Sequoioideae (*Cupressaceae*) woods from the upper Oligocene of European Turkey (Thrace)

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Abstract. Six Upper Oligocene mummified fossil wood samples originating from the Agacli Lignite Quarry near Istanbul (Turkey) were anatomically studied and identified as *Sequoioxylon*. This record increases the understanding of the palaeoenvironments of Turkey during the Oligocene and thus represents an important contribution to the poorly understood vegetation existing between Europe and Asia during the Tertiary.

Key words: fossil wood, Oligocene, palaeobotany, *Sequoioideae*, *Sequoioxylon*, Turkey

Introduction

Identification of tree species based on wood anatomy is of interest not only to taxonomists studying extant vegetation but also for studies focusing on past environments and ecosystems especially when other vegetative or reproductive parts are not available (Visscher & Jagels 2003). Few palaeobotanical studies have been undertaken on the fossiliferous deposits of Turkey and thus little is known about the Tertiary vegetation and environments of this region. Those palaeobotanical investigations that have been undertaken, on both microfossils (Sanli 1982) and macrofossils (Özgüven 1971; Eroskay & Aytug 1982; Sanli 1982; Kayacik & al. 1995; Aras & al. 2003), have concentrated on Tertiary sediments around Anatolia (the Asian part of Turkey) and Thrace (European Turkey) (Fig. 1). Within the Northern Thrace Basin (Fig. 1) evidence from petrified woods for *Carya* sp. and *Juglans* sp. (Eroskay & Aytug 1982) have been found alongside the pollen of such more exotic taxa as *Ginkgo* sp., *Podocarpus* sp., *Pseudotsuga* sp., *Cedrus* sp. and *Pinus* sp. (Sanli 1982). The Agacli Lignite Quarry has yielded ample Tertiary fossil material, including wood of *Pinus* sp., *Taxus* sp., *Juniperus* sp., *Juglans* sp., *Quercus* sp., and *Salix* sp. (Aytug & Sanli 1974), alongside *Sequoia* type pollen (Bati 1996). The only record of taxodiaceous wood was the material of *Sequoioxylon (S. egemeni)* described from Tertiary sediments within the Northern Thrace Basin (Özgüven 1971) and the wood from a second lignite quarry near Çiftalan village (Eyüp district, Istanbul; Fig. 1) with the greatest similarity to *Sequoiadendron giganteum* (Kayacik & al. 1995).

Since our understanding of the vegetation that grew in Turkey during the Tertiary is relatively poor, the aim of this study was to identify the fossil wood samples in order to further the knowledge pertaining to both the woody component of the vegetation and thereby to the palaeoenvironment that existed across Turkey during Oligocene.

Material and methods

This work focuses on six pieces of Tertiary mummified fossil wood (Plate I, Figs 1–6) originating from

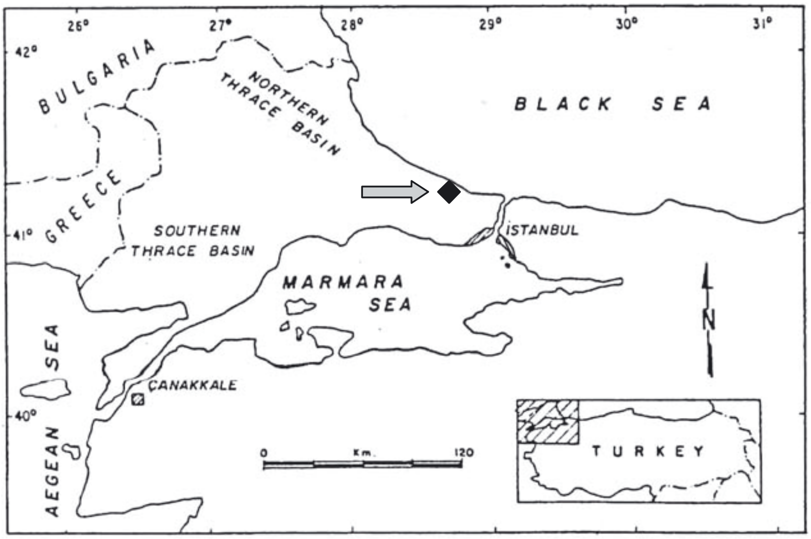

Fig. 1. Locality map indicating the location of Agacli Lignite Quarry and other places mentioned in the text.

the Agacli Lignite Quarry (41° 17' 20'' N, 28° 44' 30'' E) situated near the village of Çiftalan in the Eyüp district of Istanbul, Turkey (Fig. 1). The specimens were collected by Dr. Burhan Aytug in 1995 and are deposited in the Akkemik Collection housed in the University of Istanbul, Faculty of Forestry and Department of Forest Botany.

On the basis of extensive palynological studies it is widely accepted that the age of the coal-bearing strata within the sequence from which the wood material was found (depicted with the bold horizontal lines in Fig. 2) represents the Upper Oligocene Danismen to Çöpköy Formations (Nakoman 1968; Ediger & Bati 1988; Ediger & al. 1990; Elsik & al. 1990; Akyol & Akgün 1995).

Of the six samples retrieved from the quarry, one sample (Specimen 6) had previously been studied and assigned to *S. giganteum* on the basis of tracheid and ray characters (Kayacik & al. 1995), but has been re-examined and included here for completeness. Aras & al. (2003) later identified a second large stem (approximately 115 cm) from the same lignite quarry as *S. giganteum.*

Although *Taxodiaceae* have recently been synonymised into the *Cupressaceae* (Gadek & al. 2000; Farjon 2001), in this work the fossil material previously assigned to the Taxodiaceae will be referred to as 'taxodiaceous' rather than 'cupressaceous' for clarity.

Thin sections (20–40 μm) of the wood material were cut with a Richert microtome and prepared by standard methods, which include the staining, in Safranin T, of the three planes of section (transverse, tangential- and radial longitudinal). Anatomical analyses were performed with a light microscope and described using the terminology of the IAWA Committee (2004) for softwood identification wherever possible. Mean and maximum numbers of cells were determined from 50 replicates for each character measurement. Due to compression, measuring the tracheid lengths was problematical and only 20 (rather than 25) measurements per character were carried out for each specimen.

