



## ***Cedroxylon lesbium* (UNGER) KRAUS from the Petrified Forest of Lesbos, lower Miocene of Greece and its possible relationship to *Cedrus***

**Dimitra Mantzouka, Vasileios Karakitsios, and Jakub Sakala**

With 6 figures

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**Abstract:** The Petrified Forest of Lesbos has been the subject of the palaeobotanical research since the 19th century, but a number of inconsistencies still remain. One of them concerns the fossils described over 100 years ago that are characterized by lack of the accompanied illustrations, missing or even lost type material, rather general and uninformative descriptions and finally weak evidence about stratigraphy and exact location of fossiliferous sites. We present here an accurate interpretation of *Cedroxylon lesbium* (UNGER) KRAUS from Sigrí (Petrified Forest area, western peninsula of Lesbos Island), which is hosted at the collections of the Natural History Museum of Vienna, Austria. The specimen, which is designated here as a lectotype, is compared with living *Cedrus* wood, its attribution to *Cedroxylon* is discussed and finally, a new combination for its denomination is proposed: *Taxodioxyton lesbium* (UNGER) MANTZOUKA & SAKALA, comb. nov.

**Key words:** fossil conifer wood, modern wood of *Cedrus*, Petrified Forest of Lesbos, early Miocene, Mediterranean, Greece.

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### **1. Introduction**

Lesbos Island is highly appreciated by the scientific community because of the occurrence of the famous Miocene Petrified Forest at the western peninsula of the Island (Fig. 1), although there are numerous important plant fossiliferous findings also from other parts of the island (e.g., MANTZOUKA et al. 2016). The first references about the extraordinary fossil flora of the island belong to the famous Greek philosopher and father of botany THEOPHRASTUS (3<sup>rd</sup> century B.C.) (MANTZOUKA et al. 2013, in press). In the first half of the 19<sup>th</sup> century AD the Archduke Johann collects fossil samples from the Petrified Forest of Lesbos and

presents those in the annual fossils' exhibition at the Landesmuseum Joanneum (Graz, Austria) in 1842 (GROSS 1999). The Austrian Professor of Botany and Director of this museum's Botanical garden FRANZ UNGER described this material (UNGER 1844, 1845, 1847, 1850). One of the samples was identified by UNGER as *Peuce lesbia* UNGER. Unfortunately no stratigraphic information, full anatomical description or illustrations accompanied the identification. The present paper gives for the first time a detailed description of the lectotype of *Peuce lesbia*, known today as *Cedroxylon lesbium* (UNGER) KRAUS, and also brings a comparison with the modern *Cedrus* species for investigating its botanical affinities.

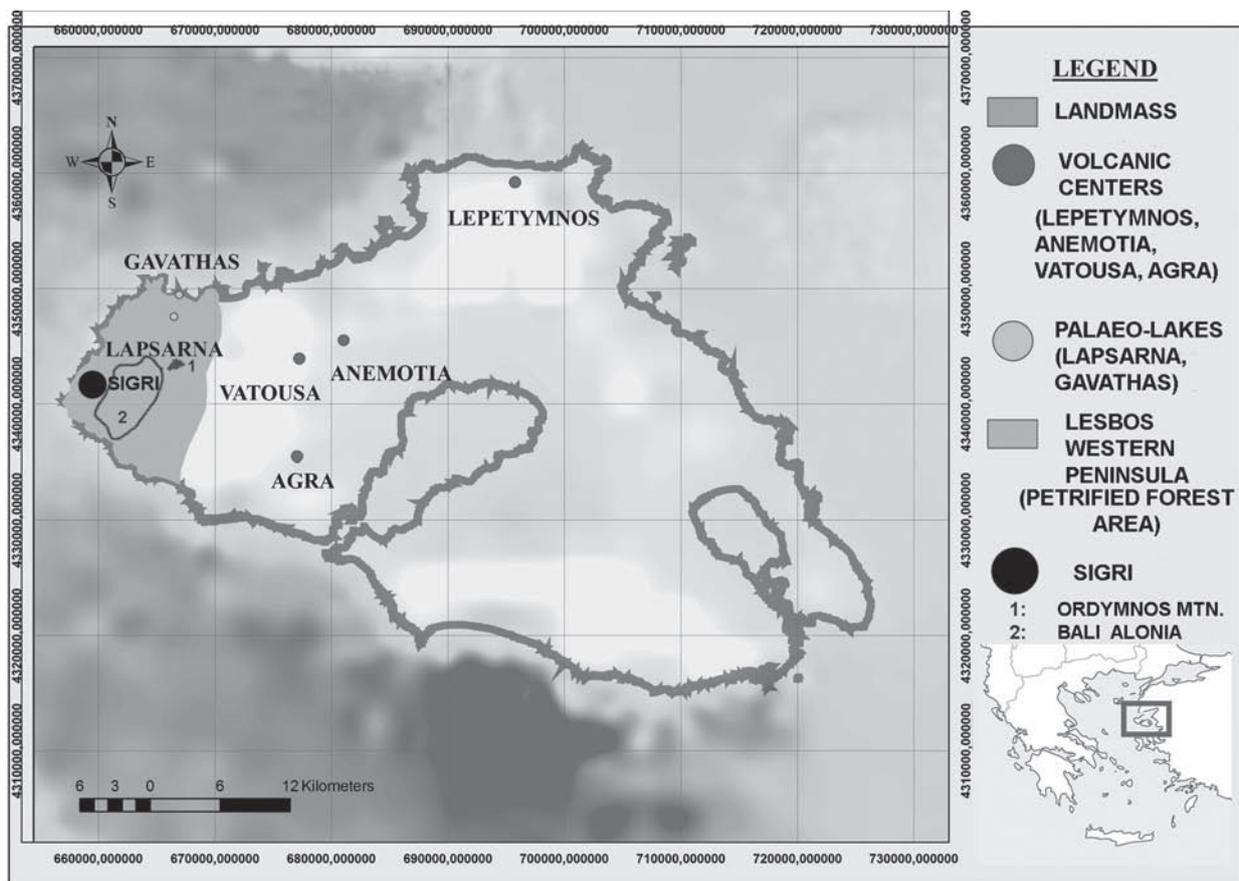


Fig. 1. Lesbos Island palaeogeographical map during early Miocene.

