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BRILL

IAWA Journal 40 (3), 2019: 488–529

iawa

Wood evolution: Baileyan trends and Functional traits in the fossil record

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Accepted for publication: 9 November 2018

ABSTRACT

We revisited questions about changes in the incidences of functional wood anatomical traits through geologic time and compared the incidences of these traits in the fossil record with modern wood anatomical diversity patterns in order to test classical ("Baileyan") and more recent ecophyletic hypotheses of xylem evolution. We contrast patterns through time for tropical and higher (paleo)latitudes. Data are from the InsideWood database. There are striking differences between woods from high and mid latitudes *versus* tropical (paleo)-latitudes. At temperate and subtropical latitudes (Laurasia *and* high latitude Gondwana), the epoch by epoch time series supports the Baileyan transformation series of vessel-bearing woody angiosperms (basal woody angiosperms and eudicots): "primitive" features such as scalariform perforations, exclusively solitary vessels, apotracheal diffuse parenchyma and heterocellular rays abound in the Cretaceous and become much less frequent in the Cenozoic, especially post-Eocene. In contrast, in the paleotropics hardly any changes occur in the incidences – each epoch has an equally "modern" spectrum of wood anatomical attributes. Although climatic gradients from the poles to the equator were less steep in the Cretaceous than in the late Cenozoic, the wood anatomical differences between mid-high latitude woods and tropical woods were much more pronounced in the Cretaceous than in later epochs. This seeming paradox is discussed but we cannot resolve it.

We suggest that tropical conditions have accelerated xylem evolution towards greater hydraulic efficiency (simple perforations), biological defense and hydraulic repair (elaborate paratracheal parenchyma patterns) as evidenced by late Cretaceous tropical latitude woods having near modern incidences of almost all traits. At higher paleolatitudes of both the Northern and Southern Hemisphere "ancestral" features such as scalariform perforations were retained in cooler and frost-prone regions where they were not selected against in mesic habitats because of lower demands on conductive efficiency, and could even be advantageous in trapping freeze-thaw embolisms. The fossil wood record remains too incomplete for testing hypotheses on the wood anatomy of the earliest angiosperms. The low incidence of so-called "xerophobic" woods *sensu* Feild with scalariform perforations with numerous (over

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Published by Koninklijke Brill NV, Leiden

DOI 10.1163/22941932-40190230

40) closely spaced bars in the Cretaceous tropical fossil record is puzzling. At *higher* paleolatitudes such woods are common in the Cretaceous.
Ring porosity, an indicator of seasonal climates and deciduousness, occurs at low levels in the Cretaceous and Paleogene at higher paleolatitudes only, and reaches modern levels in the Miocene. In Neogene and Recent temperate Northern Hemisphere, wide vessels are virtually restricted to ring-porous woods. In the tropics, there is a low incidence of ring porosity throughout all epochs.
The fossil record indicates that ecophysiological adaptation to tropical or temperate conditions was already evident in the Cretaceous with considerable latitudinal differences.

Keywords: Ecophyletic wood anatomy, functional traits, porosity, vessel perforations, axial parenchyma, ray cellular composition, septate fibers.

INTRODUCTION

The centenary of Bailey and Tupper's classical paper on xylem evolution (1918) inspired us to revisit the fossil record of angiosperm woods for an analysis of the incidence of wood anatomical traits through time with special attention to contrasting patterns at temperate *versus* tropical paleolatitudes. Adaptive scenarios of xylem evolution, liberated from irreversibility or linearity as originally claimed (Bailey 1953; cf. Olson 2012), still have Baileyan transformation series at their core, tacitly (*e.g.*, Feild *et al.* 2009; Carlquist 2012) or outspokenly (*e.g.*, Baas *et al.* 2004; Lens *et al.* 2016). At the onset we should, however, stress that our analysis can also be read independently from the Baileyan framework as a comparison of the incidences of functional wood traits through time.

Xylem diversification in angiosperms, with different cell types occurring in varying proportions and dimensions, surely is significant to the success of woody angiosperms in a variety of terrestrial environments (*e.g.*, Martinez-Cabrera *et al.* 2017). How this wood anatomical variation contributes to angiosperm success continues to inspire research (*e.g.*, Gleason *et al.* 2016; Spicer 2016; Morris *et al.* 2016, 2018). The resulting hypotheses, based on comparative anatomical and physiological studies of extant plants in combination with molecular-based phylogenies, need to be tested with evidence from the fossil record (Philippe *et al.* 2008; Wilf & Escapa 2015, 2016). The Cretaceous-Cenozoic of the Northern Hemisphere with its well-documented climate changes (*e.g.*, Upchurch & Wolfe 1987; Graham 1999; Bowen 2007; Linnert *et al.* 2014; Anagnostou *et al.* 2016) and its relatively abundant fossil wood record provides opportunities for analyzing what is essentially a long-term experiment in the relationships between wood functional traits and climate.

Despite considerable progress in our understanding of early angiosperm evolution (Friis *et al.* 2011; Sauquet & Magallón 2018), the place and time of their origin remains unresolved. There are no reliable reports of pre-Cretaceous angiosperms (Herendeen *et al.* 2017). Most early Cretaceous angiosperm records are from pollen (*e.g.*, Doyle & Endress 2010), with unequivocal flowers and leaves appearing later (*e.g.*, Herendeen

et al. 2017). There are only a few reports of early Cretaceous (Aptian-Albian) angiosperm woods with anatomical descriptions (*e.g*., Fliche 1905; Serlin 1982; Thayn *et al*. 1983, 1985; Herendeen 1991; Crawley 2001; Takahashi & Suzuki 2003; Nunes *et al*. 2018). Some of these oldest known angiosperm woods have simple perforation plates, while others have scalariform perforation plates, in one instance both wood types co-occur at the same locality (Thayn *et al*. 1983, 1985). Angiosperm woods became more abundant in the Cenomanian (late Cretaceous) and are well documented in the late Cretaceous of Antarctica (Cantrill & Poole 2005), Japan (Takahashi & Suzuki 2003), Europe (Philippe *et al*. 2008), and North America (*e.g*., Estrada-Ruiz *et al*. 2007; Wheeler & Lehman 2009; Jud *et al*. 2017). The fact that the fossil wood record of angiosperms is younger than that of other plant parts features in arguments for an herbaceous or semi-woody ancestry of the angiosperms (*e.g*., Philippe *et al*. 2008; Jud 2015).

Earlier analyses of the fossil record (Wheeler & Baas 1991,1993) provided strong support for the Baileyan trends: putatively "primitive" character states such as scalariform perforations, scalariform intervessel pits, exclusively solitary vessels, fibers with distinctly bordered pits, diffuse apotracheal parenchyma and heterocellular rays all appeared to be of much more frequent occurrence in the Cretaceous, and generally in the early Cenozoic (Paleocene and Eocene), while many "derived" features in the Baileyan sense did not reach modern incidence levels until the Oligocene/Miocene. We also found "modern" ecological trends, *i.e*., latitudinal differences, were in place from the Cretaceous onwards.

In a recent critical review of the species-rich fossil wood assemblages of the Deccan Intertrappean Beds of India, Upper Cretaceous-Lower Paleocene in age (Wheeler *et al*. 2017), we found surprisingly "modern" wood patterns. We interpreted this as an adaptive response of those assemblages to the tropical conditions the Indian subcontinent was exposed to as it rafted northward over the "Réunion Hotspot " (Smith *et al*. 2015). These results raised the question whether our earlier analyses (Wheeler & Baas 1991, 1993) were flawed, because we had lumped together all Southern Hemisphere (Gondwana) fossil records and contrasted them with Northern Hemisphere (Laurasia) ones, while a comparison of fossil woods from mid and high latitudes (subtropical and temperate) with woods from tropical paleolatitudes would have been more appropriate. We offer such a comparison here, based on the fossil wood entries in the InsideWood database (InsideWood 2004-onwards; Wheeler 2011).

Another justification for this survey is that since 1991 the number of fossil wood records, (*i.e*., individual descriptions, including new species and reports of known species from new localities) has increased, especially for the Cretaceous, Paleocene, and Eocene of the north temperate region. This improves the reliability of generalizations about changes in wood anatomical diversity patterns through time. However, the number of records for the tropics is still markedly lower than for the north temperate regions, with only the Miocene having more than 100 records, and only a few woods from tropical latitudes are pre-Maastrichtian (latest Cretaceous). For temperate South America (including Antarctica), no epoch has more than 40 records.

A third reason why this analysis is timely is that our understanding of wood anatomical features as functional traits and the tradeoffs in meeting the demands of hydraulic efficiency and safety, support, storage and wound response has improved since 1993 (Carlquist 2001, 2012; Sperry *et al*. 2008; Feild *et al*. 2009; Jansen & Nardini 2014; Lachenbruch & McCulloh 2014; Beeckman 2016; Spicer 2016; Morris *et al*. 2016, 2018; Pratt & Jacobsen 2017). This increased understanding allows a more meaningful evolutionary interpretation of any temporal or spatial patterns observed. Our analysis uses the coarse temporal (epoch) and spatial scales (large geographic areas) of the InsideWood database. Moreover, taphonomic bias limits the application of modern ecophysiological interpretations of the fossil record. For instance, one can expect that woody plants from arid environments would be underrepresented in the fossil record, while those from riparian environments would be overrepresented. Another potential source of bias for the Cenozoic wood record is that woods that are easy to identify to genus or family, *e.g*. *Quercus* and Lauraceae (species with oil cells) are more likely to be described in the literature than woods of unknown affinities.

The main purpose of this paper is to provide an updated summary of the broad trends in functional trait incidences from the Cretaceous to Pliocene, with a comparison to wood anatomical diversity today.

Methodology

We used information from the InsideWood database (InsideWood 2004-onwards, accessed February-April 2018; Wheeler 2011), which includes a multiple entry key based on the IAWA Hardwood List (IAWA Committee 1989), and a database with over 7,300 coded descriptions of modern woods and nearly 2,000 descriptions of fossil woods. The number of descriptions does not equal the number of species represented. In the modern wood database, 612 descriptions are only for genera, *e.g*. *Croton* spp. (Euphorbiaceae), and they represent a variable number of species, some descriptions represent species groups that share similar anatomy, *e.g*., one description each for the Red Oak, White Oak, and Evergreen Oak groups (*Quercus,* Fagaceae), one description for seven Malagasy species of *Tinopsis* (Sapindaceae). There also are a few commercially important or widespread species with two or more descriptions from different authors. In contrast, in the fossil wood database, which uses a subset of the IAWA Hardwood features, each description represents one report of a species or wood type. This compromises comparing the incidences in the fossil wood database with those in the modern wood database. However, there are relatively few duplicate reports for a fossil wood type and the duplications are for woods from different localities and with slightly differing anatomy, which might represent different species. In an attempt to make the fossil and modern wood datasets more comparable, for the mid to high latitude Northern Hemisphere (Laurasia) we exported all the descriptions for that region and split the descriptions for multiple species into individual species descriptions. To help with the splitting we used resources such as the Flora of North America, the Flora of China, the FFPRI Wood Database (http://db.ffpri.affrc.go.jp/WoodDB/index-E.html) and some regional wood anatomy atlases, *e.g*. Schweingruber (1990), Crivellaro & Schweingruber (2013), and the references the InsideWood descriptions were based on.

We grouped the fossil and modern woods into three broad geographic/latitudinal areas (following the IAWA Hardwood List, IAWA Committee 1989):

– Temperate (and subtropical) Northern Hemisphere (Temperate NH), also defined as Laurasia, which includes North America, Europe and temperate Asia. This was done by excluding woods from all other IAWA List regions, searching InsideWood for the absence of Central South Asia (168a), Southeast Asia and Pacific (171a), Australia and New Zealand (175a), Tropical Mainland Africa and adjacent islands (178a), South Africa (181a), Neotropics and temperate Brazil (183a), and temperate South America (188a). This grouping is similar to the NH grouping in our 1991 and 1993 papers.

– Tropical (TR) which includes Central South Asia, Southeast Asia and Pacific, tropical Mainland Africa and adjacent islands, and the Neotropics (and also temperate Brazil). This was done by searching InsideWood for the absences of North America (182a), Europe and temperate Asia (164a), Australia and New Zealand (175a), South Africa (181a), and temperate South America (188a). The Indian Deccan Intertrappean woods from localities likely to be Paleocene were included in that epoch, while those from localities likely to be Maastrichtian were included in the Cretaceous. Woods from localities whose ages may be either late Cretaceous or early Paleocene are treated as a separate category, Deccan, and in tables and graphs for the Tropics are plotted in between the Cretaceous and the Cenozoic. This grouping does not have a counterpart in our 1991 and 1993 papers because the Southern Hemisphere (SH) grouping of that paper included all Gondwanan regions.

– Temperate South America (Temperate SH), which includes fossil woods from southern South America and Antarctica (188p), is considered separately, but in view of the limited number of fossils per epoch the results for this region are only presented in a table and not in bar graphs (Table 1). This grouping did not have a counterpart in the 1991 and 1993 papers. We did not analyzse statistics for temperate Southern Africa, Australia and New Zealand for the simple reason that for most epochs very few fossil woods have been recorded for these regions.

Certainly, during times in the past, the Temperate NH and Temperate SH categories had climatic regimes that were not temperate (*e.g.*, Upchurch & Wolfe 1987; Cantrill & Poole 2005) and today, these areas encompass a variety of climates and vegetation types (*e.g.*, Olson *et al*. 2001; Kottek *et al*. 2006), but all have seasonality in at least temperature and light conditions.

As in our 1991 paper, the incidence (frequency of occurrence) of features through time is reported as a percentage. The number on which this percentage is based varies by epoch because there is a different number of records reported per geologic epoch and region. The number also varies by feature because some features are more likely to be recorded or preserved than others. For example, almost all fossil wood descriptions describe porosity because it is an important diagnostic feature and can be determined even in poorly preserved woods. Intervessel pitting also is an important diagnostic fea-

ture but might not be reported because the wood was not well-preserved and intervessel pits were not observed. Supplemental Tables S1–S8 (at the end of this paper) provide for each feature the number of entries with information on that feature per epoch and geographic region. We also include the 1991 information for the Temperate NH for comparison.

Statistics

We calculated confidence intervals for all percentages as we did before (Wheeler & Baas 1993) by estimating Standard Deviations (SD) according to Steel & Torrie (1980) and Raup (1991).

$$\text{Estimated SD} = \sqrt{\frac{p\,(1-p)}{n}}$$

where p = percentage/100 and n = number of records for that feature at that epoch. Single SD values are shown as error bars in Figures 1–18; only given above the average value, for practical reasons. It is obvious that the SDs are larger for percentages based on a small number of samples, such as most epochs for tropical Gondwana, and that differences in percentages need to be much bigger to achieve significance. The fact that the SDs or error bars represent 68% confidence intervals, and that 2× SD would represent 95% confidence intervals provide a means of visualizing whether the differences between epochs are significant.

Presentation of data

The main results are presented as bar graphs plotting the percentage incidences and confidence intervals of wood anatomical features per epoch for TempNH (aka Laurasia) and TR (aka equatorial and tropical Gondwanan regions) (Fig. 1–18).

For TempSH (Southernmost South America and Antarctica), we present the data in Table 1, not as bar graphs due to the low number of records for this region. Detailed percentage occurrences for more characters and the Deccan Woods are presented in Tables S1–S8 in the Supplement of this paper.

A limited number of the features analyzed is shown in Plates I and II. Further on, our results are briefly described and compared with the earlier findings (Wheeler & Baas 1991, 1993).

Table 1. Incidences (% of record) for Temperate South America and Antarctica (TempSH) (IAWA feature 188).

