Tauride - Anatolide Platform was due to the N-S convergence between the Pontides and Tauride - Anatolide Platform since the Late Cretaceous period after the closure of the northern branch of the Neotethys ocean along the İzmir-Ankara-Erzincan suture region (Gürer & Aldanmaz 2002).

A series of sedimentary basins were created on the Tauride-Anatolide Platform during the Late Cretaceous-Cenozoic period in different areas (Şengör & Yılmaz 1981; Görür *et al.* 1984; Cater *et al.* 1991; Gürer 1996; Poisson *et al.* 1996; Erdogan *et al.* 1996).

The Sivas Basin evolved from marine to lacustrine and fluvial sedimentary environments (Tekin 2001) and is one of the largest Central Anatolian basins which developed during the closure of the northern branch of the Neotethys ocean (Gökten 1993; Poisson *et al.* 1995) between the Pontide Orogen to the north and the Tauride Orogen to the south (Kelling *et al.* 1989; Cater *et al.* 1991). In addition, the Sivas Basin is considered as one of the most important sedimentary basins, in terms of its hydrocarbon potential, in the Central Anatolian region of Turkey (Kavak *et al.* 1997).

Ophiolitic melange, volcano-sedimentary unit, granitoid rocks and Cenozoic sediments characterize the Sivas-Divriği region including the study area (Yılmaz *et al.* 2001). The Cenozoic system is represented by different units to the north and south of the study area, including the early Eocene Subaşı formation, composed of clastic and volcanic rocks and the middle-late Eocene Bozbel formation which includes clastics and limestones (Bilgiç 2008). The latter formation is overlain unconformably by the clastics of the Oligocene Selimiye formation. Early-middle Miocene units are represented by terrestrial clastics of the Karacaören formation in the north and neritic limestones of the Başpınar formation in the south. The Divriği formation which is composed of conglomerates, sandstone and limestone with gypsum intercalations covers these units unconformably. Further, some of these units are unconformably overlain by the late Miocene-Pliocene Yamadağı volcanics and Pliocene Kangal formation and covered by Quaternary deposits (Bilgiç 2008).

The samples studied in the present paper originate from the early-middle Miocene Divriği formation, which is represented by lacustrine limestones and clastics covering large areas south of the Divriği region (Aktimur *et al.* 1988, 1990) and amount to 250 m of thickness (Bilgiç 2008) (Fig. 2).

MATERIAL AND METHODS

The fossil wood sample (Fig. 3) was collected in the vicinity of the city of Kemalîye, Erzurum province (Fig. 1). It is stored in the Department of Forest Botany, Faculty of Forestry, Istanbul University-Cerrahpaşa with the code KEM01.

A piece of the fossil wood was used to produce thin sections, which have a thickness of about 30 microns. Transversal, tangential and radial sections were taken and all microscopic descriptions and photographing were performed on these three sections. The IAWA terminology for coniferous woods (Wheeler *et al.* 2004) was followed. A number of further references (e.g. Mathiesen 1970; Tidwell *et al.*