Since accurate identification requires detailed descriptions and comparisons with well-described extant wood, preferably from vouchered specimens (Visscher & Jagels 2003), the fossil woods were compared with published literature (e.g. Jacquiot 1955; Hejnowicz 1973; Gromyko 1982; Kayacik & al. 1995; Visscher & Jagels 2003) and sections of modern material housed in the National Herbarium of the Netherlands (Utrecht Branch) and the Royal Botanic Garden, Kew (UK). Finally, the specimens were compared with similar fossils formerly assigned to the *Taxodiaceae* (e.g. Greguss 1955; Özgüven 1971; Basinger 1981; Aras & al. 2003).

The largest piece (Specimen 6) of the six wood samples collected could be used for tree-ring measurements. A tree-ring chronology was construct-

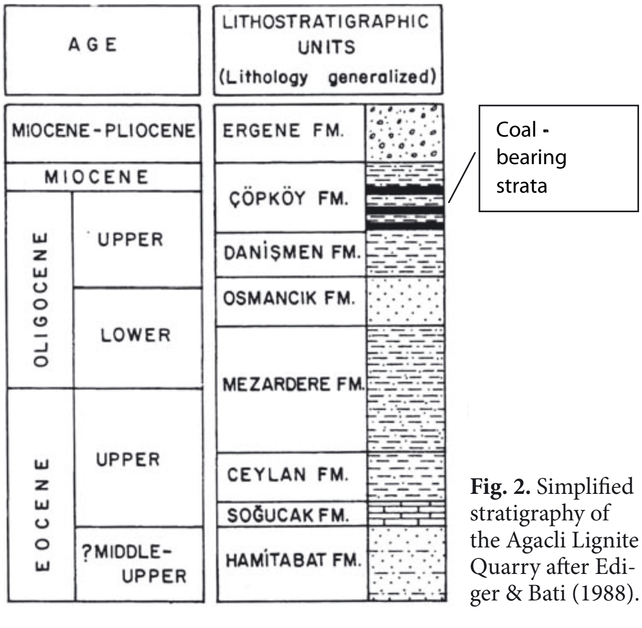

Fig. 2. Simplified stratigraphy of the Agacli Lignite Quarry after Ediger & Bati (1988).

ed with the help of CRONOL computer program (in DPL) (Grissino-Mayer & al. 1996) based on the 416 tree rings of the fossil wood No 6. This chronology was compared with the latest 1000-year period of the 3220-year long Giant Sequoia Master Chronology (Hughes & al. 1994). The frequency of extreme negative years was investigated in both the current and the fossil tree ring series. To do this the mean of the below-average values of the chronology was calculated and the "lower mean" obtained. Those values falling below the lower mean were considered to represent extremely negative years.

Results

The description of the wood is based on the anatomical characteristics of all six pieces of large organ/trunk wood, measuring 1.2–24.5 cm in diameter, and 11–97 cm in length (Table 1; Plate I, Figs 1–6).

Transverse section: Wood material is mummified, with some areas having undergone significant decay. Growth rings in Specimen 6 number over 416 tree-rings. Growth rings in the other specimens range from 13–51 in number (Table 1). Tree rings measure between 0.5 and 2 mm in width. The transition between earlywood and latewood is generally distinct – abrupt or semi-abrupt (Plate II, Fig. 1, Plate IV, Fig. 1). Tracheids of both earlywood and latewood are more or less angular in cross section. Radial diameters of the earlywood tracheids measure 55–90 μm (mean = 71 μm), whereas tangential diameters measure 40–67 μm (mean = 52 μm). In well-preserved regions, tracheid cell wall thickness ranges from 2.5–3.8 μm in the earlywood to 6.3–12 μm in the latewood. Resin canals are absent. Wood parenchyma is present and diffuse, especially in the transition zone from earlywood to latewood and within the latewood. Parenchyma cells are filled with resin-like globules (Plate II, Fig. 3) and have smaller or equivalent radial and tangential dimensions when compared with the surrounding tracheids.

Tangential longitudinal section: Tracheidal pitting is abundant, with circular bordered pits located on tangential walls of some earlywood tracheids (Plate II, Fig. 2), the circular pits ranging from 14–23 μm in diameter. Occasionally, more or less solitary pits were observed on some tangential walls of the latewood tracheids. Rays are predominantly [mean 95 % (range 88–98 %)] uniseriate, occasionally [mean 5 % (range 2–12 %)] biseriate within the body of the rays. Ray height ranges from 1 to 28 cells in specimens 1, 2, 3 and 6 (Plate II, Fig. 4), and up to 41 and 61 in specimen 5 and specimen 4 (Plate IV, Fig. 3) respectively. Ray cell walls in the tangential section measure 2.5–6.25 μm. Axial parenchyma cells generally have smooth end walls (Plate II, Figs 4–5), but sometimes and more rarely the horizontal end walls are slightly dentate.

Radial section: Tracheids range from 4.3 to 9 mm in length. Tertiary or spiral thickenings are absent. Tracheid walls have abundant circular bordered pits in uniseriate rows and oppositely arranged pits in biseriate rows; some triseriate rows were observed in Specimens 4 and 5 (Plate IV, Fig. 2) located predominantly in the earlywood tracheids. Pits are closely spaced, sometimes crowded (Plate II, Fig. 6 and Plate III, Fig. 1) and measure 16–23 μm in diameter. Degradation around the edges of some bordered pits can be clearly seen in Specimen 5 (Plate IV, Fig. 5). Crassulae are frequently observed between pits forming bi- to triseriate rows but are less frequent between uniseriate pits (Plate II, Fig. 6 and Plate III, Fig. 1). The numbers of successive biseriate-bordered pits are in the range of 19–20 in Specimens 4 and 5, and 17–42 in the remainder. Most rays appear to be homogeneous although ray tracheids are present in all specimens. Ray tracheids are most frequent in Specimens 4 and 5, where they are located in the upper or lower borders of some rays (Plate III, Fig. 2). Ray cell walls of all specimens are generally smooth and seldom dentate. Horizontal ray cell walls measure 2.5–5 μm in thickness. Half-bordered pit pairs in the cross-fields number 2–4(-7) (-8 in Specimen 2) (Plate III, Fig. 3). Cross-field pits measure 8–14 μm in diameter and are arranged in one or two horizontal rows in the cross-fields of the wider earlywood tracheids (Plate IV, Fig. 4), and in one or two vertical rows in the narrower latewood tracheids. Pit borders are broad, elliptical to round; apertures are generally oval and commonly horizontally orientated. Pits are more abundant in the uppermost and lowermost marginal ray cells, arranged in one or two horizontal rows. Axial parenchyma is composed of 6–11 cells in Specimens 4 and 5, and up to 14 cells in the remaining specimens with the marginal cells tall (1.4–1.94 mm relative to the cells (0.13–0.23 mm) located in the middle of the axial chain.

