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Zitteliana

Reihe A

Mitteilungen der Bayerischen Staatssammlung
für Paläontologie und Geologie

43



MÜNCHEN 2003

Zitteliana

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HINWEIS DES HERAUSGEBERS

Vom Jahr 2003 an erscheint die Zeitschrift *Zitteliana* in zwei Reihen.

Die *Reihe A: Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-412X) ersetzt die bisherigen „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). Die Bandzählung (zuletzt erschienen: Heft 42, 2002) wird fortgesetzt.

Die *Reihe B: Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-4138) führt die bisherige „Zitteliana - Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627) fort.

Hinweise für Autoren beider Reihen sind am Ende dieses Bandes enthalten.

EDITORIAL NOTE

Starting in 2003 the journal *Zitteliana* is published in two series.

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The *Reihe B: Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-4138) continues the previous „Zitteliana - Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627).

Instructions for authors are included at the end of this volume.



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Tertiary *Cedrela* woods (Meliaceae) from the North Alpine Foreland in Southern Germany and Austria

By
ALFRED SELMEIER

ABSTRACT

The microscopic structure of silicified *Cedrela* wood, assignable to the form genus *Cedreloxylon* SELMEIER, 1987, is described from the northern Alpine Foreland in southern Germany and Austria. Two structurally different wood types of *Cedreloxylon* can be distinguished based on cross sections. The wood of *Cedreloxylon* is compared to that seen in extant and other fossil taxa of *Cedrela*. In addition, the ring widths of 45 *Cedrela* wood fragments are recorded. The results suggest that minute anatomy and growth ring width may vary considerably

within a single tree, depending on the topographic position (e.g., stem, branch, root) of the respective fragment. Finally, a few comments are offered on the difficult task of interpreting fossil tree-rings with regard to palaeoclimatology, and some aspects are exemplified based on the material at hand.

Key words: Deciduous tree, Meliaceae, South Germany, Tertiary, Wood anatomy.

KURZFASSUNG

Berichtet wird über die anatomische Struktur von Kieselhölzern der Gattung *Cedrela*, Familie Meliaceae. Die Holzreste werden, von Ausnahmen abgesehen, in der Bayerischen Staatssammlung für Paläontologie und Geologie, München, aufbewahrt. Sie gehören zur fossilen Gattung *Cedreloxylon* SELMEIER, 1987. Zwei verschiedene Strukturtypen sind am Querschliff unterscheidbar. Von einigen Fundorten der südlichen Frankenalb beschreibt GOTTWALD (2002) verkieselte *Cedrela* Hölzer. Die Breite der Zuwachszonen dieser Funde

konnte mit Messungen an mehr als 40 weiteren *Cedrela* Hölzern verglichen werden. Rückschlüsse auf Klima und Umweltbedingungen sind jedoch nur bedingt möglich. Je nach Lage und Herkunft der fossilen Holzprobe innerhalb des einstigen Baumindividuums sind unterschiedliche Strukturen vorhanden (Stamm, Ast, Wurzel).

Schlüsselwörter: Holzanatomie, Laubbaum, Meliaceae, Süddeutschland, Tertiär

1. INTRODUCTION

The North Alpine Foreland (Switzerland, southern Germany, Austria) has yielded approximately 500 localities with permineralized Tertiary wood; over 11.000 specimens have

been collected to date and form the basis for an ongoing scientific research project (SELMEIER 1998). Nevertheless, *Cedrela* woods have been discovered at only a few of these

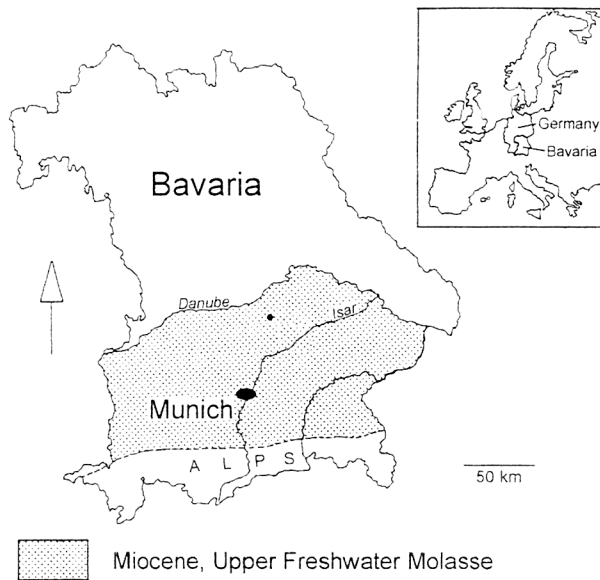


Fig. 1: Geographic position of the North Alpine Foreland Basin filled with massive Tertiary sediments with schematic illustration of the extension without Quaternary cover. - Map from GOHLICH (2002), modified.

sites, which are located in Bavaria and Austria, i.e. in the northern Alpine Foreland Basin, the so-called Molasse Basin. To the north, the Molasse Basin is bounded by the river Danube and in the south, it borders the Alps. The Molasse Basin is filled with massive Tertiary sediments. The uppermost part, which widely crops out (Fig. 1), represents the Miocene limnofluviatile Upper Freshwater Molasse (HEISSIG 1997).

The main places for easily collecting silicified wood remains are situated in the Franconian Alb between the rivers Altmühl (north) and Danube, but more rarely in the so-called Molasse basin (Fig. 2). The fossils in the Franconian Alb predominantly occur in sandy or loamy sediments, usually close to the surface (HOLLEIS & GREGOR 1986, HOLLEIS 1992). They can easily be picked up from farming fields or at waysides. The size of the usually grey to brown wood specimens from the southern Franconian Alb varies between just a few centimeters to up to 20-30 cm. Eleven hardwood families have been identified to date based on microscopical analysis. According to GOTTWALD (2002), the extant equivalents of these fossils grow in temperate, subtropical, or even tropical climates.

2. ANATOMICAL DESCRIPTION

Meliaceae

Cedreloxylon SELMEIER, 1987

Generic diagnosis (emend.): Growth rings distinct. Vessels ring-porous, early wood pores in 1-4 (-6) layers, solitary and in radial multiples of 2-3, maximal tangential diameter up to 450 μm , lumina plugged with brown to reddish deposits, late wood pores few, evenly distributed, solitary and in radial groups of 2-7, tangential diameter 50-70 μm ; intervessel pits

alternate, 5-7 μm , perforation plates simple, vessel segments generally short, tyloses absent. Fibres non-septate. Axial parenchyma terminal, sparsely paratracheal and diffuse. Rays uniseriate and multiseriate, mostly 3-4 cells wide, heterocellular to nearly homocellular, marginal cells with solitary rhomboid crystals, multiseriate rays in part with uniseriate ends. Occasionally traumatic gum canals present.

Type species: *Cedreloxylon cristalliferum*; stem rest 1 m, weight 100 kg, river Inn gravel, near Seibersdorf, Bavaria.

