

## A SURVEY OF THE FOSSIL RECORD FOR DICOTYLEDONOUS WOOD AND ITS SIGNIFICANCE FOR EVOLUTIONARY AND ECOLOGICAL WOOD ANATOMY

by

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### Summary

Data on fossil dicotyledonous wood were assembled in order to 1) test the Baileyan model for trends of specialisation in dicotyledonous wood anatomy by addressing the question – were ‘primitive’ wood anatomical features (as defined by the Baileyan model) more common in the geologic past than at present?, 2) infer, on a broad geographic scale, past climatic regimes, and long term climatic change, and 3) assess the extent of knowledge of fossil dicotyledonous woods. The resulting database has information on 91 anatomical features for over 1200 fossil dicotyledonous woods. The incidence of selected anatomical features was plotted through time (by geologic epoch) for the world and for two regional groupings (roughly corresponding to the Laurasian and Gondwanan supercontinents). For comparison to the fossil wood record, the incidence of wood anatomical features in the Recent flora was obtained from the 5260 record OPCN database for extant dicotyledonous woods.

The fossil record supports the Baileyan model for xylem evolution, as the incidence of ‘primitive’ features (e.g., scalariform perforation plates) is much higher in the Cretaceous than in the Tertiary, while the incidence of ‘advanced’ features (e.g., short vessel elements and simple perforation plates) is lower. From the Cretaceous to the Tertiary, there are pronounced changes in the incidence of features believed associated with conductive efficiency. The tempo and timing of changes in ray composition, storied structure,

and elaborate axial parenchyma distribution patterns are different from those for tracheary elements as the former increase gradually throughout the Tertiary. Incidences of features, such as ring porosity and elaborate vessel groupings, that are associated with markedly seasonal climates in the Recent flora do not approach modern levels until the Neogene. Correlations of wood anatomical features with ecology do not appear to have been constant throughout time, as in the Cretaceous different features provide conflicting interpretations of the climate. Throughout the Tertiary, there are differences between the ‘Laurasian’ and ‘Gondwanan’ regions in the incidences of wood anatomical features, and these differences are consistent with well-established ecological trends in wood anatomy in the extant flora; during the Miocene and Pliocene, wood anatomical characteristics of these two regions are nearly identical to those of the present-day. The Late Tertiary increase in seasonality of the Northern Hemisphere is recorded in the fossil wood record. Our review of the literature indicates there is a considerable need for more information on well-dated woods, particularly for woods of Paleocene age (less than 40 known world-wide), and from continuous sequences across the Cretaceous-Tertiary boundary, and the mid-Eocene to Oligocene, both times critical in the development of modern vegetation.

*Key words:* Dicotyledons, wood anatomy, fossil wood, ecological wood anatomy, paleobotany.

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## Introduction

In this paper data from the fossil record for dicotyledonous wood are used to 1) test the Baileyan model for trends of specialisation in dicotyledonous wood anatomy by addressing the question – are ‘primitive’ wood anatomical features (as defined by the Baileyan model) more common in the past than at present?, 2) infer, on a broad geographic scale, past climatic regimes, and long term climatic change, and 3) assess the extent of information available and identify some of the areas needing additional work.

Before an analysis of the data, we present as background summaries of the Baileyan trends and current concepts of ecological wood anatomy, comment on the characteristics of the fossil record for dicotyledonous wood, and outline how we prepared this database for fossil dicotyledonous wood.

### *The Baileyan trends*

The Baileyan trends of specialisation in dicotyledonous wood, as established by Bailey and Tupper (1918) and expanded and elaborated in later papers (e.g., Frost 1930a, 1930b, 1931; Kribs 1935, 1937; Tippe 1938), are based on continuous morphological series in extant plants, and were established independent of any system of angiosperm classification. These series were polarised on the basis of evidence from the fossil record that all putative ancestors of the angiosperms had vesselless xylem with long tracheids. The Baileyan trends were long considered to represent unidirectional, irreversible evolutionary specialisation, leading to a division of labour for water conduction (simply perforated vessel elements) and support (fibres with minutely bordered to simple pits). Presumed specialisations in ray composition (from heterocellular to homocellular) and parenchyma distribution (from diffuse apotracheal to predominantly paratracheal or banded) were based solely on correlations with the more ‘firmly’ established evolutionary trends in tracheary elements (see Carlquist 1975, 1988; Baas 1986; Dickison 1975, 1989; Stern 1978 for summaries of the Baileyan trends).