	Perforation plates %				Scalariform-opposite intervessel pitting %		Average vessel element length > 800 µm %		Porositty %				Exclusively solitary vessels %		Helical thickenings %	
		All Scal	Simp & Scal	All Simp						Ring	Semi-ring	Dif-fuse				
Recent:	n = 279	8	5	87	n = 276	13	n = 276	7	n = 270	2	6	92	n = 280	15	n = 286	13
Pliocene:	n = 19	0	5	95	n = 19	11	n = 19	0	n = 19	0	16	84	n = 19	11	n = 18	6
Miocene:	n = 38	18	29	53	n = 36	35	n = 36	0	n = 38	7	14	79	n = 38	11	n = 38	11
Oligocene:	n = 21	48	24	28	n = 20	58	n = 20	0	n = 21	14	10	76	n = 21	24	n = 21	10
Eocene:	n = 8	25	62	13	n = 8	69	n = 8	1	n = 8	0	25	75	n = 8	25	n = 8	0
Paleocene:	n = 12	42	16	42	n = 12	58	n = 12	14	n = 15	0	20	80	n = 12	39	n = 13	8
Cretaceous:	n = 22	55	27	19	n = 19	79	n = 19	9	n = 24	4	8	88	n = 19	30	n = 19	0

	Vessel diameter %				Septate fibers %		Rare axial parenchyma %		Axial parenchyma				Storied structure %		Ray composition			
		<100 µm	All* >200 µm	DP** >200 µtm					D, D-Ag %	Alif-confl %	Marg. %				Hom %	Hom+ het %	Het %	
Recent:	n = 286	59	3	3	n = 278	30	n = 278	8	n = 280	2	6	18	n = 278	14	n = 286	23	21	56
Pliocene:	n = 18	56	5	0	n = 13	0	n = 13	5	n = 19	0	16	11	n = 19	0	n = 19	53	0	47
Miocene:	n = 38	45	5	3	n = 17	62	n = 17	16	n = 38	7	14	8	n = 38	5	n = 38	29	16	55
Oligocene:	n = 21	43	5	2	n = 16	25	n = 16	38	n = 21	14	10	10	n = 21	0	n = 21	10	14	76
Eocene:	n = 8	100	0	0	n = 5	40	n = 5	75	n = 8	0	25	0	n = 8	0	n = 8	0	0	100
Paleocene:	n = 13	62	8	8	n = 10	40	n = 10	42	n = 12	0	20	0	n = 12	0	n = 13	8	0	92
Cretaceous:	n = 15	74	0	0	n = 15	47	n = 15	18	n = 19	4	8	0	n = 19	0	n = 23	0	13	87

* All porosity types; ** only diffuse-porous woods.
D, D-Ag = Diffuse and diffuse-in-aggregates; Alif-confl = Aliform-confluent; Marg. = marginal.
Hom = homocellular, composed of procumbent cells only; Het = heterocellular, composed of procumbent & upright / square cells.

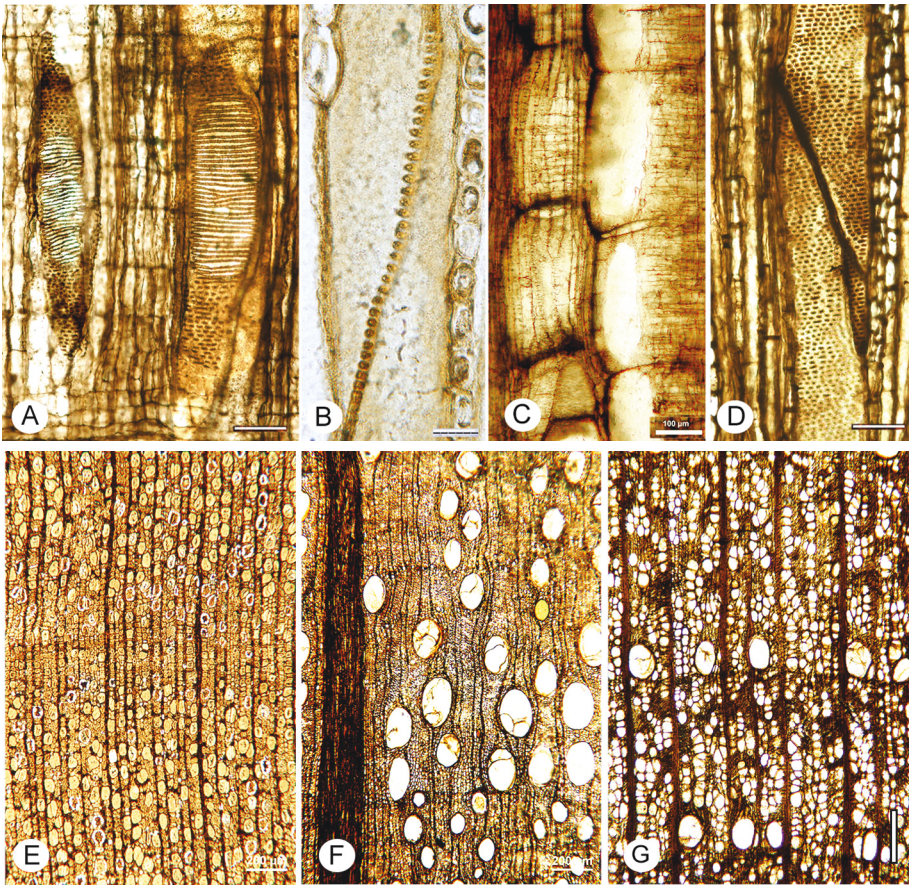


Plate I. Fossil wood features. – A: Scalariform perforation plates, "*Turpinia*" *lamarense*, early Middle Eocene, Yellowstone National Park, WYO, USA, RLS. – B: Scalariform perforation plates, The Hancock Tree (Hamamelidaceae), Middle Eocene, John Day Fossil Beds, OR, USA, TLS. – C: Series of vessel elements with simple perforations, Malvaceae, Late Eocene, OR, USA, RLS. – D: Opposite intervessel pits, "*Turpinia*" *lamarense*, early Middle Eocene, Yellowstone National Park, TLS. – E: Predominantly solitary vessels, diffuse-porous wood, Pentaphylacaceae, early Middle Eocene, Yellowstone National Park, TS. – F: Exclusively solitary vessels, semi-ring porous, *Quercinium amethystianum* (Fagaceae), early Middle Eocene, Yellowstone National Park, TS. – G: Ring-porous wood, Anacardiaceae, Late Eocene, Post, Oregon, USA, TS. — Scale bars: 200 µm in E, F, G; 100 µm in C; 50 µm in A, D; 20 µm in B.

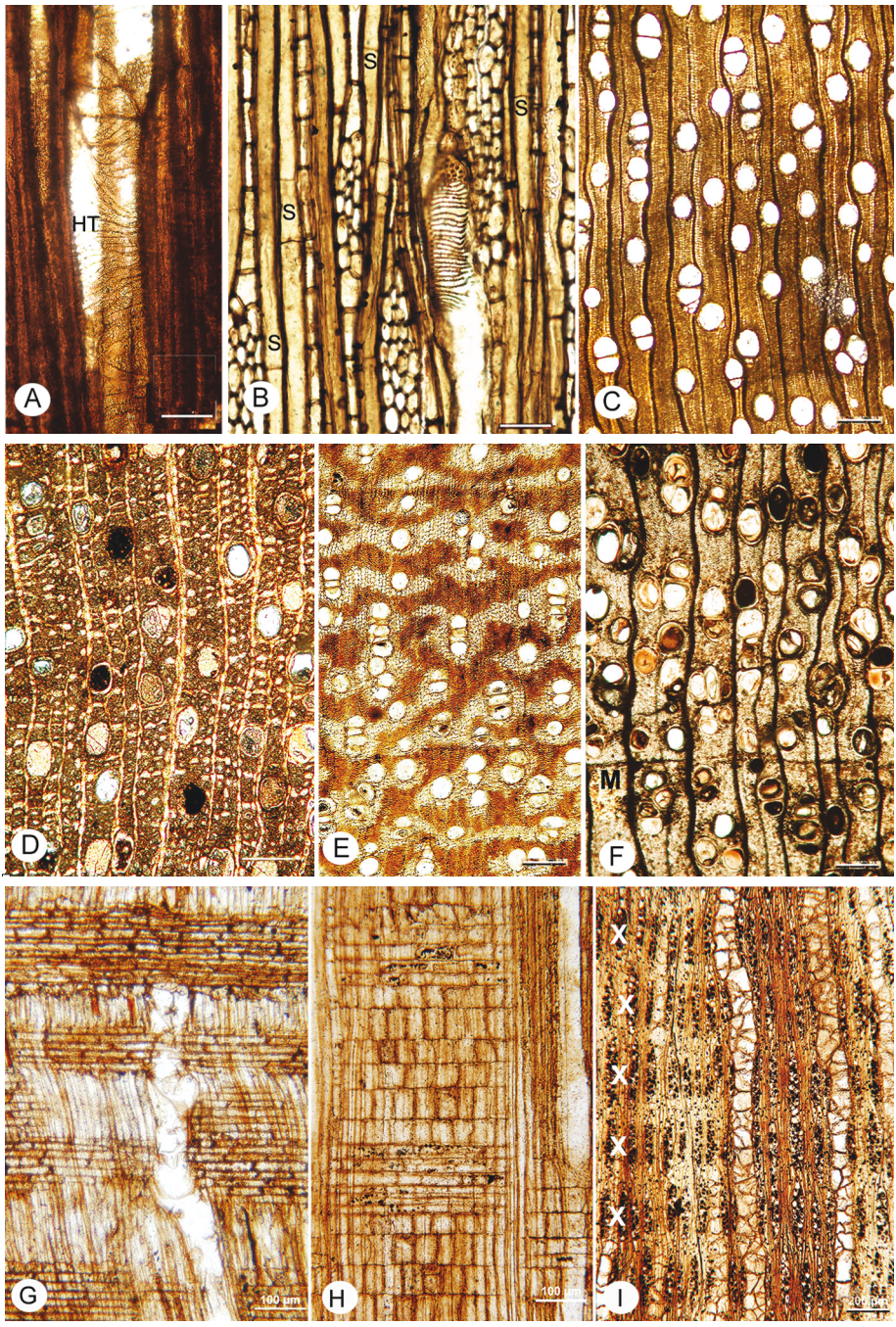

HT
A
S
S
S
S
B
C
D
E
M
F
100 µm
G
100
H
X
X
X
X
X
I

Plate II. Fossil wood features. – A: Helical thickenings (HT) in vessel elements, scalariform perforation plates with few bars, possibly parietal clade of Malpighiales, early Middle Eocene, Yellowstone National Park, WYO, USA, RLS. – B: Septate fibers (S), scalariform perforation plates with numerous bars, "*Turpinia*" *lamarense*, early Middle Eocene, Yellowstone National Park, TLS. – C: Axial parenchyma rare, *Burseroxylon preserratum* (Sapindales, Anacardiaceae/Burseraceae), latest Cretaceous-earliest Paleocene, Deccan Intertrappean Beds, India, TS. – D: Axial parenchyma diffuse and diffuse-in-aggregates, Baileyan Big Bend Type I (family unknown), late Cretaceous (Maastrichtian), Big Bend National Park, TX, USA, TS. – E: Aliform-confluent parenchyma, Fejej Wood Type 4 (family unknown), Miocene Bakate Formation, Ethiopia, TS. – F: Marginal axial parenchyma (above letter M, extending to right), Fejej Wood Type 9 (Fabaceae), Miocene Bakate Formation, Ethiopia, TS. – G: Rays composed of procumbent cells, affinities unknown, early Middle Eocene, Yellowstone National Park, RLS. – H: Ray composed of procumbent and upright cells, possibly Cornales, early Middle Eocene, Yellowstone National Park, RLS. – I: Storied rays, × marks single tiers of storied rays, *Javelinoxylon multiporosum* (Malvaceae), Late Cretaceous (Maastrichtian), Big Bend National Park, TX, USA, TLS. — Scale bars: 200 μm in C, E, F, I; 100 μm in D, G, H; 50 μm in A, B.
←

RESULTS AND DISCUSSION BY FEATURE

Hydraulic Features

Vessel perforations (Fig. 1, 2; Tables 1, S1)

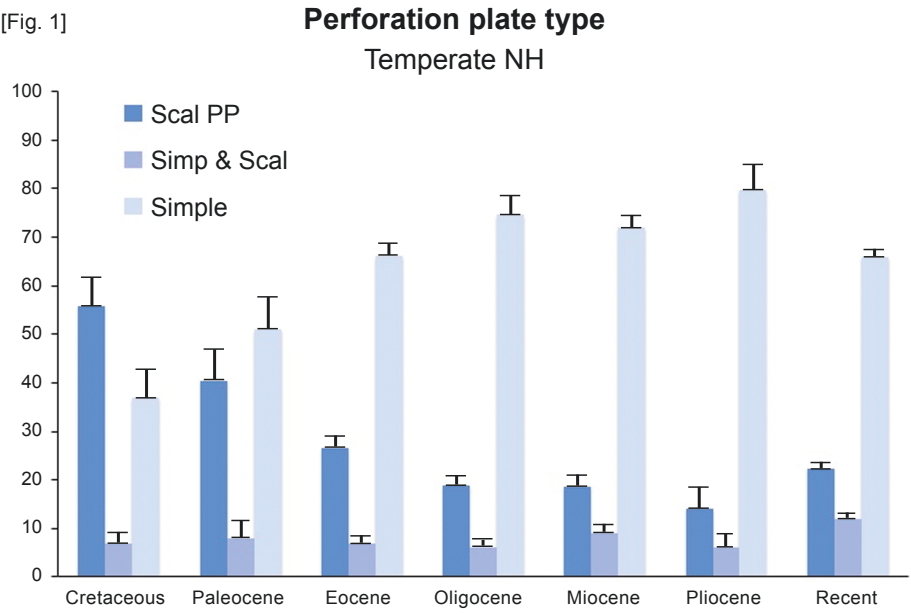
The records from Laurasia and temperate South America/Antarctica show a distinct decrease in % occurrence of scalariform perforation plates from the Cretaceous (56 & 55%) to the Eocene (27 & 25%), with the Paleocene being intermediate. In later epochs, the incidence of exclusively scalariform perforations fluctuates from 0–26%. The very high incidence in the Oligocene of the tempSH (48%) results from 13 of the 21 records for this epoch and region from a single locality having scalariform perforations (Chilean fossils as described in Nishida *et al*. 1988). The occurrence of simple perforations logically follows a contrasting trend. These results mirror those reported earlier for a smaller number of woods (Wheeler & Baas 1991, 1993).

In contrast, the records from tropical paleolatitudes do not show any obvious differences between epochs – almost all epochs showing lower incidences than the contemporary samples from higher paleolatitudes, and the Cretaceous records are virtually identical to the recent flora for the incidence of scalariform and simple perforations. This differs from our earlier report (Wheeler & Baas 1991, 1993) where the records from temperate Southern latitudes had been lumped with those from tropical paleolatitudes, resulting in a higher incidence of exclusively scalariform perforations (38%) in the Cretaceous of Gondwana. For later epochs, the results are the same as in the earlier paper.

Intervessel pits (Fig. 3; Tables 1, S1)

In the Baileyan scheme, scalariform-opposite pits are "primitive" compared to alternate pits. In the temperate NH, incidences of scalariform-opposite pits are highest in the Cretaceous and Paleocene, then decrease to the Eocene, with relatively low levels

[Fig. 1]



[Fig. 2]

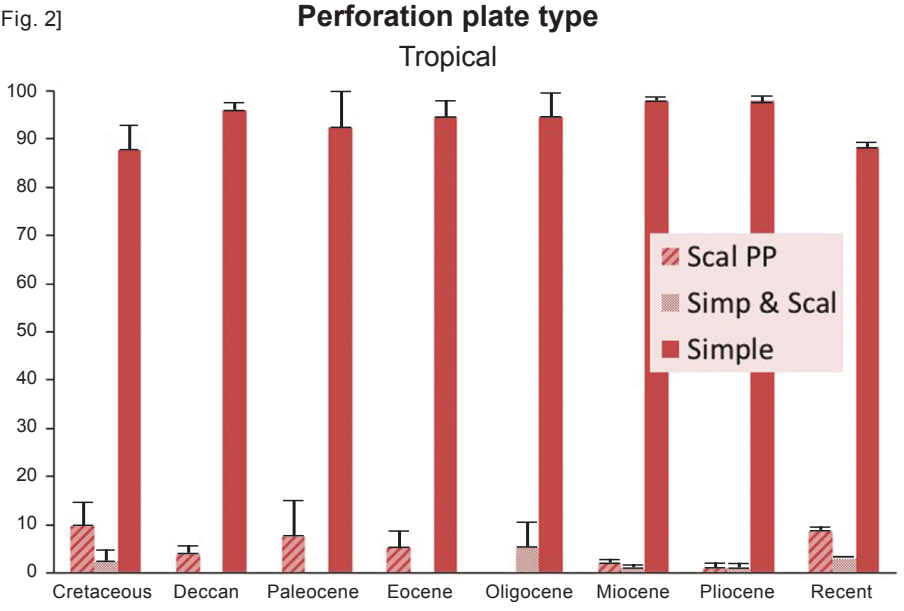
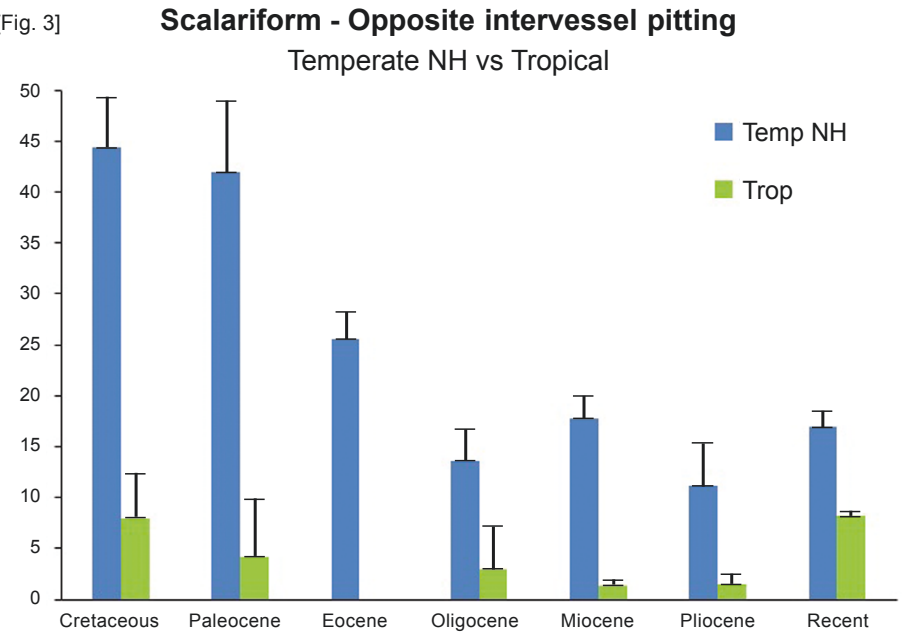


Figure 1 & 2. Incidence (% of records for fossil woods; % of taxa for Recent woody flora) of wood anatomical traits by epoch. Error bars = 1 SD, only shown one-sided above the % value (for explanation see text). – Fig. 1: Incidence (%) of types of perforation plates in the temperate Northern Hemisphere (NH). Scal PP = vessel perforations exclusively scalariform; Simp & Scal = vessel perforations mixed simple and scalariform in the same sample; Simple = vessel perforations exclusively simple.—Fig. 2: Incidence (%) of types of perforation plates at tropical (paleo)latitudes. For explanation see Fig. 1.

