BRILL

iawa

USING IDIOBLASTS TO GROUP *LAURINOXYLON* SPECIES: CASE STUDY FROM THE OLIGO-MIOCENE OF EUROPE

Dimitra Mantzouka[1,*], **Vasileios Karakitsios**[1], **Jakub Sakala**[2], and
Elisabeth A. Wheeler[3]

[1]National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment,
Department of Hist. Geology – Paleontology, Panepistimioupoli Zographou, 157 84 Athens, Greece
[2]Charles University in Prague, Faculty of Science, Institute of Geology and Palaeontology,
Albertov 6, 128 43 Prague 2, Czech Republic
[3]N.C. State University, Department of Forest Biomaterials, Campus Box 8005,
Raleigh, NC 27695, U.S.A.
*Corresponding author; e-mail: dmantzouka@yahoo.gr

ABSTRACT

Several specimens of Lauraceae fossil wood from the Cenozoic of Greece (southern part of Lesbos), the Czech Republic (Kadaň-Zadní Vrch Hill and Jáchymov), and Hungary (Ipolytarnóc) were studied. When considering whether they belonged to the speciose fossil wood genus *Laurinoxylon,* we reviewed the literature and data from InsideWood on fossil and modern woods. As a result, we propose criteria for excluding a fossil Lauraceae wood from *Laurinoxylon* and list the species that should be excluded from this genus. The criteria (filters) proposed to exclude a genus from having relationships with *Laurinoxylon* are: A. Axial parenchyma features: A1. Marginal axial parenchyma, A2. Aliform to aliform-confluent paratracheal parenchyma. B. Ray features: B1. Rays higher than 1 mm, B2. Exclusively homocellular rays, B3. Rays more than 5 cells wide, B4. Rays storied. C. Porosity features: Ring-porous. D. Idioblasts: Absence of idioblasts. Based on the distribution of idioblasts, we recognize four groups in *Laurinoxylon* (*Type 1* - with idioblasts associated only with ray parenchyma cells, *Type 2a* - with idioblasts associated with both ray and axial parenchyma, *Type 2b* - with idioblasts associated both with rays and present among the fibres, and *Type 3* - with idioblasts associated with ray and axial parenchyma and also among the fibres) and list the extant genera with features of those groups. Such grouping helps with interpreting the relationships of fossil lauraceous woods with extant genera. We discuss the Oligocene–Miocene European species that belong to these *Laurinoxylon* groups, noting that some warrant reassignment to different genera or even families. Future studies are needed to determine whether new genera should be established to accommodate these species. We propose the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala & Wheeler.

Keywords: Lauraceae, fossil wood anatomy, oil and/or mucilage cells, *Cinnamomoxylon*, Lesbos Island (Greece), UNESCO Global Geoparks, Czech Republic, Hungary.

INTRODUCTION

Lauraceae is a family distributed worldwide with about 50 genera (van der Werff & Richter 1996; Stevens 2001; Schweingruber *et al.* 2011; Johansson 2013) and more than 2500 species of mainly evergreen trees and shrubs. The great majority of the genera are tropical and subtropical. In present-day Europe, this family is represented only by the genus *Laurus* L. (Mai 1995).

According to Mai (1995), Lauraceae woods are the most common fossil woods in the Cenozoic of Europe and indicate a relatively warm climate. Lauraceous fossil woods occur on all continents, including Antarctica (Gregory *et al.* 2009). The abundance of Lauraceae in the fossil record is probably due to lauraceous woods being likely to be reported because they are easily recognizable by their idioblasts, and they are likely to enter the fossil record because many have decay resistant heartwood (Wheeler & Manchester 2002).

The relationship of fossil Lauraceae woods to extant genera is difficult to determine because many extant lauraceous woods have similar combinations of features or the fossil is not well enough preserved to observe important diagnostic features (*e.g.*, vessel-ray parenchyma pits or presence/absence of septate fibres). *Laurinoxylon* is a genus name for fossil lauraceous woods that are impossible to assign to a single present-day genus.

The diagnosis of *Laurinoxylon* was recently emended by Dupéron *et al.* (2008) as follows: "heteroxylous fossil wood with average vessels, solitary or in radial groups; perforation plates simple and sometimes scalariform; intervessel pits alternate and moderately large; tyloses present; paratracheal parenchyma; uni- to 5-seriate rays, slightly heterocellular and less than 1 mm high; ray-vessel pits large, sometimes stretched; fibres libriform or pits on radial walls; oil or mucilage (idioblasts) cells present". The term "average vessels" is a translation from "vaisseaux moyens" which according to Boureau (1957, p. 542) refers to vessels with a diameter from 100 to 200 μm. Based on the description of the type species *Laurinoxylon diluviale,* the pits on the radial walls of the fibres are not distinctly bordered, and are inconspicuous.

Oil or mucilage cells in wood, hereafter referred to as idioblasts, essentially are restricted to the Lauraceae and other Magnoliid families - Annonaceae, Canellaceae, Hernandiaceae, Magnoliaceae (Metcalfe & Chalk 1950, p. 1347, 1354; Carlquist 2001). As suggested by their name, idioblasts are usually larger than surrounding cells; they often have coloured contents. Idioblasts in Lauraceae have been known since 1676, with the first report made by Antoni van Leeuwenhoek (Baas & Gregory 1985).

Our objectives are: 1) to investigate whether idioblasts can help in relating fossil Lauraceae wood to extant genera, 2) to describe fossil Lauraceae woods from four different areas of South-eastern and Central Europe of Oligocene to Miocene age, 3) to propose a classification scheme for *Laurinoxylon* species, in part based on idioblast distribution, and 4) to suggest which *Laurinoxylon* species do not fit the emended diagnosis of *Laurinoxylon* and probably should be transferred to another genus.

Figure 1. Map of Europe with the geographical position of the studied localities indicated. – 1: Lesbos, Greece (early Miocene). – 2: Kadaň-Zadní Vrch Hill, Czech Republic (early Oligocene. – 3: Jáchymov, Czech Republic (?Oligocene). – 4: Ipolytarnóc, Hungary (early Miocene).

LOCALITIES AND GEOLOGY

The specimens described herein are from Kadaň-Zadní Vrch Hill and Jáchymov in northwestern Bohemia, Czech Republic; Ipolytarnóc in northern Hungary; and three new localities in the southern part of the island of Lesbos in the Aegean Sea in northeastern Greece (Fig. 1).

The three new localities in the Polichnitos region, in the southern part of Lesbos, were discovered by the first author (DM) in 2011. They are in a volcanic layer that underlies the ignimbrite of Polichnitos (PU unit), dated at 17.2 Ma (early Miocene) and belonging to the magnetic epoch 17 (Borsi *et al.* 1972; Pe-Piper 1980; Pe-Piper & Piper 1993; Lamera 2004; Lamera *et al.* 2004). The geology of the area and the stratigraphic sequences of these localities have recently been studied and described in detail (Mantzouka *et al.* 2013). Lesbos is known for its Miocene Petrified Forest at its western peninsula. In 2012, the whole island of Lesbos, not only the area of the Petrified Forest, was declared a European and Global Geopark. Geoparks combine the protection and promotion of geological heritage in combination with sustainable local development (Zouros 2004). At a meeting in Paris on 17 November 2015, the 195 Member States of UNESCO ratified the creation of the UNESCO Global Geoparks.

The holotype of *Laurinoxylon czechense* Prakash *et al.* (No. CNB-2 with 5 slides: G 4036, G 4037, G 4038, G 4063, G 4064), housed in the National Museum in Prague, comes from the yellowish and greenish tuffites of Kadaň-Zadní Vrch Hill in the Doupovské hory Mountains. The depositional environment is interpreted as a debris flow – lahar, and its age is considered Late Ruppelian (early Oligocene) by Sakala *et al.* (2010). The whole area is the richest site for fossil angiosperm wood in the Czech Republic (Prakash *et al.* 1971; Sakala & Privé-Gill 2004; Sakala *et al.* 2010).

The holotype of *Laurinoxylon diluviale* (Unger) Felix emend. Dupéron *et al.* (4 slides Nos. 8652–8655), housed in the Muséum National d'Histoire Naturelle in Paris, comes from Jáchymov and was recently described in detail by Dupéron *et al.* (2008). We refer mainly to this recent description, but also discuss a recently discovered part of the original holotype sample (IGP Jáchymov No. 08 with 2 slides: No. 08/A, No. 08/B now housed in the Institute of Geology and Palaeontology, Charles University, Prague), provided by R. Roessler. The fossiliferous rock, which is volcanic breccias, is probably related to the volcanics of Loučná and estimated to be Oligocene in age (Rapprich pers. comm. 2012).

The sample from Ipolytarnóc (IGP Ipolytarnóc, No. 05 with 3 slides: No. 05/A, No. 05/B, No. 05/C, Institute of Geology and Palaeontology, Charles University, Prague) was collected by the third author (J. S.) at Ipolytarnóc Fossils Nature Reserve in Hungary from a trunk embedded in the outcrop on the official pathway. Ipolytarnóc is in the European and Global Geoparks Network of UNESCO (as is Lesbos), attesting to its international significance. According to I. Szarvas (pers. comm. 2014), it is plausible that the trunk represents the type species of *Laurinoxylon mueller-stollii* Greguss (1954) emend. Süss and Mädel (1958). Consequently, we consider this sample as a potential part of the holotype of *L. mueller-stollii*. The fossiliferous sediment, which is mainly formed of a combination of sandstone and rhyolite tuff, contains plant and animal fossils as well as fossil tracks (Szarvas 2007). The site was recently radioisotopically dated to the Ottnangian regional stage of the Central Paratethys (early Miocene) by Pálfy *et al.* (2007).

MATERIALS AND METHODS

Thin sections of the Greek material were prepared at the Laboratory of the Department of Historical Geology & Paleontology, Faculty of Geology & Geoenvironment, National and Kapodistrian University of Athens; thin sections of the Czech and Hungarian material were prepared at the Czech Geological Survey in Prague. Microscopic observations were made with an Olympus BX51 microscope, Olympus DP73 camera and QuickPHOTO MICRO 3.0 image analysis software. Anatomical descriptions follow the IAWA Hardwood List (IAWA Committee 1989). Each vessel was counted separately, both for density and vessel grouping percentage, as proposed by Wheeler (1986). Identifications were made with reference to the InsideWood website (InsideWood 2004-onwards; Wheeler 2011). Idioblast frequency was determined from transverse sections.

APPROACH

The distinctions between oil and mucilage cells in structure and chemistry were reviewed by Baas and Gregory (1985), Gregory and Baas (1989), and Carlquist (2001). It is impossible to distinguish between the two in fossil woods, so throughout this paper we use the term idioblasts. Idioblasts in Lauraceae wood may occur: a) associated with the ray parenchyma; b) associated with axial parenchyma strands and/or c) amongst the fibres as individual cells.

First, we determined which extant genera differ from Dupéron *et al.*'s (2008) emended diagnosis. We relied on publications dealing with extant Lauraceae wood anatomy, especially Richter's (1981a) monograph. Other references used were: Richter (1981b, 1985, 1990), van der Werff & Richter (1985, 1996), Richter & Van Wyk (1990), Callado & Costa (1997), Loutfy (2009), Rohwer *et al.* (2014. The following features (A–D) were used as criteria (or filters) to *exclude* a genus from having relationships with *Laurinoxylon*. Lauraceous genera *without* these features possibly may be related to *Laurinoxylon*:

A. Axial parenchyma features *not* in the emended diagnosis: A1. Marginal axial parenchyma, A2. Aliform to aliform-confluent paratracheal parenchyma.
B. Ray features *not* in the emended diagnosis: B1. Rays higher than 1 mm, B2. Exclusively homocellular rays, B3. Rays more than 5 cells wide, B4. Rays storied.
C Porosity features *not* in the emended diagnosis: Ring-porous.
D. Idioblasts: Absence of idioblasts.

There are two features known to be useful for present-day Lauraceae wood that we choose not to use because they are difficult to determine unless a fossil wood is well-preserved: presence/absence of septate fibres and vessel-parenchyma pit type. Septate fibres characterize the genera of the tribe Perseae, which occur mainly in the Northern Hemisphere, but with some occurrences in Asian tropics, Australia, Africa and Madagascar (Richter 1981a; van der Werff & Richter 1996). Non-septate fibres are reported for the Northern Hemisphere tribe Laureae. Vessel-ray parenchyma pit types are considered to have considerable systematic importance (Richter 1987, in Metcalfe 1987).