Although great antiquity is not proof of a feature’s ancestral nature, tracing the incidence of wood features through time provides cir-

cumstantial evidence on the validity of the Baileyan trends. Data from the fossil record provide an estimate of the timing of innovations of different features and feature combinations. Also, such data allow comparison of the timing and tempo of changes in incidences of different features, i.e., do features significant for water conduction change at the same time and rate as do features significant for storage and mobilisation of photosynthates?

### *Ecological inferences*

One of the primary functions of wood is water conduction, therefore, changes in climate that affect water availability may be reflected in wood structure. Growth ring characteristics (distinctiveness, ring width, amount of latewood) have been used to infer seasonality and length of growing season, particularly of high latitude coniferous fossil forests (Creber & Chaloner 1985; Francis 1986; Spicer & Parrish 1990). But as Collinson (1990) remarked, the potential of wood anatomical characteristics for helping in past climatic reconstructions has not been fully realised.

By tracing the incidence of particular wood anatomical features through time, we can determine whether the incidences of wood anatomical features considered adaptations to water stress increase when seasonal climates develop, and whether the timing of changes in wood anatomical features coincide with changes in leaf physiognomy (particularly at the Cretaceous-Tertiary boundary, and at the end of the Eocene).

Carlquist (e.g., 1975, 1988) and Baas (e.g., 1986) provided information about the ecological significance of different wood anatomical characters – primarily by using correlation of the incidence of particular features and suites of features with particular environmental and geographic parameters (water availability, altitude, latitude, temperature). Figure 1 summarises ecophyletic trends in dicotyledonous wood structure (adapted from Dickison 1989). It is these trends that we use for our ecological interpretations.

A major concern with ecological interpretations of fossil wood data is whether a ‘uniformitarianism approach’ is valid, in other words, we cannot be sure that correlations

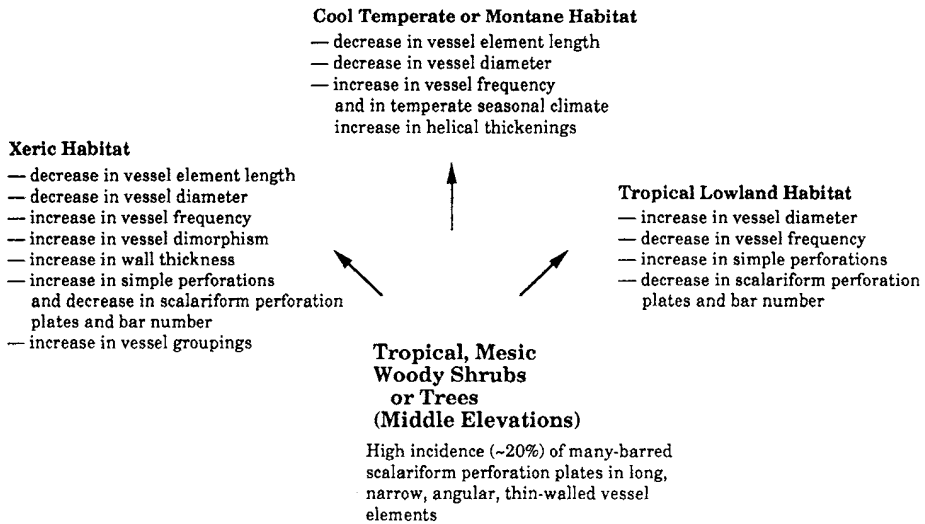


Fig. 1. Major ecophyletic trends of vessel element specialisation (adapted from Dickison 1989).

between the incidence of certain features and ecological factors were the same in the past as they are at present. Therefore, two alternative hypotheses should be considered: 1) correlations of anatomical features with ecology have been constant over time, and so their incidence can be used for inferences about climatic conditions of the past; 2) correlations with climate varied over time, because of constraints imposed by the different specialisation levels at different periods, for instance, some features considered indicators for markedly seasonal climates are also ‘specialised’ features (helical thickenings, ring porosity) and, if such features had not yet evolved, then their absence cannot be used to infer lack of seasonal climates.