All samples can be assigned to the *Sequoioideae* of the *Cupressaceae* based on the following features: (1) generally abrupt transition from earlywood to latewood; (2) absence of true resin canals; (3) predominantly two rows of opposite pits on the radial walls of tracheids; (4) crassulae conspicuous; (5) rays homogeneous, with some rays having ray tracheids present; (6) cross-field pitting predominantly taxodioid; (7) wood parenchyma present, diffuse, resinous; and (8) horizontal end walls of axial parenchyma are either smooth or very seldom nodular. The six fossil woods under consideration could be separated further on the basis of (1) ray height, where Specimens 1,2,3 and 6 attain maximum heights of < 30 cells (mean 4–6 cells) when compared with the rays of Specimens 4 and 5, where rays can reach a maximum of c. 60 cells (mean 9–10 cells); (2) ray number per mm, where Specimens 1,2,3, and 6 have ray abundances of > 40, whereas those of Specimens 4 and 5 have abundances of < 40; and (3) occasional triseriate bordered pits can be observed in the tracheids of Specimens 4 and 5. However, the differences exhibited with regard to ray height and abundance could be due to different relative ontogenetical ages of the specimens under study, whereas increase in the number of rows of tracheid pits in two of the specimens could be related to the organ of origin (cf. Falcon-Lang 2005). Therefore, although slight differences amongst the specimens have been noted, they do not warrant further subdivision.

Discussion

Comparisons with extant and fossil taxa

Identification of taxodiaceous wood to generic level is often very difficult. The main wood features of modern taxodiaceous genera are summarised in Table 2. These genera may be divided into two groups on the basis of nodular (*Glyptostrobus* and *Taxodium*) or smooth (*Sequoia, Sequoiadendron, Metasequoia, Cryptomeria, Athrotaxis, Taiwania,* and *Cunninghamia*) horizontal walls of the wood parenchyma cells (Greguss 1955; Basinger 1981). However, the findings of Jacquiot (1955) and the studies of modern taxodiaceous woods undertaken during the course of this study show that the horizontal end walls of the parenchyma can be either smooth or slightly nodular in modern *Sequoia, Sequoiadendron* and *Metasequoia* wood. On the other hand, ray tracheids present in the fossil material have only been observed in *Sequoia, Sequoiadendron*, and *Metasequoia*, in particular *M. glyptostroboides* Cheng & Hu (Greguss 1955). The presence of these features increases the similarity of these three genera with the fossil material.

The presence of occasional nodules (indentures) in the ray cell walls of the fossils (Table 1) suggests a slight but possible affinity to *Glyptostrobus* and *Taxodium* (*Taxodioideae*) and *Metasequoia*. Wood anatomical features of *Metasequoia* and *Glyptostrobus* are very similar and thus these genera have been difficult to separate. However, a recent study by Visscher & Jagels (2003) used quantitative characters to successfully separate these two genera (Table 2). According to Visscher & Jagels (2003), *Metasequoia* is characterized by the occasional separation of ray cells – a feature also observed in the fossil material. The abrupt transition from earlywood to latewood and the generally smooth horizontal end walls of the wood parenchyma cells are additional characters shared by the fossils and *Metasequoia*. However, anatomical differences between *Metasequoia* and the fossils include the arrangement of the cross-field pits. Those of *Metasequoia* are arranged in single horizontal rows within the body of the ray cells but are random in marginal ray cells, whereas in the fossils cross-field pits are arranged in one or two horizontal rows. Although the quantitative differences exhibited by the cross-field pits could be a distinguishing taxonomic character, it cannot be ruled out that there might have been an evolutionary trend towards a reduction in the number of cross-field pits.

Although ray height varies greatly both within a species and throughout a single tree, by itself this feature is considered an unreliable character for separating species (Basinger 1981; Visscher & Jagels 2003; Falcon-Lang 2005). However, maximum ray height may be useful for generic determination if extremes are reached (Basinger 1981). The fossils exhibited a range in ray heights with those of Specimens 1,2,3, and 6 of greatest similarity to the heights attained by *Sequoiadendron*, whereas Specimens 4 and 5 have heights more similar to those exhibited by *Metasequoia* and *Sequoia* respectively (Tables 1, 2). However, we consider separation at generic level difficult using this feature alone.

Tracheid length is thought to distinguish *Sequoia sempervirens, Sequoiadendron giganteum* and *Meta-*

sequoia glyptostroboides, in particular from other conifers (Basinger 1981 citing Panshin & DeZeeuw 1964). When compared with the fossil material, no clear distinction could be made between tracheid length of the fossils and the wood from modern *Sequoioideae* (Table 1). Sometimes striations similar to spiral thickenings could be seen on the radial walls of tracheids in the fossils but these could represent spiral cavities caused by soft rot following the microfibrillar structure of the cell wall (Blanchette & Simpson 1992), rather than true spiral thickening and are, therefore, not considered further.

On the basis of the above findings, along with the presence of ray tracheids and generally smooth ray cell walls, we have considered that greatest affinity lies with the genera *Sequoia, Sequoiadendron*, and *Metasequoia* of the subfamily *Sequoioideae* (Leurss.) Quinn (Gadek & al. 2000; Farjon 2001). However, anatomical differences between these fossil woods and those of modern *Sequoioideae* do exist. Such differences include (i) a greater number of successive biseriate-bordered pits, often up to 42, in the fossil woods; (ii) the greater diameters of the bordered tracheid pits in the fossil specimens relative to modern *Sequoioideae*; (iii) the number of cross-field pits in the fossil material being generally 2–4, seldom up to seven, (although eight occur in Specimen 2), whereas in modern material there are usually no more than six; and (iv) cross-fields of earlywood tracheids in the fossil material are often higher in number relative to modern *Sequoioideae* wood.