According to Richter (1981a), van der Werff and Richter (1996) and Chanderbali *et al.* (2001), Lauraceae have three tribes: Laureae, Perseae, and Cryptocaryeae, plus some genera not assigned to a tribe, *e.g.*, *Iteadaphne* and *Neocinnamomum*. In this paper, we use wood anatomical characteristics of the tribes and their genera given by Richter (1981a) and van der Werff and Richter (1996). They treated 42 genera of Lauraceae. The status of three genera has changed since their work. *Anaueria* is considered a synonym of *Beilschmiedia, Clinostemon* is an unresolved name, and *Triadodaphne* is a synonym of *Endiandra* (The Plant List 2013).

<div align="center">RESULTS</div>

Application of features A–D to exclude extant genera as matches for Laurinoxylon

A. *Axial parenchyma* – Genera differing from *Laurinoxylon* because they have marginal parenchyma (feature A1) occur in the Cryptocaryeae (a primarily Southern Hemisphere group) and include *Beilschmiedia, Cryptocarya, Endiandra, Potameia,* and *Ravensara*. Marginal parenchyma was one of the characters used to support recognition of the Cryptocaryeae tribe (Richter 1981a; van der Werff & Richter 1996).

However, not all Cryptocaryeae *sensu* Chanderbali *et al.* (2001; Rohwer *et al.* 2014) can be excluded because some do not have marginal parenchyma, *e.g.*, *Dahlgreno-dendron, Syndiclis* (P. Détienne pers. observ. for *Syndiclis lotungensis*), but Sun *et al.* (2015) reported that *S. marlipoensis* has marginal parenchyma. Moreover, the wood anatomy of some genera of Cryptocaryeae (*Sinopora, Yasunia*) is unknown.

Extant genera excluded from relationships to *Laurinoxylon* because they have aliform to aliform-confluent paratracheal parenchyma (feature A2) are: *Eusideroxylon, Hypodaphnis,* and the *Potoxylon* species once assigned to *Eusideroxylon*.

B. *Ray features* – The occurrence of rays higher than 1 mm (feature B1) excludes *Caryodaphnopsis* and *Clinostemon*.

Feature B2 (rays homocellular) excludes *Umbellularia* (NB: rays with a single marginal row with some square cells also are present in this genus).

Feature B3 (rays > 5 cells wide) excludes *Dahlgrenodendron* (Richter & van Wyk 1990, p.177).

Storied rays (feature B4) are rare in Lauraceae, reported only for *Aspidostemon;* some species of *Mezilaurus* have irregularly storied rays, but that is not a consistent feature of the genus (Richter 1990).

C. *Porosity* – The presence of ring porosity excludes *Sassafras* as a candidate for nearest living relative of *Laurinoxylon*.

D. *Idioblasts* – To date, no species of *Neocinnamomum* are known to have idio-blasts, so it is excluded.

Modern genera with features of Laurinoxylon

After using the "filters" discussed above, this leaves several extant genera with features of the emended diagnosis of *Laurinoxylon*. They are given below using Richter's (1981a) and van der Werff and Richter's (1996) grouping:

Tribe Laureae: *Actinodaphne, Laurus, Lindera* [both groups A & B], *Litsea, Neo-litsea*.

Tribe Perseae Nees: *Aiouea, Aniba, Cinnamomum, Dehaasia, Dicypellium, End-licheria, Licaria, Nectandra, Nothaphoebe, Ocotea, Persea, Phoebe, Pleurothyrium, Systemonodaphne,* and *Urbanodendron*.

Apollonias, *Cryptocarya* (species from Madagascar) and *Iteadaphne* have not been assigned to a tribe.

Grouping of Laurinoxylon species and possible matching extant genera

We used idioblast location to create four groups of *Laurinoxylon* (Tables 1–3).

Below we list those groups and the extant genera with similar idioblast location. We fully acknowledge that it may not always be possible to determine presence/absence of crystals in fossil wood. Nonetheless, we use crystal presence/absence to create two subgroups within the extant generic groups below because Richter (1981a) considered crystal occurrence a useful feature.

Type 1 - Laurinoxylon species with idioblasts associated only with ray parenchyma cells (Table 1); extant genera *Dicypellium, Laurus*, *Litsea chinensis* group, North American *Persea, Systemonodaphne,* and *Urbanodendron.*
    Subgroup 1. Genera with a high percentage of species with crystals: *Laurus*, *Litsea chinensis* group, *Systemonodaphne*.
    Subgroup 2. Genera without crystals: *Dicypellium*, North American *Persea,* and *Urbanodendron*.

Type 2a - Laurinoxylon species with idioblasts associated with both ray and axial parenchyma (Table 2a); extant genera: *Aiouea, Aniba, Apollonias, Cryptocarya* from Madagascar*, Dehaasia, Licaria, Lindera* group A, *Nothaphoebe, Persea, Phoebe, Pleurothyrium.*
    Subgroup 1. Genera with a high percentage of species with crystals: *Aniba, Apollonias, Dehaasia, Phoebe, Licaria, Pleurothyrium.*
    Subgroup 2. Genera without crystals: *Cryptocarya* from Madagascar*, Nothaphoebe*, and, according to Richter (1981a), 70 % of the species of these three genera lack crystals: *Aiouea, Persea* and *Lindera* group A.

Type 2b - Laurinoxylon species with idioblasts associated both with rays and present among the fibres (Table 2b); extant genera: *Actinodaphne* p.p.*, Nectandra* p.p., *Neolitsea* p.p.
    Crystals are present in 75 % of *Actinodaphne* species, 60 % of *Nectandra* species, and 50 % of *Neolitsea* species. Crystals are absent in 25 % of *Actinodaphne* species, 40 % of *Nectandra* species, and 50 % of *Neolitsea* species (90 % of *Actinodaphne* and *Neolitsea* species, and 84 % of *Nectandra* do not contain idioblasts among the fibres – only in rays and axial parenchyma – and belong in this category).
    If crystals are observed in a fossil, this could be useful for assigning *Laurinoxylon* Type 2b specimens to a group of modern genera, using the information on crystal types within the Lauraceae provided by Richter (1981a, p. 68–70).

Type 3 - Laurinoxylon species with idioblasts associated with ray and axial parenchyma and also among the fibres (Table 3); matching extant genera: *Actinodaphne* p.p., *Cinnamomum, Endlicheria, Nectandra* p.p.*, Neolitsea* p.p. and *Ocotea.*
    Subgroup 1. Genera with a high percentage of crystals: *Actinodaphne* p.p., *Endlicheria, Nectandra* p.p. and *Neolitsea* p.p. (10 % of *Actinodaphne* and *Neolitsea* species, and 16 % of *Nectandra* contain idioblasts also among the fibres and belong in this category).
    Subgroup 2. Genera without crystals: *Cinnamomum* and *Ocotea.*

Table 4 (see p. 484) compares some of the salient features of *Laurinoxylon* Types 1, 2a, 2b, and 3. In addition to differences in idioblast location, there are some differences between the groups in range of intervessel pit size, whether there are any scalariform perforation plates, and incidence of septate fibres. The range of the values for vessels per mm^2 for *Laurinoxylon* Types 1, 2b and 3 might in part be due to differences in counting vessels per unit area (Wheeler 1986).

There are some *Laurinoxylon* species that are not discussed in detail in this paper for reasons related to their age, or geographic location, or lack of a detailed description. However, the descriptions in the literature and in InsideWood suggest some might be assigned to a group; these are mentioned below.

   Possible *Laurinoxylon* Type 1 are *L. namsangensis* Lakhanpal, Prakash & Awasthi (1978, iss. 1981), *L. neagui* S. Iamandei & E. Iamandei (1997), and *L. perseamimatus* Petrescu (1978).

   Possible *Laurinoxylon* Type 2a are: *Laurinoxylon* sp. from Karlovy Vary, Czech Republic (Březinová 1981) and *L. stickai* Boonchai & Manchester from the Eocene of Wyoming, USA (Boonchai & Manchester 2012).

   Possible *Laurinoxylon* Type 2b species are these Indian species: *L. deomaliensis* Lakhanpal Prakash & Awasthi (1978, iss. 1981), *L. naginimariense* Awasthi & Mehrota (1989, iss. 1990), *L. siwalicus* Prasad (1989, iss. 1990), and *L. varkalaensis* Awasthi & Ahuja (1982).

   One possible *Laurinoxylon* Type 3 / *Cinnamomoxylon* is *Laurinoxylon tertiarum* Prakash & Tripathi.

Systematic descriptions – New material

   Family – Lauraceae Juss.
   Fossil genus – *Laurinoxylon* Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala & De Franceschi

Laurinoxylon Type 1

   Fossil species – *Laurinoxylon* aff. *czechense* Prakash, Březinová & Bůžek (Fig. 2A–F, Table 1).
   Material: DM 10 (2 slides), DMDA 13.1 (3 slides).
   Locality: Southeastern Lesbos, Greece.
   Stratigraphic horizon: Under Polichnitos Ignimbrite (PU unit), inside volcanics.
   Age: Early Miocene.

   Macroscopic description – These two specimens are from small stems with a diameter of 2.5 cm that were enclosed in volcanic material (Fig. 2A); they are silicified, light, porous, whitish red-brown with distinct growth ring boundaries that can be seen with the naked eye. There are also strangely coloured circles.
   Microscopic description – Growth rings: distinct (Fig. 2A). – Wood: diffuse-porous (Fig. 2A). – Vessels: 40–100 (52–74) vessels/sq. mm; 18% solitary, 50% in groups of two, 7.5% in groups of 3, 3.5% in groups of 4 and 21% clusters; tangential diameter
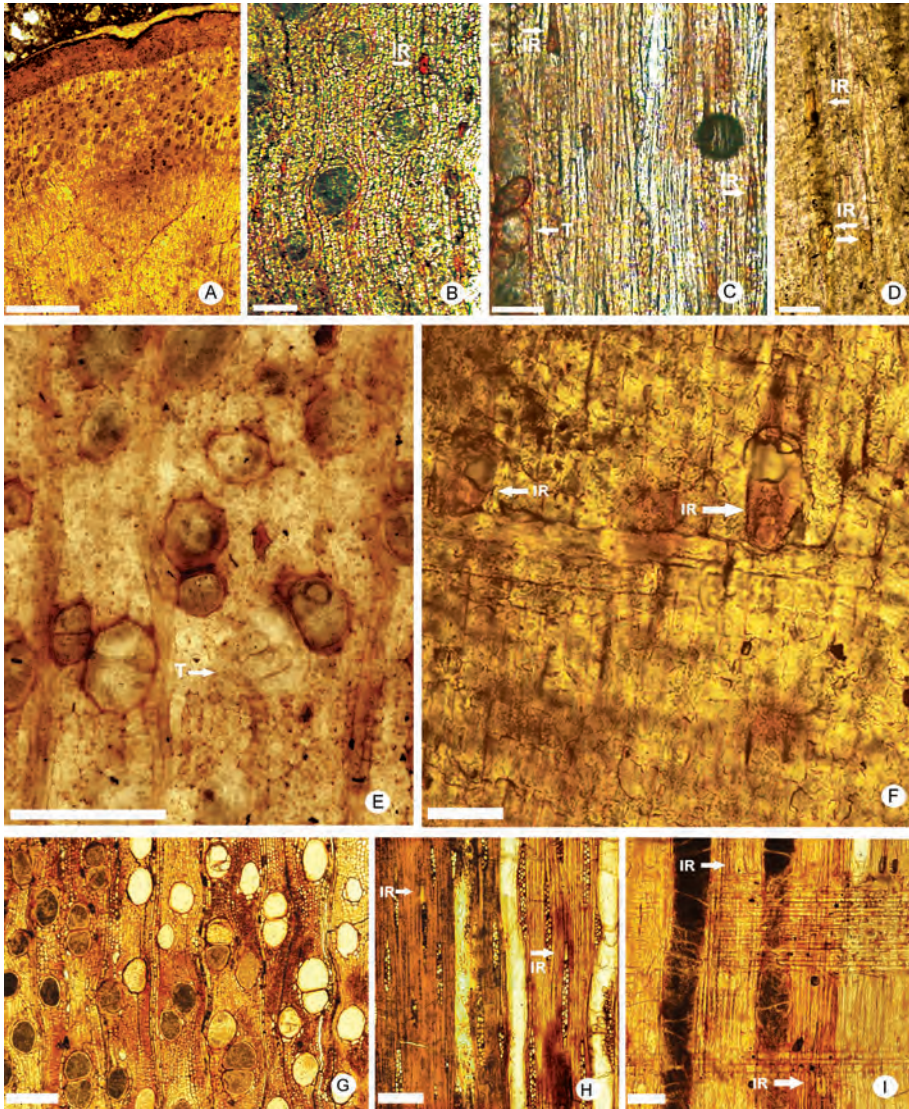
Figure 2. *Laurinoxylon* Type 1. A–F. *Laurinoxylon* aff. *czechense* Prakash *et al.* (Lesbos) (DMDA13.1). A, B: Silicified stem with a diameter of 2.5 cm, enclosed by volcanic material, growth rings distinct, diffuse-porous wood, idioblasts associated with the ray parenchyma cells (= IR),TS. – C, D: Tyloses (T), rays up to 3-seriate, idioblasts IR, mainly at the margins and less commonly in the body of the rays, TLS. – E: Outline of solitary vessels round to oval, vasicentric (scanty) paratracheal parenchyma, tyloses (T), idioblasts IR, TS. – F: Rays heterocellular, body of multiseriate rays composed of procumbent cells with one row of upright cells, idioblasts IR, RLS. – G–I. *Laurinoxylon czechense* Prakash *et al.* (part of holotype specimen CNB-2). – G: Outline of solitary vessels round to oval, vasicentric (scanty paratracheal) parenchyma, tyloses, rays up to 3-seriate, idioblasts IR, slide G 4036, TS. – H: Simple perforation plates, tyloses, idioblasts IR (at their edges and inside the ray bodies), slide G 4037, TLS. – I: Rays heterocellular, body of multiseriate rays composed of procumbent with marginal rows 1–4 of upright cells, idioblasts IR, RD. — Scale bars = 50 μm in D, F, G; 100 μm in B, C, H, I; 250 μm in E; 1000 μm in A.