**Comments on the fossil record for woods**

Although abundant, fossil wood has been underutilised as a source of information on angiosperm history. Compared to the fossil record for pollen, leaves, fruits, and seeds, there is relatively little information on well-dated fossil woods. The limitations of the fossil record (e.g., differential preservation

of different environments, differential preservation of some taxa, individual differences in definitions of fossil species) have been discussed ably and at length in different papers including those surveying changes in diversity through time (Niklas *et al.* 1980), extinction rates (Boulter *et al.* 1988) and the Tertiary history of the angiosperms (Collinson 1990; Wing 1988). All of these limitations apply to wood as much if not more so (Page 1979, 1981).

Major problems with fossil woods can be 1) poor preservation so that some diagnostic features cannot be observed (Page 1979), and 2) lack of adequate information on age because often wood is not found in place in source sediments. However, there is an abundant literature on the systematic anatomy of woody dicotyledons (see listings in Gregory 1980). Much of this information is organised into a retrievable form in computerised keys (Ilic 1987; Wheeler *et al.* 1986) and consequently, the initial comparisons of fossil woods to extant woods may be easier than the initial comparisons of fossil leaves with extant leaves.

### *Species definition*

One of the 'problems' with the fossil record that may be more acute for wood than for other plant parts is the parity/comparability of 'fossil species' with one another and with 'extant species'. Most, not just many, species of fossil wood are based on but a single sample. There are relatively few species defined on the basis of multiple samples, and those samples may or may not represent fragments from a single tree. Consequently, there is not a good understanding of variability within different 'species'.

Individual species of extant plants generally are not distinguishable by their wood structure; in some families (e.g., Annonaceae) it is impossible to distinguish different genera, while in others (e.g., Ulmaceae) it is possible. Thus, a 'species' of Annonaceae wood would not be comparable to a 'species' of Ulmaceae wood. Some families have many recognisable 'wood genera and species' while others have few.

We can only hope, and are assuming, that the difficulties in defining a fossil wood species are more or less similar throughout time.

### *Previous surveys*

Chalk (1937) compared the incidence of specialised and unspecialised features in fossil and extant genera and species. He 'lumped' together all fossil woods of different ages, and made but one comparison: fossil with modern. In 49 fossil wood genera, the percent occurrence of scalariform perforation plates was higher in fossil woods (35%) than in extant genera (11%), and the percent occurrence of storied structure lower (14%) than in extant wood genera (18%).

Bande and Prakash (1984) looked at the distribution of types of perforation plates, inclination of the vessel end wall, intervessel pit arrangement, axial parenchyma arrangement, and Kribs ray types in woods from six different Tertiary beds in India (134 species). They found that the incidence of 'advanced' parenchyma arrangements and ray type increased from the early to the late Tertiary.

### *Characteristics of the database*

Our database has over 1200 records and includes woods whose systematic affinities

are unknown. This database is a much larger compilation of information on the anatomical structure of fossil dicotyledonous woods than was previously available. Its preparation benefitted greatly from the cooperation and generous contributions of many colleagues (see Acknowledgements). Although not all inclusive, we believe it contains information on most (at least 80%, probably more) of the reasonably well-dated and reasonably well-described fossil dicotyledonous woods.