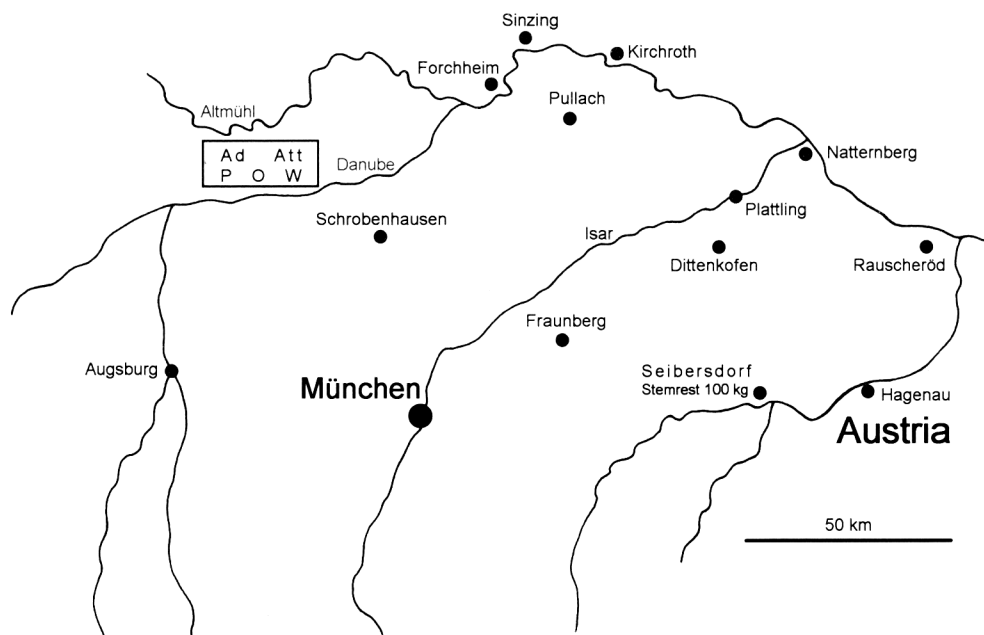


Fig. 2: Localities of *Cedrela* wood remains in the North Alpine Foreland Basin and southern Franconian Alb north of the river Danube (Ad = Adelschlag, Att = Attenfeld, P = Priehof, O = Ochsenfeld, W = Weißenkirchen).

2.1 CEDRELA WOOD TYPE A

Minute anatomy: Springwood pores usually with 4-5- (6) layers, large vessel tangential diameter > 300 µm, maximal up to 420 µm.

Hagenau

Austria, Oberösterreich, map TK 1 : 25000, No. 7744 Simbach a. Inn; castle Hagenau near Braunau a. Inn, approx. 800 m from the old river, on the shore of a lake, 2 m beneath surface.



Fig. 3: *Cedreloxylon*, silicified stem rest from Hagenau, Austria; length 26 cm, weight 5 kg. - Foto G. Janssen.

Age and horizon: Reworked, river Inn gravel, Miocene ?

Material: Stemrest, subangular, rounded at the edges by river Inn pebbles, grey, 26 cm long, perimeter 43 cm, weight 5 kg (Fig. 3); BSP 1949 I 23; leg. ERICH PFÖRTNER, München; 6 thin sections.

Natternberg

Bavaria, map TK 1 : 25000, No. 7143 Deggendorf, gravel pit HACKER near the highway Deggendorf - Regensburg; the area has been interpreted as a Holocene Danube river bottomland with peat and clay deposits, occupied by man first in the middle Neolithic (UNGER 1983).

Age and horizon: Reworked, Danube gravel, Miocene ?

Material: 9 cm long, perimeter 14 cm, leg. HEINZ HA-

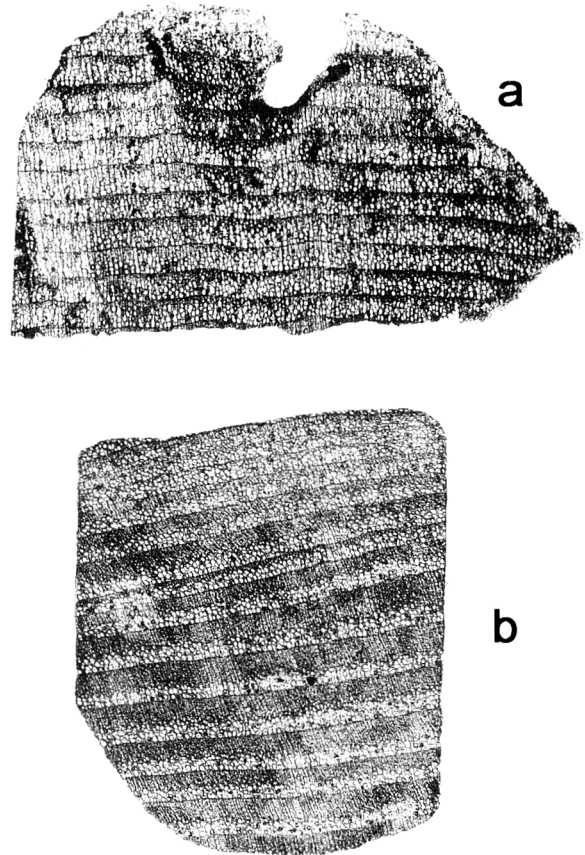


Fig. 4: *Cedreloxylon*, cross sections of thin slides with growth rings. - a: Hagenau, tangential 4.5 cm. - b: Natternberg, radial 3.6 cm.

BERDA; Deggendorf; Collection HABERDA No. 299; 5 thin sections.

Sinzing

Bavaria, map TK 1 : 25000, No. 6938 Regensburg, 1.5 km southeast of the village, discovered by digging near the so-called „am Schwalbennest“.

Age and horizon: In loess sediments over feldspar gravel, Miocene, Upper Freshwater Molasse.

Material: Bleached, conspicuously white, inner part of the wood grey-brown, length 28 cm; leg. DIETER MÜLLER 1973; BSP 1973 I 56, 3 thin sections.

Microscopic characters (Fig. 4-8): Large springwood pores, macroscopically recognizable on hand specimen and thick sections (wafers) of transversally, tangentially, and radially cut surfaces.

Growth rings pronounced, at the growth ring boundaries is a distinct zone of large springwood pores, up to 5-6 layers, the porous zones are recognizable in the radial cut surface as conspicuous, straight rims; growth ring boundaries marked by 2-3 rows of radially flattened latewood fibres and prominent differences in vessel diameter between late- and earlywood of subsequent rings; growth rings up to 4.9 mm wide.