40 to 85 μm, mean 60 μm; radial diameter of the solitary vessels 50 to 110 μm, mean 73 μm; outline of solitary vessels round to oval (Fig. 2A, B, E); vessel walls thin; perforation plates exclusively simple; tyloses common (Fig. 2C); intervessel pits alternate and polygonal in outline, about 10 μm across. – Rays: heterocellular (Fig. 2F) up to 3 cells wide (25–30 μm) (Fig. 2B, E), commonly 2–3-seriate and 280–520 μm high, body of multiseriate rays composed of procumbent cells with one row of upright cells (Fig. 2F); no crystals observed; 9–24 (mean 15) rays per mm. – Axial parenchyma: scanty paratracheal (Fig. 2E). – Fibres: most probably non-septate (difficult to determine due to the bad preservation). – Idioblasts: associated with the ray parenchyma cells only (Fig. 2B, F). Mean radial x tangential diameter of the idioblasts in transverse section: 15–22 × 26–36 μm. Number of idioblasts per sq. mm (transverse section): 35–65.

Comparison with Laurinoxylon Type I species (Table 1).

The two specimens from Lesbos have diffuse-porous wood, distinct growth ring boundaries, vessels solitary and in radial multiples of 2–3 or sometimes in clusters, simple perforation plates, alternate pitting, scanty paratracheal axial parenchyma, heterocellular 2–3-seriate rays, tyloses (common) and idioblasts associated only with the ray parenchyma cells. These features are characteristic of *Laurinoxylon* Type 1. There are several previously described fossil species that fit this type.

According to the results of our search through the InsideWood database and the literature, some of the *Laurinoxylon* species that belong to Type 1 and warrant comparison with our new material are: *L. czechense* Prakash, Březinová & Bůžek, *L. intermedium* Huard, *L. litseoides* Süss, *L. microtracheale* Süss, and *L. oligocenicum* Prakash, Březinová & Awasthi.

Süss (1958) stated that *Laurinoxylon litseoides* Süss is similar to modern *Litsea chinensis* L. and *L. citrata* Blume. The Lesbos woods described above are similar to *Laurinoxylon litseoides,* differing in vessel diameter (in *L. litseoides* slightly wider), ray seriation (1–4 in *L. litseoides*, 1–3 in Lesbos woods), idioblast density (few in *L. litseoides*, numerous in Lesbos woods) and intervessel pit size (small–medium in *L. litseoides*, large in Lesbos woods). It is probable that the difference in the vessel diameters is likely due to the Lesbos samples being small axes. We were not able to examine the original material of *L. litseoides*.

Abbreviations used in Tables 1, 2a, 2b, 3, & 4:

GR: growth ring boundaries – V Grps: vessel groupings (sol: solitary, rms: in radial multiples, cls: in clusters) – VTD: mean (range) μm; mean tangential diameter of vessel lumina (ew: in earlywood, lw: in latewood) – V/mm²: vessels per square millimetre – VEL: vessel element length – PP simple/PP scalariform: perforation plates simple -/- scalariform – IVP size (μm): intervessel pit size (sm: small, med: medium, lrg: large) – VRP: vessel-ray pitting (sim: with distinct borders; similar to intervessel pits in size and shape throughout the ray cell, red: with much reduced borders to apparently simple) – AP: axial parenchyma (scp: scanty paratracheal, vc: vasicentric, alf: aliform) – RW (cell no.): ray width (no. of cells) – RW (μm): ray width – R/mm: rays per millimetre – RH (μm): ray height – SepFib: septate fibres.

Table 1. Comparison of the anatomical characteristics among *Laurinoxylon* type 1 species.

* is used for the species that we suggest are excluded from *Laurinoxylon*. Regarding the idioblasts, it is not easy to interpret the comparison between descriptions (*e.g.* numerous or few) and numbers (*e.g.* 8–22 or 37). We believe that this connection will be feasible only when the previously described species will be re-studied.

For abbreviations used in Tables 1, 2a, b, 3 & 4, see legends on page 468.

	Laurinoxylon microtracheale*	*Laurinoxylon litseoides*	*Laurinoxylon oligocenicum*	*Laurinoxylon intermedium**	*Laurinoxylon czechense*	*Laurinoxylon czechense new observ.*	*Laurinoxylon aff. czechense*
Laurinoxylon Type 1							
Locality	Hasenberg bei Wiesa unweit Kamenz (Sachsen)	Hasenberg bei Wiesa unweit Kamenz (Sachsen)	South Bohemian basin, Czech Rep.	Landes, S. France	Kadaň (Zadní Vrch Hill), Doupovské hory Mts, Czech Rep.	Kadaň (Zadní Vrch Hill), Doupovské hory Mts, Czech Rep.	Southeastern Lesbos, Greece
Age	Middle–Upper Oligocene	Middle–Upper Oligocene	Oligocene?	Miocene	Oligocene	Oligocene	Early Miocene
GR	Distinct	Distinct	Distinct	Weak with seemingly terminal bands	Distinct	Distinct	Distinct
Porosity	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Semi-Ring / Diffuse	Diffuse
V Grps	mainly sol & in rms of 2, rarely of 3–6	mainly sol & in rms of 2, rarely of 3–6 and clusters	sol & in rms of 2–4	sol (48%), in rms of 2 (31%), of 3–5 (21%)	mainly sol, often in radial or oblique multiples of 2–3 or more	mainly sol (76%), in rms of 2 (12%), rarely in rms of 3–4 (6%) and cls (6%)	sol (18%) and cls (21%), mainly in rms of 2 (50%), sometimes rms of 3 (7.5%), rarely in rms of 4 (3.5%)
VTD: Mean (range) µm	45 (35–60)	70 (30–125)	(70–190)	(80–100) / (70–130)	(50–150)	100	60 (40–85)
V/mm²	35	35	10–14	15–27	15–25	24	52–74
VEL: Mean (range) µm	55 (40–65)	95 (40–150)	(60–225)	(90–150) / (20–90)	(60–195)	125	73 (50–110)
Tyloses	Present	Present	Present	Present?	Absent	Present	Present
PP simple / scalariform	Yes / No	Yes / No	Yes / No	No / Yes: 10 (15)–20 bars	Yes / Yes (10–15 bars)	Yes / No	Yes / No
IVP size (µm)		sm–med, 6–7.5 × 5–6	med–lrg, 8–10		med–lrg, 8–12		lrg (10 in DM 13.1)
AP	vc	scp, vc	scp, vc, tending to aliform	marginal? & concentric bands of 4–12 cells	scp	scp, vc	scp? vc
RW (cell no.)	1–5, mostly 3–4	1–4, mostly 2–3	1–3, mostly 2–3	1–5, mostly 3–4	1–3, mostly 3	1–3, mostly 2–3	1–3, mostly 2–3
RW (µm)	12–57	15–40		15–55	12–40		25–30
RH (µm)	50–320	100–470		120–700	80–900		280–520
SepFib	Yes	Yes	Yes	No	Yes	Yes	Probably non-septate
Idioblasts per mm²	Numerous	Few		8–22		37	35–65
Idioblast size (µm); R: radial T: tangential Ht: height	R: 35 (25–47), T: 21 (12–30), ? Ht: 65 (35–100)	R: 45 (27–60) T: 28 (22–42), Ht 75 (37–105)				R: 20–25, T: 40–50	R: 15–45, T: 10–36

The original material of *Laurinoxylon oligocenicum* Prakash, Březinová & Awasthi (1974) was considered for a long time lost, but small fragments were recently rediscovered and new slides were cut from them. However, their quality did not allow any detailed revision, so we based our comparison on the original description. Prakash *et al.* (1974) suggested that *L. oligocenicum* was similar to *Persea pubescens*. *Laurinoxylon oligocenicum* differs from the Lesbos wood in vessel diameter and density, number of rays per mm and presence of septate fibres.

Laurinoxylon czechense Prakash, Březinová & Bůžek (1971) appears the most similar to the Lesbos material based on microscopic examination of the holotype slides G 4036, G 4037, G 4038, G 4063, G 4064 of the specimen CNB-2 (Fig. 2G–I). It has idioblasts associated only with the ray parenchyma cells, as confirmed by Sakala *et al.* (2010). It differs from the Lesbos wood in having slightly wider vessels, occasional scalariform perforation plates, and slightly higher rays. Its idioblasts occur in the body of the rays as well as at the margins. Because of these differences, we refer these Lesbos fossil woods to *Laurinoxylon* aff. *czechense* Prakash, Březinová & Bůžek.

We think that *Laurinoxylon intermedium* Huard and *Laurinoxylon microtracheale* Süss should not be treated as species of *Laurinoxylon* (see below for discussion).

Problems and proposals – According to Huard (1967), *Laurinoxylon intermedium* has characteristics of both Persoideae and Lauroideae. The location described for its idioblasts might suggest placement in *Laurinoxylon* Type 1. However, *Laurinoxylon intermedium* Huard has only scalariform perforation plates, scalariform intervessel pits, and seemingly marginal and concentric parenchyma bands of 4–12 cells. Because of the exclusively scalariform perforation plates and scalariform intervessel pits, it should be excluded from the Lauraceae. The combination of idioblasts, exclusively scalariform perforation plates, and marginal parenchyma indicates it belongs to the Magnoliaceae. The sample needs to be examined to determine to which magnoliaceous genus it belongs. Kvaček *et al.* (2011) recently revised the leaf flora of this area. The leaf flora includes one species of Magnoliaceae, *Magnolia liblarensis* (Kräusel *et* Weyland) Kvaček. It might be possible that Huard's wood and the *Magnolia liblarensis* leaves represent the same plant.

According to Süss (1958), *Laurinoxylon microtracheale* Süss is similar to *L. nectandrioides* Kräusel & Schönfeld. However, *L. microtracheale* has predominantly homocellular rays, which does not agree with the diagnosis of *Laurinoxylon*. Homocellular rays are rare in the Lauraceae. *Umbellularia* is the one lauraceous genus known to have homocellular rays and idioblasts only associated with the rays. The type material of *L. microtracheale* needs to be examined to determine if its combination of features is consistent with *Umbellularia,* which today is a California endemic.