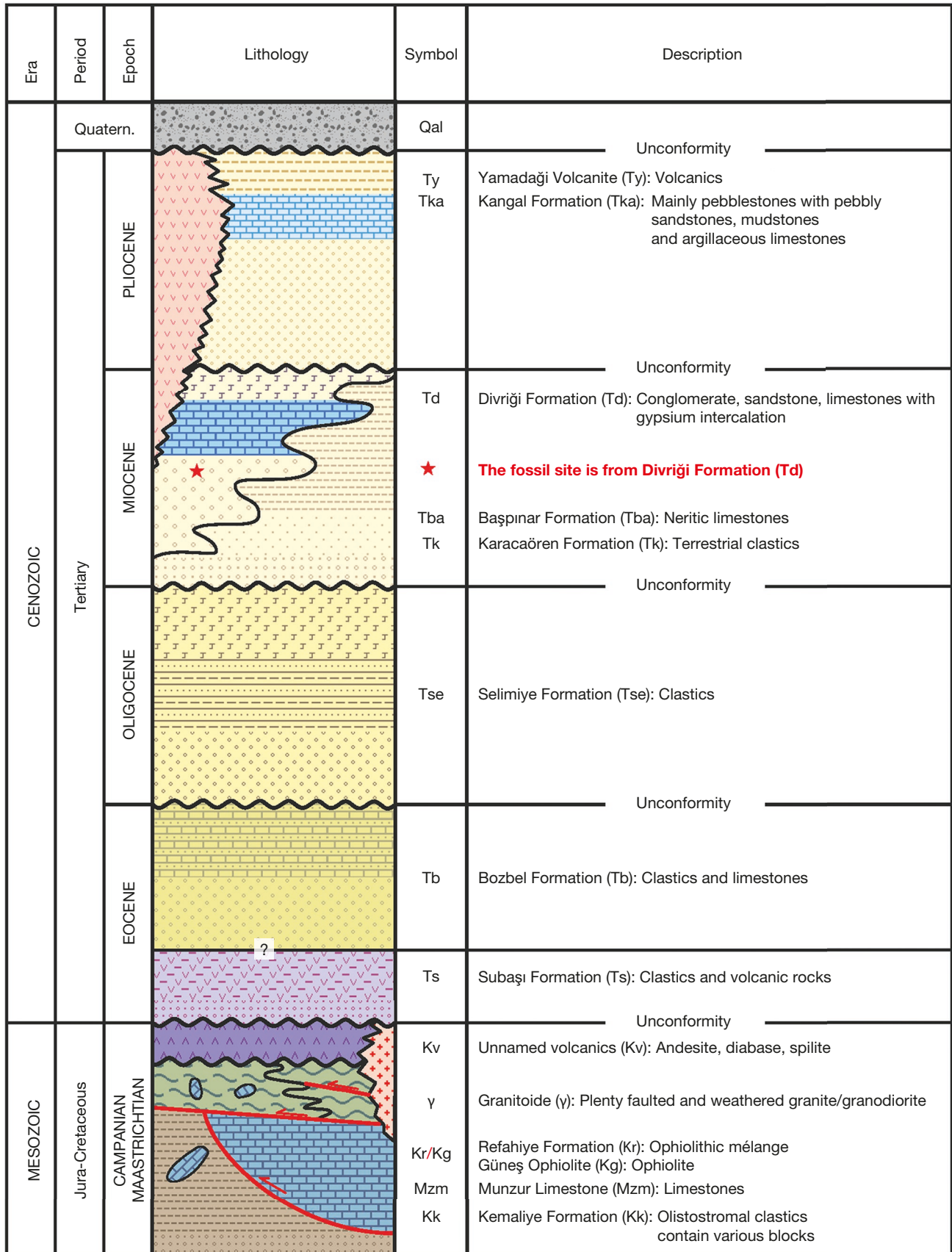


Fig. 2. — Geology and stratigraphic section of the site (early-middle Miocene Divriği formation, Erzincan province, east-central Turkey).



FIG. 3. — The petrified wood used in description (specimen KEM01, 7 × 8 × 19 cm, Istanbul University-Cerrahpasa, Faculty of Forestry).

1986; Dolezych & Schneider 2006; Philippe & Bamford 2008; Süss & Velitzelos 1994a, b, 2009, 2010; Akkemik *et al.* 2016; Blokhina & Bondarenko 2016; Iamandei *et al.*

2016a, b; Wang *et al.* 2017; Bayam *et al.* 2018; Sakala *et al.* 2018; Mantzouka *et al.* 2019; Güngör *et al.* 2019) were used in the descriptions.

TABLE 1. — Diameters of tracheids and pits.

Diameters of tracheids and pits (µm)	In earlywood	In latewood
Radial diameter	53.5 (39.8-69.6)	18.6 (11.5-29.3)
Tangential diameter	37.2 (27.2-47.8)	26.6 (17.9-36.1)
Double cell wall thickness	14.3 (11.5-19.6)	16.5 (10.6-23.3)
Bordered pits	23.5 (14.7-31.0)	–
Cross-field pits	11.3 (6.9-14.9)	–

RESULTS AND DISCUSSION

The fossil wood belongs to the family Pinaceae and to the fossil-genus *Lesbosoxylon* Süss & Velitzelos. The detailed description of the fossil wood is given as follows:

Family PINACEAE L.

Genus *Lesbosoxylon* Süss & Velitzelos

Lesbosoxylon kemaliyensis Akkemik & Mantzouka, sp. nov.
(Figs 3-6)

Plant Fossil Names Registry Number: PFN001780

HOLOTYPE. — Specimen KEM01; repository: Istanbul University-Cerrahpasa, Faculty of Forestry, Department of Forest Botany (designated here).

ETYMOLOGY. — The epithet “*kemaliyensis*” comes from the name of the main city “Kemaliye” nearby the fossil site.

TYPE HORIZON. — Divriği Formation.

AGE. — Early-middle Miocene.

TYPE LOCALITY. — Kemaliye (Eğin), Erzincan, Turkey.

DIAGNOSIS. — Coniferous wood with resin canals. Growth ring boundaries distinct, transition from earlywood to latewood mostly gradual, axial and radial resin canals with thin-walled epithelial cells, latewood tracheids thin to thick walled, bordered pits on radial walls of tracheids 1-2(-3) seriate, crassulae common, rays heterocellular, uniseriate, partly biseriate, uniseriate rays up to 27 cells high, fusiform rays up to 30 seriate high. Axial parenchyma occasionally present. Ray tracheids 2-3 rows, cell walls of ray tracheids smooth. Cross-field pitting pinoid, 1-2(-6) pits per cross-field, horizontal and end walls of ray parenchyma cells smooth and slightly nodular, horizontal walls occasionally pitted, indentures not observed.

DESCRIPTION

The petrified wood sample has grey color; dimensions are 7 × 8 × 19 cm (Fig. 3). In cross section, growth ring boundaries are distinct, transition from earlywood to latewood is mostly gradual (Fig. 4A, B). Measured diameters of tracheids and pits are given in Table 1.