[Fig. 3]



[Fig. 4]

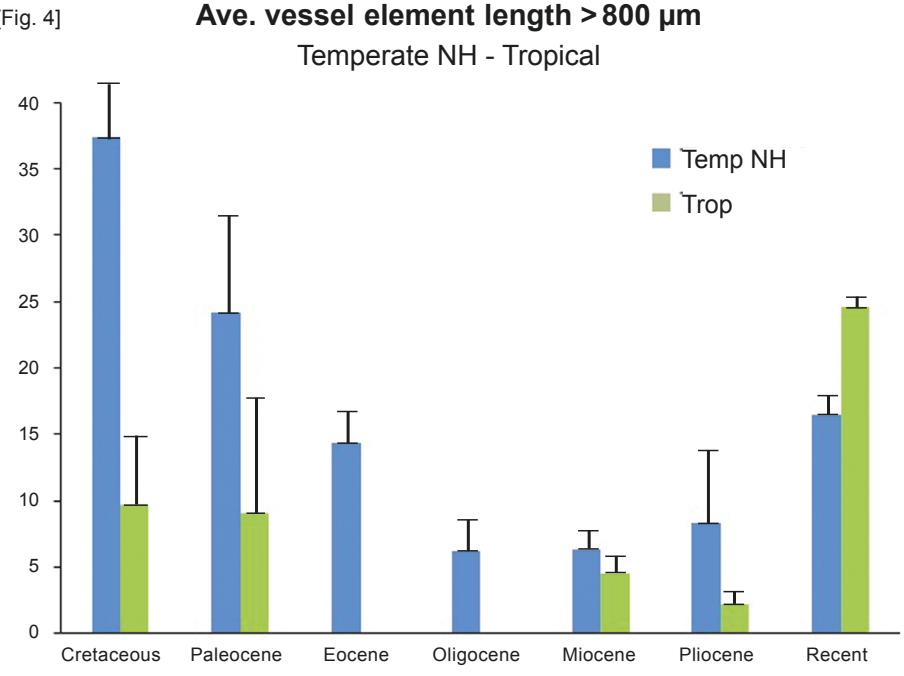


Figure 3. Incidence (%) of woods with scalariform and/or opposite, or scalariform to opposite intervessel pitting in the temperate and subtropical Northern Hemisphere (NH) and at tropical (paleo)latitudes (TR). – Figure 4. Incidence (%) of woods with long vessel elements (> 800 µm) in the temperate and subtropical Northern Hemisphere (NH) and at tropical latitudes (TR).

in the Oligocene and Pliocene and similar incidences in the Miocene and the Recent flora. In temperate SH high incidences of scalariform pits persist from the Cretaceous until the Oligocene.

In the tropics, the incidence of scalariform-opposite pits in the Cretaceous and Recent flora is similar (8 %), with fluctuating low levels throughout the Cenozoic.

Vessel element length (Fig. 4; Tables 1, S2)

According to Baileyan trends, angiosperms with long cambial initials and thus long vessel elements preceded shorter ones. Both Laurasia and tropical Gondwana show a decrease of species with long vessel elements (> 800 µm) from Cretaceous to Pliocene. This roughly agrees with our earlier findings (Wheeler & Baas 1991, 1993).

However, the recent flora has a higher incidence of long vessel elements. Most studies of recent woods measure vessel element lengths from macerations, while for fossil wood vessel element lengths are measured from sections. Measuring vessel element lengths from sections almost always results in lower values because the tips or tapering ends of the element are not easy to see, especially in fossil woods, and so vessel elements are not measured tip to tip.

The records for temperate SH do not show noteworthy differences between epochs.

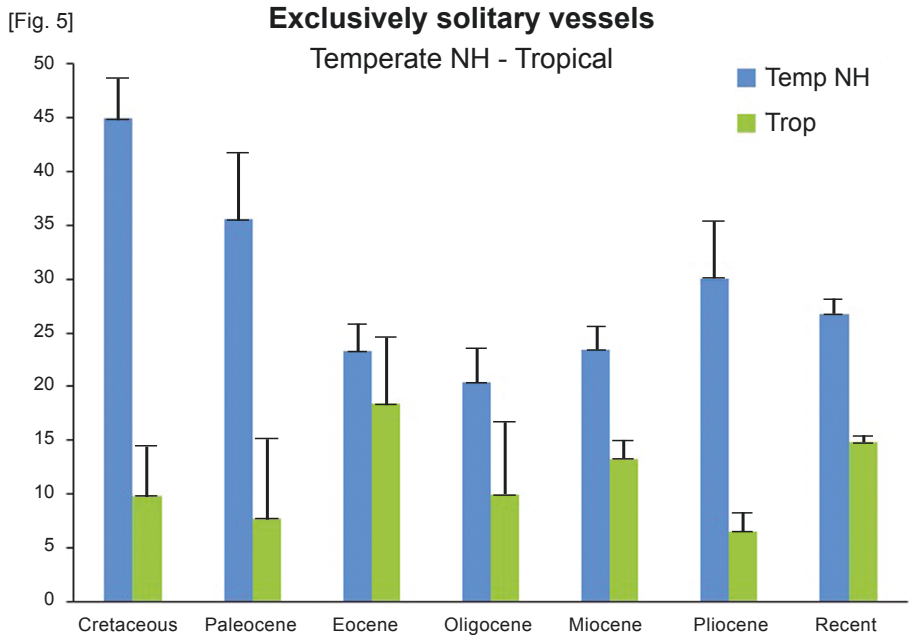
The higher incidence of long vessel elements in the recent Tropical than in Temperate floras in the InsideWood database confirms a robust ecological trend that has been validated in both floristic and taxonomic analyses (cf. Baas *et al*. 2004 for a summary). It is surprising that the fossil record for all epochs shows the reverse: temperate floras have a higher percentage of records with long vessel elements than tropical ones. This could in part be an artefact of different measurement protocols for fossil and recent woods. It is probably also related to temperate latitude fossil floras commonly including families with long vessel elements, *e.g*. Hamamelidaceae and Betulaceae, while tropical fossil floras commonly include families that do not have long vessel elements, *e.g*. Meliaceae and Fabaceae.

Solitary vessels (Fig. 5; Tables 1, S2)

In Laurasia, exclusively solitary vessels are much more common in the Cretaceous and early Cenozoic than in more recent epochs. In temperate SH, a similar, albeit somewhat weaker trend is apparent. In contrast, throughout all epochs, tropical (paleo) latitudes do not show any trend, and the incidence of exclusively solitary vessels fluctuates around relatively low levels of 10–18 %. This generally agrees with our earlier finding (Wheeler & Baas 1991, Fig. 30).

Exclusively solitary vessels with a mean tangential diameter > 100 µm that co-occur with vasicentric tracheids represents a syndrome separate from the Baileyan trends and which occurs at low levels from the Maastrichtian onwards (Table S2). In the mid to high latitude NH, from the Paleocene onwards it is almost exclusively associated with the Fagaceae. In the tropics, the earliest known occurrences of this syndrome are Myrtaceae woods in the Deccan Intertrappean Beds (Wheeler *et al*. 2017). Subsequently, it is reported at low levels in the Cenozoic, primarily in woods of Calophyllaceae, Chrysobalanaceae, and Dipterocarpaceae.

[Fig. 5]



[Fig. 6]

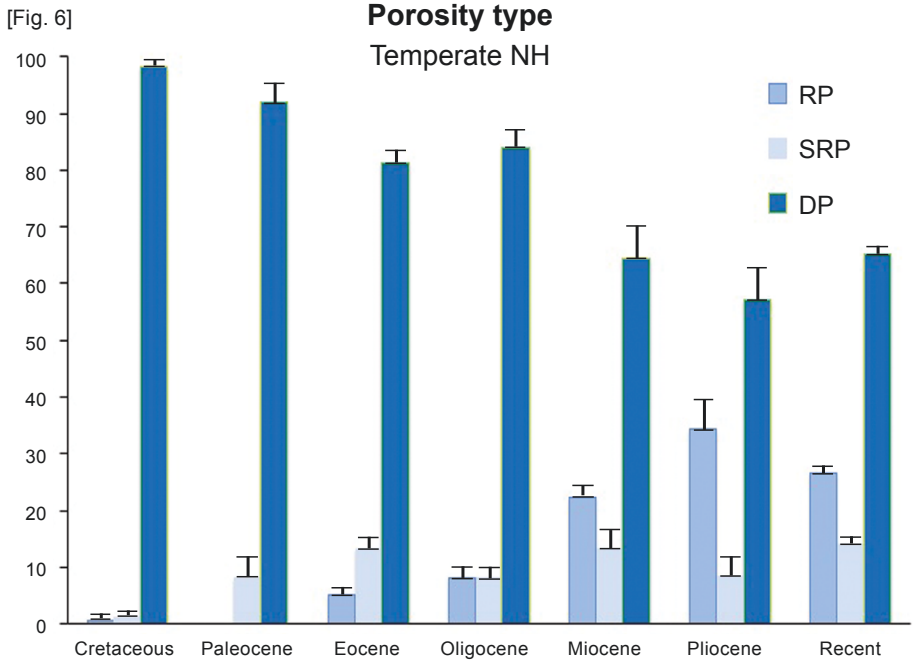


Figure 5. Incidence (%) of woods with exclusively solitary vessels in the temperate and subtropical Northern Hemisphere (NH) and at tropical latitudes (TR). – Figure 6. Incidence (%) of woods showing ring porosity (RP), semi-ring porosity (SRP) or diffuse porosity (DP) in the temperate and subtropical Northern Hemisphere (NH).

Porosity (Fig. 6, 7; Tables 1, S3)

The default condition of angiosperm woods is diffuse porosity (Wheeler *et al*. 2007). It has long been noted and recently confirmed that ring porosity is correlated with deciduousness and seasonal climates (Bailey 1924; Gilbert 1940; Boura & De Franceschi 2007). In the temperate NH, ring porosity and semi-ring porosity are rare in the Cretaceous and Paleocene, at low levels in the Eocene and Oligocene, reach near-modern incidences in the Miocene, with a peak in the Pliocene related to a high proportion of records of *Quercus, Castanea*, *Robinia* and *Fraxinus*. At temperate Southern Hemisphere latitudes, the feature peaks in the Oligocene, but remains much lower than in contemporary epochs in the temperate NH, likely related to evergreen trees being relatively common in temperate SH floras (*e.g*., Tecklin *et al*. 2011). Throughout all epochs, including the Recent, ring porosity at tropical latitudes is extremely rare. These data roughly agree with our earlier analyses (Wheeler & Baas 1991, 1993).

Vessel diameter (Fig. 8, 9; Tables 1, S4)

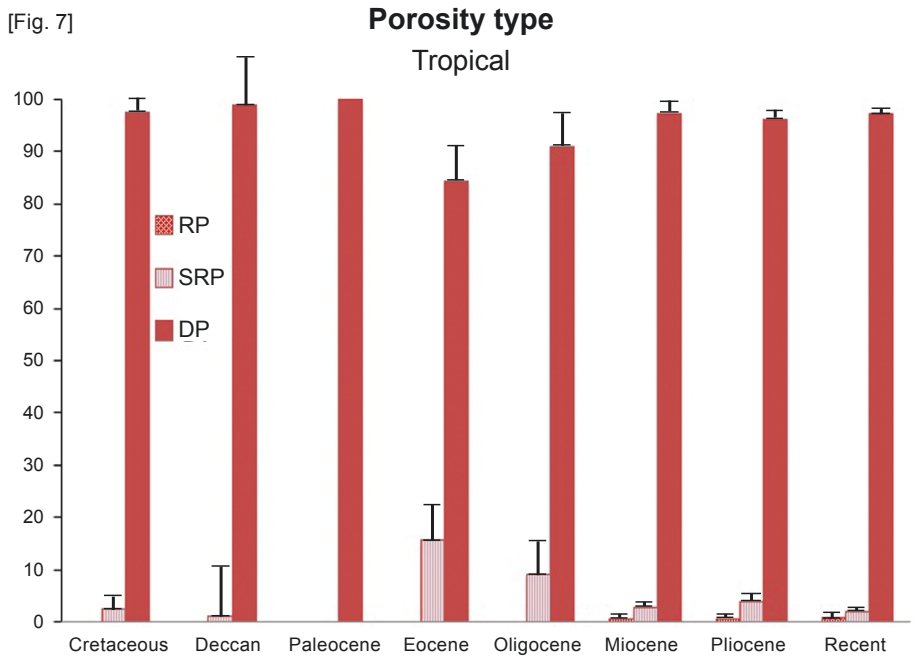
Because vessel diameter is correlated with plant size and habit (Olson *et al*. 2014; Rossell *et al*. 2017), we excluded Recent woods that are vines or only shrubs (IAWA Features 191, 190, respectively). Vessel diameters are narrower in young axes near the pith; Feature 333 of InsideWood's fossil database is for entire, small axes with pith, we also excluded these woods from the vessel diameter comparisons. We compare the incidences of woods from trees with 1) narrow vessels (mean tangential diameters < 100 μm), 2) diffuse porosity and wide vessels (mean tangential diameters > 200 μm), and 3) semi-ring-porous, ring-porous, and diffuse-porosity woods ("All" in Fig. 8 and 9) with wide vessels, for the semi-ring-porous and ring-porous wood these would be earlywood vessels.

Although at a low incidence (6%, 5%), there are Cretaceous woods with wide vessels in both the mid to high latitude NH and the tropics indicating trees were the source; this is consistent with the occurrence of Cenomanian-Campanian logs of >1 m diameter (*e.g*., Cahoon 1972; Lehman & Wheeler 2001; Estrada- Ruiz *et al*. 2012). Woods with such wide vessels should have high theoretical conductivity but low resistance to embolism (*e.g*., Martínez-Cabrera & Estrada-Ruiz 2014; Hacke *et al*. 2017).

From the Miocene onwards, diffuse-porous woods with wide vessels are rare in the north temperate zone (< 1% in the Recent flora), consistent with the riskiness (susceptibility to embolism) of wide vessels in seasonal environments, especially those with freeze-thaw cycles (Davis *et al*. 1999; Zanne *et al*. 2010, 2018; Hacke *et al*. 2017). Furthermore, in the Neogene and Recent flora of the north temperate zone, trees with wide vessels are almost always ring porous. Narrow vessels predominate in all epochs of the NH Temperate region (Fig. 8, Table S4).

Tropical Cretaceous and Paleocene have relatively high incidences of narrow vessels (43%, 50%), compared with incidences of 5–16% in the Eocene to Pliocene, and 31% in the modern flora. Because there are so few semi-ring-porous and ring-porous woods in the tropics, there is little to no difference in vessel diameter incidences between woods that are exclusively diffuse porous and woods from all porosity categories (Fig. 9, Table S4).