Information on the age and geographic source, and selected (91) anatomical features were recorded on a datasheet and subsequently computerised. The Appendix lists the literature incorporated into the database. More references than are listed in this Appendix were surveyed, but information from them was not used. Much of the older literature on fossil woods was not incorporated because the descriptions and diagnoses were very brief, and often without accompanying illustration which would have permitted reevaluation of the description. Many genera established for fossil wood are not in the database because these genera are based on either poorly preserved, poorly described, or poorly dated material. For instance, Kramer (1974a, 1974b) described many new genera and species of fossil wood from southeast Asia. His diagnoses and descriptions are detailed and well-illustrated and accompanied by careful comparisons to fossil and extant woods with similar anatomy. For that reason his papers are a valuable source of information on the anatomy of fossil woods ascribed to particular genera or families. Unfortunately, the ages of these woods are uncertain, and given as ?Tertiary, ?late Tertiary and so cannot be used in a work attempting to survey changes in wood structure through time. The controversial 'Stopes woods', whose putative middle Cretaceous (Aptian age) has been questioned, also are not included in the database (Stopes 1913, 1915; Page 1979).

Dating of some of the woods in the database is not as reliable as desirable, and some woods with 'probable' age assignments are included. When available, information on whether a wood was early or late Eocene was recorded, but there was a limited number of woods with even that level of dating. Thus,

we are only able to consider long term trends, epoch by epoch – Cretaceous, Paleocene, Eocene, Oligocene, Miocene, Pliocene.

The ages for some woods are given as Miocene-Pliocene (144 woods), for others as Oligocene-Miocene (48 woods) and so the features for, respectively, both Miocene and Pliocene, and Oligocene and Miocene are recorded for these woods.

Some epochs and regions are not well represented in the database. Most of the Cretaceous records are late Cretaceous (Campanian-Maestrichtian); there are very few mid-Cretaceous records. The Paleocene is the least known of the geological epochs with only 37 woods in the database and the age assignment for most of these woods is not definite (Koeniguer 1969, 1971). Consequently, generalisations made for the Paleocene should be considered preliminary at best. For the Oligocene there are very few woods reported for the 'southern' grouping and within the 'northern' grouping there are very few North American woods of this age. There are very few reports of fossil woods from the Southern Hemisphere and most of the woods in our 'southern' grouping are from India.

Many fossil woods are described from the Deccan Intertrappean Series, India. Bande and Prakash's (1984) survey of the Indian fossil wood record confirmed that "the Deccan Intertrappean flora was made up of a number of plant communities of different ages occurring in a wide area of Central India." For this paper we have followed Bande and Prakash's approach and have assigned the woods from the Deccan Traps to the Eocene – which permits comparison of the characteristics of these woods with those from younger Indian beds, e.g., the Cuddalore Series, and the Tipam Sandstones.

Approximately 100 of the 1200 records represent woods whose descriptions are not published; in the computer database, the locality and the investigator are recorded for those woods.

Each published report of a fossil wood species was treated as a different record, and so for some 'species' there is more than one record in the database when a 'species' has been described from more than one locality,

e.g., *Quercoxylon bavaricum* (Selmeier 1971; Privé 1975), *Cassinium borooahii* (Prakash 1973, 1976; Ghosh & Roy 1982), *Plataninum haydenii* (Scott & Wheeler 1982; Wheeler *et al.* 1977).

### Features surveyed

The features used are a subset of the IAWA Standard List of Features Suitable for Hardwood Identification (IAWA Committee 1989). Not all 91 anatomical features on the data-sheet are discussed in this paper, some features were included because they might be useful in identification (e.g., presence of crystals and their location). The database should be useful for future work with fossil wood as it will help with fossil wood identification and the comparison with previously described woods. Work on the database is continuing, with the intention of compiling information so as to update Edwards's (1931) catalogue of fossil woods and to prepare a paper similar to Muller's (1981) by-family evaluation of the fossil pollen record.

Features were scored as to whether they were 1) present, 2) absent, 3) 'variable', either with a tendency to exhibit a particular feature such as radial arrangement of vessels or vessel groups, or variable in occurrence – present in some samples and absent in others (for records based on multiple samples), or variable within the sample (e.g., diffuse-porous in one growth ring, semi-ring-porous in another), or 4) unknown (?) – unable to determine whether a feature was present or absent – either because of poor preservation, or the descriptions and illustrations did not make it possible to determine presence/absence.