Axial resin canals with thin walled epithelial cells present mostly in latewood zone (Fig. 4A, B). Traumatic resin canals present (Fig. 4C). In tangential section, rays uniseriate (Fig. 4D), and fusiform rays present (Fig. 4E). Rays occasionally biseriate or partly biseriate (Fig. 5A). Big rays with idioblast-like cells present (Fig. 5B-D). Ray cells uniform in some rays, and heterocellular, wider or narrower (Fig. 5D-E). Height of uniseriate rays up to 27 cells (Fig. 4C), height of fusiform rays up to 30 cells and wider (Fig. 4D and Fig. 5D). Average height of rays 4-15 cells. Radial resin canals with thin-walled epithelial cells. Axial parenchyma cells occasionally present, and generally smooth transverse end walls (Fig. 5F-G and I), and slightly nodular (Fig. 5H). Axial resin canal visible in radial section (Fig. 6A). Tracheid pitting in radial walls of earlywood 1-2 (-3) seriate opposite and crassulae formation common (Fig. 5B-D). Cross-field pitting pinoid in 1(-2) rows of usually 1-2(-6) pits per cross-field (Fig. 6E, F). End walls of ray parenchyma cells smooth, no indentures observed. Rays heterocellular. Ray tracheids present, 1-3 seriate, smooth walled (Fig. 6G). Ray cells smooth walled (Fig. 6E-H) and occasionally pitted. These descriptive features are also provided in Appendix A based on “Criteria used according the IAWA for fossil conifers” by Wheeler *et al.* (2004).

ate or partly biseriate (Fig. 5A). Big rays with idioblast-like cells present (Fig. 5B-D). Ray cells uniform in some rays, and heterocellular, wider or narrower (Fig. 5D-E). Height of uniseriate rays up to 27 cells (Fig. 4C), height of fusiform rays up to 30 cells and wider (Fig. 4D and Fig. 5D). Average height of rays 4-15 cells. Radial resin canals with thin-walled epithelial cells. Axial parenchyma cells occasionally present, and generally smooth transverse end walls (Fig. 5F-G and I), and slightly nodular (Fig. 5H). Axial resin canal visible in radial section (Fig. 6A). Tracheid pitting in radial walls of earlywood 1-2 (-3) seriate opposite and crassulae formation common (Fig. 5B-D). Cross-field pitting pinoid in 1(-2) rows of usually 1-2(-6) pits per cross-field (Fig. 6E, F). End walls of ray parenchyma cells smooth, no indentures observed. Rays heterocellular. Ray tracheids present, 1-3 seriate, smooth walled (Fig. 6G). Ray cells smooth walled (Fig. 6E-H) and occasionally pitted. These descriptive features are also provided in Appendix A based on “Criteria used according the IAWA for fossil conifers” by Wheeler *et al.* (2004).

DISCUSSION

A typical haploxyton *Pinuxylon* has thin walled axial and radial resin canals, pinoid type of cross-field pitting, ray tracheids with smooth horizontal and end walls of ray parenchyma (Mantzouka *et al.* 2019). The wood samples investigated in the present study meet all the anatomical features of a *Pinuxylon*, but having in addition an “unusual” occurrence of seemingly idioblastic cells in rays. Idioblasts (oil and/or mucilage cells) represent a special feature in angiosperms and have been studied in several scientific works and even categorized (e.g., Mantzouka *et al.* 2016), but they are not a common characteristic in conifers.

Many fossil pine species described with smooth or weakly dentate horizontal walls of ray tracheids (see table 1 in Wang *et al.* 2017) were described. They comprise *Pinus uniseriata* and *Pinus nanfengensis* (Wang *et al.* 2017), *Pinus albicauloides* S.K. Choi & K. Kim (Choi *et al.* 2010), *Pinus* cf. *armandii* Franchet (Yi *et al.* 2002), *Pinus chemrylensis* Blokhina (Blokhina 1995), *Pinus hatamuraenase* Jeong & Kim (Jeong *et al.* 2012), *Pinus benanensis* J.J. Yang (Yang *et al.* 1990), *Pinuxylon dakotense* (Knowlton) Read (Nishida & Nishida 1995), *Pinuxylon arjuzanxianum* Huard (van der Burgh (1973), *Pinuxylon cembraeforme* Rössler (Rössler 1937), *Pinuxylon parryoides* (Kräusel) van der Burgh (van der Burgh (1964, 1973), *Pinuxylon pinastroides* (Kraus) Stockmans & Willière (van der Burgh (1973), *Pinuxylon ponderosoides* van der Burgh (van der Burgh (1973), *Pinuxylon similkameenensis* Miller (Miller 1973), *Pinuxylon tarnocziense* (Tuzsón) Greguss (van der Burgh (1973), *Pinuxylon woolardii* Tidwell, Parker & Folkman (Tidwell *et al.* 1986), *Pinuxylon zobelianum* (Goepfert) Kräusel (van der Burgh 1964). Later, Mantzouka *et al.* (2019) demonstrated that extant pines are separated in two groups: Haploxyton pines, with smooth horizontal walls of ray tracheids, and Diploxyton pines, with dentate horizontal walls of ray tracheids. Because our *Pinuxylon* has smooth horizontal walls of ray tracheids, we classified it as