Vessels variable in size, wood ring-porous; large vessels macroscopically discernible, usually abrupt transition to the latewood of the same growth ring; early wood vessels solitary and in radial multiples of 2-(-3), vessels form a well defined

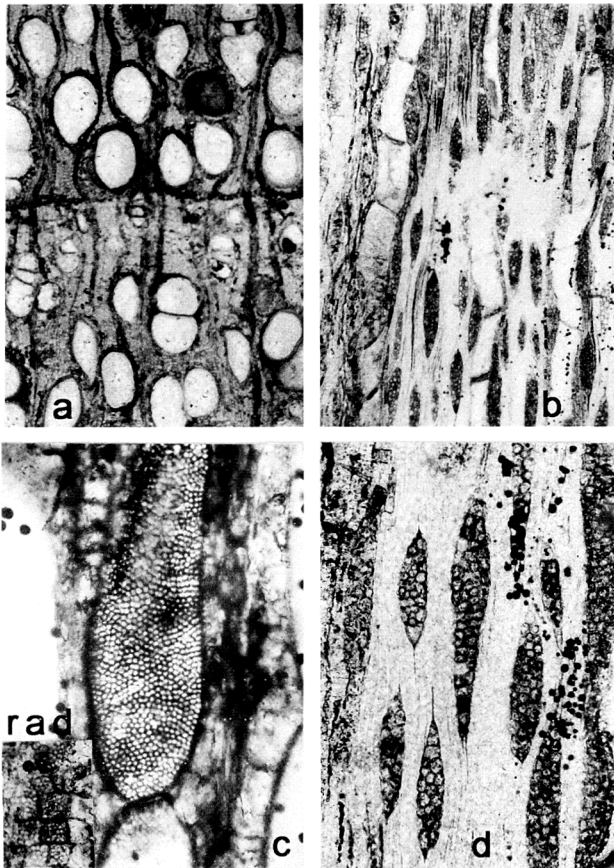


Fig. 5: *Cedreloxydon* from Hagenau. – a: cross section on growth ring boundary. x 20. – b: tangential section with simple vessel perforation. x 25. – c: tangential section with alternate vessel pitting, similar to cross field pitting (rad). x 110. – d: tangential section with weakly heterocellular ray structure. x 60.

zone with 3-5 layers, solitary vessels diameter tangential : radial, (210-392) : (294-459) μm , diameter of radial multiples of two, tangential : radial, (280-300) : (420-490) μm ; latewood vessels radial multiples of (3-8) common, locally a tendency to form small clusters of 6-(12) vessels, tangential diameter of late-wood pores 70-160 μm ; perforations exclusively simple; nearly horizontal to oblique, springwood vessel elements 233-456 (mean 309) μm , vessels truncate or abruptly tailed on one or both ends, thin-walled; intervessel pits polygonal in outline with included slit-like horizontal apertures, 5-6 μm ; vessel-ray pits similar in size and shape to intervessel pits; helical thickening absent, many vessels plugged with reddish-brown gum deposits, dumbbell-shaped deposits often occluding the perforations in tangential view; tyloses absent.

Fibres non-septate, 3-15 radial rows between two rays, relatively thick-walled, polygonal or quadratic shape in cross section, diameter about 14 μm , pits not observed.

Axial parenchyma scanty paratracheal, terminal and diffuse, 1-2-cell-wide sheaths around the vessels common, cells radial 35-49 μm , vertical up to 70 μm , pits ca. 7 μm .

Rays of two sizes. Uniseriate rays few, composed of quadratic to upright cells, 4-12 cells high, e.g. 10 (308 μm) cells; multiseriate rays, heterocellular, usually 3-4 cells wide, e.g. height 14-43 (420-830 μm) cells, some rays with 8-10 uniseriate rows of marginal cells, total ray height 700 μm , uniseriate portion 140 μm (4 cells) or total height of 25 cells with 10 cells

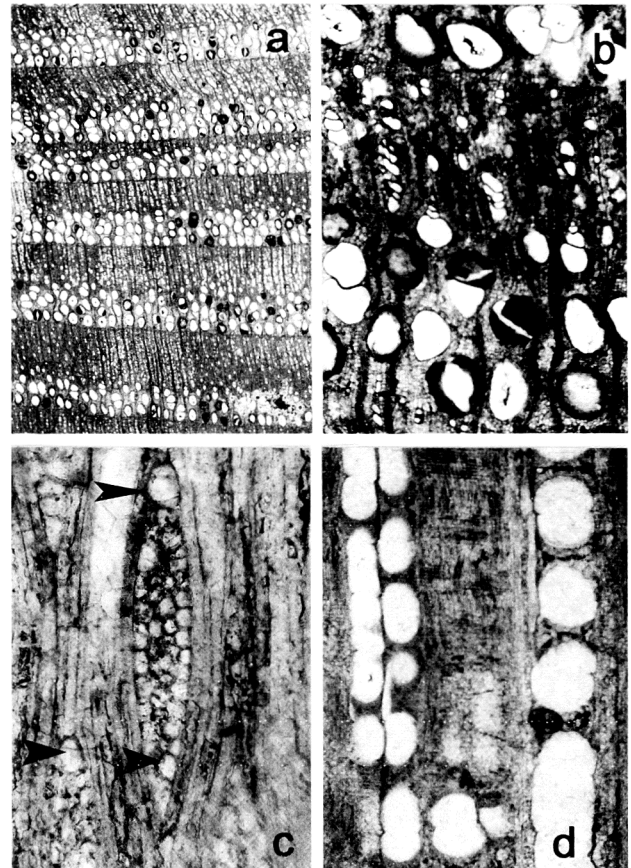


Fig. 6: *Cedreloxydon* from Natternberg. – a: cross section with six growth rings. x 3. – b: cross section with dark deposits in some vessels. x 20. – c: tangential section with heterocellular rays and solitary crystals (arrows). x 70. – d: radial section with dark, dumbbell-shaped deposits in the vessels. x 70.

uniseriate; multiseriate rays composed of procumbant, square and upright cells, marginal cells vertical 49-84 μm . Solitary rhomboid crystals in ray cells, especially in marginal cells common. (6)-8-10-(12) rays per mm tangential.

2.2 CEDRELA WOOD TYPE B

Minute anatomy: Springwood pores with commonly 1-2 layers, large vessel tangential diameter < 300 μm , maximal up to 280 μm .

Dittenkofen

Bavaria, map TK 1 : 25000, No. 7342 Landau a. d. Isar, south of Mamming, district Dingolfing a.d. Isar.

Age and horizon: Upper Miocene, so-called lower Nördlicher Vollsotter, Feinsandlage im Hangenden, +/- 410 m NN; discovered during excavation works for the construction of a water pipe.

Material: Silicified wood without bark, color brown to grey, length 10 cm; leg. H.-R. VON BERCHEM, 1964; BSP 1966 I 91; 3 thin sections.

Microscopic characters (Fig. 9): Growth rings distinct, macroscopically visible, early wood pores immediately on the growth ring boundaries, growth ring zones 0.6-4.8 (mean 1.2) mm wide.