[Fig. 7]



[Fig. 8]

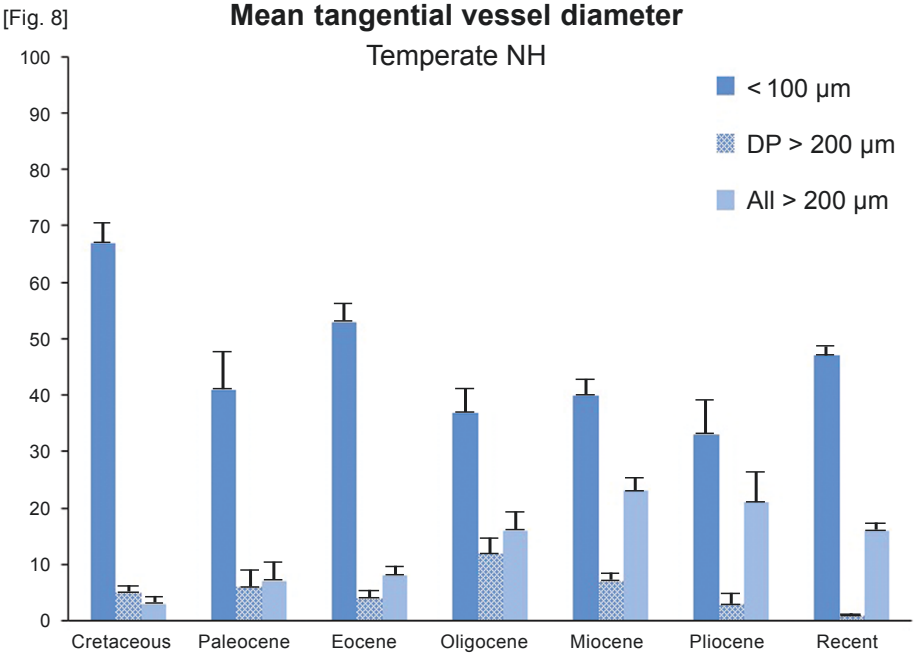
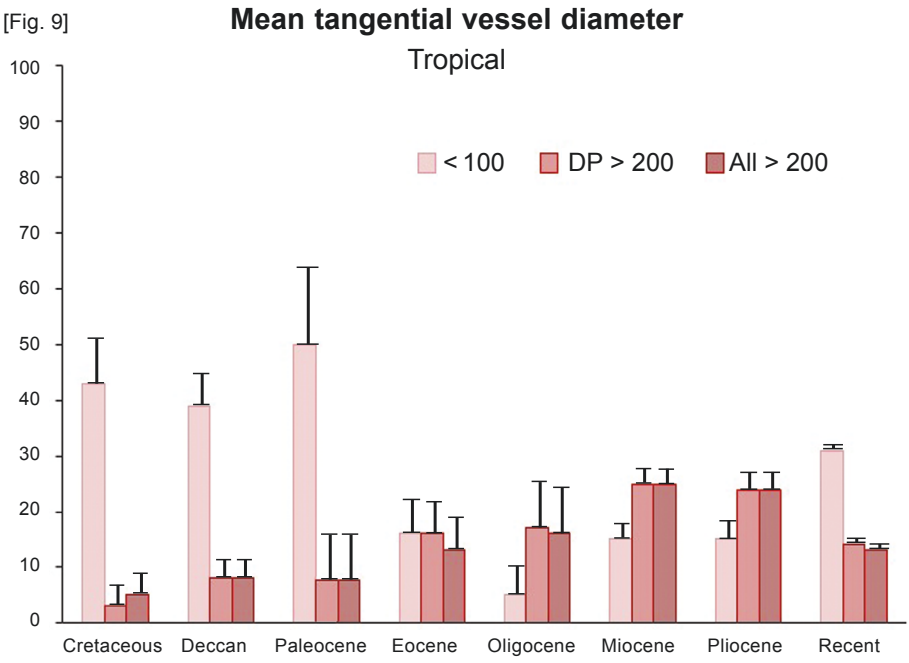


Figure 7. Incidence (%) of woods showing ring porosity (RP), semi-ring porosity (SRP) or diffuse porosity (DP) at tropical (paleo)latitudes (TR). – Figure 8. Incidence (%) of woods from tem-perate and subtropical latitudes (NH) with narrow (< 100 µm) and very wide (> 200 µm) vessels (DP = in diffuse-porous woods only; All = in diffuse-, semi-ring-, and ring-porous woods).

[Fig. 9]



[Fig. 10]

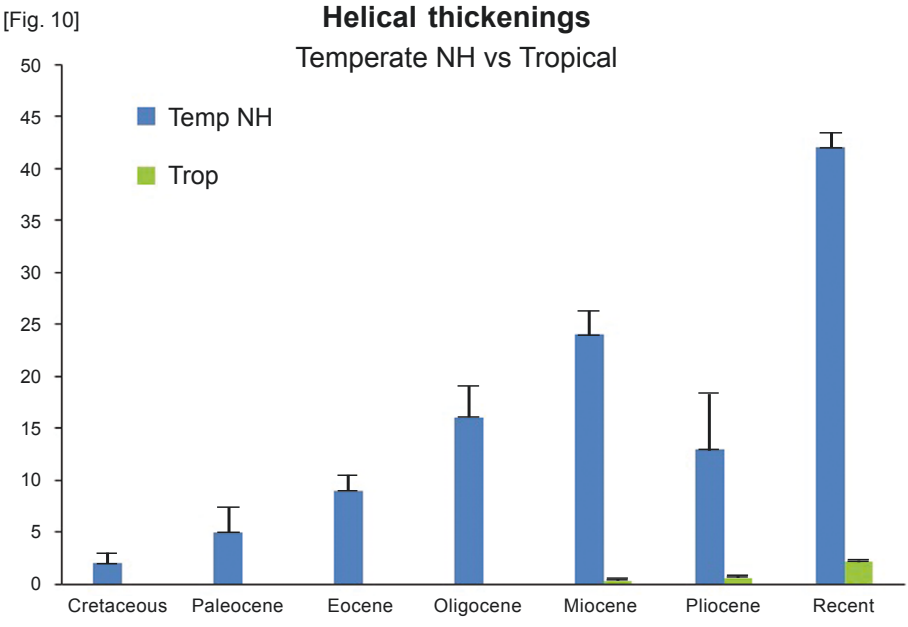


Figure 9. Incidence (%) of woods from tropical (paleo)latitudes (TR) with narrow (< 100 μm) and very wide (> 200 μm) vessels (DP = in diffuse-porous woods only; All = in diffuse-, semi-ring-, and ring-porous woods). – Figure 10. Incidence (%) of woods with helical vessel wall thickenings present in the temperate and subtropical Northern Hemisphere (NH) and at tropical latitudes (TR).

Helical thickenings (Fig. 10; Tables 1, S5)

Helical vessel wall thickenings do not feature in the Baileyan trends, but it is a feature with a strong ecological signal, being associated with regions that experience water stress caused by drought or freezing (Van der Graaff & Baas 1974; Carlquist 2001), and therefore was included in this analysis. In Temp NH, they are rare in the Cretaceous and Paleocene (< 2%, 5%), with medium frequencies (19–24%) in the Neogene, and at a very high incidence in the modern flora (42%). In the tropics (TR), throughout all epochs they are extremely rare (0–2%). The limited fossil record of temperate SH is somewhat in between, with fluctuating percentages (0–16%) in the Cenozoic, and also with a maximum in the recent flora.

It is likely that helical thickenings are underreported in fossil woods because they cannot be clearly seen unless the wood is well preserved.

Septate fibers and axial parenchyma absent or rare (Fig. 11, 12; Tables 1, S5)

The absence or rareness of axial parenchyma is often associated with presence of living fibers that are septate (Harrar 1946; Carlquist 2001, 2015; Wheeler *et al*. 2007).

Septate fibers are most common in the Cretaceous of both the temperate (and subtropical) NH (37%) and the Tropics (53%). In the temperate NH, their incidence decreases throughout the Cenozoic to 7% in the Pliocene and 9% in the Recent flora. In the Tropics, from the Eocene onwards, septate fibers are at higher incidences than in the temperate NH.

In the temperate NH, the incidence of absent-rare axial parenchyma is similar in the Cretaceous through the Eocene, with especially low levels during the Oligocene (3%), then similar in the Miocene and Pliocene (6%), with an increase into the Recent (13%). Oddly, the Tropics parallel the temperate NH in the incidence of absent-rare axial parenchyma, with the highest levels in the Cretaceous-Eocene, lowest in the Oligocene (0%), then similar in the Miocene and Pliocene (4%, 3%, respectively), with a higher level (14%) in the Recent.

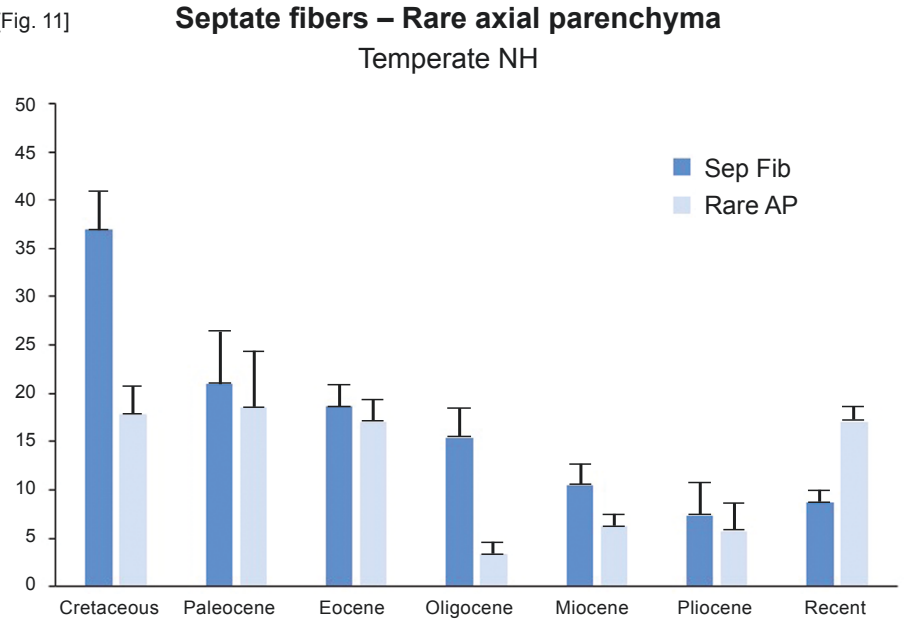
In temperate SH, incidences fluctuate widely and inexplicably for both septate fibers (0–62%) and absent-rare axial parenchyma (5–75%), probably related to the low number of records and resulting statistical noise. Septate fibers are likely underreported for fossil woods because it is difficult to be sure they are present unless the wood is well preserved.

Diffuse versus paratracheal parenchyma (Fig. 13, 14; Tables 1, S6)

We compare the incidence of woods that have *only* diffuse and/or diffuse-in-aggregates axial parenchyma with woods that have the presumably more derived paratracheal axial parenchyma types (aliform-confluent, often co-occurring with vasicentric parenchyma).

Temperate and subtropical NH shows a higher percentage of exclusively diffuse/diffuse-in-aggregates types in the Cretaceous and Paleocene (38%, 37%) than in later epochs (10–16%) and the present day (20%). In contrast, tropical Gondwana shows hardly any temporal trends, but only fluctuations with unexpected lows in the Paleocene and Eocene (0%) and a high in the Oligocene (17%).

[Fig. 11]



[Fig. 12]

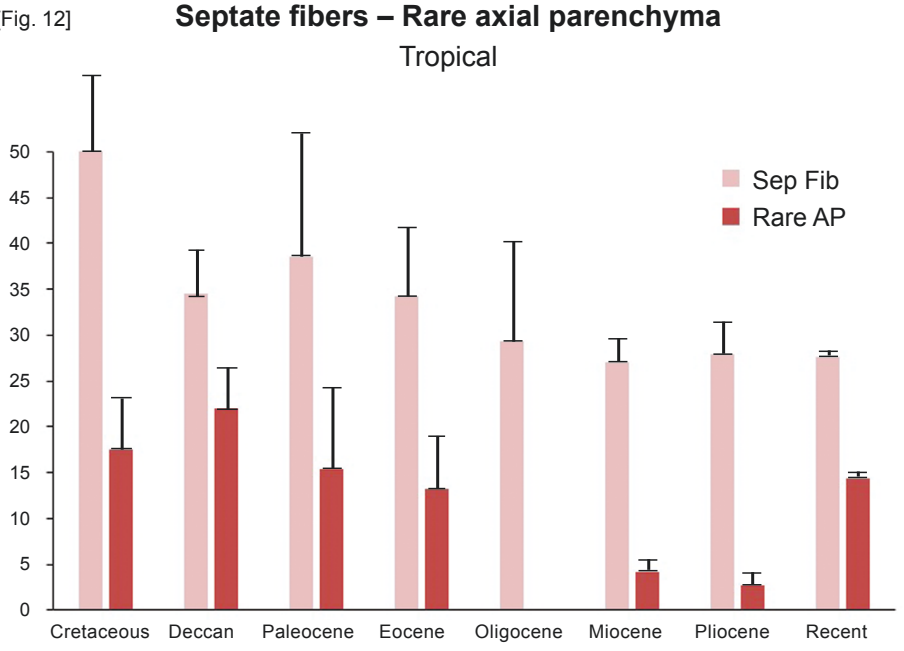
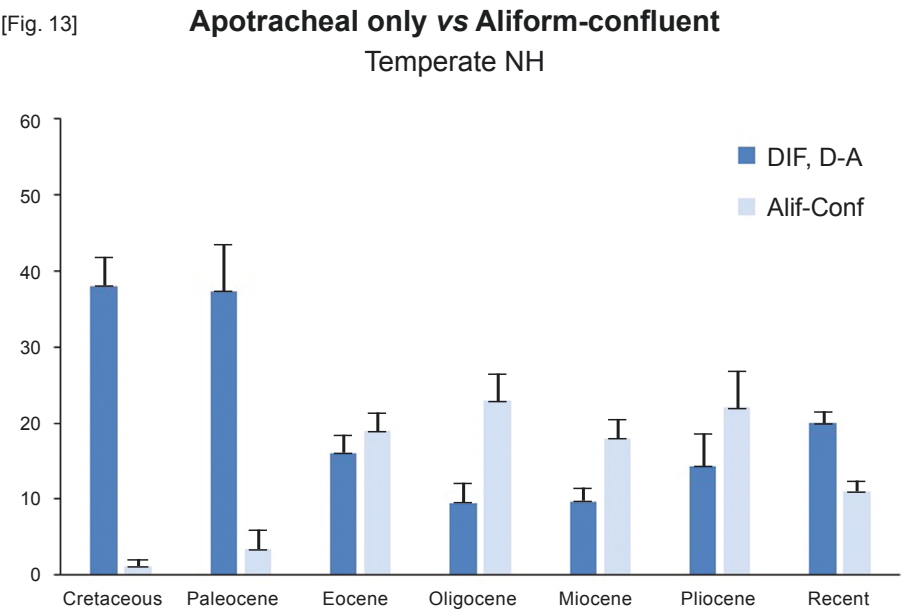


Figure 11. Incidence (%) of woods with septate fibers (Sep Fib) and axial parenchyma rare to absent (Rare AP) in the temperate and subtropical Northern Hemisphere (NH). – Figure 12. Incidence (%) of woods with septate fibers (Sep Fib) and axial parenchyma rare to absent (Rare AP) at tropical (paleo)latitudes (TR).

[Fig. 13]



[Fig. 14]

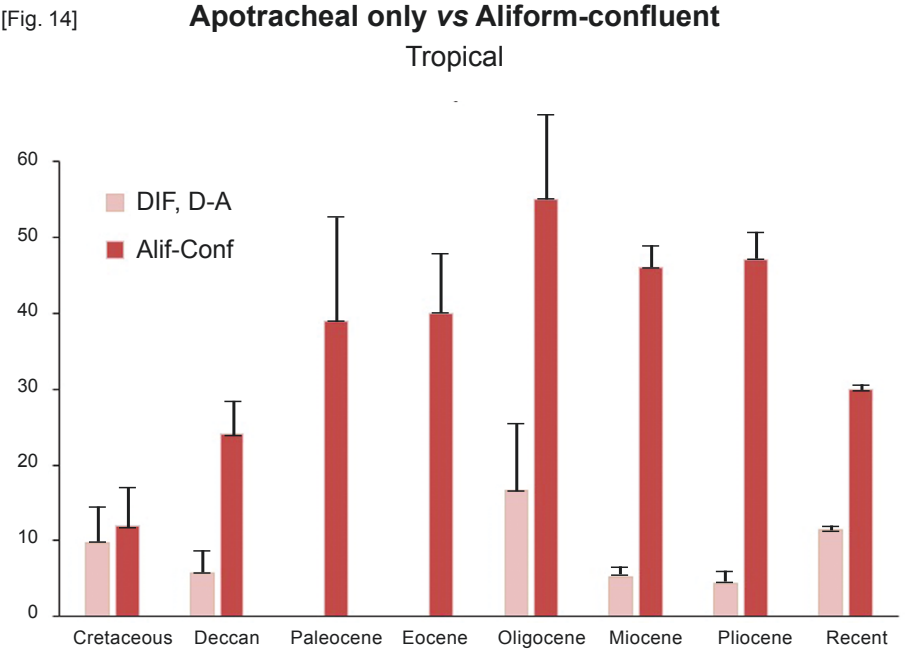


Figure 13. Incidences (%) of main parenchyma distribution types in the temperate and subtropical Northern Hemisphere (NH). DIF, D-A = parenchyma apotracheal diffuse and/or diffuse-in-aggregates; Alif-Conf = parenchyma paratracheal, aliform and/or confluent. – Figure 14. Incidences (%) of main parenchyma distribution types at tropical latitudes (TR). For explanation see Fig. 13.