Although we have suggested that greatest affinity of the fossils lies with the extant members of the *Sequoioideae*, based on the combination of wood anatomical features outlined above and summarised in Tables 1 and 2, certain identification of the fossils described herein remains problematical. Therefore, we have assigned the material to the morphogenus *Sequoioxylon* erected for fossil woods with similarities to the former *Taxodiaceae* or *Sequoioideae* of the *Cupressaceae*.

Sequoioideae wood of the Neogen age from Thrace has also been identified. Özgüven (1971) described material which he assumed as belonging to *Sequoioxylon egemeni* on the basis of tracheid diameters and the presence of taxodioid type cross-field pits, homogeneous ray cells occasionally with ray tracheids, wood parenchyma cells and crassulae. Moreover, wood considered to belong to *Sequoiadendron* has also been described. One sample formerly assigned to *S. giganteum*, namely Specimen 6, originally described by Kayacik & al. (1995) was re-studied herein and described as *Sequoioxylon*. One another big trunk identified by Aras & al. (2003) as *Sequoiadendron giganteum*, which exhibits very similar wood anatomy to the material identified as taxodiaceous herein, should also be considered as *Sequoioxylon* (Table 1). In the light of the above discussions and age of the material, we consider that our specimens and the former specimens from Ağaçli Lignite Quarry should also be placed in *Sequoioxylon* sp. Although slight differences amongst the specimens have been noted, they do not warrant further subdivision.

Palaeoenvironment

The Thrace region of Turkey lay at a palaeolatitude of c. 37° N (Meulenkamp & Sissingh 2003) during the mid-Tertiary, with members of the *Sequoioideae* forming an important component of the vegetation.

Taxodiaceous fossils from Late Cretaceous to Middle Tertiary sediments often dominate the floristic components of lowland swamp and braided river delta forests of North America, Europe and Asia (Momohara 1994; Kumagai & al. 1995; Stockey & al. 2001). The *Sequoioideae* are well represented in the fossil record from the Cretaceous onwards, with a common and widespread occurrence across two or more continents. Today their distribution has to be interpreted as relict (Farjon 2001). *Sequoia*, once more widely distributed across the Northern Hemisphere until the Pleistocene, is now restricted to California and Oregon in the United States of America (Farjon & Page 1999; Farjon 2001) where it is confined to elevations generally below 300 m (occasionally up to 1000 m) and within 60 km of the coast: a region characterised by fog (Watson 1993). *Sequoiadendron* occurs in mixed montane coniferous forests between 900–2700 m in California and in isolated groves along the western foothills of the Sierra Nevada (Watson 1993; Farjon 2001). *Metasequoia* was widely distributed in the Tertiary, reaching 80°N during the Eocene, but became almost extinct in the Pleistocene (Farjon 2001). Today it is restricted to a small area in Central China near the Sichuan-Hubei border (ca. 30° 10' N, 108° 45' E) in E Sichuan, SW Hubei and NW Hunan, at altitudes between 750–1500 m (Silba 1986).

The occurrence of *Sequoioideae* woods (Özgüven 1971; Aras & al. 2003) and *Sequoia* pollen (Ediger & al. 1990) from the same horizon of the Upper Oligocene deposits, which represent former swamp-communities, could be used to support the hypothesis of warm, humid conditions existing in Turkey at that time (Nakoman 1968). The occurrence of *Taxodioxylon* wood of the Late Oligocene – Miocene age on the Lesvos Island (Greece) (Velitzelos & Zouros 1997) also supports this hypothesis. This is also in agreement with other studies which indicate that the mean annual temperature in Turkey in the Early Oligocene was c. 15 °C and had subsequently dropped to c. 10 °C by the beginning of the Miocene (Wolfe 1978; Aleksandrova & al. 1987). This cooling trend from the Early Oligocene through the Miocene resulted in a change from subtropical to temperate-subtropical humid conditions (Ediger & al. 1990), which also reflected on the vegetation.

From the Upper Oligocene into the Miocene there was a change in the microflora represented in the Agacli Lignite Quarry. That change is characterized by taxodiaceous taxa being replaced by members of the *Pinaceae* (Nakoman 1968) so that the new vegetation was distinguished by species of *Pinus* (such as *P. nigra, P. pinea* and *P. brutia*) that came to dominate the forests across that region (Aytug & Sanli 1974). Today, vegetation of the Northern Thrace can be separated into different zones: the humid broadleaved forest with *Quercus petraea, Q. robur*, *Q. frainetto*, *Fagus orientlis*, *Castanea sativa, Carpinus betulus, Tilia argentea, Ulmus minor*; the anthropogenic steppe; the macchia-pseudo-macchia; and the coastal zone (Dönmez 1968). Even though *Pinus brutia* is still widespread in Southern Thrace to the north, with the exception of several small stands of *P. nigra* representing the relict Miocene flora, conifers characteristic of the Tertiary no longer dominate the vegetation of that area (Yaltirik 1966).

From growth ring analysis the numbers of extreme negative years, below the lower mean (Fig. 3 and Table 3) in each 100-year period ranged between 13–22 in the present chronology and 17–20 in the fossil wood. On this basis we can conclude that climate in the Thrace region during the upper Oligocene, when the woods were living, is similar to the prevailing climate where the *Sequoiadeae* are distributed today.

In conclusion this paper outlines new records of fossil woods with anatomy most similar to the *Sequoioideae* (*Cupressaceae*) from Oligocene coal deposits of the Thrace Basin to the northwest of Istanbul. These woods represent an important contribution to the poorly understood vegetation that existed between Europe and Asia during the Middle Tertiary. These fossils help confirm that taxodiaceous conifers formed an important part of the swamp community under a prevailing warm temperate-subtropical climate regime, prior to the onset of the post Oligocene climatic deterioration. It is through the documentation of records such as this that the vegetation dynamics leading to the evolution of the present-day ecosystem in Europe can be more fully understood.