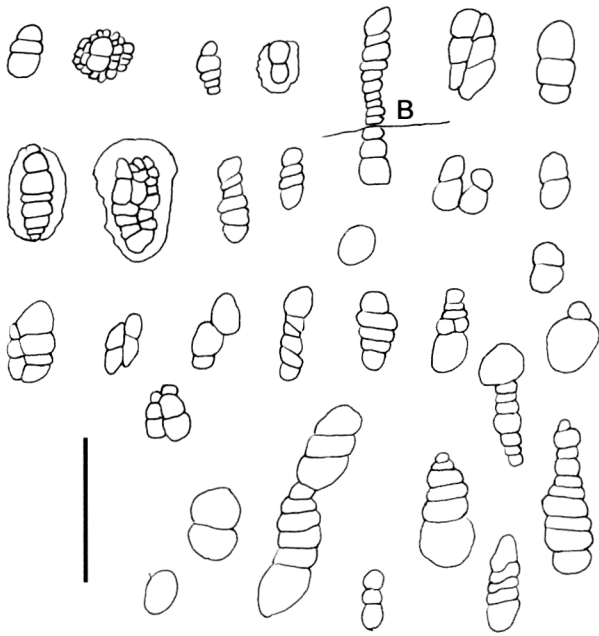


Fig. 7: *Cedreloxyton* from Natternberg, cross section. Latewood pores with radial multiples up to 9 and partly with small clusters. B = growth ring boundary. Bar scale 100 μ m.

Vessel arrangement ring-porous, portion of early pores on broad growth ring about 20 %, on narrow rings ca. 50% in radial direction, solitary vessels (80 %), radial multiples (17 %), multiples of 3 pores (3 %); tangential diameter of solitary earlywood vessels 147-248 (mean 200) μ m, lumina often plugged with brown to yellowish gum deposits, dumbbell-shaped in tangential and radial section, gum deposits vertical 140-210 μ m, vessel segments relatively short, e.g. 140-280 μ m; latewood vessels solitary (76 %), radial multiples of two (21 %), three (3 %), or four (2 %), tendency to form tangential groups, tangential diameter of the utmost latewood pores 45 μ m; 11-27 (mean 18) vessels per mm² (counting each vessel separately; WHEELER 1986).

Fibres non-septate, 2-12 radial rows between two rays, polygonal in cross section, diameter 10-18 μ m.

Axial parenchyma scanty paratracheal, terminal and diffuse, locally short tangential lines, (1)-2-4 cells wide.

Rays uniseriate and multiseriate of 2-3, heterocellular to nearly homocellular, multiseriate rays usually 330-520 μ m high, occasionally up to 910 μ m high, multiseriate rays partly with uniseriate portions at one of the ends; 7-9 rays per mm tangential.

Kirchroth

Bavaria, map TK 1 : 25000, No. 7041 Münster, locality northwest of Straubing.

Age and horizon: Reworked, Danube gravel, Miocene?

Material: Small fragment, length 10 cm, diameter 4.5 cm; leg. JAKOB BOGNER, Oberzeitldorn near Kirchroth; 5 thin sections.

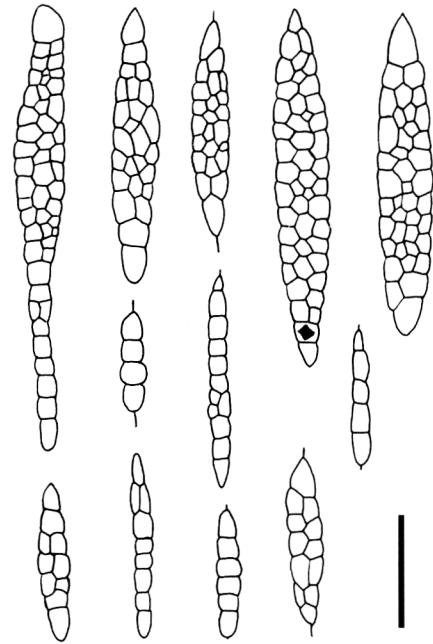


Fig. 8: *Cedreloxyton* from Natternberg, tangential section. Uni- and multiseriate rays, partly with marginal rows of upright and square marginal cells. Bar scale 100 μ m.

Microscopic characters (Fig. 10-11): Branch wood with pith remain, without bark; wood structure compressed, and thus deformed prior to mineralisation.

Growth rings, 11-14 zones more or less in concentric arrangement, 0.8 - 4.4 mm wide.

Vessels ring porous; solitary and in radial multiples of 2,

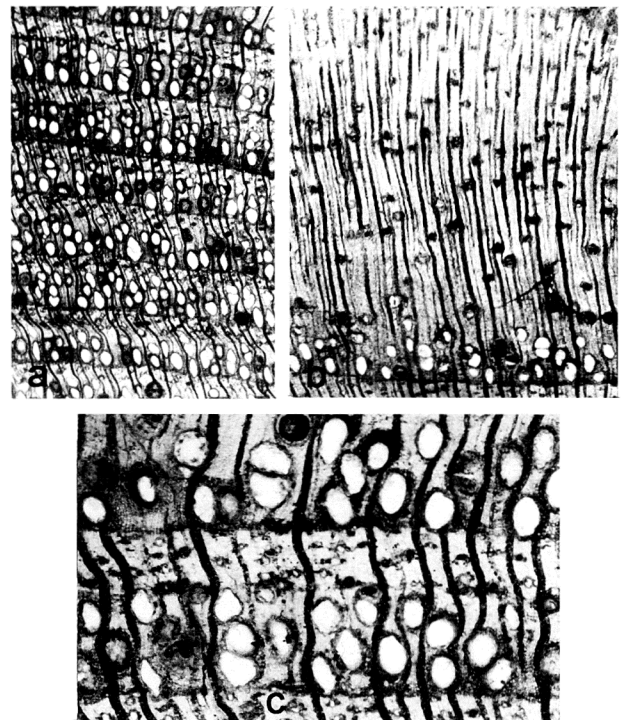


Fig. 9: *Cedreloxyton* from Dittenkofen, 3 cross sections. – a: growth boundaries distinct, marked by differences in vessel diameter. x 8. – b: growth rings interrupted by a single anomalous broad zone. x 8. – c: abrupt change in vessel diameter between early- and latewood. x 20.