Botanical affinities – The Lesbos *Laurinoxylon* aff. *czechense* has no crystals. Therefore, we believe it is possibly related to *Dicypellium*, *Urbanodendron* or the North American *Persea*. Because it does not have septate fibres it seems more closely related to North American *Persea*; this group of *Persea* species is close to Laureae tribe, which has non-septate fibres. Leaves of Lauraceae are known from Lesbos (Velitzelos *et al.* 1981a, b, 1999; Mantzouka *et al.* 2013).
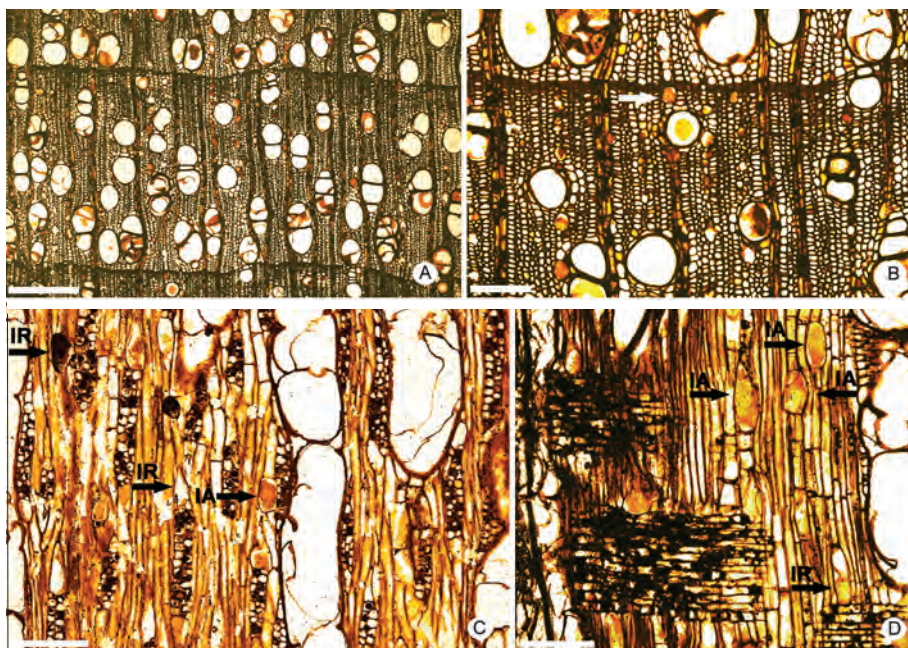
Figure 3. *Laurinoxylon* Type 2a, *Laurinoxylon mueller-stolli* Greguss emend. Süss & Mädel (IGP Ipolytarnóc No. 05, potential part of the holotype of *L. mueller-stolli*: Fig. 3A–3D, slide IGP Ipolytarnóc No. 05/A: Fig. 3A, 3B, slide IGP Ipolytarnóc No. 05/C: Fig. 3C, slide IGP Ipolytarnóc No. 05/B: Fig. 3D). – A, B: Distinct growth rings, diffuse-porous wood, vessels solitary and in multiples of 2–4 with round outline, tyloses, vasicentric parenchyma, idioblasts associated with the ray and axial parenchyma (= IR, IA), TS. – C: Idioblasts IR and IA, vasicentric parenchyma, abundant tyloses, fibres probably septate, TLS. – D: Heterocellular rays with procumbent body cells and one row of upright and/or square marginal cells, idioblasts IR and IA, RLS. — Scale bars = 200 μm in B, C, D; 500 μm in A.

Laurinoxylon **Type 2a**

Fossil species – *Laurinoxylon mueller-stollii* Greguss emend. Süss & Mädel (Fig. 3A–D, Table 2a).

Material: specimen IGP Ipolytarnóc No. 05 + 3 slides: No. 05/A, 05/B & 05/C (potential part of the holotype of *L. mueller-stollii*).

Locality: Ipolytarnóc Fossils Nature Reserve, Hungary.

Stratigraphic horizon: rhyolite tuff.

Age: early Miocene.

Macroscopic description – Slightly flattened trunk, 50 × 35 cm in diameter, directly embedded in rock with only a part of transverse surface exposed.

Microscopic description – Growth rings: distinct (Fig. 3A, B). – Wood: diffuse-porous (Fig. 3A, B). – Vessels: 12–18 vessels/sq. mm; 56% solitary, 25% in groups of two, 19% in groups of 3–4; tangential diameter of the solitary vessels 85 to 200 μm, mean 160 μm; radial diameter of the solitary vessels 85 to 240 μm, mean 175 μm;

Table 2a. Comparison of the anatomical characteristics among species of *Laurinoxylon* type 2a.

* is used for the species that we suggest are excluded from *Laurinoxylon*. For abbreviations used in Tables 1, 2a, b, 3 & 4, see legends on page 468.

	Laurinoxylon endiandroides*	*Laurinoxylon aniboides**	*Laurinoxylon nectandrioides**	*Laurinoxylon annularis**	*Laurinoxylon (+ cf.) hasenbergense*	*Laurinoxylon ehrendorferi*	*Laurinoxylon müller-stollii*
	***Laurinoxylon* Type 2a**						
Locality	Hasenberg at Wiesa close to Kamenz, Saxony, Germany	Ipolytarnóc, Komitat Nograd, Hungary	Netherlands (Holland), Germany	East Bavarian Molasse near Ortenburg close to Passau	Hasenberg, Wiesa, Saxony, Germany	Lemnos island (2 km SSE of, Mudros), Greece	Ipolytarnóc (Hungary) and Wiesa, Kamenz (Germany)
Age	Middle–Upper Oligocene	Early Miocene	Miocene	Allochthonous from Lower Eocene age inside Lower Miocene fluvial sediments	Middle–Upper Oligocene (Süss), Early Mocene (Greguss)	Early or Middle Miocene	Early Miocene (Burdigallan)
GR	Distinct	Distinct	Weak (Berger), distinct (K-S) or indistinct-absent (van der Burgh)	Distinct	Distinct (but 'blurred')	Weakly distinct	Distinct
Porosity	Diffuse	Diffuse	Semi-ring or diffuse	Ring-porous	Diffuse	Diffuse	Diffuse
V Grps	sol, rms of 2, rarely in rms of 3–6	sol, rms of 2, often in rms of 3–4, rarely cls	mainly sol, rarely in rms of 2–3	sol, rms of 2–4	sol, rms of 2, rarely rms of 3–4	sol, rms of 2, rarely rms of 3	sol (56%), rms of 2 (25%) and 3–4 (19%)
VTD: Mean (range) μm	67 (30–90)	133 (55–220)	(50–180)	80–95	60–95 (25–130)	up to 200	160 (85–200)
V/mm²	10	25	10–20		10–25, 30–45	12	12–18
VEL: Mean (range) μm	90 (30–135)	180 (65–280)	250–400	110–135	70–100 (30–170) 105–140 (30–230)	500	175 (85–240)
Tyloses	Present	Present	Present	Probably present	Present		Present
PP simple/ scalariform	Yes / No	No / Yes	Yes / No	Yes / Yes	Yes / No	Yes / ?	Yes / Yes
IVP size (μm)	sm–med, 7.5 × 6–7.5	med–lrg, 7–10 × 7–15	sm–med, 6–7	sm, 4–6	sm–lrg, 5–10(–12)	lrg	lrg
VRP			red		sim	sim, red	sim, red
AP	alf to cfl	vc	scp, vc, alf, cfl, marg	vc (ring 3 cells width)	vc (ring 1–3 cells wide)	scp, vc	scp, vc
RW (cell no.)	1–3 (mostly 2, rarely 4)	1–4 (mostly 2–3, rarely 5)	1–4, mostly 2–3	1–3	1–3	2–4	1–3, mostly 2
RW (μm)	28 (10–60)	37 (20–60)	12–16		12–52		25–30
R/mm	9–11	7–8			6–11	5	5–8
RH (μm)	270 (85–620)	460 (110–1230)	50–100		250–390 (60–1200)	up to 800	260–500
SepFib	Yes	No	Yes	No	Yes	Yes	
Idioblasts per mm²	Very numerous	Numerous					35–65
Idioblast size (μm);	R: 48 (35–67), T: 33 (25–52), Ht: 130 (55–310)	R: 56 (30–75) T: 47 (25–70), Ht: 120 (60–320)	R: 40–75, T: 30–50		R: 40-50 (15-100), T: 25–32 (10–65), Ht: 85–130 (30–300)	Ht: 200, width: 80 in TLS	Ht: 40–75, width: 30–50
Prismatic crystals	Yes	Yes	Yes	Not observed	Yes	Not observed	Not observed

outline of solitary vessels round to oval (Fig. 3A, B); perforation plates simple and scalariform (Fig. 3D); tyloses common (Fig. 3A–D), intervessel pits alternate about 10–15 μm, vessel-ray pits with distinct or much reduced borders, similar to intervessel pits in size and shape. – Rays: heterocellular (Fig. 3D) up to 3 cells wide (25–30 μm) (Fig. 3A–D), commonly 2-seriate and 10–15 cells high, body of multiseriate rays composed of procumbent cells with 1–4 or more (mostly 2–4) rows of upright and/or square marginal cells (Fig. 3D); no crystals observed; 5–8 rays per mm. – Axial parenchyma: vasicentric (Fig. 3A–C) 15–20 μm wide circle around the vessel. – Fibres: with simple to minutely bordered pits, probably septate (Fig. 3C, D). – Idioblasts: associated with the ray and axial parenchyma, tangential height 40–75 μm, width 30–50 μm (Fig. 3C, D). Number of idioblasts per sq. mm (transverse section): 35–65.

Comparison with Laurinoxylon Type 2a species (Table 2a).

IGP Ipolytarnóc No. 05, potential part of the holotype of *Laurinoxylon muellerstollii* Greguss emend. Süss & Mädel of Lower Miocene (A. Burdigalian) age from Ipolytarnóc (Hungary) was examined and assigned to *Laurinoxylon* Type 2a because it has idioblasts associated with the ray and axial parenchyma (Fig. 3A–D). In the original description by Süss and Mädel (1958), 'cells as upright prisms of 20–75 μm height and 7–22 μm width' are mentioned, and we believe this refers to the idioblasts associated with the axial parenchyma cells. The values for idioblast size are new observations (Table 2a).

Our search of the InsideWood database and the literature suggests the Type 2a *Laurinoxylon* species that should be compared with our material are: *L. aniboides* Greguss emend. Süss & Mädel, *L. annularis* Gottwald, *L. ehrendorferi* Berger, *L. endiandroides* Süss, *L. hasenbergense* Süss, *L.* cf. *hasenbergense*, and *L. nectandrioides* Kräusel & Schönfeld.

Laurinoxylon aniboides Greguss emend. Süss & Mädel (1958) differs in dimensions of idioblasts and vessels and it has only scalariform perforation plates (a characteristic which excludes this species from the Lauraceae, see discussion below).

Laurinoxylon annularis Gottwald (1997) differs in porosity (is a ring-porous wood), vessel diameter, intervessel pit size, and the presence of parenchyma bands up to 3 cells wide (characteristics not in accordance with the emended diagnosis for *Laurinoxylon*).

Berger (1953) suggested *L. ehrendorferi* was closely related to *L. nectandrioides*, based on idioblast characteristics, and was similar to the extant lauraceous genera *Acrodiclidium, Aiouea, Cinnamomum, Cryptocarya, Persea* and *Phoebe*. We agree that *Laurinoxylon ehrendorferi* Berger is similar to *L. nectandrioides,* except for more frequently grouped vessels in *L. ehrendorferi* and more abundant axial parenchyma in *L. nectandrioides*. There are differences between *L. ehrendorferi* and *L. mueller-stollii* in mean radial vessel diameter, the size of the intervessel pits, ray height, and occurrence of some scalariform perforation plates (Table 2a).

Süss (1958) described *Laurinoxylon endiandroides* as having idioblasts associated with both ray and axial parenchyma. However, this species has aliform to confluent parenchyma and thus does not fit the emended description of *Laurinoxylon* (see also the

"Problems and proposals" paragraph below). There are additional differences between the Hungarian material we studied and *L. mueller-stollii*, such as the vessel density, vessel diameter, the occurrence of scalariform perforation plates, and the size of the intervessel pits (Table 2a).