Mean vessel diameter, frequency, and vessel element length are recorded in categories (IAWA Committee 1989). Vessel diameter, frequency, and vessel element length are affected by cambial age, i.e., there is variation pith to bark in these features (Panshin & De Zeeuw 1980). In general, vessel diameters are smaller, vessel frequencies higher, and vessel elements shorter in small axes and wood from near the pith than they are in mature bolewood of trees. Thirty-one of the

98 records for the Cretaceous are known to be small axes (Page 1979, 1980, 1981), and so vessel diameter and vessel element length data are presented separately for these woods (labelled K-S). Vessel frequencies were not reported for these small Cretaceous axes. The other 67 Cretaceous woods are a mixture of woods from trees and fragments from axes of unknown size.

#### *Presentation of the data*

The incidence (frequency of occurrence) of features through time is reported as a percentage. The number on which this percentage is based varies through time (obviously because there is a different number of records per geologic epoch) and by feature (because some features are more likely to be either recorded or preserved than others). For example, almost all wood descriptions indicate whether a wood is diffuse-porous or ring-porous because porosity is considered an important diagnostic feature and can be determined even in very poorly preserved woods. In contrast, distinctiveness of fibre pitting cannot be determined in poorly preserved material; vessel-ray pitting type often was not mentioned or illustrated either because of poor preservation or because some individuals did not consider it an important diagnostic character.

The percent incidence of features is presented for the world as a whole (designated 'W' on the graphs and tables), and for two different geographic regions. For practical reasons, we have distinguished only two geographical areas. One is a grouping designated 'N' on the graphs and tables, which is equivalent to Laurasia, including North America, Europe and North and Northeast Asia, and which now includes subtropical, temperate and boreal floras. In the past (particularly the Cretaceous and early Tertiary) this region ('N') was presumably subjected to a much warmer climate with less latitudinal gradient in climate (Wolfe 1978; Upchurch & Wolfe 1987; Collinson 1990). The other is a grouping designated 'S' on the graphs and tables, this category ('S') contains all major tropical regions of the world and the subtropical to temperate regions of New Zealand,

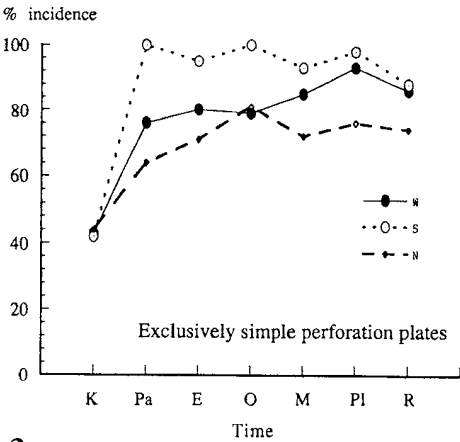
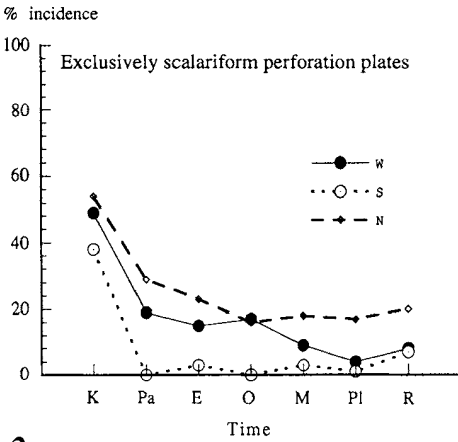
Tasmania, South America (Argentina and Chile p.p.) and South Africa and roughly coincides with the landmasses derived from the Gondwana supercontinent. The bulk of the fossil records for this second region are from areas that have been in tropical latitudes throughout time. For the Oligocene, however, 20 of the 42 records for this 'southern' region are from southern South America and Antarctica, consequently for this epoch, when there are marked differences between the high latitude and tropical regions, on the graphs a data point for the 'tropical region' is given.

Tables 1–21 (pages 302–313) give for each feature the number of entries with information on that feature per time unit and geographic grouping. These numbers are the numbers on which the percentages used in the Results and Discussion section are based.