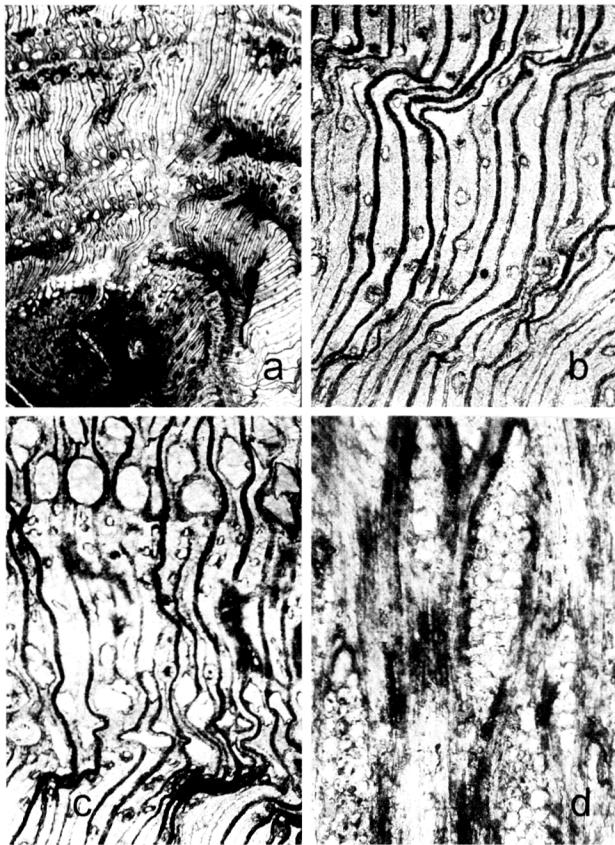


Fig. 10: *Cedreloxyton* from Kirchroth. – a: cross section with 5 growth rings in concentric arrangement, pith rest obscured. x 12. – b: small latewood pores evenly distributed between the distorted rays. x 90. – c: cross section, deformed, with 2 growth ring boundaries. x 40. – d: tangential section with uni- and multiseriate rays. x 120.

tangential diameter of springwood pores 135–248 (mean 165) μm , tangential diameter of late wood vessels 35–70 μm ; perforation plates simple, vessel lumina often plugged with yellowish or brown deposits, large dumbbell-shaped deposits visible in longitudinal sections, vertical length 147–280 μm .

Fibres non-septate, diameter 10–20 μm .

Axial parenchyma scanty paratracheal and diffuse.

Rays uniseriate and multiseriate of 2–3, heterocellular to nearly homocellular; uniseriate rays e.g. 3 cells (70 μm) high, 6 cells (130 μm), 10 cells (189 μm), solitary rhomboid crystals in marginal cells, diameter of crystals 22–26 μm ; rays occasionally

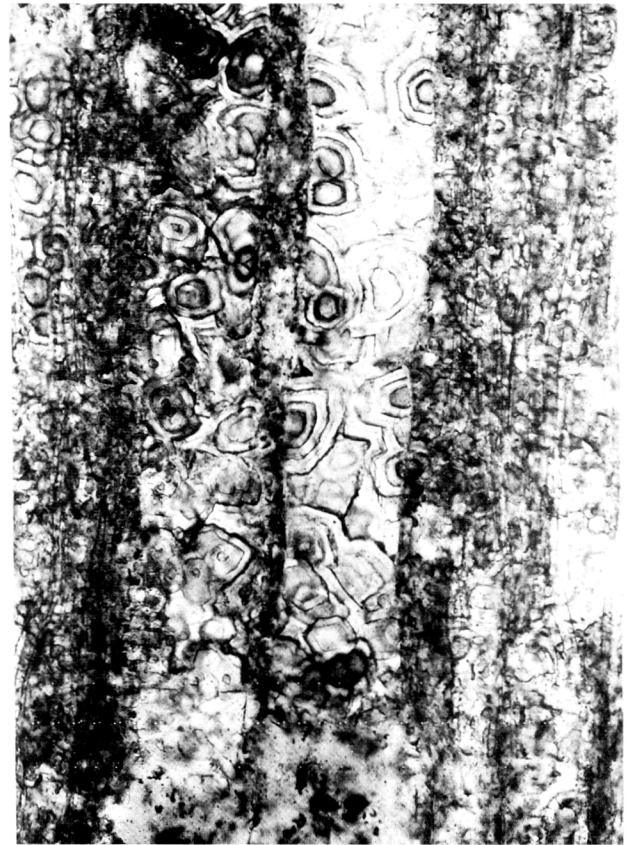


Fig. 11: *Cedreloxyton* from Kirchroth, radial section. Wood tissue obscured, vessels filled with stratified quartz crystals as a result of mineralisation processes. x 140.

forming uniseriate ends (80–100 μm) with quadratic or upright cells, height of multiseriate rays usually 300–560 (15–30 cells) μm , ray cells in tangential view polygonal; marginal ray cells, vertical about 50 μm , partly with crystals; 10–12–(18) rays per mm.

Pith cells with dark contents, large cells 35 x 70 μm , usually 28–35 μm in diameter.

Comments: Vessel-ray parenchyma pits could not be identified with certainty due to the meagre preservation of the specimen. The ray cells often display dark-colored contents that obscure analysis of the pits. Fungal hyphae not observed.

3. AFFINITIES

The affinities of the fossil woods were initially determined by consulting the wood-anatomical descriptions given in „Anatomy of the Dicotyledons” (METCALFE & CHALK 1950) and BRAZIER & FRANKLIN (1961), CARLQUIST (2001), GOTTWALD (1992), KRIBS (1968), LEMMENS et al. (1995), PANSHIN (1979), PEARSON & BROWN (1932), PURKAYASTHA (1996), RECORD & HESS (1943) and WAGENFÜHR & SCHEIBER (1989).

The 5 silicified woods (Hagenau, Natternberg, Sinzing, Dittenkofen, Kirchroth) are characterized by distinct growth rings; wood ring-porous, springwood pores large to very large, vessels solitary or in radial rows of 2–6, open or included with brown to nearly black gummy deposits, dumbbell-shaped in

tangential or radial section, perforation plates exclusively simple, vessel elements short, fibres non-septate; paratracheal parenchyma sparse, terminal and diffuse; rays uni- to multiseriate of 2–4, multiseriate rays in part with uniseriate portions, rays heterocellular to nearly homocellular, solitary rhomboid crystals in ray cells; tyloses absent. This suite of anatomical features is characteristic for the extant genus *Cedrela/Toona* (family Meliaceae).

A comparison of anatomical features of extant *Cedrela/Toona* species and the Tertiary woods is provided in Table 1 and 2.

Microscopic features	<i>Cedrela odorata</i>	Tertiary <i>Cedrela</i> woods
Growth rings		
distinct	+	+
Vessels		
ring porous	+	+
maximal tangential diameter	300 (up to 480) μm	280 (up to 390) μm
perforation plates	simple	simple
Fibres		
non-septate	+	+
heterocellular	+	+
up to 0.5 mm high	+	+
4-8 (-14) per mm	+	(6-)8-10(-12)
silica bodies absent	+	?
ray cells with solitary crystals	?	present
Axial intercellular canals		
traumatic type	occasionally	not observed

Tab. 1: Comparison of selected anatomical features of *Cedrela odorata* BROWNE (LEMMENS et al. 1995: 124) and silicified *Cedrela* woods from Hagenau, Natternberg and Sinzing.