Laurinoxylon hasenbergense Süss (Süss 1958) and *L.* cf. *hasenbergense* (Greguss 1969) differ from this Hungarian sample in having exclusively simple perforation plates, narrower vessels, parenchyma bands up to 3 cells wide and no conical idioblasts (Table 2a). The presence of rays up to 1200 μm tall does not agree with the emended diagnosis of *Laurinoxylon*. This "problematic characteristic" is discussed in the "Problems and proposals" paragraph below. The description of *Laurinoxylon nectandrioides* Kräusel & Schönfeld (Kräusel & Schönfeld 1924; van der Burgh 1964, 1973) is not clear about the occurrence of idioblasts among the fibres; it deserves re-examination. We also found some differences in tangential (but also in radial) vessel diameter, occurrence of scalariform perforation plates, size of the intervessel pits, ray width and presence of tracheids (observed in *Laurinoxylon nectandrioides* Kräusel & Schönfeld according to van der Burgh 1973, p. 166). The main difference is the presence of aliform–confluent vasicentric paratracheal parenchyma and seemingly marginal bands in *Laurinoxylon nectandrioides*, features not mentioned in the generic diagnosis of *Laurinoxylon.*

The vessel element lengths reported for five of the seven Type 2a lauraceous woods (Table 2a) are very low (means < 250 μm) compared with modern lauraceous woods (typically means > 350 μm). Possible explanations are that distances between tyloses walls were measured instead of between vessel element end walls. Another factor is that the studied samples were from very near the pith and vessel elements are expected to be shorter in juvenile wood than in mature wood.

Problems and proposals – Laurinoxylon aniboides Greguss emend. Süss & Mädel has rays higher than 1 mm and only scalariform perforation plates. Because of the exclusively scalariform perforation plates, it should be excluded from the Lauraceae. Further investigation is needed to determine whether it belongs to the Magnoliaceae or Canellaceae (*e.g.*, *Warburgia stuhlmannii*), two families in which idioblasts and exclusively scalariform perforation plates co-occur.

Laurinoxylon annularis Gottwald has aliform-confluent parenchyma and 3-cell wide parenchyma bands and is ring-porous. This is not typical for *Laurinoxylon*; therefore, we recommend excluding it from this genus and that it be assigned to *Sassafrasoxylon* Březinová & Süss. This wood needs further study to determine whether it is conspecific with *Sassafrasoxylon gottwaldii* Poole, Richter & Francis or *S. lipnicense* Březinová & Süss or whether if differs enough from those two species so that a new combination could be proposed.

For the three species listed below, study of the type material is needed to determine whether their characteristics fit any existing genus for fossil lauraceous woods or if new genera should be created.

Laurinoxylon endiandroides Süss has aliform to confluent axial parenchyma, a characteristic not in accordance with the emended diagnosis of *Laurinoxylon*. We propose that the type be examined to determine whether there are idioblasts associated

with the fibres as alluded to by Süss (1958, p. 32, "einige scheinbar in der Holzmasse verstreut"). If idioblasts among the fibres are present, this species might be assigned to *Cinnamomoxylon*. On the other hand, if there are no idioblasts among the fibres, then it might be assigned to the Cryptocaryeae Nees tribe (because of its axial parenchyma type).

Laurinoxylon hasenbergense Süss and *Laurinoxylon* cf. *hasenbergense* have an idioblast distribution that places them in our *Laurinoxylon* Type 2a. However, their published descriptions indicate that they have some characteristics not in accordance with the emended diagnosis of *Laurinoxylon*, *e. g.*, the 3-cell wide parenchyma bands and the rays up to 1.2 mm high. Rays 1.2 mm high in combination with the presence of crystals and exclusively simple perforation plates suggest that a relationship with *Licaria* needs investigation.

Laurinoxylon nectandrioides Kräusel & Schönfeld has confluent parenchyma (and seemingly marginal bands), septate fibres and crystals. The parenchyma distribution suggests relationships with genera of the Cryptocaryeae tribe, but the occurrence of septate fibres suggests relationships with the Perseae tribe. Further study is required for determining its placement within the Lauraceae.

Botanical affinities – Laurinoxylon mueller-stollii has septate fibres and no crystals, so it could be related to the extant genera with features of *Laurinoxylon* Type 2a that do not have crystals and belong to the tribe Perseae Nees: *Aiouea, Cryptocarya* from Madagascar, *Nothaphoebe* and *Persea*. Fossil lauraceous leaves also occur at Ipoly-tarnóc (Hably 1983) (*e.g.*, *Persea braunii* Heer or *Persea speciosa* Heer in Hably 1983, p. 140), so there may be a correlation between *Laurinoxylon mueller-stollii* and those *Persea* leaves.

Laurinoxylon **Type 2b**

Fossil species – Laurinoxylon aff. *diluviale* (Unger) Felix emend. Dupéron *et al.* (Fig. 4A–J, Table 2b).

Material: DMKO 1 (3 slides), DMDA 2 (4 slides), DMDA 7 (5 slides).

Locality: Southeastern Lesbos, Greece.

Stratigraphic horizon: Under Polichnitos Ignimbrite (PU unit), inside volcanics.

Age: early Miocene.

Macroscopic description – Two specimens are from small stems (the pith is preserved) which are enclosed in the surrounding volcanic material with the following dimensions (in cm): $18 \times 9 \times 4$, $12 \times 3.5 \times 2$ and one is from a part of a stem with knots (the pith was not preserved), which is silicified, heavy, red-brown with the dimension of $31 \times 21 \times 11$ cm. They are silicified, light, whitish brown with distinct growth ring boundaries that can be seen with the naked eye. There is a strange colouration type of circles, due to fossilization processes (Fig. 4A).

Microscopic description – Growth rings: distinct. – Wood: diffuse-porous. – Vessels: 20–100 vessels/sq. mm; 29 % solitary, 50 % in groups of two, 17 % in groups of 3, and 4 % in groups of 4; tangential diameter 40–110 μm, mean 70 μm; radial diameter of solitary vessels 50–150 μm, mean 90 μm; outline of solitary vessels round to
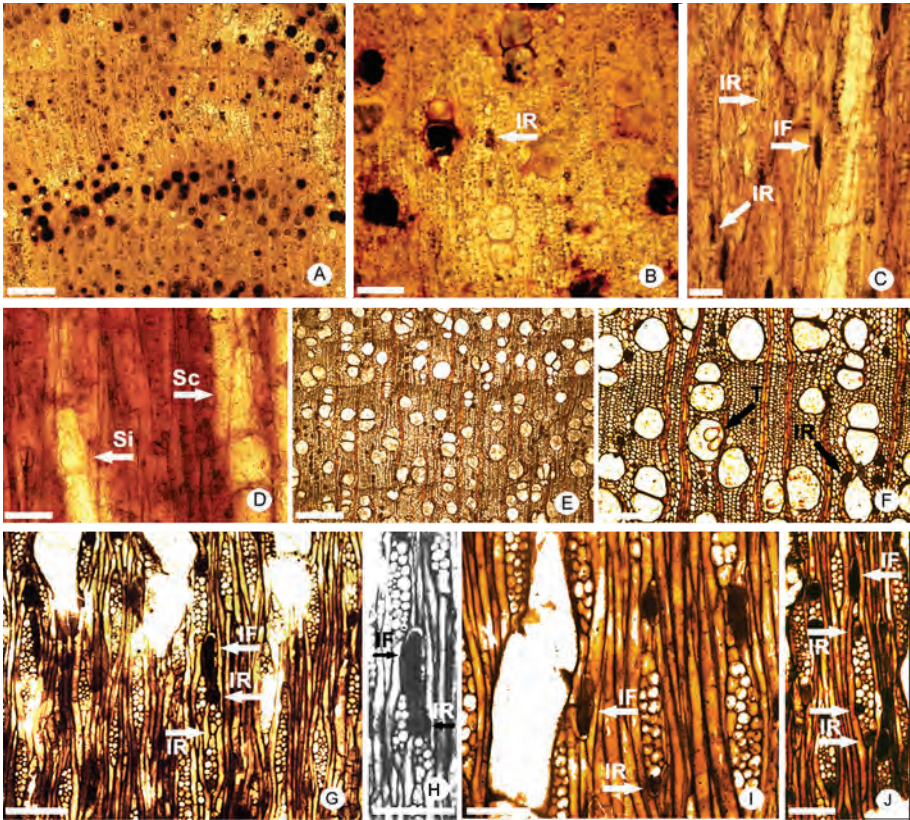
Figure 4. *Laurinoxylon* Type 2b, *Laurinoxylon* aff. *diluviale* (Unger) Felix emend. Dupéron *et al.* (DMDA7: Fig. 4A, B; DMDA2: Fig. 4C; DMKO1: Fig. 4D). – A, B: Distinct growth ring boundaries, diffuse-porous, circular regions with strange colouration, outline of solitary vessels round to oval, tyloses, scanty paratracheal parenchyma, idioblasts associated with the ray parenchyma cells and among the fibres (= IR, IF), TS. – C: Idioblasts IR and IF, TLS. – D: Idioblasts IR and IF, perforation plates simple (Si) and scalariform (Sc), TLS. – E–J. *Laurinoxylon diluviale* Unger (Felix) emend. Dupéron *et al.* (part of the holotype specimen IGP Jáchymov No. 08: Fig. 4H–J, slide IGP Jáchymov No. 08/B: Fig. 4E, 4F, slide IGP Jáchymov No. 08/A: 4G--5J). – E, F: Distinct growth ring boundaries; diffuse-porous, tyloses (T), scanty paratracheal parenchyma, idioblasts IR and IF, TS. – G, I, J: Idioblasts IR (at the edges of the rays and in their bodies) and IF, septate fibres (SF), TLS. – H: Detail from 4G, in black & white for better separation of the IR idioblast from the IF idioblast, septate fibres, TLS. — Scale bars = 50 μm in B, C, D; 100 μm in I, J; 200 μm in F, G, H; 500 μm in A, E.

oval (Fig. 4A, B); vessel walls thin; perforation plates mostly simple (Fig. 4C, D), some scalariform with 6–12 bars; polygonal alternate intervessel pits small (5 μm) to medium (7.5 μm), tyloses common (Fig. 4A, B). – Rays: heterocellular up to 3 cells wide (extremely rarely 4 cells), (20–60 μm), and 160–650 μm high (Fig. 4C); body of multiseriate rays composed of procumbent and upright cells, marginal rows of 1–4 upright

Table 2b. Comparison of the anatomical characteristics among species of *Laurinoxylon* type 2b.

* is used for the species that we suggest are excluded from *Laurinoxylon*. For abbreviations used in Tables 1, 2a, b, 3 & 4, see legends on page 468.

	Laurinoxylon (*Ulminium*) *diluviale*	*Laurinoxylon perfectum**	*Laurinoxylon compressum**	*Laurinoxylon* aff. *diluviale* (n=3)
***Laurinoxylon* Type 2b**				
Locality	Jachymov (Bohemen), Czech Republic	Landes, S. France	Landes, S. France	Southeastern Lesbos
Age	? Oligocene	Miocene	Miocene	Lower Miocene
GR	Distinct	Distinct	Distinct	Distinct
Porosity	Diffuse	Diffuse	Ring-porous	Diffuse
V Grps	sol (75%), rms of 2 (20%), of 3–4 (2%), and in cls (3%)	sol (35%), rms of 2 (35%) and 3–4 (29%)	mostly sol, rarely in rms of 2–3	sol (29%) and in rms of 2 (50%), 3 (17%), and 4 (4%)
VTD: Mean (range) µm	ew: 100–154; lw: 44–72	ew: 100 (75–140), lw: 55 (40–70)	ew: 110–150, lw: 70–95	40–110
V/mm²	9–33	10–15		20–100
VEL: Mean (range) µm	300–550	lw: 57 (48–80); ew: 125 (65–160)	ew: 180–240; lw: 110–150	50–150
Tyloses	Present	Present	Present	Present
PP simple/ scalariform	Yes / Yes (6–12 bars)	Yes / No	Yes / No	Yes / Yes (6–12 bars)
IVP size (µm)	med–lrg (7–15)	lrg (10–15)		sm–med (occ. lrg)
VRP		red	red–sim	
AP	scp, vc (1–2 cells wide rows)	scp, sometimes tends to alf	scp, vc	scp?, vc
RW (cell no.)	1–5 (3s–51%) 4s 29%	1–3 (mostly 2)	1–3 (mostly 2)	1–4 (mostly 2–3)
RW (µm)		20–48		20–60
R/mm	6–9	16		11–16
RH (µm)	60–820 (frequently: 220–420)	1s: 170 (60–370), 2s: 290 (220–420), 3s: 390 (250–500)	avg: 270 (150–500)	160–650
SepFib	Probably	Yes	No	Probably
Idioblasts per mm²	0–18	Abundant	25–33	Usually 35–70
Idioblast size (µm)	At ray edges: R: 50–80, T: 27–60 Inside rays: R: 37, T: 27	Large (max. ht: 300)	Tangential: height: 115 (65–180), width: 64 (55–80) or transversal: 35–60 radial diam.: 50–90	R: 25–70, T: 15–40 (in TS)
Prismatic crystals	No	No	No	No

cells; crystals not seen; rays per mm: 11–16. – Axial parenchyma: scanty paratracheal (Fig. 4B). – Fibres: probably septate. – Idioblasts: associated with the ray parenchyma cells and among the fibres (Fig. 4C, D), idioblasts in transverse section with radial diameter × tangential diameter from 25 × 15 up to 70 × 40 µm; number of idioblasts per sq.mm in transverse section, in general, 35–70/sq. mm.