## 2. Geology and stratigraphy of the study area

Lesbos Island is located at the NE part of Aegean and it belongs to the Pelagonian geotectonic zone of Greece which represents a fragment of the Cimmerian Continent (MOUNTRAKIS 1986) with the bending of the geotectonic zones to the E / NE to the Sakaraya Zone of Asia Minor (THOMAIDOU 2009).

The geology of Lesbos has been described by several scientists (FYTIKAS et al. 1984; HECHT 1971-1974; KATSIKATSOS et al. 1982, 1986; MOUNTRAKIS 1986; PE-PIPER 1980; PE-PIPER & PIPER 1993; THOMAIDOU 2009), and it consists of: a) an autochthonous unit of Permo–Triassic age (basically extended in the south-eastern part of the Island) and b) two allochthonous units representing the volcanosedimentary nappe and the ophiolite nappe.

The central and western part of the Island is covered by Neogene volcanic rocks (of calcium–alkaline and shoshonitic composition) originating from the volcanic activity which took place at the Central-Northern Aegean area (volcanic arc) and ended at the Western Anatolia during the upper Oligocene – middle Miocene (FYTIKAS et al. 1984).

Concerning *Cedroxylon* findings from Lesbos Island, FLICHE (1898) described without giving further details 4 types of *Cedroxyla* among his findings from Ordymnos area (*Cedroxylon* type 1: samples No. 4, 31, *Cedroxylon* type 2: samples No 13-16, 23, *Cedroxylon* type 3: samples No 3, 18, 24-30, *Cedroxylon* type 4: sample No 8). Only one is permineralised (*Cedroxylon* type 4) among these fossils, the others are lignitic. Taking into account that the lignitic horizon is located in Lapsarna (Fig. 1) we come to the hypothesis that

FLICHE performed two different samplings. One with all lignitic samples was at the Lapsarna area, which some millions years ago (most probably in Otnangian stage, MANTZOUKA 2009; VASILEIADOU & ZOUROS 2012) hosted a palaeolake with a general low palaeoaltitude. The other one, hosting the permineralised tree trunks studied by FLICHE, was at the higher altitudes of Ordymnos Mountain. There is the Petrified Forest Park (Bali Alonia).

Although there is no stratigraphic evidence about the exact fossiliferous locality, the fossils UNGER (1844) had in his disposal come very possibly from Sigri area (or from Sigri until Ordymnos area, western peninsula of Lesbos Island) which was easily accessible by boat. Moreover, this hypothesis is also supported by the reddish colour and the type of silicification (the fossil in hand is permineralised) of the original material that we re-studied. The reddish colour is connected with the reddish early Miocene stratigraphic horizon (enriched in iron oxides) which hosts mostly permineralised stumps. According to PE-PIPER & PIPER (1993, 2002), Sigri pyroclastic deposits belong to the Skoutaros Formation and have been dated to  $18.4 \pm 0.5$  Ma with the use of K/Ar method.

### 3. Material and methods

The studied sections belong to the sample D.38 of UNGER's collection housed in the Natural History Museum of Vienna. Apart from the already existing sections, the Natural History Museum of Vienna made a new transverse one from the same type material UNGER had studied. The anatomical description is in accordance with IAWA Softwood List (IAWA COMMITTEE 2004). For their microscopic observation the facilities of the Faculty of Botany, Department of Biology, National and Kapodistrian University of Athens (Olympus CX41 optical microscope, Nikon D5000, 12.3 megapixel camera), Laboratory of Electron Microscopy of the Agricultural University of Athens (Scanning Electron Microscope Jeol 6360, Olympus BX40 Light microscope equipped with accessories for fluorescence microscopy, dark field and phase contrast, DP71 Olympus 12.5 megapixel digital camera and "Soft Imaging System-CELL" Olympus image analysis software), and Institute of Geology and Paleontology, Faculty of Science, Charles University in Prague (Olympus BX51 microscope, Olympus DP73 camera and QuickPHOTO MICRO 3.0 image analysis software) were used. The modern wood specimens have been taken from "Julia & Alexander N. Diomedes" Botanic Garden of the University of Athens. The preparations of the modern wood specimens for the observation at the light and scanning electron microscope were made at the Laboratory of Electron Microscopy of the Agricultural University of Athens (with the usage of a Reichert Sledge microtome and then samples were cleaned, dried, mounted on stub and coated with gold).

### 4. Systematic part

Family Cupressaceae GRAY sensu FARJON 2005

Genus *Taxodioxylo* HARTIG

*Taxodioxylo lesbium* (UNGER) MANTZOUKA & SAKALA, comb. nov.

Fig. 2A-H

Homotypic (nomenclatural) synonyms:

1844 *Peuce lesbia* UNGER, p. 37.

1848 *Pinites lesbius* (UNGER). – GOEPPERT, p. 976.

1870 *Cedroxylon lesbium* (UNGER). – KRAUS, p. 372.

**Material:** One piece of wood (Fig. 2F) and four slides among them three old and one new, sample No. D.38, UNGER's collection in the Natural History Museum of Vienna (lectotype, designated here).

**Emended diagnosis:** Homoxylous wood. Distinct growth rings with abrupt transition from earlywood to latewood. Tracheid pitting opposite, uniseriate to predominantly biseriate. Crassulae present, helical and other wall thickenings absent. Axial parenchyma diffuse to tangentially zonate with smooth transverse end walls. Rays uniseriate or partly biseriate and very height (more than 30 cells). Ray tracheids absent. Ray walls, both horizontal and end (tangential), thin and smooth. Cross-field pits taxodioid in earlywood and cupressoid in latewood, mostly 1-3 per field arranged in one horizontal row (in marginal cells up to 4 per field arranged in two horizontal rows). Axial and radial intercellular (resin) canals absent.