Microscopic features	<i>Toona ciliata</i>	Tertiary <i>Cedrela</i> woods
Growth rings		
distinct	+	+
Vessels		
weakly semi-ring prous	+	+/?
max. tangential diameter	200-305 μm	150-250 (mean 200) μm
perforation plates	simple	simple
Fibres		
non-septate	+	+
Rays		
2-4 sciate	+	(1-)2-3(-4)
heterocellular	+	+
up to 0.9 mm high	+	0.7-0.9
4-12 per mm	+	(6-)8-10(-18)
silica bodies absent	+	?
ray cells with solitary crystals	?	present
Axial intercellular canals		
traumatic type	occasionally	not observed

Tab. 2: Comparison of selected anatomical features of *Toona ciliata* (ENDLICHER) ROEMER (LEMMENS et al. 1995: 494) and silicified *Cedrela* woods from Dittenkofen and Kirchroth.

3.1 SIMILARITIES WITH EXTANT WOODS

There is considerable disagreement among plant taxonomists relative to the circumscription of the Meliaceae and the grouping of Meliaceae genera into tribes and sub-families. PENNINGTON & STYLES (1975) subdivided the Meliaceae in 4 subfamilies: Melioideae (6 tribes), Swietenioideae (3 tribes), and two genera confined to Madagascar.

Sub-Family Swietenioideae

Tribe Xylocarpeae
Tribe Swietenioideae
Tribe Cedreleae

Tribe Cedreleae
Cedrela BROWNE, 1756

Origin and geographic distribution (New World):
The genus *Cedrela* consists of 8 species, which were originally

Locality	Map number	Samples	Material deposited	leg. / ded.
Adelschlag, J 1	7133	1	Jura Museum Eichstätt	–
Adelschlag, 7	7133	1	BSP	A. SELMEIER
Adelschlag, 374	7133	1	BSP	W. JUNG
Attenfeld	7133	2	Naturmuseum Augsburg	A. SELMEIER
Attenfeld	7133	4	Hist. Verein Neuburg a.d. Donau	P. HOLLEIS
Augsburg	7631	2	BSP	–
Dittenkofen	7342	1	BSP	H. VON BERCHEM
Forchheim	7136	13	BSP	H. VON BERCHEM
Frankenalb	7133	1	Jura Museum Eichstätt	–
Fraunberg	7637	1	BSP	K. HEISSIG
Hagenau	7744	1	BSP	E. PFÖRTNER
Kirchroth	7041	1	BSP	J. BOGNER
Natternberg	7143	1	BSP	H. HABERDA
Ochsenfeld	7132	1	BSP	L. FRUTH
Plattling	7243	1	BSP	J. SIMNETH
Priehof	7133	3	BSP	A. SELMEIER
Pullach	7139	1	BSP	QUEL
Rauscheröd	7445	1	Naturmuseum Augsburg	R. BAUMGARTNER
Schrobenhausen	7433	3	BSP	REISCHL
Seibersdorf	7743	1	BSP, Holotyp	G. MARKTMÜLLER
Sinzing	6938	1	BSP	D. MÜLLER
Südliche Frankenalb, J 8	7133 ?	1	Jura Museum Eichstätt	–
Weißkirchen	7133	1	BSP	A. SELMEIER
Wittenfeld	7133	1	Naturmuseum Augsburg	P. HOLLEIS

Tab. 3: Sites in the North Alpine Foreland, Upper Freshwater Molasse yielding Tertiary *Cedrela* woods. Topographic Maps (TK) 1 : 25000 and number of samples are recorded. The material is deposited in Munich (BSP), in Augsburg (Museum für Naturkunde) and Neuburg a. d. Donau (Collection Historischer Verein e. V.).

confined to the New World tropics, but are today planted throughout the tropical regions. Trade groups Spanish cedar, Cedro: *Cedrela odorata* L.; synonyms *C. guianensis*, *C. mexicana*, *C. glaziovii*.

There used to be some confusion about the distinction of the genera *Cedrela* (from the New World) and the genera *Toona* (from the Old World). This has resulted in a complex taxonomy at the intraspecific level.

Note: All Old World species of *Cedrela* have been transferred to the genus *Toona* (LEMMENS et al., 1995, p. 124).

Tribe Cedreleae

Toona (ENDLICHER) ROEMER, 1846

Origin and geographic distribution (Old World): *Toona* consists of 4 or 5 species and is naturally distributed from Pakistan and China to Australia. Some species are today widely cultivated in the tropics. Trade group Surian: (e.g.) *Toona ciliata*, *T. sinensis*, *T. sureni*.

Selection of synonyms:

Toona ciliata ROEMER, - (syn.: *Cedrela toona* ROXBURGH, *T. australis*, *T. microcarpa*, *T. termaliense*).

Toona microcarpa (DE CANDOLLE) HARMS, - (syn. *Cedrela microcarpa* DE CANDOLLE)

Toona sinensis (JUSSIEU) ROEMER, - (syn. *Cedrela serrata* ROYLE).

Toona sureni (BLUME) MERTENS, - (syn. *Cedrela fabrifuga* BLUME).

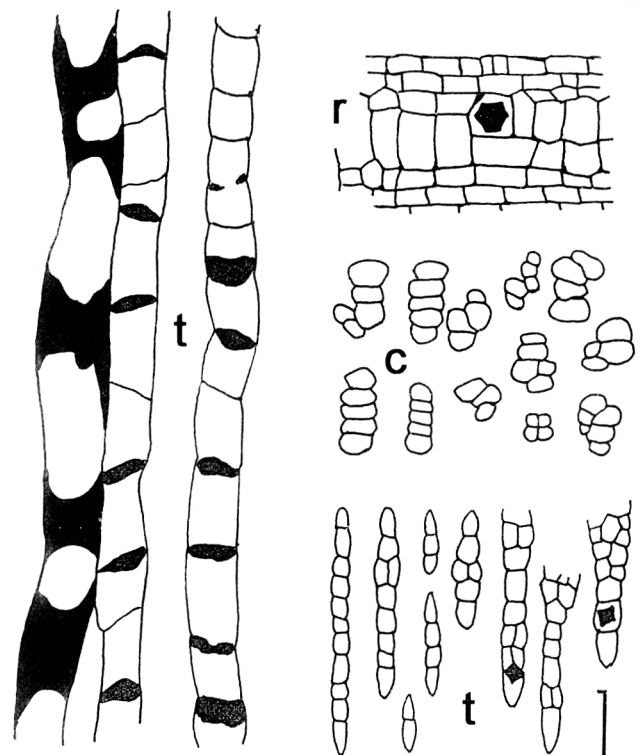


Fig. 12: *Cedreloxylon* from Attenfeld. Cross section (c) with latewood vessels, tangential section (t) with simple perforation plates, dark deposits and uniseriate rays, (r) radial section; specimens VI 16, 19. Bar scale 100 µm.