#### *Comparison with the extant flora*

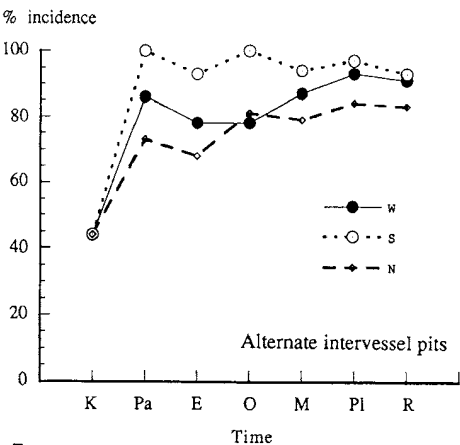
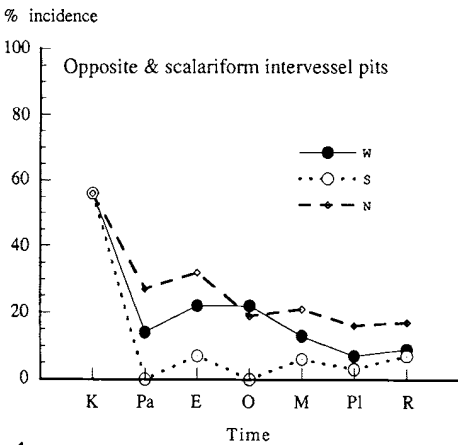
The data from the fossil wood record are compared with the extant flora. Data on the incidence of different characters were obtained from recent literature on ecological trends as based on floristic inventories (Baas 1976, 1982, 1986; Baas & Schweingruber 1987; Baas *et al.* 1983; Carlquist 1975; Carlquist & Hoekman 1985), and the OPCN computer database (Wheeler *et al.* 1986; Wheeler 1991). The OPCN database contains 5260 entries, most based on data Chalk and his co-workers recorded on marginally perforated cards prepared while accumulating information for the first edition of 'Anatomy of the Dicotyledons' (Metcalf & Chalk 1950), plus additional information from the Princes Risborough key (Brazier & Franklin 1961), CTFT (Centre Technique Forestier Tropical – D tienne & Jacquet 1983; Normand & Paquis 1976), IPT (Instituto de Pesquisas Tecnol gicas), and recent literature (as given in Gregory 1980) and original observations.

For a number of features data for the modern flora are not directly comparable with the data for the fossil record. This is due to variations in feature definitions in the wood anatomical literature; these problems will be discussed for individual features.