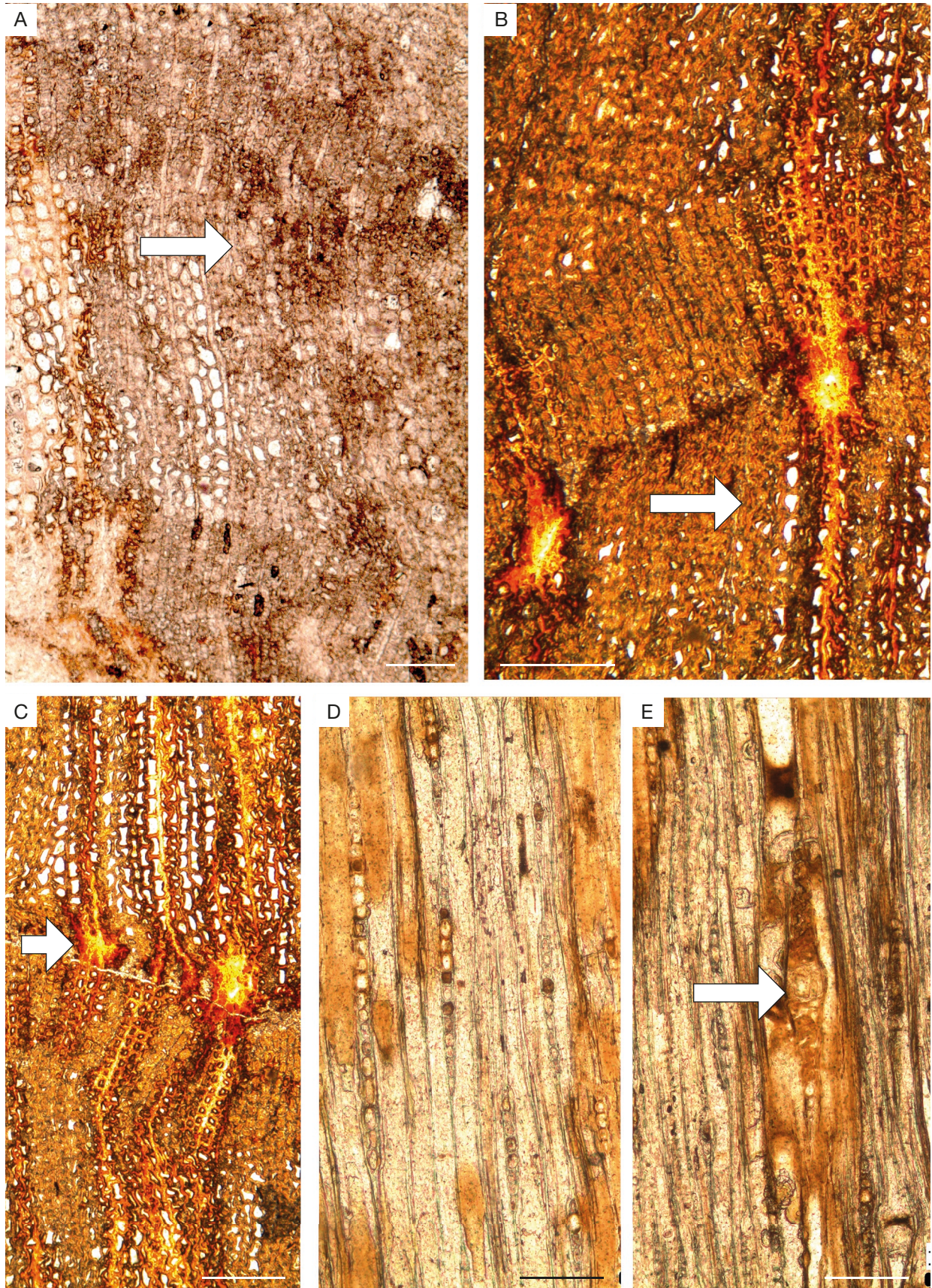


FIG. 4. — Wood features of *Lesbosoxylon kemaliyensis* Akkemik & Mantzouka, sp. nov.: **A, B**, transversal section with gradual transition from earlywood to latewood (**arrow**); **C**, traumatic resin canals in transversal section (**arrow**); **D**, uniseriate rays in tangential section (**arrow**); **E**, fusiform ray with horizontal resin canal, and resinous cells around the ray (**arrow**). Scale bars: A-C, E, 200 μ m; D, 100 μ m.

a Haploxyton pine. Some Haploxyton fossil pine woods were also mentioned in Mantzouka *et al.* (2019). They are *Pinuxylon haploxyloides* Greguss, with a single pinoid cross field pit per cross-field (Sakala *et al.* 2018), *Pinuxylon succiniferum* (Göppert) Kräusel emend. Dolezych (Dolezych *et al.* 2011) without axial parenchyma, and *Pinuxylon nightigalense* Vozenin-Serra (Vozenin-Serra 1971) with taxodioid to ooporoid pittings in cross-fields.

Axial parenchyma present in the here studied fossil wood clearly sets them apart from numerous species, which have smooth or weakly dentate horizontal walls of ray tracheids given in Wang *et al.* (2017). The fossil *Pinuxylon* species with axial parenchyma are *Pinus chemrylensis* Blokhina (Blokhina 1995) and *Pinus hatamuraenase* Jeong & Kim (Jeong *et al.* 2012). Furthermore, Süß & Velitzelos (1993) described *Pinoxylon parenchymatosum* Süß & Velitzelos with axial parenchyma. Another fossil pine wood, *Pinuxylon* sp. cf. *Pinus sylvestris* L. (Iamandei *et al.* 2011, 2016b) has also axial parenchyma and 2-3 seriate rays, and the same is true for *Pinuxylon marinasii* Iamandei & Iamandei (Iamandei & Iamandei 1999). *Pinoxylon yabei* Shimakura (Shimakura 1936) has also axial parenchyma in growth ring boundaries (Kim *et al.* 2005). Hence, to our knowledge, only six fossil pine species have axial parenchyma cells.

In *Pinus chemrylensis*, cross-field pitting is piceoid, taxodioid and cupressoid, and tracheidal pitting is uniseriate (Blokhina 1995). In our wood, cross-field pitting is pinoid, and tracheidal pitting is biseriate and, commonly, with crassulae.