In mid- to high-latitude Laurasia, the pattern for aliform-confluent parenchyma incidence complements that for the apotracheal types, with lows in the Cretaceous and Paleocene (1%, 3%), Eocene-Pliocene incidences varying from 13–19%, and modern levels of 11%.

In the tropics, aliform-confluent parenchyma occurs at high incidences from the Paleocene onwards with the Deccan woods (K-Pg boundary) at intermediate levels, and high incidences in the Oligocene (55%), Miocene (46%), and Pliocene (47%).

These data (Fig. 13, 14, Table S6) indicate that the present-day trend of aliform-confluent parenchyma being more common in tropical than in temperate floras (Wheeler *et al*. 2007; Morris *et al*. 2016) has existed since the Cretaceous.

Marginal parenchyma (Fig. 15; Tables 1, S6)

Marginal parenchyma is rare-absent from the Cretaceous of all regions. The single record of marginal parenchyma in the Upper Cretaceous of California (Page 1980) is questionable (Wheeler, personal observation of sample CAS 60427). In tropical Gondwana, levels of this feature fluctuate between 15–25% through time (with the Deccan woods at 10%), and with a peak of 32% in the Oligocene. At higher (paleo) latitudes, marginal parenchyma reaches more or less modern levels of incidence either in the Oligocene (temperate Gondwana) or the Eocene (Laurasia).

Strangely, the modern trend for marginal parenchyma to be more common in temperate regions than in tropical regions is reversed in the fossil record, where tropical woods have higher incidences of marginal parenchyma from the Paleocene to Pliocene. We cannot provide a reasonable explanation of this paradox. One partial explanation might be that Meliaceae and Fabaceae with marginal or marginal-like parenchyma bands are over-represented in the tropical fossil records because such woods are relatively easy to assign to family and so are more frequently described in the literature.

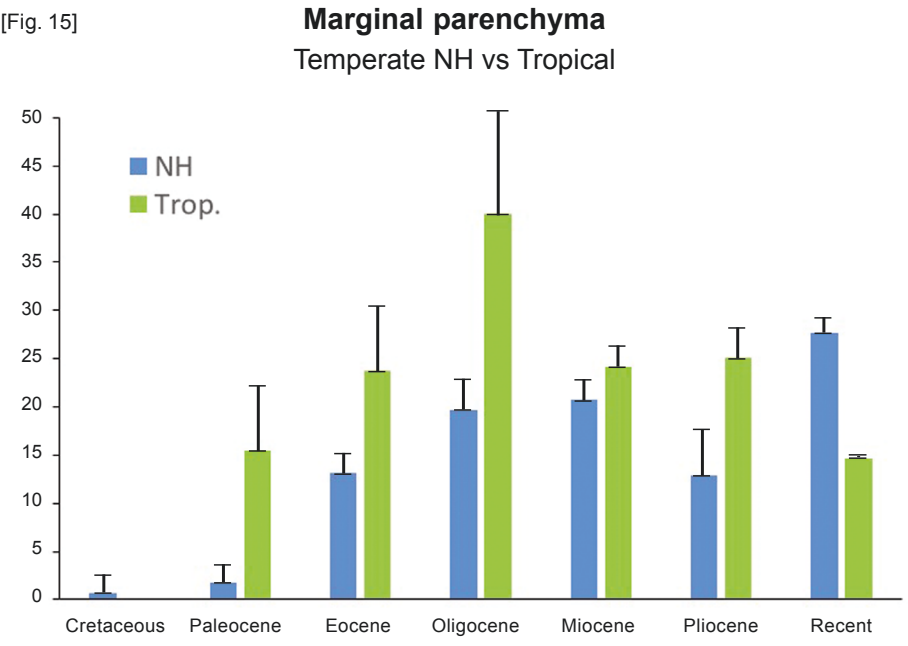
Ray composition (Fig. 16, 17; Tables 1, S7)

In the Baileyan canon, heterocellular rays composed of procumbent central cells and square to upright marginal cells preceded homocellular rays composed of procumbent cells only (Kribs 1935). We plotted the incidences of woods with exclusively heterocellular, both heterocellular and homocellular, and exclusively homocellular rays.

In the Cretaceous, Paleocene, and Eocene of Laurasia and temperate SH, homocellular rays are infrequent (0–15%), while heterocellular rays are very common. Incidences of homocellular ray types are generally similar in the Oligocene and Miocene of Laurasia (~40%). The Pliocene has the highest incidences (51 & 53%) of exclusively homocellular rays. The Recent flora has only 28 & 23% exclusively homocellular rays, but there is a higher incidence of woods that have both homocellular and heterocellular rays (23%, 21%).

In the tropics, there is no clear trend for incidences of ray types between the Cretaceous and Recent floras with homocellular ray occurrence at 17 and 15%, respectively, and then peaks at 38 and 30% in the Oligocene and Miocene. The incidence of heterocellular rays shows a contrasting pattern. These results differ from our earlier analysis (Wheeler & Baas 1991), which showed a nearly perfectly linear increase of homocellular rays and a decrease of heterocellular rays over time.

[Fig. 15]



[Fig. 16]

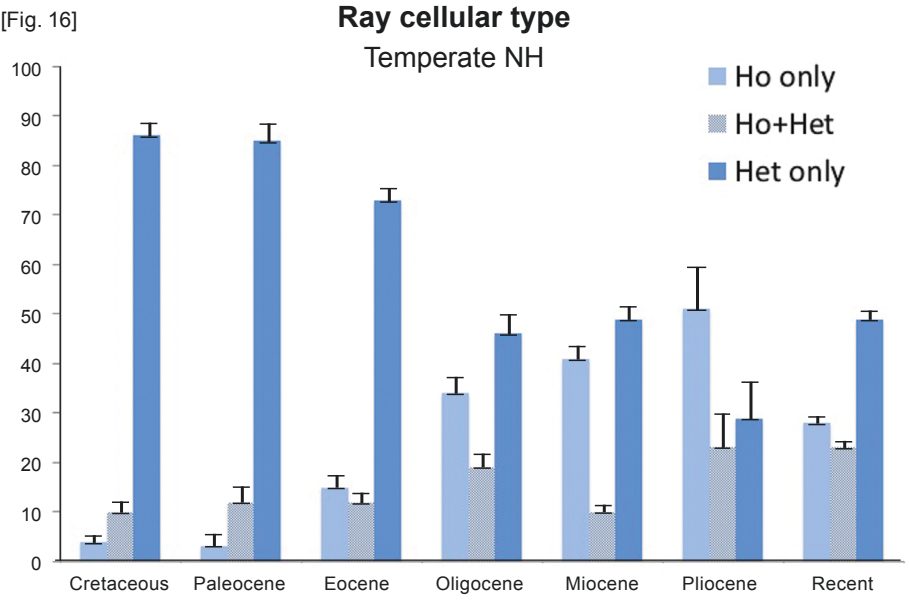
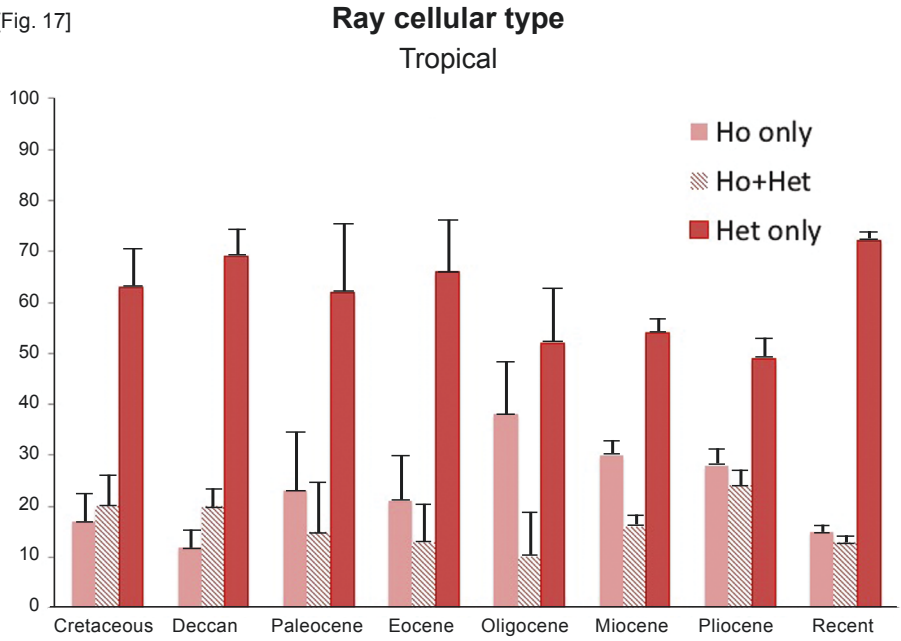


Figure 15. Incidences (%) of woods with marginal parenchyma bands present in the temperate and subtropical Northern Hemisphere (NH) and at tropical latitudes (Trop). – Figure 16. Incidences (%) of main types of cellular ray composition in the temperate and subtropical Northern Hemisphere (NH). Ho only = rays all homocellular and composed of procumbent cells only; Ho + Het = both homocellular and heterocellular rays present; Het only: all rays heterocellular and composed of central procumbent cells and marginal rows of square to upright cells.

[Fig. 17]



[Fig. 18]

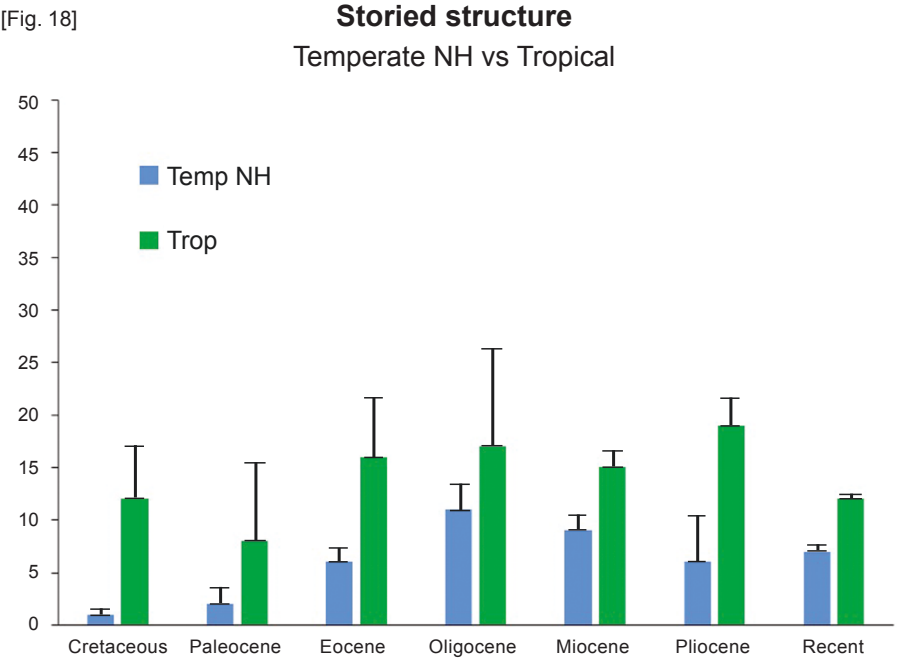


Figure 17. Incidences (%) of main types of cellular composition at tropical (paleo)latitudes (TR). For explanation see Fig. 16. – Figure 18. Incidences (%) of woods with storied structure in the temperate and subtropical Northern Hemisphere (NH) and at tropical latitudes (TR).

It should be noted that raylessness, common among recent secondarily woody clades such as Amaranthaceae (including Chenopodiaceae) and a number of other largely herbaceous families (Carlquist 2001), is completely absent from the fossil record. Whether this is due to their very recent origins or mostly xeric ecologies (Lens *et al*. 2013), making fossilization unlikely, remains an unanswered question.

Storied structure (Fig. 18; Tables 1, S8)

Because of the correlation of storied structure with short vessel elements and simple vessel perforations, this feature has been considered derived in the Baileyan sense (Bailey & Tupper 1918; Kribs 1935, 1937; Metcalfe & Chalk 1950). There is a weak trend at high paleolatitudes for storied structure to increase over time from absence or very low incidences in the Cretaceous and Paleocene (also the Eocene in temperate SH) with fluctuations up to or above modern levels in later epochs.

For the Tropics, storied rays are already relatively well represented (12%) in the Cretaceous, with no clear patterns in later epochs. These results are at variance with our earlier data (Wheeler & Baas 1991), which showed a slow, but consistent, increase in the combined incidence of storied rays from the Cretaceous up to the Recent in both the SH and NH.

GENERAL DISCUSSION

Our results show very contrasting temporal patterns between the mid and high latitudes (subtropical and temperate zones) of Laurasia and temperate Gondwana (South America and Antarctica) and the tropics. Fossil woods from mid-high latitudes broadly confirm the Baileyan trends of xylem evolution: "primitive" character states such as scalariform perforations, scalariform to opposite intervessel pits, exclusively solitary vessels, apotracheal diffuse and diffuse-in-aggregates parenchyma, and heterocellular rays are significantly more common in the Cretaceous, and also usually so in the early Cenozoic (Paleocene, Eocene) than in later Cenozoic epochs and the Present-day. In contrast, in the tropics, none of these key features of the Baileyan transformation series show marked differences between the Cretaceous, Cenozoic, and Recent. In this paper, we have emphasized relationships between broad climatic regions and wood anatomical traits through time; however, we appreciate that other factors have effects, *e.g*., soils, phylogenetic restraints.

Incidences of ring porosity and helical thickenings in the temperate NH broadly reflect Cenozoic climatic changes and become more common in the Neogene when seasonality increases (Liu *et al*. 2009; Hren *et al*. 2013). These results are paralleled in studies of smaller geographic areas. Elliott and Foster (2014) determined growth ring distinctiveness and porosity type in a large number (>1900) of samples (not species!) from southwestern Oregon, ranging in age from early Middle Eocene to Lower Miocene. They found that semi-ring-porous to ring-porous woods were absent from the early Middle Eocene, but represented 19% of the late Eocene samples, 59% of the late Oligocene samples, and 70% of the Lower Miocene samples.

Marginal parenchyma, another marker of seasonality, was virtually absent in the Cretaceous, with fluctuating incidences in the Cenozoic, and unexpectedly higher incidences in the tropics than in the temperate fossil floras.

These main patterns will be discussed below in terms of ecophysiologically adaptive xylem evolution. For reviews of functional xylem anatomy see Baas (1986), Carlquist (2001, 2012), Baas *et al*. (2004), and Spicer (2016); many reviews focus on how woods can simultaneously provide hydraulic safety and efficiency, storage, response to injury, and meet physical/mechanical demands, *e.g*., Lachenbruch & McCulloh (2014), Pratt & Jacobsen (2017), Hacke *et al*. (2017).

With the InsideWood dataset we used, we can only broadly contrast wood anatomical traits for tropical *versus* temperate and subtropical latitudes and how changes in the incidences of these traits parallel broad changes in late Cretaceous-Cenozoic climates, especially for the Cenozoic of mid to high latitude regions (see Upchurch & Wolfe 1987; Prothero 1994; Graham 1999; Zachos *et al*. 2001; Scotese 2003; Upchurch *et al*. 2007; Zanazzi *et al*. 2007; Friis *et al*. 2011). In a summary such as this one it is a cliché to state, but nonetheless important to emphasize, that there is a need for additional information and continued investigation. For fossil wood, this is especially true for low latitudes where there are few fossil wood reports. Also, additional localities spanning critical intervals in angiosperm history (late Cretaceous-earliest Paleocene; late Eocene-early Oligocene of North America) are needed to better understand the response of woody plants to major shifts in climate and detect any coordinated changes in functional traits. Well-dated localities with co-occurring woods and leaves deserve special attention as the ecology and climate inferred from leaves and woods can be compared, and whether and how changes in leaf physiognomy and wood anatomy are related, as a whole, by geographic regions, as well as within individual orders, families, and genera (*e.g*., Wiemann *et al*. 2001; Cretaceous Olmos Formation, Mexico, Martinez-Cabrera & Estrada-Ruiz 2014; Eocene, Blue Rim, Wyoming, USA, Allen 2017).