**Description:** The slides come from a reddish permineralised sample, about 10 centimeters in size.

Transverse section: Nine distinct growth ring boundaries with a width from 0.4 to 1.2 mm (mean: 0.8 mm), transition from earlywood to latewood abrupt. The latewood is relatively wide and composed of 11-19 cells (mean: 14, SD: 2.4). False rings are absent. Latewood tracheids thin-walled, torus well-defined, disc-shaped (Fig. 2A, B), axial parenchyma mainly diffuse, sometimes tangentially zonate (Fig. 2A, B), axial intercellular (resin) canals absent.

Tangential longitudinal section: axial parenchyma is present, transverse end walls smooth (Fig. 2H), the rays are very high, with more than 30 cells (Fig. 2G, H) and up to biseriate in width (Fig. 2G, H), radial intercellular (resin) canals absent.

Radial longitudinal section: bordered pits in tracheids (Fig. 2C, E). The pits in radial walls of tracheids can be uniseriate but mainly tracheids have 2 rows of bordered pits (tracheid pitting predominantly biseriate), arrangement of tracheid pitting in radial walls opposite (occasionally seems alternate but it is due to the crowded pits), crassulae present, circular pits outline (Fig. 2C, E) of a diameter of 18 (15-20)  $\mu\text{m}$ , cross-field pitting cupressoid in latewood and taxodioid in earlywood (Fig. 2D) commonly arranged in one horizontal row of two pits per cross-field, but in some cases even 3 pits in one horizontal row (or 4 pits arranged in two rows, e.g.

Fig. 2D, in marginal cells). Uniseriate pits in radial walls of tracheids have a diameter of 20–27  $\mu\text{m}$  (with the majority of them at 25  $\mu\text{m}$ ) and the biseriate pits have a diameter of 17–20  $\mu\text{m}$ , ray tracheids absent. Horizontal and tangential (end) walls of ray parenchyma cells are smooth and thin.

## 5. History of the studied species

According to UNGER's original description (1844: 37) *Peuce lesbia* had “growth rings of 0.5–2 mm distance, uni- to biseriate pits, medullary rays consisted of 1–40 cells and no resin ducts”. The only stratigraphic information which was given is that probably the specimen comes from a Tertiary formation of Lesbos Island.

Our description could recall UNGER's one because the distance between the growth rings is about 1 mm, the rays are up to biseriate and very high (with even more than 30 cells) and there are also no resin ducts.

The name *Cedroxylon lesbium* given to our fossil specimen by KRAUS (1870) leads us to investigate the similarities and differences with the genus *Cedroxylon*. According to KRAUS (1870: 370–371), *Cedroxylon* represents the ‘simplest’ type of coniferous wood without resin ducts and axial parenchyma, being composed only of tracheids and thin rays. He also compared this fossil type with the wood of modern *Cedrus* and *Abies*.

More specimens from Lesbos Island western peninsula attributed to *Cedroxylon* had been also studied by FLICHE (1898) who had two samples in hand, only one of which was well preserved. According to his descriptions the width of the growth rings was about 2.5 mm at the first and 0.75–1.5 mm at the second specimen, with rays' height consisting of 7–11 at the first and 5–13 cells at the second sample, and with the characteristics of *Cedroxylon*. He also observed the disarrangement of the ray tracheids. This

observation could indicate high compression during the fossilization. Unfortunately, thinking that FLICHE's identification outlines a possible *Cedroxylon lesbium* representative cannot be supported.

## 6. Remarks on *Cedroxylon*

According to SCHIMPER & SCHENK (1890: 862) and SEWARD (1919) axial parenchyma is mostly present at the latewood of *Cedroxylon* while in *Cupressinoxylon* is not limited. SEWARD (1919) believed that the character of the rays (instead of parenchyma) provides a more satisfactory distinction between *Cedroxylon* and *Cupressinoxylon*. In the same publication is stated that in *Cedroxylon* there is abietineous pitting in all the walls of ray parenchyma cells and that the axial parenchyma can be in great amounts or completely absent depending on the *Cedroxylon* species. Other characteristics of *Cedroxylon* include circular and, if in more than one row, opposite bordered pits (SEWARD 1919; KRÄUSEL 1949; MORGANS 1999). This characteristic is also seen in our specimen.

In this point a short explanation on the terminology usage seems obligatory and is given below in order to avoid any ambiguity: we use the term “abietineous pitting” as the English equivalent of ‘Abietineentüpfelung’ (compare SÜSS & MÜLLER 2015) in its wider sense according to KRÄUSEL (1949), which refers to distinctly pitted horizontal and end (tangential) walls of ray parenchyma cells (Fig. 5H, K). On the other hand, ‘Abietineentüpfelung’ sensu GOTHAN, as explained by PHILIPPE & BAMBORD (2008: 186; Fig. 2E, F), has a more strict meaning for describing only the distinctly pitted end (tangential) walls of ray parenchyma cells (Fig. 5F). Concerning the English terms “abietoid” (or “abietean”), we propose to use them only for the opposite type of pitting in radial tracheid walls.

**Fig. 2.** *Taxodioxyton lesbium* (UNGER) MANTZOUKA & SAKALA, comb. nov. **A, B** – Distinct growth ring boundaries with a mean width of 0.8 mm, transition from early- to latewood abrupt, wide latewood composed of eleven to nineteen cells, axial parenchyma in diffuse arrangement, no intercellular or traumatic resin canals, latewood tracheids thin-walled, torus well-defined of disc-shaped (indicated by an arrow). **C, E** – Bordered pits in tracheids with tori preserved, biseriate tracheid pitting in radial walls, opposite arrangement of tracheid pitting in radial walls, crassulae present, circular pits outline. **D** – Taxodioid pits commonly arranged in horizontal rows of two pits per cross-field. **F** – Specimen No D38 (NHMW), reddish in colour. The sample is given in 2 photographs for estimating a 3D interpretation of it. **G** – Rays very high (with even more than 30 cells) and partly biseriate. **H** – Transverse end walls of axial parenchyma smooth, uni- to biseriate rays. A, B = TS; C–E = RLS; G, H = TLS. TS, TLS, and RLS denote transverse, tangential longitudinal and radial longitudinal sections, respectively. Scale bars: F = 3 cm; A = 0.5 mm; E, G = 0.1 mm; B, C, D, H = 0.05 mm.