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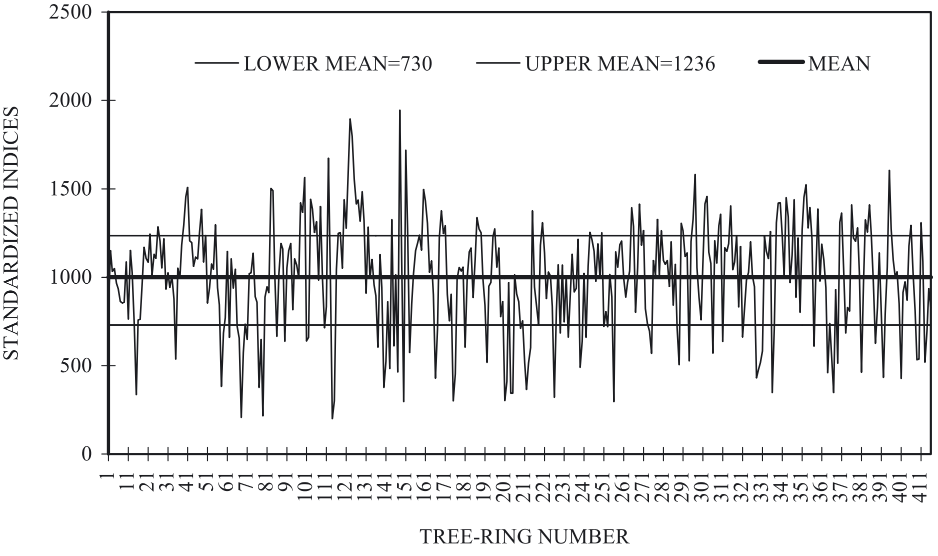


Fig. 3. Tree-ring chronology of specimen 6.

Table 1. The wood anatomical chartacteristic of the fossil woods copared with the specimen previously identified as ^{a,b} *S. giganteum* from the same locality and *S. egemeni* (Özgüven, 1971) from Thrace.

Wood character	Specimen-1	Specimen-2	Specimen-3	Specimen-4	Specimen-5	^{a}Specimen-6	^{b}*Sequoiadendron giganteum* Aras & al. (2003)	*Sequoioxylon egemeni* Özgüven (1971)
Ø x length (cm)	2.2 x 27	3.5 x 25	1.2 x 11	2.5 x 24	5 x 97	24.5 x 80		
ETØ (cm) based on growth ring curvature	>100	>100	>100	>100	>100	>100	a complete trunk of 115 cm	
no. of growth rings	15	32	13	28	51	416		
ring width range (mm)	1-2	1-2	1-2	1-2	0.5-2	0.5-1		
Tracheids: length (mm)	8.26 (7.20-8.95)	5.30 (4.30-6.70)	6.00 (4.60-7.44)	6.32 (4.80-7.24)	--	5.81 (4.45-7.25)		
radial Ø (μm)	74.10 (±6.22)	69.70 (±9.83)	72.80 (±7.22)	77.55 (±10.91)	72.60 (±6.19)	62.65 (±8.01)		60-76
tangential Ø (μm)	46.30 (±5.82)	46.50 (±5.77)	48.20 (±6.15)	49.35 (±6.52)	51.30 (±6.65)	58.65 (±8.05)		34-54
transversal section	angled and polygonal	angled and polygonal	angled and polygonal	angled and polygonal	angled and polygonal	angled and polygonal	angled or polygonal	polygonal or rectangular
pit Ø (radial walls, μm)	17-22	17-23	16-22	17-22	17-23	17-22		12-22
pit arrangement (RS)	uni-biseriate	uni-biseriate	uni-biseriate	uni-triseriate	uni-triseriate	uni-biseriate	uni-biseriate	uni-biseriate
no. successive biseriate pits	17	42	19	20	19	23		
Crassulae	many	many	many	many	many	many		many
Rays	homogeneous^{c}	homogeneous^{c}	homogeneous^{c}	Homogeneous^{c}	Homogeneous^{c}	Homogeneous^{c}	Homogeneous^{c}	Homogeneous^{c}
maximum height (cells)	25	26	28	61	41	21	22	32
average height (cells)	6	5	5	10	9	4	5-12	7
no. per mm	40-46	41-47	40-47	30-35	31-37	44-53		29-35
separation of ray cells	absent	absent	absent	absent	absent	absent		
ray tracheids	present	present	present	present	present	present		present
cell walls	generally smooth	generally smooth	generally smooth	generally smooth	generally smooth	generally smooth		
cross field pits:								
no. of taxodioid	2-7	2-8	2-7	2-7	2-7	2-7	2-4	2-5
Ø (μm)	10.5 (±1.88)	11.13 (±1.75)	11.25 (±3.13)	10.38 (±1.30)	10.38 (±1.33)	11.24 (±1.18)		10-12
Arrangement	mostly 1-2 horizontal rows and rarely random	mostly 1-2 horizontal rows and rarely random	mostly 1-2 horizontal rows and rarely random	mostly 1-2 horizontal rows and rarely random	mostly 1-2 horizontal rows and rarely random	mostly 1-2 horizontal rows and rarely random		mostly 1-2 horizontal rows
Parenchyma no. of successive cells	17	42	19	20	19	27		
relative abundance	abundant	abundant	abundant	abundant	abundant	abundant		
horizontal walls	Generally smooth or rarely nodular	generally smooth or rarely nodular	generally smooth or rarely nodular	smooth or slightly nodular	smooth or slightly nodular	generally smooth or rarely nodular		smooth