Comparison with Laurinoxylon Type 2b species (Table 2b).

These three specimens from Lesbos have features characteristic of *Laurinoxylon* Type 2b. According to the results of our search through the InsideWood database and the literature, *Laurinoxylon* species that belong to our Type 2b and that warrant comparison with our new material are: *Laurinoxylon compressum* Huard, *L. perfectum* Huard and *L. diluviale* Unger.

Laurinoxylon compressum Huard was described as ring-porous to semi-ring-porous (closely related to *Ocotea* and *Sassafras* according to Huard 1967)*,* so it is not similar to the samples from Lesbos. *Laurinoxylon perfectum* Huard differs from the Lesbos wood because its parenchyma tends to be aliform, with 1–3-seriate rays, lower vessel frequency and fewer rays per mm. Both *L. compressum* and *L. perfectum* should be excluded from *Laurinoxylon* (for explanation see the "Problems and proposals" paragraph)*.*

Laurinoxylon diluviale from Jáchymov appears the most similar to the Lesbos material. It has been studied by Unger (1842), Felix (1883), and, most recently, Dupéron *et al.* (2008), who made a detailed re-examination of the original type slides. We examined new slides from the newly re-discovered part of the holotype given to us by R. Roessler (holotype specimen IGP Jáchymov No. 08, 2 slides, Fig. 4E–J). We observed the following features: wood diffuse-porous; vessels rounded to slightly angular; 9–33 vessels per sq. mm; 6–9 rays per mm, fibres possibly septate, and tyloses common (Fig. 4F). Our observations of quantitative features generally agree with Dupéron *et al.* (2008), but we found idioblasts to be larger and associated with ray parenchyma and also dispersed among the fibres (Fig. 4E–J). We also observed in tangential sections some idioblasts that looked as if they had been shifted some microns away from the rays' bodies (as if the idioblast's edge was detached from the rest of the ray). They can appear to be idioblasts among the fibres, but we believe that they were originally associated with the rays. This strange phenomenon also occurs in the Lesbos material. The Lesbos wood is similar to *Laurinoxylon diluviale* (Table 2b), because it has simple and scalariform perforation plates and 1–5-seriate rays, but differs in vessel diameter and idioblast size and abundance. These differences (Table 2b) may be in fact related to the individual variability as the samples probably come from different parts of the tree.

Problems and proposals – Laurinoxylon compressum Huard is ring-porous. This characteristic is not in accordance with the emended diagnosis of *Laurinoxylon*. We believe that its ring-porosity and low rays indicate it should be assigned to *Sassafrasoxylon* Březinová & Süss. Additional study is needed to determine if it is conspecific with *Sassafrasoxylon lipnicense*.

Laurinoxylon perfectum Huard tends to have some aliform parenchyma. This type of parenchyma is not typical for *Laurinoxylon*. A re-examination of the specimen is recommended for better assessing its affinities.

Botanical affinities – We did not observe crystals in *Laurinoxylon* aff. *diluviale* from Lesbos or in *Laurinoxylon diluviale* from Jáchymov, so our material belongs to the Subgroup 2 of *Laurinoxylon* Type 2b. We observed septate fibres in this material. Septate fibres occur in *Nectandra*, a genus belonging to the Perseae Nees tribe, and therefore we suggest that *Laurinoxylon* aff. *diluviale* might have affinities with the group of *Nectandra* species without crystals.
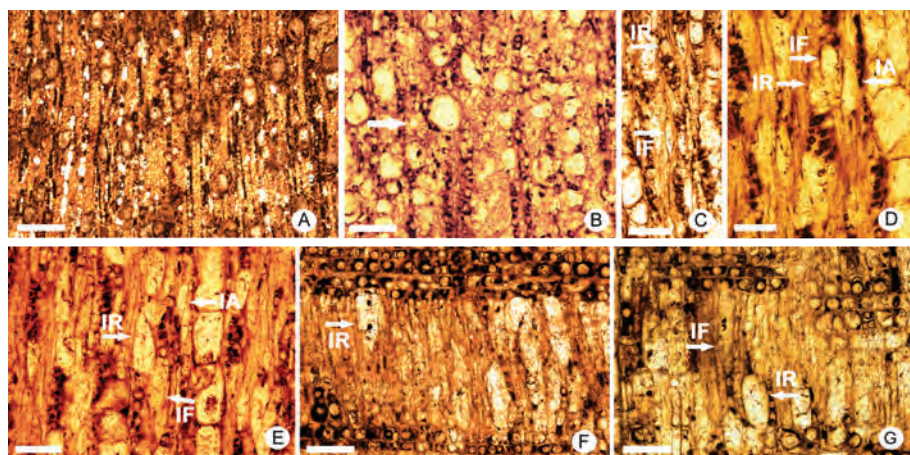
Figure 5. *Cinnamomoxylon* Gottwald (= *Laurinoxylon* Type 3), *Cinnamomoxylon seemannianum* (Mädel) Gottwald (DMDA6a, DMDA6b, DMDA6c). – A, B: (Scanty) vasicentric paratracheal parenchyma, slightly confluent forming bands, outline of solitary vessels mainly angular, idioblasts associated with the ray (= IR) and axial (= IA) parenchyma cells and among the fibres (= IF), TS. – C, D: Idioblasts IR, IA and IF, TLS. – E: Axial parenchyma: scanty paratracheal with a thickness of 15–40 μm, idioblasts IR, IA and IF, TLS. – F, G: Heterocellular rays, body ray cells procumbent with one row of upright and/or square marginal cells, idioblasts IR and IF, RLS. — Scale bars = 50 μm in B; 100 μm in D, E, F, G; 200 μm in A, C.

Laurinoxylon **Type 3** / *Cinnamomoxylon* Gottwald

Fossil species – Cinnamomoxylon seemannianum (Mädel) Gottwald (Fig. 5A–G, Table 3).

Material: DMDA 6 (7 slides).

Locality: Southeastern Lesbos, Greece.

Stratigraphic horizon: Under Polichnitos Ignimbrite, inside volcanics.

Age: early Miocene.

Macroscopic description – The specimen belongs to one of three small stems found enclosed in volcanic material with the following dimensions: $4.5 \times 2 \times 2$ cm. This stem and the other two are silicified, light, whitish brown with distinct growth ring boundaries that can be seen with the naked eye.

Microscopic description – Growth rings: distinct. – Wood: diffuse-porous. – Vessels: 40–100 vessels/sq. mm; 17% solitary, 33% in groups of two, 14% in groups of 3, 15% in groups of 4 and 21% in clusters; tangential diameter 45–50 μm, mean 47 μm; radial diameter 60–110 μm, mean 90 μm; outline of solitary vessels mainly round to oval (sometimes the vessels' outline seems angular because the sample is contorted and compressed) (Fig. 5B); vessel walls thin; perforation plates simple (Fig. 5D, E); tyloses common (Fig. 5A); intervessel pits alternate. – Rays: heterocellular, up to 5-seriate (mostly 2–3-seriate) (50–60 μm), and 300–500 μm high, body of multiseriate rays composed of procumbent body ray cells with one row of upright and/or square marginal cells (Fig. 5F, G); crystals not seen; rays 9 (7–14) per mm. – Axial parenchyma: scanty

paratracheal, vasicentric to confluent (Fig. 5A, B, D, E). – Fibres: probably non-septate. – Idioblasts: associated with the ray and axial parenchyma cells and among the fibres (Fig. 5A–G). Idioblasts in the transverse view radial × tangential diameter in μm from 30 × 135 to 50 × 160 and per sq. mm 15–33.

Table 3. Comparison of the anatomical characteristics among species of *Laurinoxylon* type 3.

* is used for the species that we suggest are excluded from *Laurinoxylon*. For abbreviations used in Tables 1, 2a, b, 3 & 4, see legends on page 468.

	Cinnamomoxylon limagnense* [syn. *Laurinoxylon limagnense*]	*Laurinoxylon variabile**	*Laurinoxylon bergeri*	*Cinnamomoxylon seemanianum** [syn. *Laurinoxylon seemannianum*]	*Cinnamomoxylon seemannianum* [syn. *Laurinoxylon seemannianum*] DMDA 6
Laurinoxylon Type 3					
Locality	d'Aigueperse (Puy-de-Dome), France	d'Aigueperse (Puy-de-Dome), France	Hasenberg at Wiesa close to Kamenz (Saxony, Germany)	Randecker Maar (SW Germany)	Southeastern Lesbos, Greece
Age	Oligocene	Oligocene	Middle–Upper Oligocene	Upper Miocene	Early Miocene
GR	Distinct	Distinct	Distinct	Distinct	Distinct
Porosity	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
V Grps	sol (66%), rms of 2 (28%), 3 (6%), and 4 (1%)	sol (52%), rms of 2 (36%), 3 (9%), 4 (2%) and 5 (1%)	sol, rms of 2, rarely of 3–4	sol and rms of 2 –3	sol (17%), rms of 2 (33%), 3 (14%) and 4 (15%), and cls (21%)
VTD: Mean (range) μm	93 (60–140)	164 (65–225)	80–87 (30–135)	99 (25–150)	45–50
V/mm²	12–15	3–5	5–40	20 (13–29)	40–100
VEL: Mean (range) μm	187	295	105–110 (30–180)	115 (45–180)	60–110
Tyloses	Present		Present	Present	Present
PP simple/ scalariform	Yes / Occasion-ally (5–8 bars)	Yes / No	Yes / No	Yes / No	Yes / No
IVP size (μm)	9–12	6–7			
VRP	Elliptic (4–7 x 7–15 μm) or cir-cular (6–10 μm)	6–7	sim		
AP	vc, cfl	alf–cfl	scp, vc	scp, vc	scp, vc
RW (cell no.)	1–4	1–3(–4)-seriate	1–3	1–3 (2–3)	1–5
RW (μm)	60		25 (7–40)	15–35	50–60
R/mm	7–8	3–8	9–11	5–10	7–14 (mostly 9)
RH (μm)	620	50–225)	200–230 (25–800)	100–400	300–500
SepFib	Possibly	No	No	Some	Possibly
Idioblasts per mm²	very numerous		very numerous	numerous	15–33
Idioblast size (μm)	20–75 × 40–170	26–70 × 30–150 (in TS)	R: 50 (25–75), T: 25 (15–40), Ht: 110 (50–250/ 70 (55–120)	R: 53 (20–95), T: 38 (20–50), Ht: 130 (50–150)	R: 30–50, T: 90–175
Prismatic crystals	No	No	No	No	No

Comparison with Laurinoxylon Type 3 species and Cinnamomoxylon (Table 3).

As indicated by the description above, this specimen from Lesbos has characteristics of *Laurinoxylon* Type 3. The revised diagnosis of *Laurinoxylon* is not clear about how abundant axial parenchyma can be within the genus. We think that the new Lesbos material with the idioblast distribution of the *Laurinoxylon* Type 3 group should be assigned to *Cinnamomoxylon sensu* Gottwald (1997). As implied by its name, this fossil genus has features seen in present-day *Cinnamomum*, which according to Richter (1981a) also has features seen in some species of *Lindera*, *Litsea* and *Persea*.

We think that the diagnosis of *Cinnamomoxylon* Gottwald should be modified to include rays up to 5-seriate (as described in Richter 1981a for extant *Cinnamomum*), rather than 2–4 cells.