Spatial patterns

The fact that throughout the Cenozoic the different % incidences in tropical *versus* temperate and subtropical paleolatitudes more or less fit well established ecological trends known for the modern flora, may be used to support adaptive interpretations postulated before (Carlquist 1975, 2001, 2012; Baas *et al*. 2004) emphasizing greater needs for conductive efficiency in tropical conditions, and greater safety from freeze-thaw embolisms in temperate regions. Christman and Sperry's (2010) studies indicate that scalariform perforation plates "doubled lumen flow resistance". This would "explain" the low incidence of scalariform perforations in tropical and seasonally hot and dry conditions. Explanations for their much higher incidence as "relictual" features at higher latitudes are less clear. Zimmermann (1983), Ewers (1985), and Tyree & Zimmermann (2002) speculated about a functional role of scalariform perforations in limiting the spread of freeze-thaw embolisms. Later studies (Christman & Sperry 2010; Ewers personal communication 2018) have questioned these hypotheses in view of the dominant role of vessel diameter in limiting the spread of freeze-thaw embolisms. However, we cannot imagine that a trait that has survived in such high percentages in

boreal and alpine floras (Baas 1976; Baas & Schweingruber 1987; Jansen *et al*. 2004), did so *only* as a neutral trait, because there was "no selective pressure for higher conductive efficiency to eliminate it".

A similar adaptive argumentation could be valid for the elimination from tropical latitudes of other features often associated with scalariform perforations: solitary vessels, scalariform to opposite intervessel pits, diffuse axial parenchyma and heterocellular rays. Their large-scale replacement in tropical conditions with grouped vessels, alternate intervessel pits, elaborate, mainly paratracheal axial parenchyma patterns, and higher proportions of procumbent ray cells could be advantageous in tropical lowland trees (and drought-tolerant species) demanding high conductive efficiency, repair of embolisms (admittedly controversial), strong biological defense, and improved radial transport of metabolites as facilitated by strongly procumbent ray cells (cf. Braun 1970).

Cretaceous records of tropical (paleo)latitudes, including India, fit the same pattern as modern tropical woods. Recently, we have argued that tropical conditions in the Deccan Intertrappean region of India accelerated xylem evolution when the Indian plate was rafting northwards over the Réunion Hot Spot at the K-Pg boundary to produce a "surprisingly modern" incidence of derived wood anatomical features in the Baileyan sense (Wheeler *et al*. 2017). Our present data show that "surprisingly modern" applies to *all* tropical Cretaceous floras.

Paradoxes: xerophobic angiosperms and "bipolar" distribution of primitive wood features

Feild *et al*. (2009) hypothesized an early stage of *xerophobic* angiosperms with xylem characterized by primitive Baileyan features, especially vessel elements that still looked like tracheids with numerous bars per scalariform perforations (> 40) and that did not have a higher conductive efficiency than vesselless angiosperms. Only the advent of simple perforation plates allowed greater conductive efficiency (Sperry *et al*. 2007; Feild & Wilson 2012). Yet, the origin of vessel elements created possibilities for diversification in other cell types with opportunities for optimizing mechanical storage, and biological defense functions. In this respect it is noteworthy that one of the most commonly occurring Cretaceous angiosperm woods is *Paraphyllanthoxylon*, which has simple perforation plates, and is a tree. Carlquist (2012) also argued that early angiosperm woods were adapted to a mesic ecology.

The hypothesized ecology of xerophobic angiosperms in (sub)tropical mesic muddy terrains suggests an environment with a good chance of being represented in the fossil record; one would expect xerophobic woods to be more common among tropical Cretaceous woods. However, they are virtually absent from the tropics and instead are not uncommon in the temperate latitudes in the Upper Cretaceous of the Northern and Southern Hemisphere (cf. InsideWood – fossil records). The following genera, mostly with unknown familial affinities, were retrieved in an InsideWood search for Cretaceous woods with scalariform perforations with over 40 bars: *Baasia, Chaloneroxylon, Cornoxylon, Frutecoxylon, Hamamelidoxylon, Hortonioxylon, Icacinoxylon, Illioxylon, Mastixioxylon, Mulleroxylon, Nyssoxylon,* plus several unnamed types described by Page (1981); all are from extra-tropical localities.

How to harmonize the occurrence of "primitive" woods in the mid-high latitudes of both hemispheres during the Cretaceous with a tropical belt in between with woods with derived features in the Baileyan sense? There are hardly any pre-Maastrichtian angiosperm woods at tropical latitudes, yet, if it is true that woody angiosperms arose in the tropics (Feild *et al*. 2009), it is odd that Cretaceous woods with "ancestral" features are found almost exclusively in extratropical latitudes. An alternative and contrasting model postulating wood with simply perforated vessels and paratracheal parenchyma or septate fibers as primitive, with wood with scalariform vessel perforations and apotracheal, diffuse parenchyma as derived would better fit this latitudinal pattern in the early history of the angiosperms. However, this total reversal of the Baileyan transformation series would be at odds with evidence from DNA-based phylogenies of woody angiosperms which support vesselless woods and woods with scalariform perforations and other "primitive" Baileyan features as basal in angiosperms (Herendeen *et al*. 1999; Baas *et al*. 2003; Lens *et al*. 2016; unpublished results Wheeler and Baas).

Moreover, many early Cretaceous angiosperm pollen types and leaves or reproductive structures have living relatives with very primitive wood in the Baileyan sense, such as Chloranthaceae, Buxaceae, and Winteraceae (Doyle 2015). We therefore prefer to interpret our current data largely in support of the Baileyan model, with adaptive preservation of "primitive" character states in North and South Temperate zones, or possibly even some reversals towards their ancestral state in features such as perforation plates and intervessel pit arrangement.

Modern and fossil woods – effects of glaciations?

It is striking that some functional traits linked with cool and/or seasonal temperate climates, such as scalariform perforations, narrow vessels, helical vessel wall thickenings, and marginal parenchyma show relatively high incidences in the Recent mid and high latitude NH flora as compared with the Pliocene (Fig. 1, 8, 10, 15; Tables S1, S4, S5, S6). The high incidence in the Recent flora of these features could reflect selection for them during the Pleistocene glaciations, with local extinctions of woods with simple perforations and wider vessels, from which the recent high latitude (and high altitude!) floras have not yet completely recovered (cf. Baas & Wheeler 2011).

CONCLUSION

Our broad analysis of the fossil wood record confirms the Baileyan model for evolution only at mid to high latitudes, while the tropical fossil record hardly shows any changes from the Cretaceous to the Present. We do not have a satisfactory scenario to explain this paradox. Climatic gradients from low to high latitudes were less steep in the Cretaceous than in later epochs (Friis *et al*. 2011; Upchurch *et al*. 2015), while the wood anatomical differences between temperate and tropical latitudes were greater in the Cretaceous.

There is a great need for enriching the early Cretaceous fossil wood record, especially in the tropics. Above we discuss only part of the evolutionary and functional significance of the patterns retrieved from the InsideWood database, which is a relatively comprehensive source of data for angiosperm fossil woods and most recent ones. Some of these patterns raise more questions than we provide answers for. However,

we encourage all students of modern ecological and functional wood anatomy and tree biology to take these patterns into account in their studies and conclusions. Fossil data can effectively be used to falsify *or* support speculative hypotheses involving functional wood traits.

ACKNOWLEDGEMENTS

Thanks are due to all wood anatomists and paleoxylotomists who have provided data for InsideWood, to Shirley Rodgers and the NC State Libraries for maintaining and hosting the InsideWood web site, Emma van Nieuwkoop for help with the figures, Emily Griffith (Department of Statistics, NC State) for statistical advice, and Lisa Boucher, Anne-Laure Decombeix, and Jonathan Wilson, conveners of an IAWA Symposium on *Hydraulic architecture of plants through time* at IOPC, Salvador de Bahia, and EPPC, Dublin, at which portions of this manuscript were presented. We also thank Lisa Boucher, Steven Jansen and Jakub Sakala for their thoughtful and useful comments on this manuscript.

REFERENCES

Allen SE. 2017. Reconstructing the local vegetation of the Lower Eocene Blue Rim site of southwestern Wyoming using fossil wood. Int. J. Plant Sci. 178: 689–714. DOI: 10.1086/694186.

Anagnostou E, John EH, Edgar KM, Foster GL, Ridgwell A, Inglis GN, Pancost RD, Lunt DJ, Pearson PN. 2016. Changing atmospheric CO_2 concentration was the primary driver of early Cenozoic climate**.** Nature 533 (7603): 380–384M. DOI: 10.1038/nature17423.

Baas P. 1976. Some functional and adaptive aspects of vessel element member morphology. In: Baas P, Bolton AJ, Catling DM (eds.), Wood structure in biological and technological research. Leiden Botanical Series 3: 157–181. Leiden University Press.

Baas P. 1986. Ecological patterns of xylem anatomy. In: Givnish J (ed.), On the economy of plant form and function: 327–352. Cambridge University Press, Cambridge, New York.

Baas P, Ewers FW, Davis SD, Wheeler EA. 2004. The evolution of xylem physiology. In: Hemsley AR, Poole I (eds.), Evolution of plant physiology. From whole plants to ecosystems: 273–296. Linnaean Society Symposium Series No. 21. Elsevier Academic Press.

Baas P, Schweingruber FH. 1987. Ecological trends in wood anatomy of trees, shrubs and climbers from Europe. IAWA Bull. n.s. 8: 245–274. DOI: 10.1163/2241932-90001053.

Baas P, Wheeler EA. 2011. Wood anatomy and climate change. In: Hodkinson TR, Jones MB, Waldren S, Parnell J (eds.), Climate change and systematics: 141–155. The Systematics Association Special Vol. 78, Cambridge University Press.

Baas P, Wheeler EA, Jansen S. 2003. Ecological adaptations and deep phylogenetic splits - evidence and questions from the secondary xylem. In: Stuessy TF, Mayer V, Horändel E (eds.), Deep morphology - toward a renaissance of morphology in plant systematics: 221–239. Regnum Vegetabile Vol. 141, Gartner Verlag, Liechtenstein.

Bailey IW. 1924. The problem of identifying the wood of Cretaceous and later dicotyledons: *Paraphyllanthoxylon arizonense*. Ann. Bot. 38: 439–451.

Bailey IW. 1953. Evolution of the tracheary tissue of land plants. Amer. J. Bot. 40: 4–8. DOI: 10.1002.j.1537-2197.1953.tb06441.x.

Bailey IW, Tupper WW. 1918. Size variation in tracheary cells. I. A comparison between the secondary xylems of vascular cryptograms, gymnosperms and angiosperms. Proc. Amer. Acad. Arts Sci. 54: 149–204. DOI: 0.2307/20025747.

Beeckman H. 2016. Wood anatomy and trait-based ecology. IAWA J. 37: 127–151. DOI: 10.1163/22941932-20160127.

Boura A, De Franceschi D. 2007. Is porous wood structure exclusive of deciduous trees? C. R. Palevol 6: 385–391. DOI: 10.1016/j.crpv.2007.09.009.
Bowen GJ. 2007. When the world turned cool. Nature 445: 607–608. DOI: 10.1038/445607a.
Braun HJ. 1970. Funktionelle Histologie der sekundären Sprossachse. I. Das Holz. Encyclopedia of Plant Anatomy Band IX, part 1. Gebrüder Borntraeger, Berlin, Stuttgart.
Cahoon EJ. 1972. *Paraphyllanthoxylon alabamense* – a new species of fossil dicotyledonous wood. Amer. J. Bot. 59: 5–11. DOI: 10.1002/j.1537-2197.1972.tb10057.x.
Cantrill DJ, Poole I. 2005. Taxonomic turnover and abundance in Cretaceous to Tertiary wood floras of Antarctica: implications for changes in forest ecology. Palaeogeogr., Palaeoclim., Palaeoecol. 215: 205–219.
Carlquist S. 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley.
Carlquist S. 2001. Wood anatomy: Systematic, ecological, and evolutionary aspects of dicotyledonous wood. Ed. 2. Springer Series in Wood Science.
Carlquist S. 2012. How wood evolves: a new synthesis. Botany 90: 901–940. DOI: 10.1139/b2012-048.
Carlquist S. 2015. Living cells in wood. 1. Absence, scarcity and histology of axial parenchyma as keys to function. Bot. J. Linn. Soc. 177: 291–321. DOI: 10.1111/boj.12247.
Christman MA, Sperry JS. 2010. Single-vessel flow measurements indicate scalariform perforation plates confer higher flow resistance than previously estimated. Plant Cell Environ. 33: 431–443. DOI: 10.1111/j.1365-3040.2009.02094.x.
Crawley M. 2001. Angiosperm woods from British Lower Cretaceous and Palaeogene Deposits. Special Papers in Palaentology 66. The Palaeontological Association. 100 pp.
Crivellaro A, Schweingruber FH. 2013. Atlas of wood, bark and pith anatomy of eastern Mediterranean trees and shrubs with a special focus on Cyprus. Springer.
Davis SD, Sperry JS, Hacke UG. 1999. The relationship between xylem conduit diameter and cavitation caused by freezing. Amer. J. Bot. 86: 1367–1372. DOI: 10.2307/2656919.
Doyle JA. 2015. Recognising angiosperm clades in the Early Cretaceous fossil record. Historical Biology: Intern. J. Paleobiol. 27: 414–429. DOI: 10.1080/08912963.2014.938235.
Doyle JA, Endress P. 2010. Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: Magnoliidae and eudicots. J. Syst. Evol. 48: 1–35. DOI: 10.1111/j.1759-6831.2009.00058.x.
Elliott Jr WS, Foster JD. 2014. Petrified wood of southwestern Oregon: Implications for Cenozoic climate change. Palaeogeogr., Palaeoclim., Palaeoecol. 402: 1–11. DOI: 10.1016/j.palaeo.2014.03.004.
Estrada-Ruiz E, Martínez-Cabrera HI, Cevallos-Ferriz SRS. 2007. Fossil woods from the late Campanian-early Maastrichtian Olmos Formation, Coahuila, Mexico. Rev. Palaeobot. Palynol. 145: 123–133. DOI: 10.1016/j.revpalbo.2006.09.003.
Estrada-Ruiz E, Parrott JM, Upchurch Jr GR, Wheeler EA, Thompson DL, Mack GH, Murray MM. 2012. The wood flora from the Upper Cretaceous Crevasse Canyon and McRae Formation, south-central New Mexico, USA: A progress report: 503–518. New Mexico Geological Society Guidebook, 63rd Field Conference, Warm Springs Region.
Ewers F. 1985. Xylem structure and water conduction in conifer trees, dicot trees, and lianas. IAWA Bull. n.s. 6: 393–407. DOI: 10.1163/22941932-90000959.
Feild TS, Chatelet DS, Brodribb TJ. 2009. Ancestral xerophobia: a hypothesis on the whole plant ecophysiology of early angiosperms. Geobiology 7: 237–264. DOI: 10.1111/j.1472-4669.2009.00189.
Feild TS & Wilson JP. 2012. Evolutionary voyage of angiosperm vessel structure-function and its significance for early angiosperm success. Int. J. Plant Sci. 173: 596–609. DOI: 10.1086/666099.

FFPRI Wood Database. Forestry and Forest Products Research Institute, Ibaraki, Japan. Published online: http://db.ffpri.affrc.go.jp/WoodDB/index-E.html.

Fliche P. 1905. Note sur les bois fossils de Madagascar. Bull. Soc. Géol. France 4, sér. 5: 346–358.

Friis EM, Crane PR, Pedersen KR. 2011. Early flowers and angiosperm evolution. Cambridge University Press. 585 pp.

Gilbert SG. 1940. Evolutionary significance of ring porosity in woody angiosperms. Bot. Gaz. 102: 105–120.

Gleason SM, Westoby M, Jansen S, Choat B, Hacke UG, Pratt RB, Bhaskar R, Brodribb TJ, Bucci SJ, Cao K-F, Cochard H, Delzon S, Domec J-C, Fan Z-X, Feild TS, Jacobsen AL, Johnson DM, Lens F, Maherali H, Martínez-Vilalta J, Mayr S, McCulloh KA, Mencuccini M, Mitchell PJ, Morris H, Nardini A, Pittermann J, Plavcová L, Schreiber SG, Sperry JS, Wright IJ, Zanne A. 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. New Phytologist 209: 123–136. DOI: 10.1111/nph.13646.

Graham A. 1999. Late Cretaceous and Cenozoic history of North American vegetation. Oxford University Press, New York.

Hacke UG, Spicer R, Schreiber SG, Plavcová L. 2017. An ecophysiological and developmental perspective on variation in vessel diameter. Plant Cell Environ. 40: 831–845. DOI: 10.1111/pce.12777.

Harrar ES. 1946. Notes on starch grains in septate fiber-tracheids. Trop. Woods 85: 1–9.

Herendeen PS. 1991. Charcoalified angiosperm wood from the Cretaceous of eastern North America and Europe. Rev. Palaeobot. Palynol. 69: 225–239. DOI: 10.1016/0034-6667(91)90004-M.

Herendeen PS, Friis EM, Pedersen KR, Crane PR. 2017. Palaeobotanical redux: revisiting the age of the angiosperms. Nature Plants 3, Article number 17015. DOI: 10.1038/nplants.2017.15.

Herendeen PS, Wheeler EA, Baas P. 1999. Angiosperm wood evolution and the potential contribution of paleontological data. Bot. Rev. 65: 278–300. DOI: 10.1007/BF02857632.