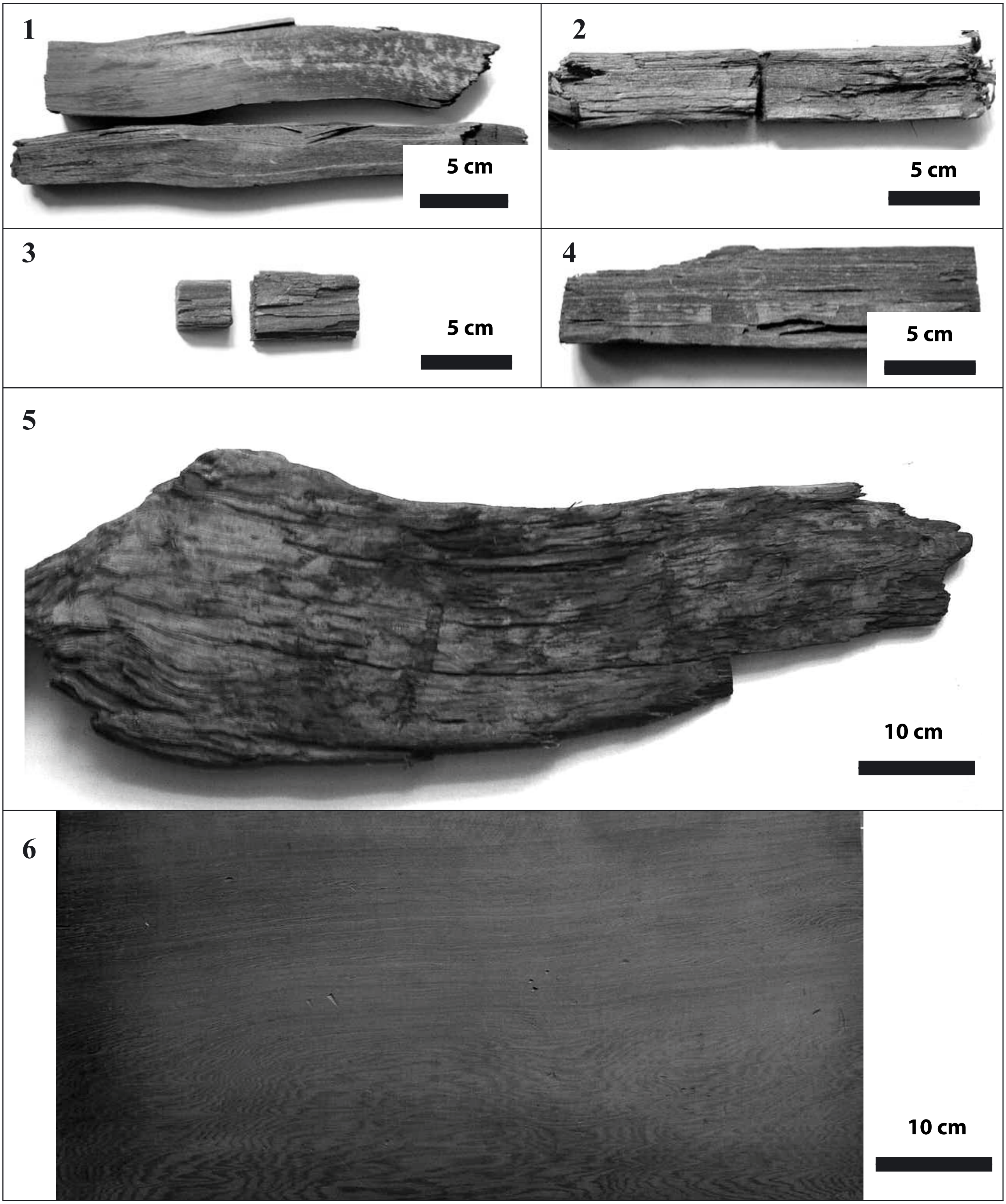
^{c} – some rays have ray tracheids and thus are cinsidered to be heterogeneous; Et – estimated total; Ø diameter; no. – number, RS – radial section.

Table 2. Summary of the anatomical features of the six genera of *Taxodiaceae*.

Wood characters	***Sequoia***	***Sequoiadendron***	***Metasequoia***	***Glyptostrobus***	***Taxodium***	***Cryptomeria***
Axial parenchyma						
horizontal end walls	often nodular and pitted[1]; smooth thickenings[6]	smooth, unpitted[1]	smooth[2] ; usually smooth, occasionally slightly nodular[3]	tangential one node[2] radial 2-3 nodes, usually nodular, ocassionally smooth[3]	nodular[1]	unpitted[1]
Distribution	abundant[1]	abundant[1]	not abundant[2]; scattered[4]; sparse[5]; diffuse[3]	present in every ring[2] fairly abundant[3,5]	abundant[1]	abundant[1]
Ray						
height (cells)	1-40+[6]; 10-15 (max 30+)[1]; 1-20 max. 30[2]; max. 60[5]	1-26+[6]; 1-3 (max 30)[1]; 1-5-12 max.30[2]; max. 30[5]	1-20+[6]; 1-34[4] max. 38[3]; 5-11 max. 34[3]; 1-16 max. 20[2]	1-20+[6]; 1-30[4]; max. 29[3]; 1-18 max. 30[2]	1-60+[6]; 4-5(15) max. 60[1]; 1-24 max. 60[2]	1-4 max. 30[1]; 1-20 max. 24[2]
no. per mm^2	30-40[5]	40-45[5]; 60[1]	45-50[5]	85-90[5]	50-60[5]	40-45[5]
indentures and pitting in horizontal walls	pitted[1]	upitted[1]	present[6] rarely pitted[3]	rarely pitted[3]	occasional, sparsely pitted[1]	present, pitted[1]
ray-tracheids	present[1,5]	present[1,5]	present[5]	absent[5]	absent[1,5]	absent[1,5]
Cross-field pitting	2-6 taxodioid[1]; 1-5 taxodioid[5]	2-4 large taxodioid[1]; 1-6 taxodioid[5]	1-3 cupressoid-taxodioid[4]; 1-4 cupressoid-taxodioid[2,5]; 1-5 cupressoid-taxodioid[3]	1-4 cupressoid[2]; 1-5 cupressoid-taxodioid[5]; 1-6 cupressoid-taxodioid[3]	1-7 cupressoid-taxodioid[1]; 1-8 taxodioid-cupressoid[5]	2-6 taxodioid[1]; 1-5 cupressoid-taxodioid[5]
Tracheids						
EW-LW transition			abrupt[3]	gradual[3]		
tangential Ø (μm)	45[3]; max. 80[5]	60[3]	max. 75[7]; max. 69[3]; max. 65[5]	max. 45[3]	max. 80[5]	
radial Ø (μm)	max. 80[5]	max. 90[5]	max. 85[5]; max. 95[6]	max. 50[5]		
Ø of bordered pits (μm)	15-17[5]; 18-22[8]	14-17; 17-20	20-22[5]; 17-23[6]; 15-20[8]	12-13[5]	12-15[5]	13-14[5]