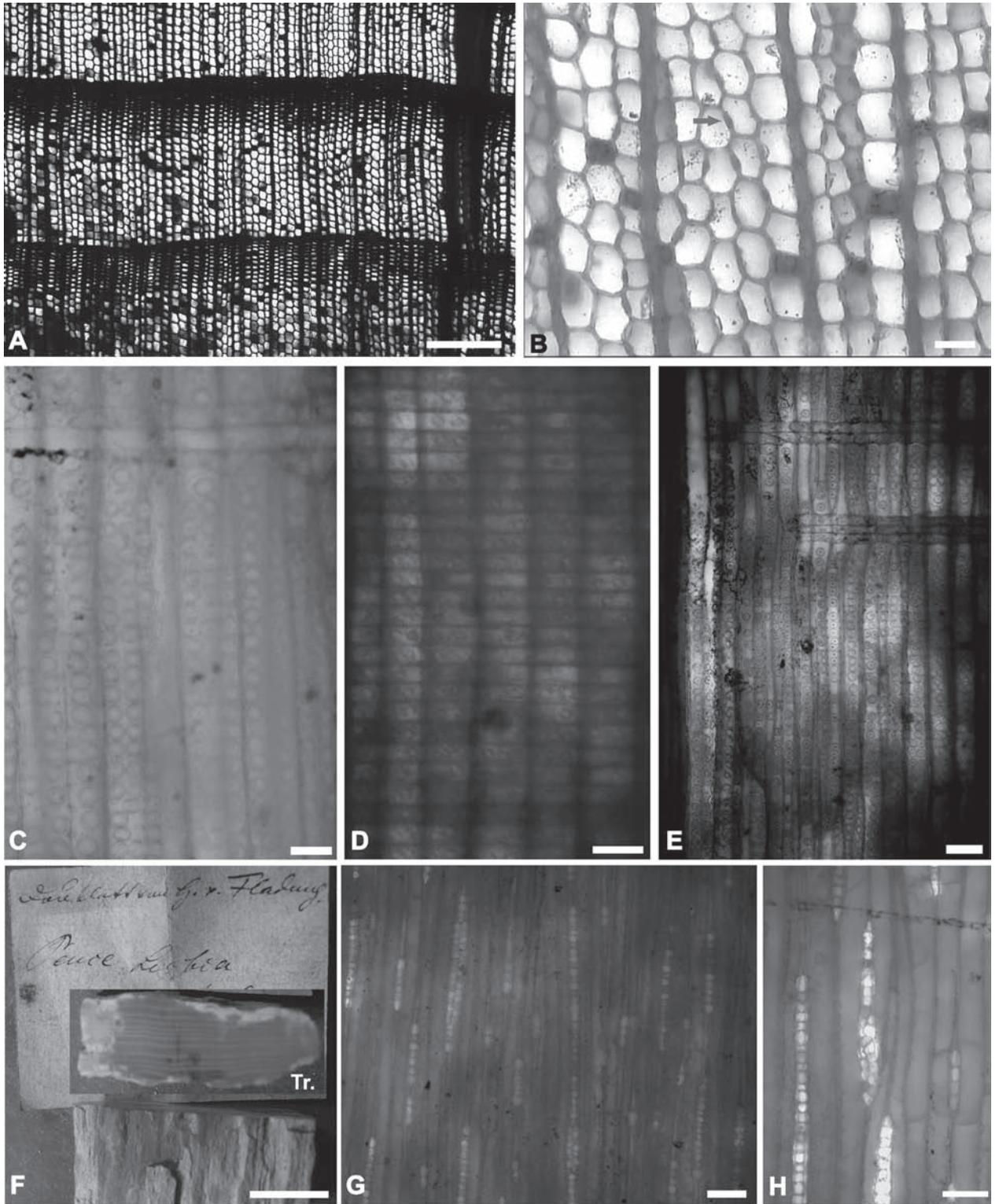


Fig. 2.