In *Pinus hatamuraenase*, cross-field pitting is pinoid and taxodioid, and tracheidal pitting is biseriate (Jeong *et al.* 2012). Our wood is similar to this fossil species, but differs in having crassulae and idioblasts. Our specimen has also been compared with *Pinuxylon* sp. cf. *Pinus sylvestris* (Iamandei *et al.* 2011, 2016b) from the Romanian Carpathians which has axial parenchyma and 2-3-seriate rays. *Pinoxylon yabei* Shimakura is completely different from our fossil having axial parenchyma only in growth ring boundaries, bordered pits arranged in three rows, thick-walled epithelial cells of resin canals, occurrence of traumatic canals and 1-3 seriate rays with up to 70 cells height.

In *Pinuxylon marinasii* Iamandei & Iamandei (Iamandei & Iamandei 1999), the wood has features very close to our fossil pine sample. It has axial parenchyma, which may rarely be seen in longitudinal section. Ray heights up to 35 cells, horizontal walls of ray tracheids are smooth and slightly wavy, or with small denticles on inner walls. Tracheid pits 1(-2) seriate, crassulae rare, and 1-3(4) taxodioid small pits in cross-fields. In contrast, our wood has large pinoid type cross-field pits, 1-2 (very rarely up to 5) per cross-field, and ray tracheids are not denticulate in inner walls.

Comparing our specimen with the fossil pine woods from Greece many differences occur: *Pinoxylon paradoxum* Süß & Velitzelos (Süß & Velitzelos 1994b) from Lesbos Island is characterized by the presence of spiral thickenings and *P. pseudoparadoxum* Süß & Velitzelos (Süß & Velitzelos 1994b, Lesbos Island) has high rays of up to 50 cells.

Süß & Velitzelos (2009, 2010) have introduced the genus *Lesbosoxylon* as a special wood type of *Pinuxylon* with idio-

blastic cells in rays established from anatomical studies from “in situ” (*L. paradoxum* [Süß & Velitzelos 1994b, 2010]) in the area of Bali Alonia Petrified Forest Park and from dispersed (not “in situ”) small wood remnants (“lose Stücke” as stated in Süß & Velitzelos 1994b and wood pebbles in rubble: “Kieselholzfunde”, “lose Gerölle” as stated in Süß & Velitzelos 2009, 2010) from Chamandroula (near Eressos) and Megalonissi (Nisiopi) islet (*L. pseudoparadoxum* [Süß & Velitzelos 1994b, 2010]) and Eressos area (*L. ventricosuradiatum*, *L. diversiradiatum*, *L. graciliradiatum* [Süß & Velitzelos 2010]). This genus is still regarded as a distinct genus represented only by the fossil “protopinaceous” woods from Lesbos Island (e.g., Velitzelos *et al.* 2014). The present study showed that this fossil “protopinaceous” wood is also found in Anatolia during the early Miocene.

Süß & Velitzelos (2009) also mentioned this unusual feature in modern wood of *Pinus pseudostrobus* but we did not find mentioning about the occurrence of idioblasts in this modern species when doing a literature search. In the same paper (Süß & Velitzelos 2009), resin ducts are mentioned reported in the work of Werker & Fahn (1969).

Pinoxylon parenchymatosum Süß & Velitzelos (Süß & Velitzelos 1993) from Lemnos Island is characterized by the occurrence of axial parenchyma, a feature in accordance with our fossil. Our specimen is closely similar to two more species from Lesbos Island identified by Süß & Velitzelos (2009): *Lesbosoxylon* (= *Pinoxylon*) *diversiradiatum* Süß & Velitzelos because the latter has bi-seriate rays and *L.* (= *Pinoxylon*) *graciliradiatum* Süß & Velitzelos which has large rays with “idioblast-like” cells. It might also be very similar to *Lesbosoxylon* (= *Pinoxylon*) *ventricosuradiatum* Süß & Velitzelos (e.g. rays with “idioblast-like” cells and pits in the cross-field and ray tracheids not ascertainable) (Süß & Velitzelos 2010).

Based on a number of diagnostic characteristics, coniferous wood with resin canals, distinct growth ring boundaries, axial and radial resin canals with thin-walled epithelial cells, 1-2(-3) seriate of bordered pits on radial walls of tracheids, heterocellular, uniseriate to partly biseriate rays, presence of axial parenchyma, smooth walls of ray tracheids and having big rays with idioblast-like cells, we consider our wood to represent a new fossil *Lesbosoxylon* species and named it *Lesbosoxylon kemalijensis* Akkemik & Mantzouka, sp. nov.

BOTANICAL AFFINITIES

According to the discussion in Tidwell *et al.* (1986), the family Pinaceae is represented by 10 genera in the extant flora (note that Tidwell did not consider *Nothotsuga* in his classification; for a modern classification of Pinaceae, see e.g., Neale & Wheeler 2019). Neale & Wheeler (2019) suggested 11 genera within the family Pinaceae including *Nothotsuga*, and recognized two subfamilies Pinoideae and Abietoideae. Furthermore, based on ray morphology and whether normal horizontal and vertical resin ducts are present in their wood, four groups have been distinguished (Greguss 1955; Watari 1956; Roy & Hills 1972) as follows:

– Group 1: Pinaceous woods having heterogeneous rays with both horizontal and vertical resin ducts [*Pinus* L.,