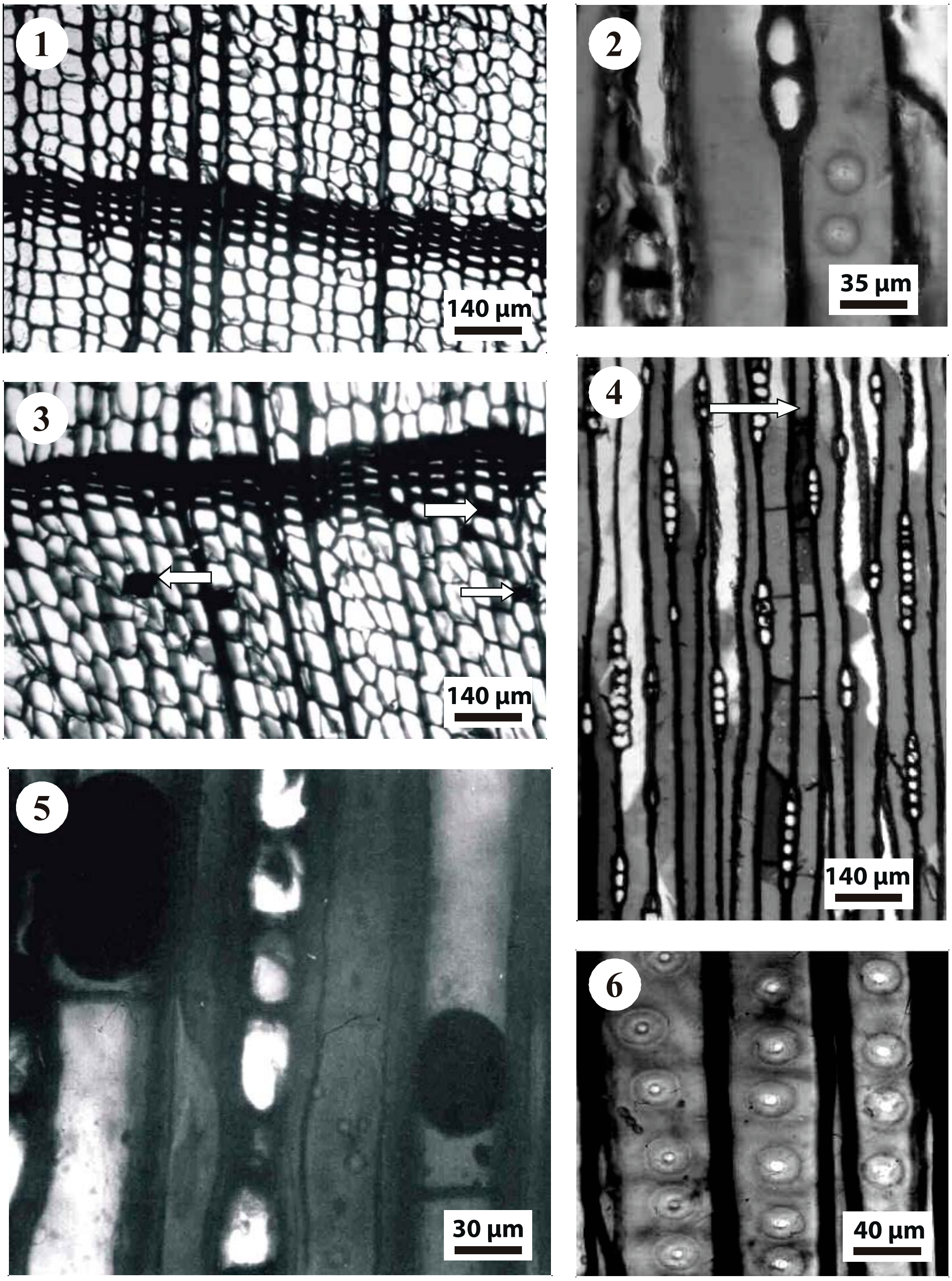
EW-LW – earlywood-latewood; max. – maxsimum; data from: [1] Jacquoit 1955, [2] Gromyco 1982, [3] Visscher and Jgels 2004, [4] Hejnowich 1973, [5] Greguss 1955, [6] Basinger 1981, [7] Florin 1952, [8] personal observation from cultivated trees in Istanbul; Ø – diameter; no. – number.

Plate I



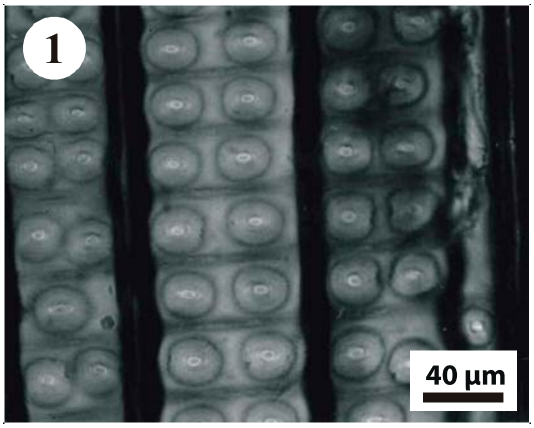
Figs 1-6. Mummified fossil wood specimens with the figure numbers coinciding with the specimen number.