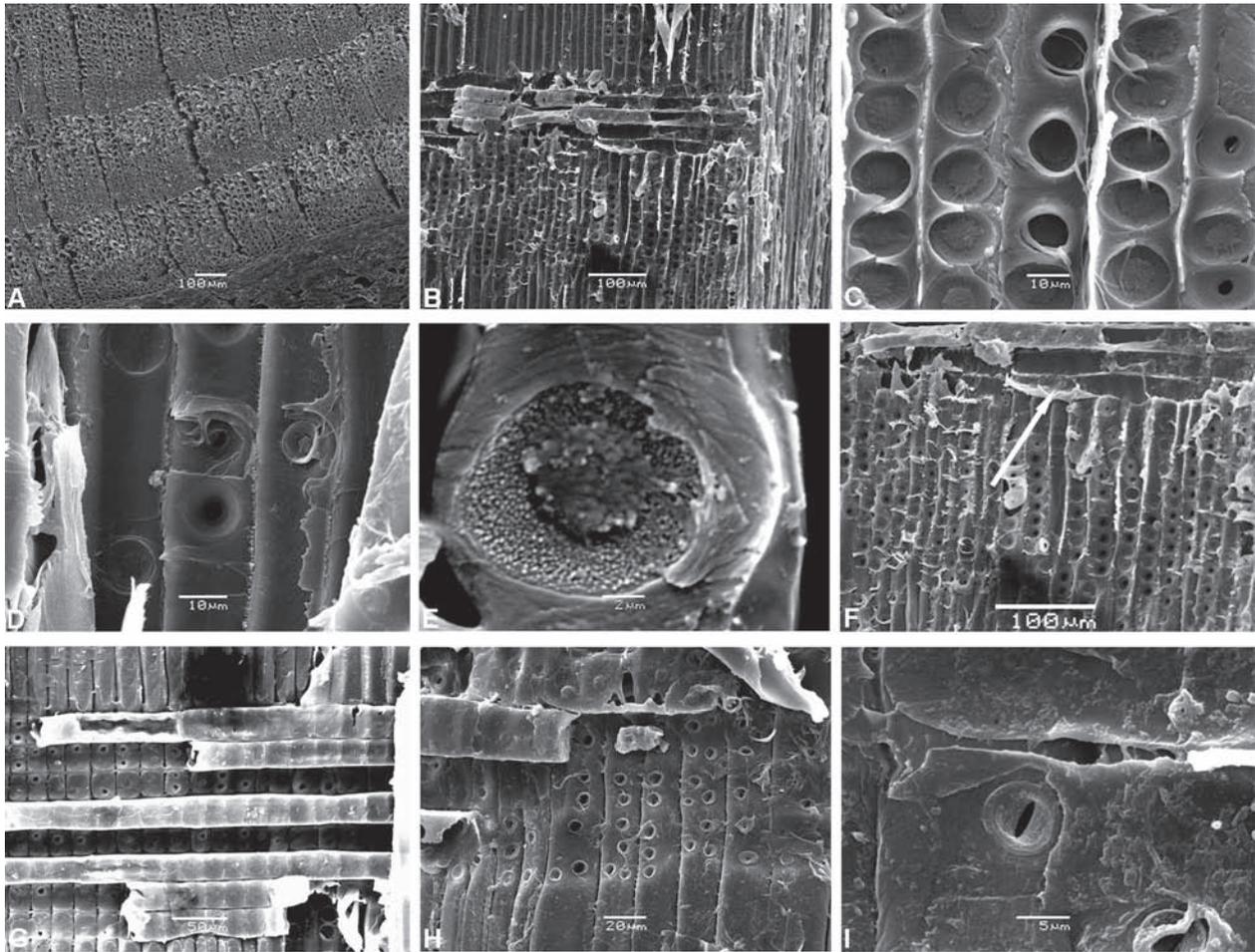
**Fig. 3.** Extant *Cedrus* species. **A** – *Cedrus deodara* tree (trunk-branches) in its growth position; **B** – *C. deodara* branch with needles; **C** – *C. atlantica* tree (trunk-branches) in its growth position; **D** – *C. atlantica* branch with needles; **E** – *C. libani* tree (trunk-branches) in its growth position; **F** – *C. libani* branch with needles.

SEWARD (1919) summarizes the description of *Cedroxylon* giving the following characteristics: “Annual rings well marked, bordered pits on the radial walls of the tracheids usually circular and separate and if in more than one row, opposite, but in some species the Araucarian type of pitting also occurs, the pits being contiguous and alternate or sometimes arranged in stellate clusters. Xylem-parenchyma typically confined to the end of an annual ring, but sometimes absent. Medullary rays generally uniseriate and composed exclusively of parenchyma though horizontal tracheids may occur. Pits on all the walls of medullary-ray cells as in the Abietineae. On the radial walls there may be 1-6 apparently simple circular pits in the field. There are no resin-canals except as the result of injury”.

BAILEY (1933) has proposed that Mesozoic pinaceous woods be identified as one of three comprehensive genera: *Pinoxylon* (*Pinus*), *Piceoxylon* (*Picea*, *Larix*, and *Pseudotsuga*), or *Cedroxylon* (*Keteleeria*, *Pseudolarix*, *Cedrus*, *Tsuga*, and *Abies*).

According to KRÄUSEL (1949) *Cedroxylon* has the following characteristics: pits on radial walls of tracheids circular and, where multiseriate, oppositely arranged, never typically araucarioid, normal wood without resin canals, spiral thickenings absent and abietineous (‘Abietineentüpfelung’) ray wall pitting present.

In LEMOIGNE (1988: 157) there is a discussion on the distinction among *Brachyoxylon* HOLLICK & JEFFREY, *Araucarioxylon* KRAUS and *Cedroxylon* KRAUS based