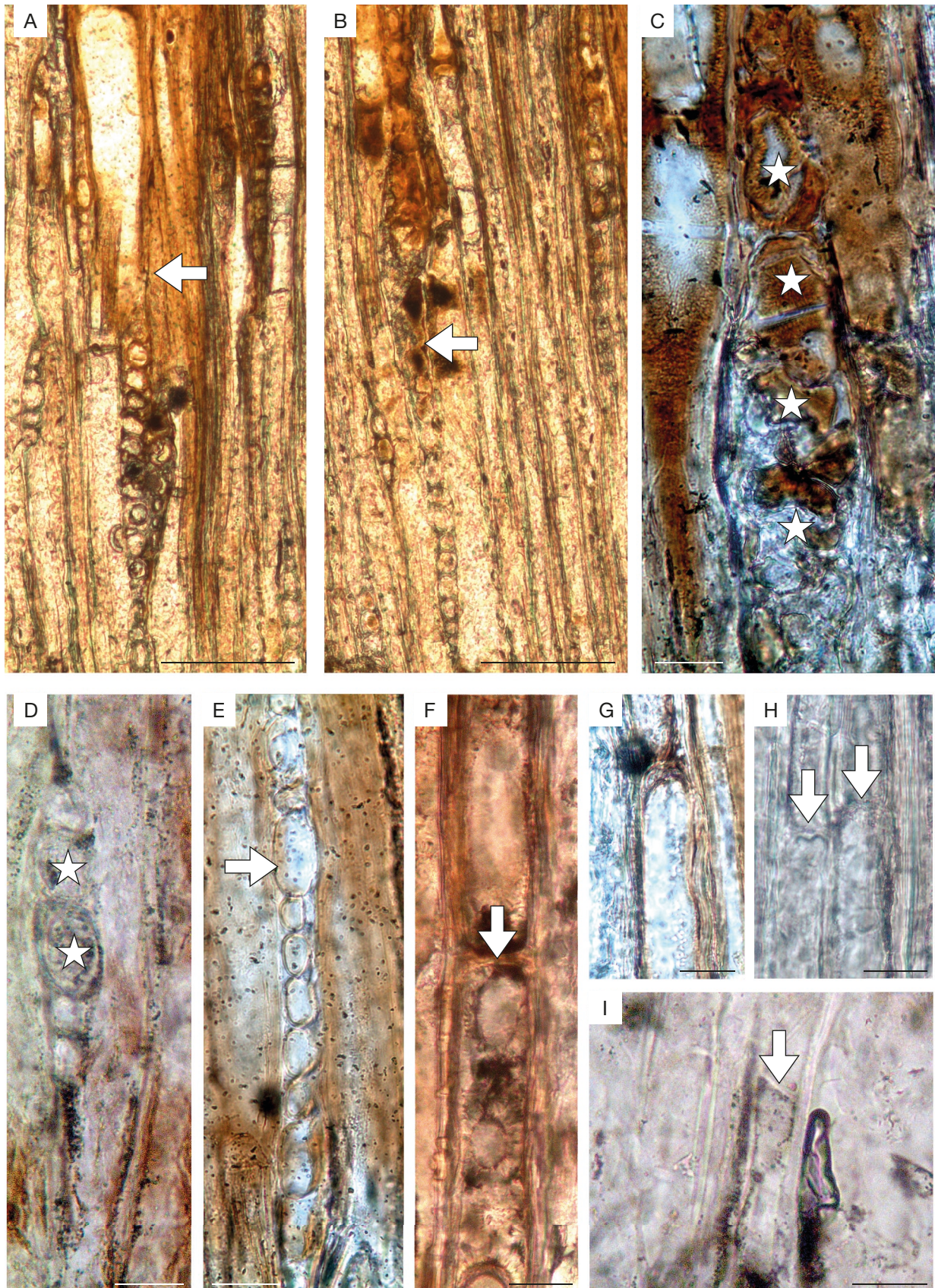


FIG. 5. — Wood features of *Lesbosoxylon kemaliyensis* Akkemik & Mantzouka, sp. nov.: **A**, Biseriate ray (black arrow) and tracheids with resin material (white arrow); **B**, a tall fusiform ray (arrow); **C**, **D**, big rays with idioblast-like cells (asterisk); **E**, heterocellular ray cells in a ray; **F**, **G**, **H**, **I**, axial parenchyma cells with smooth end walls (white arrows), and slightly nodular end walls (black arrow). Scale bars: A, B, E, 100 μ m; C, D, F-I, 20 μ m.

Picea A. Dietrich, *Larix* Miller, *Cathaya* Chun & Kuang (Hu & Wang 1984), and *Pseudotsuga* Carrière]. This group reflects a monophyletic group within Pinaceae (Neale & Wheeler 2019). Our wood, which has heterogeneous rays with horizontal and vertical resin ducts, falls clearly into this group.

– Group 2: Pinaceous woods with heterogeneous rays, without normal resin ducts (*Cedrus* Trew. and *Tsuga* (Endlicher) Carrière). This may reflect the plesiomorphic state in Pinaceae, where *Cedrus* is sister to the rest of the family.

– Group 3: Pinaceous woods with homogeneous rays and only vertical resin ducts (*Keteleeria* Carrière).

– Group 4: Pinaceous woods having homogeneous rays and lacking any resin ducts (*Pseudolarix* (J. Nelson) Rehder and *Abies* Miller). The loss of resin ducts may have occurred independently in these two genera (cf. Neale & Wheeler 2019).