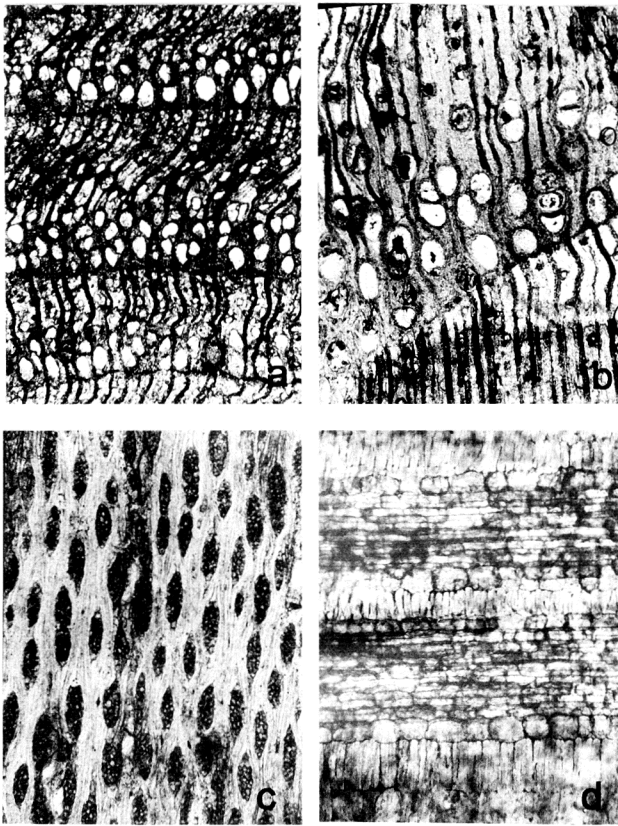


Fig.13: *Cedreloxylon* from Ochsenfeld. – a: cross section with 3 growth rings. x 8. – b: cross section, great differences in vessel diameter between late- and early wood. x 12. – c: tangential section with dark multiseriate rays. x 25. – d: radial section with enlarged marginal ray cells. x 60.

Many species of *Cedrela* examined by wood anatomists show a considerable variation in density and growth ring structure, varying from ring-porous to diffuse-porous. Small crystal-druses, usually in chambered cells, occur in some of the *Toona* species (BRAZIER & FRANKLIN 1961; GOTTWALD 1992).

Comparison with extant thin sections: Detailed microscopic examination of the wood structure was carried out to determine the nearest living equivalent to the here considered fossil woods. Approximately 27 specimens of the genera *Cedrela* and *Toona* are available in the Xylothech, Wood Research Institute, Technical University Munich (STERN 1988). The highest degree of correspondence exists between *Cedrela/Toona sinensis* and the fossils, wood type A.

3.2 SIMILARITIES WITH FOSSIL WOODS

Woods with characteristics of *Cedrela/Toona* have previously been described from several Tertiary localities in Germany, including the Eocene of Helmstedt (GOTTWALD 1992) and the Upper Freshwater Molasse of the North Alpine Foreland (GOTTWALD 1997, 2002, SELMEIER 1987, WHEELER 1991). Vessel element dimensions, diameter and length, and the combination of all other consistent anatomical features of these fossils are remarkably similar to the here presented material. Qualitative and quantitative differences in the anatomical features may be regarded as being within the normal range of intraspecific variability.

Tertiary Localities	Number of growth rings	min. mm	max. mm	mean mm
Adelschlag, J 1	8	1.3	2.5	1.9
Adelschlag, 7	16	1	2.4	1.6
Adelschlag, 374	6	3.5	5.6	4.9
Attenfeld [*]), 26	12	1.4	2.1	1.6
Attenfeld [*]), 48	9	2.1	3.3	2.8
Attenfeld, 16	1	–	–	–
Attenfeld, 19	8	1.6	3.9	2.6
Attenfeld, 280	7	1.3	3.4	2.4
Attenfeld, 295	2	6.4	8.8	7.6
Augsburg, 108	3	2.6	10.5	5.7
Dittenkofen	21	0.6	4.8	1.2
Forchheim, 25	5	3	4.9	4.1
Forchheim, 18	5	2.8	4.9	3.8
Forchheim, 19	3	4.1	5.2	4.6
Forchheim, 20	5	3.7	6.1	4.8
Forchheim, 21	6	1.6	3.2	2.6
Forchheim, 22	5	2.4	3.6	3.1
Forchheim, 23	4	3.5	5.9	4.6
Forchheim, 24	3	3.3	4.5	3.8
Forchheim, 24	4	3.8	4.5	4
Forchheim, 24	3	4.5	7.5	5.6
Forchheim, 27	3	4	4.9	4.6
Forchheim, 28	4	3.9	5.2	4.5
Forchheim, 29	5	2.8	12.8	6.6
Fraunberg	4	2	3	2.7
Hagenau, Austria	11	1.7	2.4	2.1
Hagenau, Austria	14	1.3	3.7	2.3
Helmstedt [*]), brown coal	–	2	6	3.6
Kirchroth	13	1	4.3	1.8
Natternberg	12	1.2	4.2	2.6
Natternberg	14	1.2	3.7	2.3
Ochsenfeld	2	5	5.4	5.2
Plattling	5	1.5	2.4	2.1
Prielhof, 135	4	2.6	4.8	3.5
Prielhof, 152	11	0.9	2.4	1.6
Prielhof, 90	6	1.9	3.7	2.5
Pullach	7	1.4	2.6	1.8
Rauscheröd [*]), 1101	4	2.8	3.6	–
Schrobenhausen, 58	11	0.5	2.3	1.3
Schrobenhausen, 59	9	1	1.9	1.3
Schrobenhausen, 60	11	0.8	2.7	1.9
Seibersdorf, Holotype	12	3.3	5.5	4
Sinzing	2	4.4	4.9	4.6
Südlische Frankenalb, J 8	11	1.3	3.2	2
Weißkirchen	6	1.9	8.6	4.8
317				

Tab. 4: Silicified *Cedrela* wood. The growth ring boundaries are distinct and usually display an abrupt change at the boundaries. To avoid confusion, collection numbers are partly mentioned if necessary. Localities marked with an asterisk indicate material described by GOTTWALD (1992, 1997, 2002).