Hren MT, Sheldon ND, Grimes ST, Collinson ME, Hooker JJ, Bugler M, Lohmann KC. 2013. Terrestrial cooling in Northern Europe during the Eocene-Oligocene transition. Proc. Nat. Acad. Sci. 110: 7562–7567. DOI: 10.1073/pnas.1210930110.

IAWA Committee. 1989. IAWA List of microscopic features for hardwood identification. IAWA Bull. n.s. 10: 219–332.

InsideWood. 2004-onwards. Published on the Internet: http://insidewood.lib.ncsu.edu/search.

Jansen S, Baas P, Gasson P, Lens F, Smets E. 2004. Variation in xylem structure from tropics to tundra: Evidence from vestured pits. Proc. Nat. Acad. Sci. 101: 8833–8837. DOI: 10.1073/pnas.0402621101.

Jansen S, Nardini A. 2014. From systematic to ecological wood anatomy and finally plant hydraulics: are we making progress in understanding xylem evolution? New Phytologist 203: 12–15. DOI: 10.1111/nph.12839.

Jud NA. 2015. Fossil evidence for a herbaceous diversification of early eudicot angiosperms during the Early Cretaceous. Proc. Roy. Soc. B Biol. Sci. 282(1814). DOI: 10.1098/rspb.2015.1045.

Jud NA, Wheeler EA, Rothwell GW, Stockey RA. 2017. Angiosperm wood from the Upper Cretaceous (Coniacian) of British Columbia, Canada. IAWA J. 38: 141–161. DOI: 10.1163/22941932-20170164.

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006. World map of the Köppen-Geiger climate classification updated. Meteorol. Zeitschr. 15: 259–263. DOI: 10.1127/0941-2948/2006/0130.

Kribs DA. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz. 96: 547–557. DOI: 10.1086/334500.

Kribs DA. 1937. Salient lines of structural specialization in the wood parenchyma of dicotyledons. Bull. Torrey Bot. Club 64: 177–187. DOI: 10.2307/2481141.

Lachenbruch B, McCulloh KA. 2014. Traits, properties, and performance: how woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. New Phytologist 204: 747–764. DOI: 10.1111/nph.13035.

Lehman TM, Wheeler EA. 2001. A fossil dicotyledonous woodland/forest from the Upper Cretaceous of Big Bend National Park, Texas. Palaios 16: 102–108. DOI: 10.1669/0883-1351(2001)016<0102:AFDWFF>2.0.CO;2.

Lens F, Davin N, Smets E, & del Arco M. 2013. Insular woodiness on the Canary Islands: a remarkable case of convergent evolution. Int. J. Plant Sci. 174: 992–1013. DOI: 10.1086/670259.

Lens F, Vox RA, Charrier G, van der Niet T, Merckx V, Baas P, Guterrez JA, Jacobs B, Dóris LC, Smets E, Delzon S, Janssens SB. 2016. Scalariform-to-simple transition in vessel perforation plates triggered by differences in climate during the evolution of Adoxaceae. Ann. Bot. 118: 1043–1056. DOI: 10.1093/aob/mcs151.

Linnert C, Robinson SA, Lees JA, Bown PR, Pérez-Rodríguez I, Petrizzo MR, Falzoni F, Littler K, Arz JA, Russell EE. 2014. Evidence for global cooling in the Late Cretaceous. Nature Communications 5: 4194. DOI: 10.1038/ncomms5194.

Liu Z, Pagani M, Zinniker D, DeConto R, Huber M, Brinkhuis H, Shah SR, Leckie RM, Pearson A. 2009. Global cooling during the Eocene-Oligocene climate transition. Science 323 (5918): 1187–1190. DOI: 10.1126/science.1166368.

Martínez-Cabrera HI, Estrada-Ruiz E. 2014. Wood anatomy reveals high theoretical hydraulic conductivity and low resistance to vessel implosion in a Cretaceous fossil forest from northern Mexico. PLoS ONE 9 (10): e108866. DOI: 10.1371/journal.pone.0108866.

Martínez-Cabrera HI, Zheng J, Estrada-Ruiz E. 2017. Wood functional disparity lags behind taxonomic diversity in angiosperms. Rev. Palaeobot. Palynol. 246: 251–257. DOI: 10.1016/j.revpalbo.2017.07.008.

Metcalfe CR, Chalk L. 1950. Anatomy of the dicotyledons. Vol. 1 & 2. Clarendon Press, Oxford, U.K.

Morris H, Gillingham MAF, Plavcová L, Gleason SM, Olson ME. Coomes DA, Fichtler E, Klepsch MM, Martínez-Cabrera HI, McGlinn DJ, Wheeler EA, Zheng J, Zieminska K, Jansen S. 2018. Vessel diameter is related to amount and spatial arrangement of axial parenchyma in woody angiosperms. Plant Cell Environ. 41: 245–260. DOI: 10.1111/pce.13091.

Morris H, Plavcová L, Cvecko P, Fichtler E, Gillingham MAF, Martinez-Cabrera HI, McGlinn DJ, Wheeler E, Zheng J, Zieminska K, Jansen S. 2016. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. New Phytologist 209: 1553–1565. DOI: 10.1111/nph.13737.

Nishida M, Nishida H, Nasa T. 1988. Anatomy and affinities of the petrified plants from the Tertiary of Chile. V. J. Plant Res. 10: 293–309. DOI: 10.1007/BF02488606.

Nunes CI, Pujana RR, Escapa IH, Gandolfo MA, Cúneo NR. 2018. A new species of *Carlquistoxylon* from the Early Cretaceous of Patagonia (Chubut province, Argentina): the oldest record of angiosperm wood from South America. IAWA J. 39: 406–426. DOI: 10.1163/22941932-20170206.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR. 2001. Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51: 933–938. DOI: 10.1641/0006-3568(2001)051(0933:TEOTWA]2.0.CO;2.

Olson ME. 2012. Linear trends in botanical systematics and the major trends of xylem evolution. Bot. Rev. 78: 154–183. DOI: 10.1007/s12229-012-9097-0.

Olson ME, Anfodillo T, Rosell JA, Petit G, Crivellaro A, Isnard S, León-Gómez C, Alvarado-Cárdenas LO, Castorena M. 2014. Universal hydraulics of the flowering plants: vessel diameter scales with stem length across angiosperm lineages, habits and climates. Ecology Letters 17: 988–997. DOI: 10.1111.ele.12302.

Page VM. 1980. Dicotyledonous wood from the Upper Cretaceous of central California. II. J. Arnold Arbor. 61: 723–748. https://www.jstor.org/stable/43782080.

Page VM. 1981. Dicotyledonous wood from the Upper Cretaceous of central California. III. Conclusions. J. Arnold Arbor. 62: 437–455. https://www.jstor.org/stable/43782095.

Philippe M, Gomez B, Girard V, Coiffard C, Daviero-Gomez V, Thévenard F, Billon-Bruyat J-P, Guiomar M, Latil J-L, Le Loeuff J, Néraudeau D, Olivero D, Schlogl J. 2008. Woody or not woody? Evidence for early angiosperm habit from the Early Cretaceous fossil wood record of Europe. Palaeoworld 17: 142–152. DOI: 10.1016/j.palwor.2008.06.001.

Pratt RB, Jacobsen AL. 2017. Conflicting demands on angiosperm xylem: Tradeoffs among storage, transport and biomechanics. Plant Cell Environ. 40: 897–913. DOI: 10.1111/pce.12862.

Prothero DR. 1994. The Eocene–Oligocene transition: Paradise lost. Columbia University Press, New York. https://doi.org/10.1017/S0016756800009183.

Raup DM. 1991. The future of analytical paleobiology. In: Gilinsky NL, Signor RW (eds.), Analytical paleobiology. Short courses in paleontology, No. 4: 207–214 (1996). Paleontological Society, University of Tennessee, Knoxville.

Rossell JA, Olson ME, Anfodillo T. 2017. Scaling of xylem vessel diameter with plant size: causes, predictions, and outstanding questions. Curr. For. Reports 3: 46–59. DOI: 10.1007/s40725-017-0049-0/.

Sauquet H, Magallón S. 2018. Key questions and challenges in angiosperm macroevolution. New Phytologist 219: 1170–1187. DOI: 10.1111/nph.15104.

Schweingruber FH. 1990. Anatomy of European woods. Verlag Paul Haupt, Publishers, Bern, Stuttgart.

Scotese CR. 2003. Paleomap Project. http://www.scotese.com.

Serlin BS. 1982. An early Cretaceous fossil flora from northwest Texas: its composition and implications. Palaeontographica 182B: 52–86.

Smith SY, Manchester SR, Samant B, Mohabey DM, Wheeler EA, Baas P, Kapgate D, Srivastava R, Sheldon N. 2015. Integrating paleobotanical, paleosol, and stratigraphic data to study critical transitions: A case study from the Late Cretaceous-Paleocene of India. In: Polly PD, Head JJ, Fox DL (eds.), Earth-Life transitions: Paleobiology in the context of earth system evolution. Paleontological Society Papers 21: 137–166. Yale Press, New Haven, CT.

Sperry JS, Hacke UG, Feild TS, Sano Y, Sikkema EH. 2007. Hydraulic consequences of vessel evolution. Int. J. Plant Sci. 168: 1127–1139. DOI: 10.1086/520726.

Sperry JS, Meinzer FC, McCulloh KA. 2008. Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. Plant Cell Environ. 31: 632–645. DOI: 10.1111/j.1365-3040.2007.01765.x.

Spicer, R. 2016. Variation in angiosperm wood structure and its physiological and evolutionary significance. In: Groover AT, Cronk QCB (eds.), Comparative and evolutionary genomics of angiosperm trees. Plant Genetics and Genomics: Crops and Models Vol. 21: 19–60. Springer. DOI: 10.1007/978-3-319-49329-9.

Steel RGD, Torrie JH. 1980. Principles and procedures of statistics. A biometrical approach, Ed. 2. McGraw-Hill, New York.

Takahashi K, Suzuki M. 2003. Dicotyledonous fossil wood flora and early evolution of wood characters in the Cretaceous of Hokkaido, Japan. IAWA J. 24: 269–309. DOI: 10.1163/22941932-90001597.

Tecklin D, DellaSala DA, Luebert F, Pliscoff P. 2011. Valdivian temperate rainforests of Chile and Argentina. In: DellaSala DA (ed.), Temperate and boreal rainforests of the world: ecology and conservation. Chapter 5: 121–153. Island Press.

Thayn GF, Tidwell WD, Stokes WL. 1983. Flora of the Lower Cretaceous Cedar Mountain Formation of Utah and Colorado. Part I. *Paraphyllanthoxylon utahense*. Great Basin Naturalist 43: 394–402. https://scholarsarchive.byu.edu/gbn/vol43/iss3/3.

Thayn GF, Tidwell WD, & Stokes WL. 1985. Flora of the Lower Cretaceous Cedar Mountain Formation of Utah and Colorado. Part III. *Icacinoxylon pittiense* n. sp. Amer. J. Bot. 72: 175–180. DOI: 10.1002/j.1537-2197.1985.tb08281.x.

Tyree MT, Zimmermann MH. 2002. Xylem structure and the ascent of sap. Springer Series in Wood Science. Springer, Berlin, Heidelberg. DOI: 10.1007/978-3-662-04931-0.

Upchurch GR, Kiehl JT, Shields CA, Scherer J, Scotese C. 2015. Latitudinal temperature gradients and high-latitude temperatures during the latest Cretaceous: Congruence of geologic data and climate models. Geology 43: 683–686. DOI: 10.1130/G36802.1.

Upchurch GR, Lomax BH, Beerling DJ. 2007. Paleobotanical evidence of climatic change across the Cretaceous-Tertiary boundary, North America: Twenty years after Wolfe and Upchurch. Cour. Forsch.-Inst. Senckenberg 258: 57–74.

Upchurch GR, Wolfe JA. 1987. Mid-Cretaceous to Early Tertiary vegetation and climate: Evidence from fossil leaves and woods. In: Friis EM, Chaloner WG, Crane PR (eds.), The origins of angiosperms and their evolutionary consequences: 75–105. Cambridge University Press, Cambridge.

Van der Graaff NA, Baas P. 1974. Wood anatomical variation in relation to latitude and altitude. Blumea 22: 101–121.

Wheeler EA. 2011. InsideWood - A web resource for hardwood anatomy. IAWA J. 32: 199–211. DOI: 10.1163/22941932-90000051.

Wheeler EA, Baas P. 1991. A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. IAWA Bull. n.s. 12: 272–332. DOI: 10.1163/22941932-90001256.

Wheeler EA, Baas P. 1993. The potentials and limitations of dicotyledonous wood anatomy for climatic reconstructions. Paleobiology 19: 487–498. DOI: 10.1017/S00948373000 1410X.

Wheeler EA, Baas P, Rodgers S. 2007. Variations in dicot wood anatomy: A global analysis based on the InsideWood database. IAWA J. 28: 229–258. DOI: 10.1163/22941932-90001638.

Wheeler EA, Lehman TM. 2009. New Late Cretaceous and Paleocene dicot woods of Big Bend National Park, Texas and review of Cretaceous wood characteristics. IAWA J. 30: 293–318. DOI: 10.1163/22941932-90000220.

Wheeler EA, Srivastava R, Manchester SR, Baas P. 2017. Surprisingly modern. Latest Cretaceous–earliest Paleocene woods of India. IAWA J. 38: 456–542. DOI: 10.1163/22941932-20170174.

Wiemann MC, Dilcher DL, Manchester SR. 2001. Estimation of mean annual temperature from leaf and wood physiognomy. Forest Science 47: 141–149. DOI: 10.1093/forestscience/47.2.141.

Wilf P, Escapa IH. 2015. Green Web or megabiased clock? Plant fossils from Gondwanan Patagonia speak on evolutionary radiations. New Phytologist 207: 283–290. DOI: 10.1111.nph.13114.

Wilf P, Escapa IH. 2016. Molecular dates require geologic testing. New Phytologist 209: 1359–1362. DOI: 10.1111/nph.13831.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to Present. Science 292 (5517): 686–693. DOI: 10.1126/science.1059412.

Zanazzi A, Kohn MJ, MacFadden BJ, Terry DO. 2007. Large temperature drop across the Eocene-Oligocene transition in central North America. Nature 445: 639–642. DOI: 10.1038/nature05551.

Zanne AE, Pearse WD, Cornwell WK, McGlinn DJ, Wright IJ, Uyeda JC. 2018. Functional biogeography of angiosperms: life at the extremes. New Phytologist 218: 1697–1709. DOI: 10.1111/nph.15114.

Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SE, Coomes DA. 2010. Angiosperm wood structure: global patterns in vessel anatomy and their relationship to wood density and potential conductivity. Amer. J. Bot. 97: 207–215. DOI: 10.3732/ajb.0900178.

Zimmermann MH. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.

Edited by Lisa Boucher

Supplement (Tables S1–S8)

Table S1. Incidence (%) of perforation plate types and scalariform-opposite intervessel pits.

	Perforation plates			Intervessel pits	
	All Scal	Simp & Scal	All Simp		Scal / Opp
Recent Temp NH, n = 827	22	12	66	Recent Temp NH, n = 816	17
1991, n = 677	*20*	*3*	*74*	*1991, n = 677*	*17*
Recent -Trop, n = 4881	9	3	88	Recent -Trop, n = 5048	8
Pliocene Temp NH, n = 64	14	6	80	Pliocene Temp NH, n = 64	11
1991, n = 54	*17*	*7*	*76*	*1991, n = 54*	*16*
Pliocene Trop, n = 182	1	1	98	Pliocene Trop , n = 169	2
Miocene Temp NH, n = 334	19	9	72	Miocene Temp NH, n = 296	18
1991, n = 206	*18*	*19*	*72*	*1991, n = 214*	*21*
Miocene Trop, n = 354	2	1	97	Miocene Trop, n = 321	1
Oligocene Temp NH, n = 152	19	6	75	Oligocene Temp NH, n = 132	14
1991, n = 165	*16*	*4*	*75*	*1991, n = 153*	*19*
Oligocene Trop, n = 19	0	5	95	Oligocene Trop, n = 17	1
Eocene Temp NH, n = 279	27	7	66	Eocene Temp NH, n = 262	26
1991, n = 130	*23*	*8*	*69*	*1991, n = 150*	*32*
Eocene Trop, n = 38	5	0	95	Eocene Trop, n = 37	0
Paleocene Temp NH, n = 57	41	8	51	Paleocene Temp NH, n = 50	42
1991, n = 14	*29*	*7*	*64*	*1991, n = 14*	*29*
Paleocene Trop, n = 13	7,7	0	92	Paleocene Trop, n = 12	4
Deccan, n = 87	4	0	96	Deccan, n = 87	7
Cretaceous Temp NH, n = 167	56	7	37	Cretaceous Temp NH, n = 154	44
1991, n = 71	*54*	*3*	*44*	*1991, n = 73*	*56*
Cretaceous Trop, n = 41	10	2	88	Cretaceous Trop, n = 39	8

Table S2. Incidences (%) vessel element lengths > 800 µm, exclusively solitary vessels.