Regarding the presence of wood parenchyma, in Patel (1971) based on Bailey (1909): in *Pinus*, as has been noted, Gothan asserts the absence of spirals, yet Penhallow (1907) has described them as occurring in *Pinus taeda* L. Bailey (1909) also observed this feature in *Pinus attenuata* Lemm (Patel 1971). Recently, DM (co-author of this paper) has also observed them in *Pinus attenuata* and several other species. Furthermore, spiral thickenings occur in the ray tracheids of *Pinus balfouriana* A. Murr., they are strongly developed in certain specimens and only feebly in others. *Pinus strobiformis* Engelm. and other pines from the southwestern United States show traces of their occurrence. The occurrence of spiral thickening in the wood of radiata pine described by Barker (1927) was in fact, the spiral checking which is associated with an abnormality called compression wood (Patel 1971).

However, Tidwell *et al.* (1986) stated, based on Greguss (1955) and Penhallow (1907), that wood parenchyma might occur very rarely in some *Pinus* species such as *P. monophylla* Torr. & Frem. and *P. massoniana* Lamb., whereas spiral thickenings were described in *Pinus taeda*.

Güner *et al.* (2017) described 3-needle and 2-needle pine macrofossils from middle Miocene strata in southwestern Turkey. Three-needled samples were compared to *Pinus canariensis* C. Sm. (subgenus *Pinus*; diploxylon pines) and members of the North American section *Trifoliae* in the same subgenus. Two-needled pine samples were also closer to the subgenus *Pinus*. From early Miocene strata of Güvem, cones with affinities to subgenus *Pinus* and leaf fascicles with affinities to subgenera *Pinus* and *Strobis* (haploxylon pines) are known (Kasaplıgil 1977; Denk *et al.* 2017a). Fossil pine cones and seeds from Greece have been related to *Pinus roxburghii* Sarg. and *P. canariensis* C.Sm. (Mai & Velitzelos 2007; Boyd 2009; Kvaček *et al.* 2014). In the palynological record, diploxylon and haploxylon pines have been distinguished for many early and middle Miocene sites in Turkey (Bouchal *et al.* 2016, 2017; Bouchal 2018; Denk *et al.* 2017a). These findings show that both haploxylon and diploxylon pines were present during the Miocene in Turkey. Due to the smooth ray tracheids, our wood can be considered to represent a haploxylon pine species.

Taking into account the work by Esteban *et al.* (2004) and mainly after using the presence of diffuse axial parenchyma and of axial and radial resin canals as the most important

“filters”, the following modern pines are closely similar to our fossil-species: *Pinus canariensis* C. Sm in Buch, *P. douglasiana* Martínez, *P. hartwegii* Lindl., *P. lawsonii* Roehl ex Gordon, *P. montezumae* Lamb., *P. tabuliformis* Carrière and *P. thunbergii* Parl. in Candolle. From the above mentioned species we excluded the following ones:

Pinus douglasiana Martínez is excluded because it does not have well-defined growth rings; *P. hartwegii* Lindl., and *P. thunbergii* Parl. in Candolle are excluded because they do not have thin-walled epithelial cell resin canals; *P. lawsonii* Roehl ex Gordon is excluded because it has spiral thickenings in all the axial tracheids (a feature not in accordance with our wood); *P. tabuliformis* Carrière is excluded because it does not have pinoid cross-field pits.

Among the remaining species, *Pinus canariensis* C. Sm in Buch and *P. montezumae* Lamb., taking into account also the “whole plant concept” *sensu* Sakala (2004) and Kvaček (2008), we suggest that our fossil is more closely related to *Pinus canariensis* C. Sm & Buch. However, some features of this species such as: 1) spiral thickenings present but not in all the axial tracheids; 2) bordered pits present on the tangential walls of the axial tracheids; and 3) dentate ray tracheids with the height of the dentations < 2.5 µm, are not seen in our sample. Ray parenchyma with nodular axial walls and ray parenchyma with resin canal are features shared by *Pinus canariensis* and *Lesbosoxylon kemaliyensis* Akkemik & Mantzouka, sp. nov. Based on cone and leaf imprints, Kasaplıgil (1977) also described *P. canariensis* from the early Miocene of central Anatolia.

CONCLUSION

In this study, we describe a new pine species (*Lesbosoxylon kemaliyensis* Akkemik & Mantzouka, sp. nov.) from the Miocene of Turkey and compare it to fossil and living pine species. Among living species, the fossil-species resembles most closely the endemic *P. canariensis* (subgenus *Pinus*, diploxylon pines) from the outer Canary Islands. A large number of macrofossils (leaf fascicles and cones) and microfossils (dispersed pollen) demonstrate that both diploxylon and haploxylon pines were common in Turkey during the early and middle Miocene. Today, Turkey has only five diploxylon pine species (*Pinus brutia* Ten., *P. halepensis* Mill., *P. nigra* Arnold, *P. pinea* L., and *P. sylvestris* L.), and all haploxylon pine species are extinct. The here described fossil-species suggests that the lineage leading to the modern *P. canariensis* had a much greater distribution during large parts of the Cenozoic.