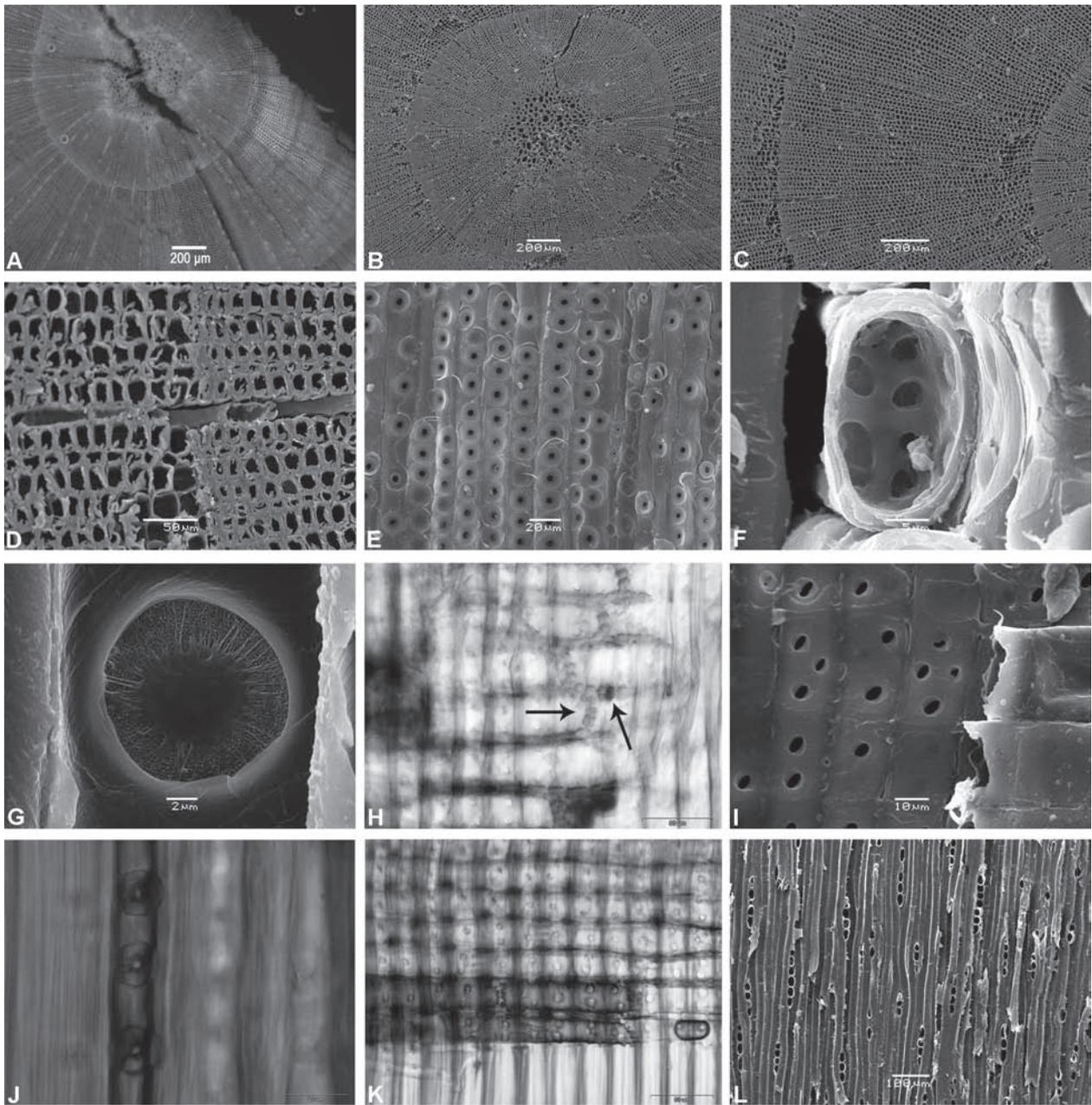
**Fig. 4.** *Cedrus deodara* (SEM images). **A** – Distinct growth ring boundaries, no axial parenchyma or traumatic resin canals, transition from earlywood to latewood abrupt. **B** – Uniseriate pitting in radial walls of earlywood tracheids. **C, D** – Uniseriate pitting in radial walls of earlywood tracheids, circular outline of pits, crassulae present, scalloped tori in earlywood tracheids’ pits. **E** – Detail of a scalloped torus in earlywood tracheids’ pits. **F, G, H** – Uniseriate pitting in radial walls of earlywood tracheids, taxodioid and cupressoid cross-field pitting, 1-4 number of pits per cross-field in earlywood in perpendicular arrangement of up to 2 rows. The arrow indicates the existence of ray tracheids. **I** – Piceoid cross-field pit. A= TS; B-I = RLS. TS and RLS denote transverse and radial longitudinal sections, respectively.

on their wood anatomical features. As mentioned by BAMFORD & PHILIPPE (2001), the name *Cedroxylon* is a later synonym of *Tiloxylon* HARTIG and *Peuce* LINDLEY & W. HUTTON. Its status was considered superfluous and its use for softwoods as unjustified (PHILIPPE 1993).

In HARLAND et al. (2007) there is a discussion about *Cedroxylon* and its first representatives: “*Cedroxylon* is the coniferous wood without either resin canals or conspicuous storage parenchyma. On the contrary, woods, which are provided with abundant axial parenchyma, are designated *Cupressinoxylon*. The pitting in both categories is opposite”.

## 7. Overview of the wood anatomy of modern *Cedrus*

According to ESTEBAN & DE PALACIOS (2009) *Cedrus* has distinct growth rings, not a specific transition from early- to late wood, tracheid pitting in radial walls normally uniseriate and when biseriate then opposite or rarely alternate, well defined disc-shaped tori in earlywood pits, scalloped tori, some species have a warty layer in the inner layer of the secondary wall, present but sparse axial parenchyma, normally distributed along the growth ring boundaries in single



**Fig. 5.** *C. atlantica* (SEM and light microscope images). **A, B** – Pith preserved, distinct growth ring boundaries, no axial parenchyma or traumatic resin canals, transition from earlywood to latewood abrupt. **C, D** – Thick-walled latewood tracheids. **E** – Uniseriate pitting of earlywood tracheids is predominant, outline of tracheid pits circular, crassulae present. **F** – Nodular end walls of ray parenchyma cells ('Abietineentüpfelung' sensu GOTHAN). **G, J** – Scalloped torus in earlywood tracheids' pits, crassulae present. **H** – Distinctly pitted horizontal and end (tangential) walls of ray parenchyma cells, as indicated by arrows ('Abietineentüpfelung' sensu KRÄUSEL). **I** – Taxodioid and cupressoid cross-field pitting, 1-4 pits per cross-field in earlywood, the arrangement is perpendicular in up to 3 rows. **K** – Taxodioid and cupressoid cross-field pitting, 1-4 pits per cross-field in earlywood, the arrangement is perpendicular in up to 3 rows, nodular end walls and well pitted horizontal walls of ray parenchyma cells ('Abietineentüpfelung' sensu KRÄUSEL), ray tracheids present. **L** – Exclusively uniseriate rays of medium height (up to 10-15 cells), no axial parenchyma. **A, J, K** = Light microscope images; **B-I, L** = Electron microscope images. **A-D** = TS; **E, G-K** = RLS; **L, F** = TLS. TS, TLS, and RLS denote transverse, tangential longitudinal and radial longitudinal sections, respectively.

cells in the first row of earlywood or in the last row of latewood, nodular transverse end walls of axial parenchyma, frequent ray tracheids, occurrence of degenerated cells, distinctly pitted horizontal walls of the ray parenchyma cells and nodular end walls, with not obvious indentures, taxodioid or piceoid pitting, although cupressoid pitting has also been observed, similarly to *Abies* and *Tsuga* (PHILLIPS 1941; GREGUSS 1955) no normal intercellular (resin) canals, but both axial and radial traumatic resin canals can be present as well as calcium oxalate crystals in ray parenchyma. Unfortunately, the height of the rays of *Cedrus* was not a matter of discussion in this paper.

## 8. Comparison with extant *Cedrus* species

According to the karyotype analysis made by BOU DAGHER-KHARRAT et al. (2001, 2007) *Cedrus* is subdivided into three species, *C. atlantica*, *C. deodara* and *C. libani*, considering *C. brevifolia*, the endemic taxon from the Island of Cyprus, as a variety of *C. libani*.