Vessel element lengths > 800 µm		**Exclusivly solitary vessels**		**Exclusively solitary vessels > 100 µm**	
Recent Temp NH, n = 699	18	Recent Temp NH, n = 850	19	Recent Temp NH, n = 831	10
1991 World	*25**	*1991, n = 677*	*16*	*1991, not done*	
Recent -Trop, n = 5123	25	Recent -Trop, n = 5123	15	Recent Trop, n = 5048	3
Pliocene Temp NH, n = 24	8	Pliocene Temp NH, n = 70	27	Pliocene Temp NH, n = 70	2
1991, n = 31	*3*	*1991 n =71*	*21*	*1991, not done*	
Pliocene Trop, n = 139	2	Pliocene Trop, n = 186	7	Pliocene Trop, n =186	4
Miocene Temp NH, n = 208	6	Miocene Temp NH, n = 334	23	Miocene Temp NH, n = 334	4
1991, n = 160	*4*	*1991, n = 214*	*17*	*1991, not done*	
Miocene Trop, n = 242	5	Miocene Trop, n = 368	13	Miocene Trop, n = 368	8
Oligocene Temp NH, n = 97	6	Oligocene Temp NH, n = 147	20	Oligocene Temp NH, n = 147	10
1991, n = 94	*4*	*1991, n = 168*	*15*	*1991, not done*	
Oligocene Trop, n = 17	0	Oligocene Trop, n = 20	10	Oligocene Trop, n = 20	0
Eocene Temp NH, n = 205	15	Eocene Temp NH, n = 287	23	Eocene Temp NH, n = 287	5
1991, n = 126	*10*	*1991, n = 138*	*16*	*1991, not done*	
Eocene Trop, n = 35	0	Eocene Trop, n = 38	18	Eocene Trop, n = 38	8
Paleocene Temp NH, n = 33	24	Paleocene Temp NH, n = 59	36	Paleocene Temp NH, n = 59	3
1991, n = 14	*18*	*1991, n = 14*	*14*	*1991, not done*	
Paleocene Trop, n = 11	9	Paleocene Trop, n = 13	8	Paleocene Trop, n = 13	0
Deccan, n = 73	3	Deccan, n = 86	7	Deccan, n = 82	7
Cretaceous Temp NH, n = 131	37	Cretaceous Temp NH, n = 169	45	Cretaceous Temp NH, n = 169	8
1991, n = 66	*27*	*1991, n = 69*	*33*	*1991, not done*	
Cretaceous Trop, n = 31	10	Cretaceous Trop, n = 41	10	Cretaceous Trop, n = 41	7

* Data from Metcalfe & Chalk (1950).

Table S3. Porosity type %.

Ring porous	RP	Semi-ring porous	SRP	Diffuse porous	DP
Recent Temp NH, n = 850 *	27	Recent Temp NH, n = 850	14	Recent Temp NH, n = 850	65
1991, n = 677	*24*	*1991, n = 677*	*21*	*1991, n = 677*	*55*
Recent Trop, n = 5123	1	Recent -Trop, n = 5123	2	Recent -Trop, n = 5123	97
Pliocene Temp NH, n = 64	34	Pliocene Temp NH, n = 64	9	Pliocene Temp NH, n = 64	57
1991, n = 73	*29*	*1991, n = 73*	*8*	*1991, n = 73*	*64*
Pliocene Trop, n = 186	< 1	Pliocene Trop , n = 186	4	Pliocene Trop , n = 186	96
Miocene Temp NH, n = 334	22	Miocene Temp NH, n = 334	13	Miocene Temp NH, n = 334	65
1991, n = 238	*17*	*1991, n = 238*	*13*	*1991, n = 238*	*71*
Miocene Trop, n = 368	< 1	Miocene Trop, n = 368	3	Miocene Trop, n = 368	97
Oligocene Temp NH, n = 147	8	Oligocene Temp NH, n = 147	8	Oligocene Temp NH, n = 147	84
1991, n = 182	*9*	*1991, n = 182*	*6*	*1991, n = 182*	*85*
Oligocene Trop, n = 20	0	Oligocene Trop, n = 20	9	Oligocene Trop, n = 20	91
Eocene Temp NH, n = 287	5	Eocene Temp NH, n = 287	13	Eocene Temp NH, n = 287	82
1991, n = 148	*3*	*1991, n = 148*	*10*	*1991, n = 148*	*86*
Eocene Trop, n = 38	0	Eocene Trop, n = 38	16	Eocene Trop, n = 38	84
Paleocene Temp NH, n = 59	0	Paleocene Temp NH, n = 59	8	Paleocene Temp NH, n = 59	92
1991, n = 15	*0*	*1991, n = 15*	*7*	*1991, n = 15*	*93*
Paleocene Trop, n = 13	0	Paleocene Trop, n = 13	0	Paleocene Trop, n = 13	100
Deccan, n = 86	0	Deccan, n = 86	1	Deccan, n = 86	99
Cretaceous Temp NH, n = 169	1	Cretaceous Temp NH, n = 169	1	Cretaceous Temp NH, n = 169	98
1991, n = 71	*0*	*1991, n = 69*	*1*	*1991, n = 69*	*99*
Cretaceous Trop, n = 41	0	Cretaceous Trop, n = 41	2	Cretaceous Trop, n = 41	98

* For Recent, total % > 100 % because some species have more than one porosity type.

Table S4. Mean vessel tangential diameters %.

Trees only. Excludes vines and species that are shrubs only

MTDs < 100 µm		**Diffuse porous & MTD > 200 µm**		**All records MTD > 200 µm**	
Recent Temp NH, n = 831	47	Recent Temp NH, n = 533	< 1	Recent Temp NH, n = 831	16
1991, n = 677	*62*	*1991, not done*	*n/a*	*1991, n = 677*	*1*
Recent Trop, n = 5048	44	Recent Trop, n = 5048	13	Recent Trop, n = 5048	13
Pliocene Temp NH, n = 61	33	Pliocene Temp NH, n = 30	3	Pliocene Temp NH, n = 61	21
1991, n = 58	*34*	*1991, not done*	*n/a*	*1991, n = 58*	*19*
Pliocene Trop, n = 144	25	Pliocene Trop, n = 137	23	Pliocene Trop, n = 144	24
Miocene Temp NH, n = 320	40	Miocene Temp NH, n = 196	5	Miocene Temp NH, n = 320	23
1991, n = 223	*36*	*1991, not done*	*n/a*	*1991, n = 238*	*17*
Miocene Trop, n = 287	19	Miocene Trop, n = 279	19	Miocene Trop, n = 287	20
Oligocene Temp NH, n = 137	37	Oligocene Temp NH, n = 113	11	Oligocene Temp NH, n = 137	16
1991, n = 182	*32*	*1991, not done*	*n/a*	*1991, n = 182*	*15*
Oligocene Trop, n = 20	5	Oligocene Trop, n = 18	16	Oligocene Trop, n = 20	16
Eocene Temp NH, n = 284	53	Eocene Temp NH, n = 200	5	Eocene Temp NH, n = 284	8
1991, n = 149	*38*	*1991, not done*	*n/a*	*1991, n = 149*	*9*
Eocene Trop, n = 38	16	Eocene Trop, n = 32	13	Eocene Trop, n = 38	13
Paleocene Temp NH, n = 58	41	Paleocene Temp NH, n = 50	5	Paleocene Temp NH, n = 58	7
1991, n = 15	*21*	*1991, not done*		*1991, n = 15*	*7*
Paleocene Trop, n = 12	50	Paleocene Trop, n = 12	8	Paleocene Trop, n = 12	8
Deccan, n = 84	43	Deccan, n = 83	5	Deccan, n = 84	5
Cretaceous Temp NH, n = 109	67	Cretaceous Temp NH, n =105	2	Cretaceous Temp NH, n = 109	5
1991, n = 72	*61*	*1991, not done*		*1991, n = 72*	*3*
Cretaceous Trop, n = 37	43	Cretaceous Trop, n = 36	3	Cretaceous Trop, n = 37	5

Table S5. Helical thickenings, septate fibers, rare axial parenchyma.

Helical thickenings %		Septate fibers		Rare axial parenchhyma %	
Recent Temp NH, n = 797	42	Recent Temp NH, n = 849	9	Recent Temp NH, n = 850	17
1991, n = 677	*45*	*1991, n = 677*	*10*	*1991, n = 677*	*10*
Recent -Trop, n = 5122	2	Recent -Trop, n = 5114	28	Recent -Trop, n = 5213	14
Pliocene Temp NH, n = 37	13	Pliocene Temp NH, n = 54	7	Pliocene Temp NH, n = 70	6
1991, n = 70	*17*	*1991, n = 50*	*8*	*1991, n = 59*	*7*
Pliocene Trop, n = 183	0,5	Pliocene Trop, n = 172	28	Pliocene Trop, n = 169	3
Miocene Temp NH, n = 314	24	Miocene Temp NH, n = 294	11	Miocene Temp NH, n = 334	6
1991, n = 215	*20*	*1991, n = 194*	*15*	*1991, n = 219*	*5*
Miocene Trop, n = 363	0,3	Miocene Trop, n = 345	27	Miocene Trop, n = 364	4
Oligocene Temp NH, n = 139	16	Oligocene Temp NH, n = 130	15	Oligocene Temp NH, n = 147	3
1991, n = 143	*12*	*1991, n = 135*	*15*	*1991, n = 167*	*4*
Oligocene Trop, n = 19	0	Oligocene Trop, n = 17	30	Oligocene Trop, n = 18	0
Eocene Temp NH, n = 281	9	Eocene Temp NH, n = 262	19	Eocene Temp NH, n = 287	17
1991, n = 143	*6*	*1991, n = 129*	*18*	*1991, n = 139*	*5*
Eocene Trop, n = 38	0	Eocene Trop, n = 38	34	Eocene Trop, n = 38	13
Paleocene Temp NH, n = 59	5	Paleocene Temp NH, n = 58	21	Paleocene Temp NH, n = 59	19
1991, n = 15	*0*	*1991, n = 14*	*36*	*1991, n = 15*	*20*
Paleocene Trop, n = 13	0	Paleocene Trop, n = 12	39	Paleocene Trop, n = 12	15
Deccan, n = 89	1	Deccan, n = 87	35	Deccan, n = 86	22
Cretaceous Temp NH, n = 167	2	Cretaceous Temp NH, n = 138	33	Cretaceous Temp NH, n = 169	18
1991, n = 70	*0*	*1991, n = 46*	*37*	*1991, n = 70*	*6*
Cretaceous Trop, n = 41	0	Cretaceous Trop, n = 36	58	Cretaceous Trop, n = 41	17

Table S6. Axial parenchyma: diffuse and diffuse-in-aggregates only, aliform-confluent, marginal.

Diffuse and Diffuse-in-aggregates only %		**Aliform / Confluent %**		**Marginal %**	
Recent Temp NH, n = 850	20	Recent Temp NH, n = 849	11	Recent Temp NH, n = 850	28
1991, n = 677	*22*	*1991, n = 677*	*11*	*1991, n = 677*	*21*
Recent -Trop, n = 5123	11	Recent -Trop, n = 5123	30	Recent -Trop, n = 5213	15
Pliocene Temp NH, n = 70	14	Pliocene Temp NH, n = 70	22	Pliocene Temp NH, n = 70	17
1991, n = 50	*17*	*1991, n = 50*	*21*	*1991, n = 59*	*15*
Pliocene Trop, n = 183	4	Pliocene Trop, n = 185	47	Pliocene Trop, n = 169	25
Miocene Temp NH, n = 334	10	Miocene Temp NH, n = 311	19	Miocene Temp NH, n = 334	21
1991, n = 194	*21*	*1991, n = 194*	*19*	*1991, n = 219*	*24*
Miocene Trop, n = 364	5	Miocene Trop, n = 360	46	Miocene Trop, n = 364	24
Oligocene Temp NH, n = 147	10	Oligocene Temp NH, n = 142	23	Oligocene Temp NH, n = 147	20
1991, n = 135	*24*	*1991, n = 135*	*22*	*1991, n = 167*	*19*
Oligocene Trop, n = 18	17	Oligocene Trop, n = 17	55	Oligocene Trop, n = 19	44
Eocene Temp NH, n = 287	16	Eocene Temp NH, n = 284	19	Eocene Temp NH, n = 287	13
1991, n = 129	*24*	*1991, n = 129*	*19*	*1991, n = 139*	*18*
Eocene Trop, n = 38	0	Eocene Trop, n = 38	40	Eocene Trop, n = 38	24
Paleocene Temp NH, n = 59	37	Paleocene Temp NH, n = 58	3	Paleocene Temp NH, n = 59	2
1991, n = 14	*21*	*1991, n = 14*	*7*	*1991, n = 15*	*0*
Paleocene Trop, n = 13	0	Paleocene Trop, n = 13	39	Paleocene Trop, n = 13	15
Deccan, n = 86	6	Deccan, n = 88	24	Deccan, n = 86	10
Cretaceous Temp NH, n = 169	38	Cretaceous Temp NH, n = 136	1	Cretaceous Temp NH, n = 169	1
1991, n = 46	*54*	*1991, n = 46*	*6*	*1991, n = 70*	*0*
Cretaceous Trop, n = 41	10	Cretaceous Trop, n = 41	12	Cretaceous Trop, n = 41	0

Table S7. Ray cellular composition %.

Homocellular only		Homocellular & Heterocellular		Heterocellular only	
Recent Temp NH, n = 790	28	Recent Temp NH, n = 790	23	Recent Temp NH, n = 790	49
1991, n = 677	*23*	*1991, n = 677*	*9*	*1991, n = 677*	*68*
Recent -Trop, n = 4950	15	Recent -Trop, n = 5123	13	Recent -Trop, n = 5213	72
Pliocene Temp NH, n = 35	51	Pliocene Temp NH, n = 35	23	Pliocene Temp NH, n = 35	29
1991, n = 52	*55*	*1991, n = 52*	*14*	*1991, n = 52*	*31*
Pliocene Trop, n = 185	28	Pliocene Trop, n = 185	24	Pliocene Trop, n = 185	49
Miocene Temp NH, n = 328	40	Miocene Temp NH, n = 328	10	Miocene Temp NH, n = 328	49
1991, n = 204	*41*	*1991, n = 204*	*5*	*1991, n = 204*	*54*
Miocene Trop, n = 365	30	Miocene Trop, n = 365	16	Miocene Trop, n = 365	54
Oligocene Temp NH, n = 146	34	Oligocene Temp NH, n = 146	19	Oligocene Temp NH, n = 146	46
1991, n = 153	*37*	*1991, n = 153*	*3*	*1991, n = 153*	*60*
Oligocene Trop, n = 21	38	Oligocene Trop, n = 17	10	Oligocene Trop, n = 20	52
Eocene Temp NH, n = 277	15	Eocene Temp NH, n = 277	12	Eocene Temp NH, n = 277	73
1991, n = 135	*21*	*1991, n = 129*	*9*	*1991, n = 139*	*70*
Eocene Trop, n = 38	21	Eocene Trop, n = 38	13	Eocene Trop, n = 38	66
Paleocene Temp NH, n = 58	3	Paleocene Temp NH, n = 58	12	Paleocene Temp NH, n = 59	85
1991, n = 15	*7*	*1991, n = 15*	*13*	*1991, n = 15*	*80*
Paleocene Trop, n = 13	23	Paleocene Trop, n = 13	15	Paleocene Trop, n = 13	62
Deccan, n = 86	12	Deccan, n = 86	20	Deccan, n = 86	68
Cretaceous Temp NH, n = 161	4	Cretaceous Temp NH, n = 161	10	Cretaceous Temp NH, n = 161	86
1991, n = 66	*3*	*1991, n = 66*	*5*	*1991, n = 66*	*92*
Cretaceous Trop, n = 41	17	Cretaceous Trop, n = 41	20	Cretaceous Trop, n = 41	63

Table S8. Storied structure %.

	Temp NH		Tropical
Recent Temp NH, n = 797	7	Recent TRop, n = 5123	12
1991, n = 677	*12*		
Pliocene Temp NH, n = 59	10	Pliocene Trop, n = 186	19
1991, n = 66	*9*		
Miocene Temp NH, n = 314	9	Miocene Trop, n = 363	15
1991, n = 226	*5*		
Oligocene Temp NH, n = 142	12	Oligocene Trop, n = 18	17
1991, n = 158	*4*		
Eocene Temp NH, n = 287	6	Eocene Trop, n = 38	16
1991, n = 141	*3*		
Paleocene Temp NH, n = 59	2	Paleocene Trop, n = 13	8
1991, n = 14	*0*		
		Deccan, n = 89	6
Cretaceous Temp NH, n = 160	0,6	Cretaceous Trop, n = 41	12
1991, n = 72	*0*		