According to the results of our search through the InsideWood database and the literature, fossil species belonging to Type 3 warranting comparison with our new Lesbos material are: *Cinnamomoxylon limagnense* (Privé-Gill & Pelletier) Gottwald, *Laurinoxylon bergeri* Süss, *Cinnamomoxylon seemannianum* (Mädel) Gottwald, and *Laurinoxylon variabile* Privé-Gill & Pelletier.

Cinnamomoxylon limagnense differs from DMDA 6 in vessel grouping, mean vessel diameter, sporadic occurrence of scalariform perforation plates, vessel density and parenchyma arrangement (Privé-Gill & Pelletier 1981) (Table 3).

Süss (1958) suggested that *Laurinoxylon bergeri* resembled extant *Lindera polyantha* and *Aniba ovalifolia*. Later, Gottwald (1997) suggested it had similarities with the modern tropical Asian species of *Actinodaphne*, *Cinnamomum*, *Litsea* and *Persea*. Süss also suggested that *Laurinoxylon bergeri* was similar to *Laurinoxylon aromaticum* Felix, *L. bakeri* Berry, *L. ehrendorferi* Berger, *L. hasenbergense* Schönfeld, *L. linderoides* Schönfeld, and *L. nectandroides* Kräusel.

The Lesbos specimen differs from *Laurinoxylon variabile* in vessel grouping, mean vessel diameter, vessel density, and septate fibre occurrence (Table 3). The most important difference is the occurrence of aliform-confluent parenchyma forming oblique or tangential bands in *Laurinoxylon variabile* (Privé-Gill & Pelletier 1981). There are also differences in rays: *L. variabile* has an extremely low number of rays per mm. Idioblast dimensions of *L. variabile* and Lesbos wood samples are similar.

Süss and Mädel (1958) described *Laurinoxylon seemannianum* Mädel, now *Cinnamomoxylon seemannianum* (Mädel) Gottwald, as having idioblasts associated with ray and axial parenchyma and among the fibres. Their description indicates that the idioblasts of *L. seemannianum* Mädel have similar dimensions as the Lesbos Type 3 wood. The only differences between the Lesbos wood and *Cinnamomoxylon seemannianum* are in dimensions of vessels and rays. Differences are likely to be ontogenetic. Most recently, *Cinnamomoxylon seemannianum* was described by Koutecký & Sakala (2015) from the Oligocene of the Czech Republic.

Laurinoxylon cf. *seemannianum* described by Selmeier (1967, 1969, 1984) and Gottwald (1992) seems problematic (see the "Problems and proposals" paragraph) because these two authors have reported idioblasts associated only with the ray parenchyma. Therefore, DMDA 6 was compared only with *Laurinoxylon seemannianum* Mädel and not with *Laurinoxylon* cf. *seemannianum*.

We have named the specimen from Lesbos as *Cinnamomoxylon seemannianum* (Mädel) Gottwald (syn. *Laurinoxylon seemannianum* Mädel). There are only minor differences between the Lesbos wood and *Laurinoxylon seemannianum* Mädel which are of the type seen within a single tree, *i.e.* differences between trunk and branch wood. Unfortunately, our species is not well enough preserved to observe some important details, such as type of vessel-ray parenchyma pits.

Problems and proposals – The parenchyma distribution of *Laurinoxylon variabile* Privé-Gill & Pelletier is aliform-confluent forming oblique or tangential bands differing from the emended diagnosis of *Laurinoxylon*. The occurrence of this type of parenchyma and its other features recommends its assignment to *Cinnamomoxylon*.

We propose the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala & Wheeler.

Laurinoxylon cf. *seemannianum* was described by Selmeier (1967, 1969, 1984) and Gottwald (1992) as having idioblasts associated only with the ray parenchyma. This description is not in accordance with the one by Süss and Mädel (1958). Because there are no idioblasts in axial parenchyma and amongst the fibres, *Laurinoxylon* cf. *seemannianum* is not comparable to *L. seemannianum,* but with the representatives of *Laurinoxylon* Type 1 group.

Consequently, we suggest that *Laurinoxylon* cf. *seemannianum* specimens be re-examined and compared with the *Laurinoxylon* species of the Type 1 group. Based on that re-examination they might be assigned to a species in that group or named as a new species.

Botanical affinities – The material from Lesbos has no crystals and it has septate fibres as do *Cinnamomum* and *Ocotea* (tribe Perseae Nees).

We suggest that fossil woods should be assigned to *Cinnamomoxylon*, rather than to *Laurinoxylon,* when their axial parenchyma is vasicentric to confluent or aliform to confluent and rays are 2–5-seriate. This has already been done for two other species: *Cinnamomoxylon limagnense* (Privé-Gill & Pelletier) Gottwald (1987) and *Cinnamomoxylon seemannianum* (Mädel) Gottwald (1987), and we propose the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala & Wheeler.

Velitzelos *et al.* (1981b) described leaves of *Cinnamomum polymorphum* Heer *sensu* Grangeon from the area of the Petrified Forest of Lesbos (appendix in Mantzouka *et al.* 2013). It is possible that the wood described here is related to these leaves.

CONCLUSION

Laurinoxylon is a large fossil genus (Gregory *et al.* 2009), which generally has functioned as a catch-all for fossil lauraceous woods. Based on the revised diagnosis of the genus (Dupéron *et al.* 2008), we suggest that the following features indicate that a fossil wood should *not* be assigned to *Laurinoxylon*:

A. Axial parenchyma features not characteristic of *Laurinoxylon*: A1. Occurrence of marginal bands, A2. Aliform to aliform-confluent paratracheal parenchyma.
B. Ray features not characteristic of *Laurinoxylon*: B1. Rays higher than 1 mm, B2. Exclusively homocellular rays, B3. Rays more than 5 cells wide, B4. Rays storied.
C. Porosity not characteristic of *Laurinoxylon*: Ring-porous wood.
D. The absence of idioblasts (oil and/or mucilage cells).

We found that *Laurinoxylon* has features that occur in some extant genera of the tribes Laureae (*Actinodaphne, Laurus, Lindera* A and B, *Litsea, Neolitsea*) and Perseae (*Aiouea, Aniba, Cinnamomum, Dehaasia, Dicypellium, Endlicheria, Licaria, Nectandra, Nothaphoebe, Ocotea, Persea* - North American species, *Phoebe, Pleurothyrium, Systemonodaphne, Urbanodendron*), and also in genera whose tribal affinities are as yet unclear: *Apollonias, Cryptocarya* of Madagascar and *Iteadaphne*.

We recognized four groups of *Laurinoxylon* species based on the location of the idioblasts:

Type 1 with idioblasts associated only with ray parenchyma cells, as seen in extant *Dicypellium, Laurus,* the *Litsea chinensis* group, North American *Persea, Systemonodaphne, Urbanodendron*.

Type 2a with idioblasts associated with both rays and axial parenchyma, as seen in extant *Aiouea, Aniba, Apollonias, Cryptocarya* from Madagascar, *Dehaasia, Licaria, Lindera* group A, *Nothaphoebe, Persea, Phoebe, Pleurothyrium*.

Type 2b with idioblasts associated with rays and present among the fibres; as seen in extant *Actinodaphne* p.p., *Nectandra* p.p. and *Neolitsea* p.p.

Type 3 with idioblasts associated with ray and axial parenchyma cells and present among the fibres, as seen in *Actinodaphne* p.p., *Cinnamomum, Endlicheria, Nectandra* p.p., *Neolitsea* p.p. and *Ocotea*.

We described new fossil woods from the Lesbos (Types 1, 2b and 3) and Ipolytarnóc (Type 2a) UNESCO Global Geoparks and added information from the original slides of the types of *Laurinoxylon czechense* from Kadaň-Zadní Vrch Hill (Type 1) and *L. diluviale* from Jáchymov (Type 2b). Characteristics of *Laurinoxylon* species described earlier were discussed with regard to placing them in one of the groups we propose.

We suggest that using criteria or filters (A – axial parenchyma features, B – ray features, C – ring porosity, D – absence of idioblasts) that preclude assigning a fossil wood to *Laurinoxylon* and idioblast location is useful for relating fossil lauraceous woods to groups of extant lauraceous genera. Further study of the co-occurrence of fossil lauraceous wood, leaves, and reproductive organs may allow doing 'Whole Plant' reconstructions (Sakala 2004; Kvaček 2008, Manchester *et al.* 2014), as was done for an extinct Eocene tree belonging to the Platanaceae (Manchester 1986).

During this study, we found evidence suggesting that some *Laurinoxylon* species deserve further study and, in some cases, assignment to another genus. We proposed the new combination *Cinnamomoxylon variabile* (Privé-Gill & Pelletier) Mantzouka, Karakitsios, Sakala, & Wheeler. There are some species that should be excluded from the Lauraceae: *Laurinoxylon intermedium* Huard with features of the Magnoliaceae and *Laurinoxylon aniboides*, which possibly is Magnoliaceae or Canellaceae.

Table 4. Comparison of the anatomical characteristics among *Laurinoxylon* types.

For abbreviations used in Tables 1, 2a, b, 3 & 4, see legends on page 468.

	Type 1	Type 2a	Type 2b	Type 3
Idioblast location	Rays	Rays & Axial parenchyma	Rays & Among fibres	Rays & Axial paenchyma & Among fibres
Vessel grouping	Solitary, rms 2–4	>50% solitary, rms 2–4	Solitary, mostly rms 2–4	Solitary, rms 2–4
MVTD μm	50–150	60–160	50–160	45–164
Vessels / mm²	20–100	10–45	9–100	5–100
Tyloses	Present	Present	Present	Present
Perforation plates	si, si + sc	si, si + sc	si, si + sc	si, si + sc
IV pits size	Large	Medium–large	Small–large	–
Axial parenchyma	Scanty paratracheal, vasicentric	Scanty paratracheal, vasicentric	Scanty paratracheal, vasicentric	Scanty paratracheal, vasicentric
Ray seriation	1–3	1–3(–4)	1–5	1–5
Septate fibres present	Yes and No	Yes	Yes and No	Yes

REFERENCES

Awasthi N & Ahuja M. 1982. Investigation of some carbonised woods from the Neogene of Varkala in Kerala coast. Geophytology 12: 245–259.

Baas P & Gregory M. 1985. A survey of oil cells in the dicotyledons with comments on their replacement by and joint occurrence with mucilage cells. Israel J. Bot. 34: 167–186.

Berger W. 1953. Jungtertiäre Pflanzenreste aus dem Gebiete der Ägäis (Lemnos, Thessaloniki). Ann. Géol. Pays. Hellén. 5: 34–64.

Boonchai N & Manchester SR. 2012. Systematic affinities of early Eocene petrified woods from Big Sandy Reservoir, Southwestern Wyoming. Int. J. Plant Sci. 173: 209–227.

Borsi S, Ferrara G, Innocenti F & Mazzuoli R. 1972. Geochronology and petrology of Recent volcanics in the eastern Aegean Sea (West Anatolia and Lesbos Island). Bull. Volcanol. 36: 473–493.

Boureau E. 1957. Anatomie vegetale. Vol. 3. Presses Univ. France, Paris: 525–752.

Březinová D. 1981. Fossil-Hölzer aus der Umgebung von Karlsbad. Acta Musei Nationalis Pragae 37B: 137–160.

Callado CH & Costa CG. 1997. Wood anatomy of some *Anaueria* and *Beilschmiedia* species (Lauraceae). IAWA J. 18: 247–259.

Carlquist S. 2001. Comparative wood anatomy. Systematic, ecological, and evolutionary aspects of dicotyledon wood. Ed. 2. Springer Verlag, Berlin, Heidelberg.

Chanderbali AS, van der Werff H & Renner SS. 2001. Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. Ann. Missouri Bot. Gard. 88: 104–134.

Dupéron J, Dupéron-Laudoueneix M, Sakala J & De Franceschi D. 2008. *Ulminium diluviale* Unger: historique de la découverte et nouvelle étude. Ann. Paleontol. 94: 1–12.

Felix J. 1883. Untersuchungen über fossile Hölzer. I. Zeitschrift der Deutschen Geologischen Gesellschaft 35: 59–92.

Gottwald H. 1992. Hölzer aus Marinen Sanden des Oberen Eozän von Helmstedt (Niedersachsen). Palaeontographica B 225: 27–103.

Gottwald H. 1997. Alttertiäre Kieselhölzer aus miozänen Schottern der ostbayerischen Molasse bei Ortenburg. Documenta nat. 109: 1–83.