A comparison between our fossil wood and the modern cedars was not efficient only by literature because of the lack of detailed wood anatomical works on all *Cedrus* species. Several wood anatomical characteristics of *Cedrus libani* were published (CARTWRIGHT 2001; YAMAN 2007; AKKEMIK & YAMAN 2012; CRIVELLARO & SCHWEINGRUBER 2013) along with a work on *Cedrus brevifolia* (CRIVELLARO & SCHWEINGRUBER 2013) while the work by XU et al. (2012) on *Cedrus deodara* was focused on proving that the formation process of traumatic resin canals is the same with the process of the “normal” ones and the work by CHRYSLER (1915) was focused on the rays of *Cedrus* without following IAWA (2004) terminology. There was not a direct comparison among all the modern cedar species focused on their wood anatomy. Therefore, after deciding a further comparison with the modern cedars we used not only published literature as CRIVELLARO & SCHWEINGRUBER (2013) and others, but we also studied samples from small branches of *Cedrus deodara* (Fig. 3A, B), *C. atlantica* (Fig. 3C, D), and *C. libani* (Fig. 3E, F) from the trees growing in “Julia & Alexander N. Diomedes” Botanical Garden of the University of Athens. Observing their wood anatomy under the light and electron microscope we have found the following anatomical details:

1. *Cedrus deodara* (ROXBURGH ex D. DON) G. DON (Himalayan cedar): a. Transverse section: Growth

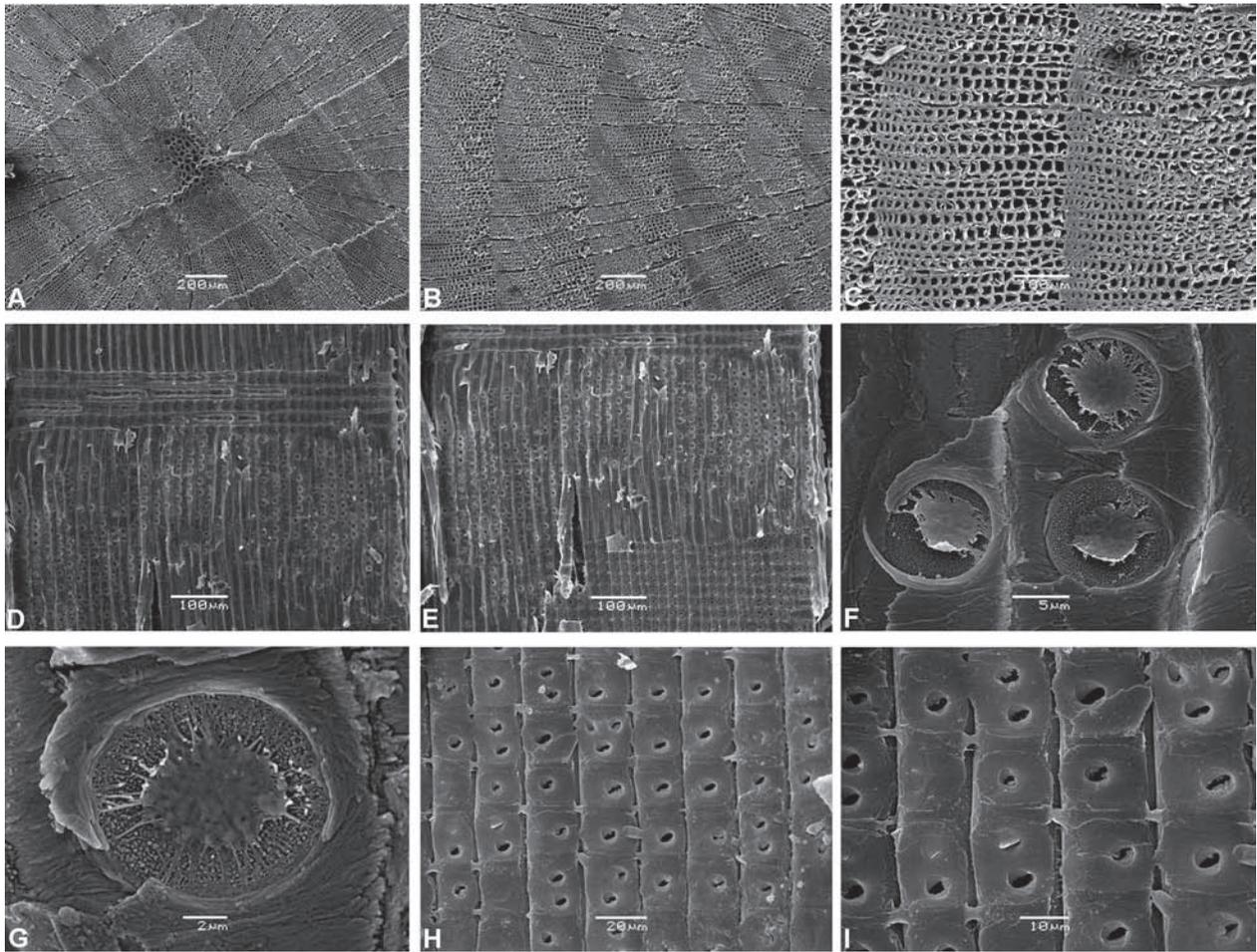
ring boundaries distinct, transition from earlywood to latewood abrupt, no axial parenchyma, no traumatic resin canals observed (Fig. 4A); b. Radial longitudinal section: Pitting in radial walls of earlywood tracheids is predominantly uniseriate (Fig. 4B-D, F), the pits are circular in outline, crassulae present (Fig. 4D), torus in earlywood tracheids’ pits scalloped (Fig. 4A-E), cross-field pitting taxodioid and cupressoid (Fig. 4F-H), even piceoid (Fig. 4I), number of pits per cross-field in earlywood 1-4 in perpendicular arrangement of up to 2 horizontal rows (Fig. 4F-H), ray tracheids present (Fig. 4F). Unfortunately we did not have a tangential longitudinal section.