Localities	Extant Taxa	Number of growth rings	min. mm	max. mm	mean mm
Burma, HM	<i>C. loona</i>	2	4.3	4.6	4.5
India, HM	<i>C. loona</i>	3	3.4	4.7	4.1
Hamburg, 11.102	<i>C. sinensis</i>	6	1.1	2	1.5
Hamburg, 11.102	<i>C. sinensis</i>	6	1.2	1.7	1.4
Hamburg, 11.102	<i>C. sinensis</i>	5	1	1.5	1.4

Tab. 5: Growth rings of extant *Cedrela* woods from Asia and Hamburg cult.; Xylothech Institute of Wood Research, TU Munich

3.3 OTHER LOCALITIES YIELDING *CEDRELA* WOODS

About 45 silicified wood fragments assignable to *Cedreloxylon cristalliferum* (SELMEIER, 1987) are today known from Upper Freshwater Molasse localities in Bavaria. Most of these specimens are deposited in the Bavarian State Collection of Palaeontology and Geology (BSP), four specimens from Attenfeld are housed in Neuburg a. d. Donau (SELMEIER 2003), the rest in Augsburg and Eichstätt (Tab. 3). The anatomical structure of the 45 thin sections is very similar (e.g. Fig. 12, 13).

3.4 GROWTH RINGS

Tree rings represent a valuable source of information about past climates. However, unlike tree-ring analysis of „modern“ wood, fossil tree rings cannot (or cannot normally) be used for dating. Nevertheless, fossil tree rings offer a unique opportunity to study annual growing conditions, seasonality, and hypothesize paleotemperatures, and water availability (CREBER & FRANCIS 1999).

Thus, it is interesting to note that the Tertiary *Cedrela* fragments show considerable variation in growth ring width. The width in millimeters per increment and/or the number of cells may represent a climatic (or some other environmental) signal. In addition, vessel diameter, vessel abundance and vessel member length are wood anatomical characters that may be used as palaeoecological proxy markers. However, as stated by CHAPMAN (1994), it is pivotal to determine from which part of the tree the fossil material comes since the minute anatomy may vary within a single tree depending upon topographic position (Fig. 14). The 18 most useful parameters for the palaeoecological interpretation of fossil wood fragments are listed by CHAPMAN (1994, p. 31). In the here presented study, however, only two of these features could be analyzed with certainty, i.e. (1) mean ring width and (2) vessel diameter. Table 4 records the width of 317 fossil *Cedrela* growth rings, table 5 records the width of cultivated *Cedrela* species.

Comments: No fossilized stumps *in situ* of *Cedrela* are available. The 45 *Cedrela* cross sections show a maximum of up to 21 growth rings. Thus, palaeoclimatological interpretations have to be regarded as problematical. Earlywood-latewood ratio shows in some slides a conspicuous fluctuation. Most of the 21 growth rings, e.g. the wood from Dittenkofen is only 0.6 mm wide, but interrupted by a single growth ring 4.8 mm

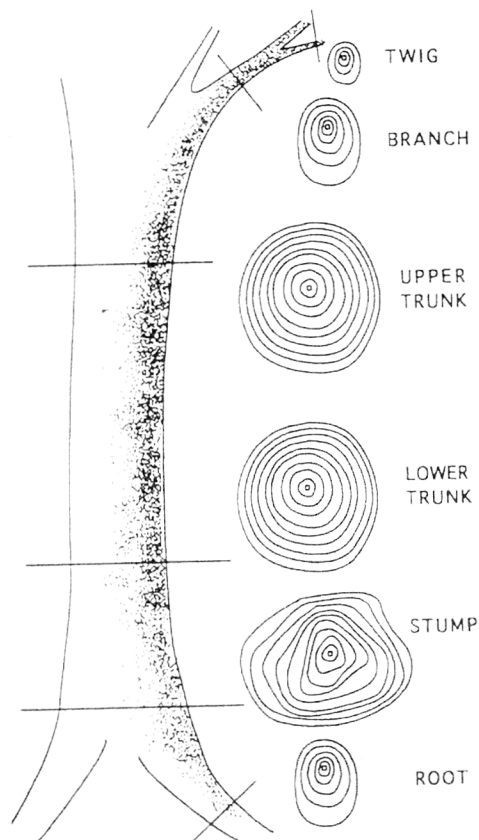


Fig. 14: Main characteristics of different positions within a tree that are important for the identification of isolated fossil material. After CHAPMAN (1994).

wide. A longer, more favourable growing season generally leads to production of a higher percentage of latewood (CREBER & FRANCIS 1999).

It is suggested that the specimens from Augsburg, Attenfeld-295, Forchheim-29, Hagenau, Natternberg, Ochsenfeld, Prielhof-135, and Seibersdorf are isolated fragments of very large tree individuals with growth rings up to 12.8 mm wide (Table 4). The majority of the 45 fossil *Cedrela* specimens presumably represent fragments of stems, with the exception of the material from a) Dittenkofen (20 rings x ca. 0.6 mm) and b) Kirchroth with pith rest presumable of a branch.

Note: A global analysis from 500 sites worldwide of the relationship between climate and extant growth ring parameters (e.g. mean ring width) makes it unlikely that such conditions can ever be met in fossil studies. According to FALCON-LANG (2003) the validity of using quantitative tree-ring parameters as indicators of Pre-Quaternary climates seems highly questionable.

4. MELIACEAE

The Meliaceae, the Mahogany family, consists of some 51 genera with over 550 species of trees, shrubs, and woody herbs. The family, named after the genus *Melia*, is widely distributed throughout the tropical regions of the world, with a few species extending into sub-tropical and temperate regions.

Cedrela timber is most widely used to manufacture cigar boxes, substituted today by *Aucoumea klaineana*, family Burseraceae, from Gabun or Kongo. *Cedrela* is occasionally planted for shade and as an ornamental along roads. *Cedrela* trees, deciduous and medium-sized to fairly large (up to 40-60

m tall), are branchless up to 25 m; diameter of the stem 1.2-3 m. The Spanish cedar (*Cedro*) occurs in areas with high annual rainfall (2000-3000 mm). The various species of *Toona* occur from sea-level up to 3000 m altitude. *Toona* trees, deciduous or

semi-evergreen, medium-sized to fairly large trees reach about 50 m height. The mean annual diameter increment of *T. ciliata* plantations is 0.8-2.5 cm (LEMMENS et al. 1995).

5. CONCLUSIONS

To date, 44 fossil remains of *Cedreloxydon crystalliferum* have been identified in the North Alpine Foreland, limno-fluvial Upper Freshwater Molasse. A single *Cedrela* is recorded from the Eocene browncoal open-cast mine Helmstedt near Braunschweig, Germany (GOTTWALD 1992).

Two wood types can be distinguished: (A) springwood with 4-5 vessel layers, tangential vessel diameter > 300 µm, (B) springwood with 1-2 vessel layers, tangential vessel diameter < 300 µm.

Variations in growth ring width are presumably due to different ecological conditions, such as rainfall, soil composition, light, and limiting temperatures. However, genetic determination of growth ring width and differences related to the topographic position of the wood fragment must also be taken into consideration as a possible explanation.

The cross sections of silicified *Cedrela* woods show maximal 21 growth rings. The growth rings are up to 12.8 mm wide, and presumably represent portions from large trees.

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