Gregory M & Baas P. 1989. A survey of mucilage cells in vegetative organs of the Dicotyledons. Israel. J. Bot. 38: 125–174.

Gregory M, Poole I & Wheeler EA. 2009. Fossil dicot wood names. An annotated list with full bibliography. IAWA J., Suppl. 6: 220.

Greguss P. 1954. Az ipolytarnóci alsó-miocén kövesedett famaradványok. Földtani Közlöny 84: 91–109.

Greguss P. 1969. Tertiary angiosperm woods in Hungary. Akademiai Kiado, Budapest.

Hably L. 1983. Early Miocene plant fossils from Ipolytarnóc, N. Hungary. Geol. Hung. Ser. Paleont. 45: 77–255.

Huard J. 1967. Étude de trois bois de Lauracées fossiles des formations a lignite néogènes d'Arjuzanx (Landes). Rev. Gen. Bot. 74: 81–105.

Iamandei E & Iamandei S. 1997. Xylotomical study of some fossil dicot trunks of Techereu in the Metalliferous Carpathians. Acta Palaeontologica Romaniae. 1. The First Romanian National Symposium on Palaeontology, 17-18 October, 1997, Bucharest, pp. 107–112.

IAWA Committee (eds. Wheeler EA, Baas P & Gasson PE). 1989. IAWA list of microscopic features for hardwood identification. IAWA Bull. n.s. 10: 219–232.

InsideWood. 2004-onwards. Published on the Internet (http://insidewood.lib.ncsu.edu/search) [last visit 5/11/2015].

Johansson JT. 2013-onwards. The phylogeny of angiosperms. Published online (http://angio.bergianska.se) [last visit 10/09/2014].

Koutecký V & Sakala J. 2015. New fossil woods from the Paleogene of Doupovské hory and České středohoří Mts. (Bohemian Massif, Czech Republic). Acta Mus. Nat. Pragae, Ser. B Hist. Nat. 71: 377–398.

Kräusel R & Schönfeld G. 1924. Fossile Hölzer aus der Braunkohle von Süd-Limburg. Abh. Senck. Naturf. Ges. 38: 272–282.

Kvaček Z. 2008. Whole-plant reconstructions in fossil angiosperm research. Int. J. Plant Sci. 169: 918–927.

Kvaček Z, Teodoridis V & Roiron P. 2011. A forgotten Miocene mastixioid flora of Arjuzanx (Landes, SW France). Palaeontographica B 285: 3–111.

Lakhanpal RN, Prakash U & Awasthi N. 1978 (1981). Some more dicotyledonous woods from the Tertiary of Deomali, Arunachal Pradesh, India. The Palaeobotanist 27: 232–252.

Lamera S. 2004. The Polychnitos Ignimbrite of Lesvos Island. PhD diss. (in Greek). University of Patras, Greece.

Lamera S, Tzortzi J, Zelilidis A, Seymour KS & Kouli M. 2004. A Lahar-like deposit at the Sole of the Polychnitos Ignimbrite, Lesvos Volcanic Field Northern Aegean, Hellas. Proc. 7th International Conf. of the Hellenic Geographical Society, Lesbos, Greece: 408–414.

Loutfy MHA. 2009. Wood anatomy and its implications on the taxonomy of *Apollonias* Nees (Lauraceae). Feddes Repert. 120: 75–90.

Mai DH. 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fisher Verlag, Jena.

Manchester SR. 1986. Vegetative and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of western North America. Bot. Gaz. 147: 200–226.

Manchester SR, Calvillo-Canadell L & Cevallos-Ferriz SRS. 2014. Assembling extinct plants from their isolated parts. Bol. Soc. Geol. Mexicana 66: 53–63.

Mantzouka D, Sakala J, Kvaček Z & Karakitsios V. 2013. Palaeobotanical study of Polichnitos region, southern part of Lesbos Island, Greece (preliminary results on angiosperm wood). Bull. Geol. Soc. Greece 47: 204–215.

Metcalfe CR. 1987. Anatomy of the Dicotyledons Vol. III. Magnoliales, Illiciales, and Laurales (*sensu* Armen Takhtajan). Clarendon Press, Oxford.

Metcalfe CR & Chalk L. 1950. Anatomy of the Dicotyledons. Vol. I, II. Clarendon Press, Oxford.

Pálfy J, Mundil R, Renne PR, Bernor RL, Kordos L & Gasparik M. 2007. U-Pb and 40Ar/39Ar - dating of the Miocene fossil track site at Ipolytarnóc (Hungary) and its implications. Earth Planet Sc. Lett. 258: 160–174.

Pe-Piper G. 1980. The Cenozoic volcanic sequence of Lesbos, Greece. Z. Dt. Geol. Ges. 131: 889–901.

Pe-Piper G & Piper DJW. 1993. Revised stratigraphy of the Miocene volcanic rocks of Lesbos, Greece. N. Jb. Geol. Paläont. Mh. H2: 97–110.

Petrescu I. 1978. Etudes sur les flores paléogènes du nord-ouest de la Transsylvanie et de la Moldavie Central. Mém. Inst. Géol. Géophys. 27: 113–184 (Univ. Cluj-Napoca, Bucarest).

Prakash U, Březinová D & Awasthi N. 1974. Fossil woods from the Tertiary of South Bohemia. Palaeontographica B 147: 107–123.

Prakash U, Březinová D & Bůžek Č. 1971. Fossil woods from the Doupovské hory and České středohoří Mountains in northern Bohemia. Palaeontographica B 133: 103–128.

Prasad M. 1989 [1990]. Occurrence of a lauraceous wood in the Siwalik sediments, India. Geophytology 19: 191–192.

Privé-Gill C & Pelletier H. 1981. Sur quelques bois silicifiés du Tertiaire de Limagne, dans la région d'Aiguerperse (Puy-de-Dôme), France. Rev. Palaeobot. Palynol. 34: 369–405.

Richter HG. 1981a. Anatomie des sekundären Xylems und der Rinde der Lauraceae. Sonderb. Naturwiss. Vereins Hamburg 5: 1–148. Parey, Hamburg.

Richter HG. 1981b. Wood and bark anatomy of Lauraceae. I. *Aniba* Aublet. IAWA Bull. n.s. 2: 79–87.

Richter HG. 1985. Wood and bark anatomy of Lauraceae. II. *Licaria* Aublet. IAWA Bull. n.s. 6: 187–199.

Richter HG. 1990. Wood and bark anatomy of Lauraceae. III. *Aspidostemon* Rohwer & Richter. IAWA Bull. n.s. 11: 47–56.

Richter HG & van Wyk AE. 1990. Wood and bark anatomy of Lauraceae IV. *Dahlgrenodendron* J.J.M. Van der Merwe & Van Wyk. IAWA Bull. n.s. 11: 173–182.

Rohwer JG, de Moraes PLR, Rudolph B & van der Werff H. 2014. A phylogenetic analysis of the *Cryptocarya* group (Lauraceae), and relationships of *Dahlgrenodendron*, *Sinopora*, *Triadodaphne*, and *Yasunia*. Phytotaxa 158: 111–132.

Sakala J. 2004. The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic, with particular reference to fossil wood. PhD diss. Université Pierre-et-Marie, Paris & Charles University, Prague.

Sakala J & Privé-Gill C. 2004. Oligocene angiosperm woods from northwestern Bohemia, Czech Republic. IAWA J. 25: 369–380.

Sakala J, Rapprich V & Pecskay Z. 2010. Fossil angiosperm wood and its host deposits from the periphery of a dominantly effusive ancient volcano (Doupovské hory Volcanic Complex, Oligocene-Lower Miocene, Czech Republic): systematic, volcanology, geochronology and taphonomy. Bull. Geosci. 85: 617–629.

Schweingruber FH, Börner A & Schulze ED. 2011. Atlas of stem anatomy in herbs, shrubs and trees. Vol. 1. Springer.

Selmeier A. 1967. Ein Lauraceenholz aus dem Miozän der Fränkischen. Alb. Geol. Bl. 17: 70–84.

Selmeier A. 1969. Ein Lorbeerholz aus jungtertiären Schichten Südbayerns (Overschneitbach). N. Jb. Geol. Paläont. Mh. 12: 731–741.

Selmeier A. 1984. Fossile Bohrgänge von *Anobium* sp. in einem jungtertiären Lorbeerholz aus Egweil (Südliche Frankenalb). Archaeopteryx 2: 13–29.

Stevens PF. 2001-onwards. Angiosperm Phylogeny Website. Version 12, July 2012 [and more or less continuously updated since] (http://www.mobot.org/MOBOT/research/APweb/) (last visit: 10/9/2014).

Sun J, Wu J, Wang X, Gu J & Gao Z. 2015. Comparative wood anatomy of 56 species of Lauraceae from Yunnan, China. Brazil. J. Bot. 38: 645–656.

Süss H. 1958. Anatomische Untersuchungen über die Lorbeerhölzer aus dem Tertiär des Hasenberges bei Wiesa in Sachsen. Abh. Deut. Akad. Wiss. Berlin Jahrb. 8: 1–59.

Süss H & Mädel E. 1958. Über Lorbeerhölzer aus miozänen Schichten von Randeck (Schwäbische Alb) und Ipolytarnóc (Ungarn). Geologie 7: 80–99.

Szarvas I. 2007. Case study of the Ipolytarnóc track site, Hungary. In: Lucas SG, Spielmann JA & Lockley MG (eds.), Cenozoic vertebrate tracks and traces: 303–307. New Mexico Museum of Natural History and Science Bulletin 42.

The Plant List. 2013. Version 1.1. Published on the Internet (http://www.theplantlist.org/) [last visit 1/1/2015].

Unger F. 1842. Synopsis lignorum fossilium plantarum acramphibryarum. In: Endlicher S (ed.), Genera plantarum secundum ordines naturales disposita: 100–102. Suppl. II. Appendix. Wien.

van der Burgh J. 1964. Hölzer der niederrheinischen Braunkohlenformation. 1. Hölzer der Braunkohlengrube "Anna" zu Haanrade (Niederrheinisch Limburg). Acta Bot. Neerl. 13: 250–301.

van der Burgh J. 1973. Hölzer der niederrheinischen Braunkohlenformation. 2. Hölzer der Braunkohlengrube "Maria Theresia" zu Herzogenrath, "Zukunft West" zu Eschweiler und "Victor" (Aulpich Mitte) zu Zulpich, nebst einer systematisch-anatomischen Bearbeitung der Gattung *Pinus* L. Rev. Palaeobot. Palynol. 15: 73–275.

van der Werff H & Nishida S. 2010. *Yasunia* (Lauraceae), a new genus with two species from Ecuador and Peru. Novon: A Journal for Botanical Nomenclature 20: 493–502.

van der Werff H & Richter HG. 1985. *Caryodaphnopsis* Airy-Shaw (Lauraceae), a genus new to the Neotropics. Syst. Bot. 10: 166–173.

van der Werff H & Richter HG. 1996. Toward an improved classification of Lauraceae. Ann. Missouri Bot. Gard. 83: 409–418.

Velitzelos E, Petrescu I & Symeonidis N. 1981a. Tertiary plant reminants from Aegiis. Macro–Palaeo–Flora of Lesbos Island (in Greek). Ann. Géol. Pays Hellén. Athens XXX/2: 500–514.

Velitzelos E, Petrescu I & Symeonidis N. 1981b. Tertiäre Pflanzenreste von der Ägäischen Insel Lesbos (Griechenland) [Tertiary plant fossils from Lesbos Island (Aegean, Greece)]. Cour. Forsch. Inst. Senckenberg Frankfurt 50: 49–50.

Velitzelos E, Zouros N & Velitzelos D. 1999. Contribution to the study of the palaeoflora of the Lesbos Petrified Forest. International Symposium 'Protected natural areas and environmental education' Sigri Lesbos Island.

Wheeler EA. 1986. Vessels per square millimeter or vessel groups per square millimeter? IAWA Bull. n.s. 7: 73–74.

Wheeler EA. 2011. InsideWood: a web resource for hardwood anatomy. IAWA J. 32: 199–211.

Wheeler EA & Manchester S. 2002. Woods of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon, USA. IAWA J. Suppl. 3, 188 pp.

Zouros N. 2004. The European Geoparks Network: Geological heritage protection and local development. Episodes 27: 165–171.