2. *Cedrus atlantica* (ENDL.) G. MANETTI ex CARRIÈRE (Atlas cedar): a. Transverse section: Pith preserved (Fig. 5A, B). Growth ring boundaries distinct, transition from earlywood to latewood abrupt (Fig. 5A-C). No resin/traumatic canals. No axial parenchyma (Fig. 5A-D). Latewood tracheids thick-walled (Fig. 5D); b. Radial longitudinal section: Pitting in radial walls of earlywood tracheids is predominantly uniseriate, the pits are circular (Fig. 5E), torus in earlywood tracheids’ pits scalloped, crassulae present (Fig. 5G, J), nodular end walls and distinctly pitted horizontal walls of ray parenchyma cells (Fig. 5H, K), ray tracheids present (Fig. 5K), cross-field pitting taxodioid and cupressoid (Fig. 5I, K), number of pits per cross-field in earlywood 1-4 in perpendicular arrangement of up to 3 horizontal rows (Fig. 5I, K); c. Tangential section: rays exclusively uniseriate of up to 10-15 cells, distinctly pitted end walls of ray parenchyma cells, no axial parenchyma observed (Fig. 5F, L).

3. *Cedrus libani* A. RICH. (Cedar of Lebanon): a. Transverse section: Pith preserved (Fig. 6A), growth ring boundaries distinct, abrupt transition from early- to latewood, latewood tracheids thick-walled, no axial parenchyma, no traumatic resin canals observed (Fig. 6A-C); b. Radial longitudinal section: Pitting in radial walls of earlywood tracheids is uniseriate (in some cases seems to be biseriate), crassulae (Fig. 6D, E), torus in earlywood tracheids’ pits scalloped (Fig. 6F, G), cross-field pitting mainly cupressoid (but also taxodioid), number of pits per cross-field in earlywood 1-3 in perpendicular arrangement of two rows (Fig. 6E, H, I).

## 9. Conclusions

The studied sample, designated here as a lectotype, is hosted at the Natural History Museum of Vienna



**Fig. 6.** *C. libani* (SEM images). **A, B** – Preserved pith, distinct growth ring boundaries, no axial parenchyma or traumatic resin canals, transition from earlywood to latewood abrupt, latewood tracheids thick-walled. **C** – Distinct growth ring boundaries, no axial parenchyma or traumatic resin canals, transition from earlywood to latewood abrupt, latewood tracheids thick-walled. **D, E** – Uniseriate (in some cases seems also biseriate) pitting in radial walls of earlywood tracheids, crassulae, cross-field pitting cupressoid (and taxodioid), number of pits per cross-field in earlywood 1-3 in perpendicular arrangement of two rows. **F, G** – Scalloped tori in earlywood tracheids' pits. **H, I** – Cross-field pitting mainly cupressoid but taxodioid as well, number of pits per cross-field in earlywood 1-3 in perpendicular arrangement of two rows. A-C= TS; D-I = RLS. TS and RLS denote transverse and radial longitudinal sections, respectively.

(Naturhistorisches Museum Wien) with No. D 38, and belongs to the Lesbos samples studied and identified by Franz Unger. Unger had described it as *Peucelesbia* and published his observations on the material from Lesbos Island in his *Chloris protogaea* (UNGER 1844: 34, 37). In this publication, there is only original brief wood anatomical description, with no illustration of its anatomy. The information about the locality is unknown, probably Sigri (Bali Alonia) and there are no anatomical details and measurements. No illustration

and anatomy description accompanied the renaming of the species as *Pinites lesbius* by GÖPPERT (1848). Finally, KRAUS (1870: 372) denominated our fossil as *Cedroxylon lesbium*.

SCHIMPER & SCHENK (1890) and SEWARD (1919) had stated that *Cedroxylon* stands for fossil wood agreeing generally with that of recent species of *Cedrus*, and also *Abies* and *Tsuga* with or without tracheids in the medullary rays (ray or horizontal tracheids). Therefore, we had compared our fossil with the modern *Cedrus*

investigating their possible relationship and drawing the similarities and the differences between *Cedroxylon lesbium* and the wood of living *Cedrus*.

This investigation was even more reinforced taking into account the hypothesis that the ancestor of Mediterranean cedars most probably reached South Europe during the early Miocene. QIAO et al. (2007) have placed the divergence between *C. atlantica* (North African species) and *C. libani* and *C. brevifolia* (eastern Mediterranean species) between 23.49+3.55 to 18.81+1.25 Ma. So, a possible “lost link” of the same age with the Petrified Forest of Lesbos in *Cedrus* chain should be investigated.

The fossil specimen that we examined has neither resin ducts, normal or traumatic, nor ray (horizontal) tracheids. On the other hand, it has abundant axial parenchyma, which is a regular feature of Cephalotaxaceae, Cupressaceae and most Podocarpaceae (IAWA COMMITTEE 2004), but not of Pinaceae. Moreover, it does not present scalloped tori, which are typical of the present day *Cedrus* species. These main characteristics lead us to the conclusion that *Cedroxylon lesbium* ( $\equiv$  *Peuce lesbia*) is not related to the modern genus *Cedrus* or to other members of the Pinaceae as e.g. *Abies*. Wood anatomy study together with nomenclatural restrictions also shows that its attribution to the fossil genus *Cedroxylon* is problematic and it should rather be attributed to *Taxodioxylon* HARTIG, characterized by rather abundant axial parenchyma, mostly biseriate opposite pitting in radial tracheid walls and cupressoid to taxodioid type of cross-field pits (see TEODORIDIS & SAKALA 2008). Consequently, we propose a new combination: *Taxodioxylon lesbium* (UNGER) MANTZOUKA & SAKALA, comb. nov.

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**Addresses of the authors:**

DIMITRA MANTZOUKA, VASILEIOS KARAKITSIOS, National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Historical Geology and Palaeontology, Athens, Greece;

e-mail: dmantzouka@geol.uoa.gr, vkarak@geol.uoa.gr

JAKUB SAKALA, Charles University in Prague, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, 12843, Prague 2, Czech Republic;

e-mail: rade@natur.cuni.cz