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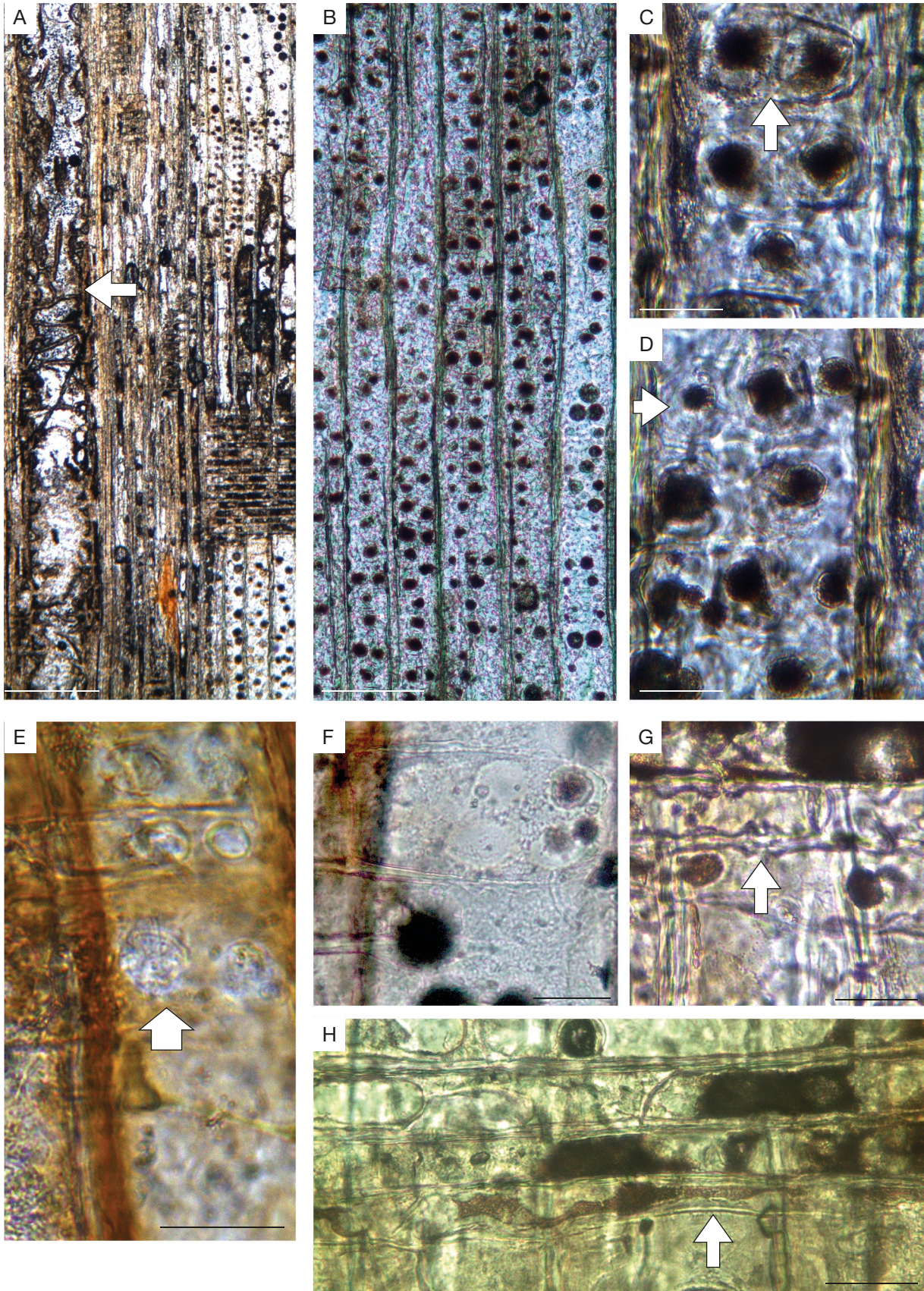


FIG. 6. — Wood features of *Lesbosoxylon kemaliyensis* Akkemik & Mantzouka, sp. nov.: **A**, radial section with axial resin canal (arrow); **B-D**, 1-3 seriate of tracheidal pitting, and crassulae formation common (white arrow); **E**, pinoid type cross-field pitting, 1-2 pits per cross-field on one row, and smooth end wall of ray cell; **F**, six pits on two rows in a cross-field (arrow); **G**, pit border on ray tracheids (arrow); **H**, one-two seriate of smooth-walled ray tracheids (arrow). Scale bars: A, 200 μ m; B, 100 μ m; C-G, 20 μ m; H, 30 μ m.

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APPENDIX 1. — The observed descriptive features for softwoods by Wheeler *et al.* (2004). Special feature observed in the present work is shown in **bold**.

- 40 Growth ring boundaries distinct;
43 Transition from earlywood to latewood mostly gradual;
45 Tracheid pitting in radial walls of earlywood 1-2 (-3) seriate;
46 Arrangement of tracheid pitting opposite;
54 Latewood tracheids generally thin-walled;
56 Torus presents;
72 Axial parenchyma occasionally presents;
73 Diffuse;
76 Transversal end walls of axial parenchyma smooth;
78 Slightly nodular;
79 Ray tracheids present, 1-3 seriate;
85 Ray cells smooth walled;
86 End walls of ray parenchyma cells smooth;
87 Ray cells smooth walled and occasionally pitted;
91 Cross-field pitting pinoid;
98 Predominantly 1-2 (rarely up to 6) pits per cross-field on 1(-2) rows;
103 Average height of rays generally 4-15 cells (rarely up to 30 cells);
107 Rays uniseriate, and fusiform rays present;
108 Rays occasionally biseriate or partly biseriate;
109 Axial resin canals presents;
111 Traumatic resin canals presents;
117 Epithelial cells with thin walled.
Idioblast-like cells present in rays.