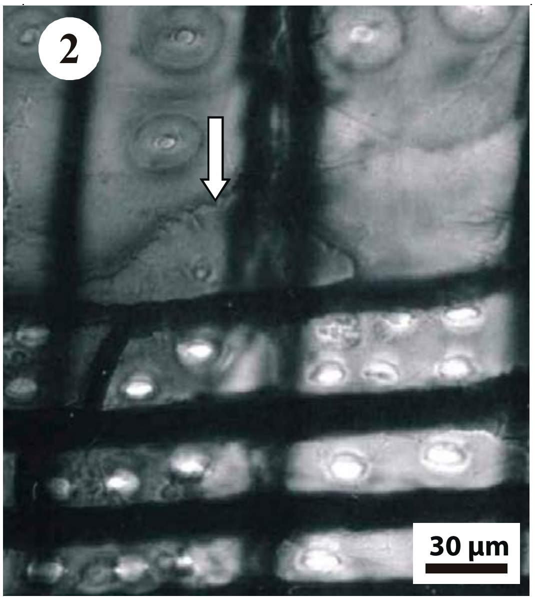
Plate II

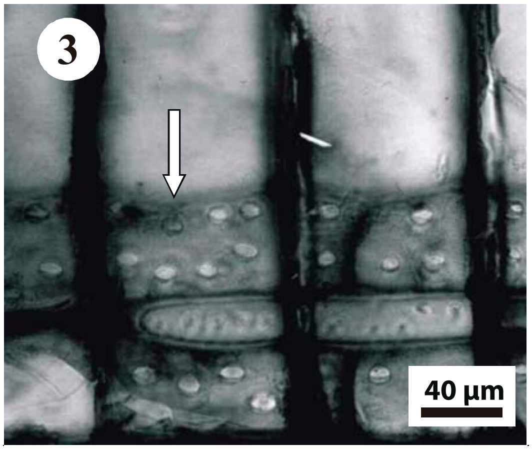


Figs 1-6. Photomicrographs of fossil *Sequoioideae* wood specimens assigned to Group 1:
1, specimen 6 showing abrupt transition from earlywood to latewood; **2,** specimen 6 showing bordered pits in earlywood tracheids and rays of two cells in tangential section; **3**, specimen 2 showing wood parenchyma cells (arrowed) in transverse section with filled a probable resinous material; **4**, specimen 6 showing smooth end wall of axial parenchyma cells (arrowed) and uniseriate rays; **5**, specimen 2 showing axial parenchyma cells with filled resinous material and smooth end walls; **6,** specimen 6 showing crassulae between successive uniseriate bordered pits.

Plate III







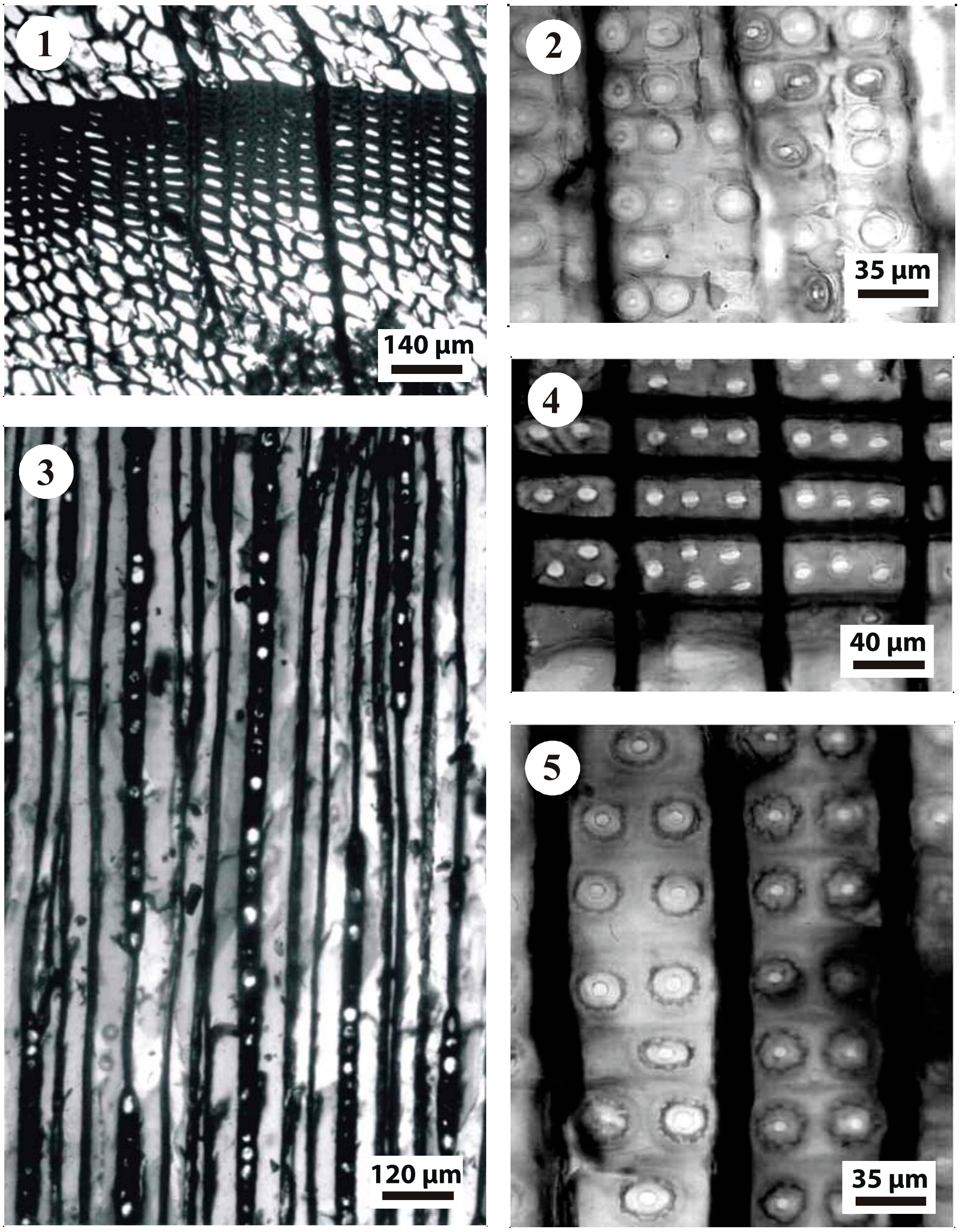
Figs 1-3. Photomicrografs of radial longitudinal sections of fossil *Sequoioideae* woods:
1, crassulae between bordered pit paris of specimen 6; **2,** ray tracheids (arrowed) in specimen 3; **3,** ray cells in specimen 2 with up to eight taxodioid pits per cross field.

Table 3. The frequency of extremely negative years in 100-year period both the fossil and the current master chronologies.

Periods	Chronology of the fossil wood
1st 100 year	17
2nd 100 year	20
3rd 100 year	20
4th 100 year	17

Periods	Current master chronology
1st 100 year	22
2nd 100 year	13
3rd 100 year	19
4th 100 year	15
5th 100 year	20
6th 100 year	14
7th 100 year	14
8th 100 year	16
9th 100 year	13
10th 100 year	13

Plate IV



Figs 1-5. Photomicrographs of fossil *Sequoioideae* woods:
1, tangential section of specimen 4 showing abrupt transition from earlywood to latewood; **2,** triseriatae bordered pits in radial longitudinal section (RLS) of specimen 4; **3,** specimen 4 tangential longitudinal section showing uniseriate rays including part of the tallest ray (total 61 cells) seen in specimen; **4,** RLS showing taxodioid cros-field pits in the earlywood to the specimen 5 aligned in two rows in upper and lower (marginal) cells and in one row in the cells of the body of the ray; **5,** RLS showing tracheidal pitting in specimen 5 with outer borders showing degradation.

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