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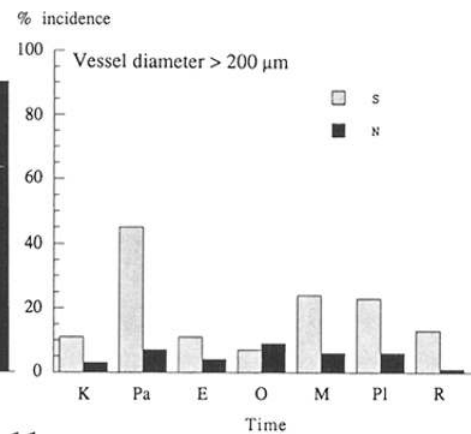
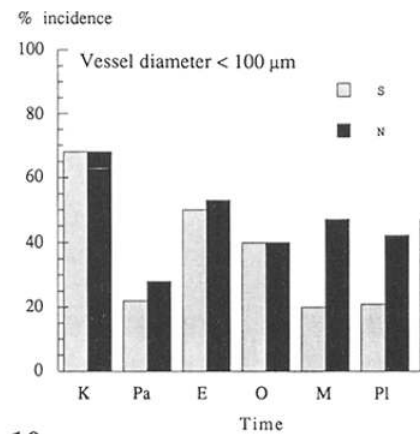
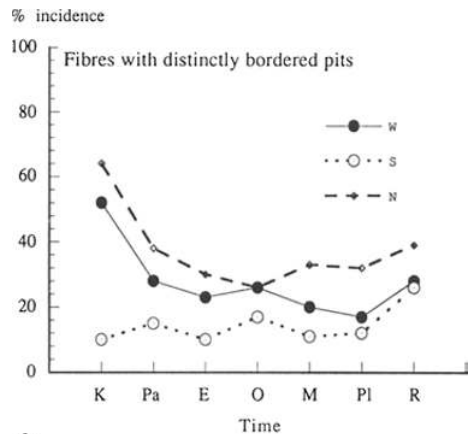
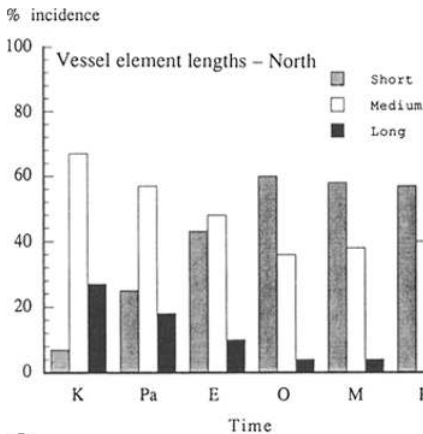
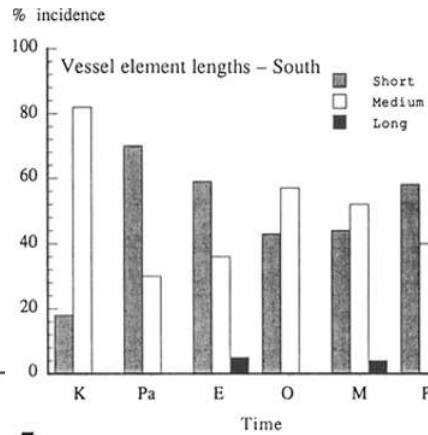
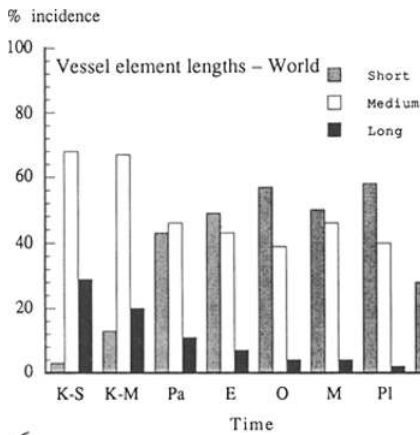
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Figs. 2–5. Incidences of perforation plates and intervessel pit arrangement types through time. – 2: Exclusively scalariform perforation plates. – 3: Exclusively simple perforation plates. – 4: Opposite and scalariform intervessel pits. – 5: Alternate intervessel pits. — K = Cretaceous; Pa = Paleocene\*; E = Eocene; O = Oligocene; M = Miocene; Pl = Pliocene; R = Recent. — W = World; S = ‘Southern’/Gondwanan grouping; N = ‘Northern’/Laurasian grouping. \* Note for Paleocene fewer than 40 records.

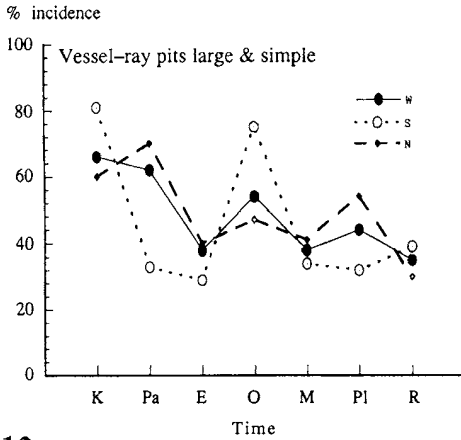
**Results and Discussion**

The results of the survey of incidences of dicotyledonous wood features through time are summarised in Figures 2–35 and Tables 1–21. Some wood anatomical features show either a marked increase (Figs. 3, 5, 15) or decrease (Figs. 2, 4, 9, 14) in incidence from the Cretaceous to the Tertiary, while during

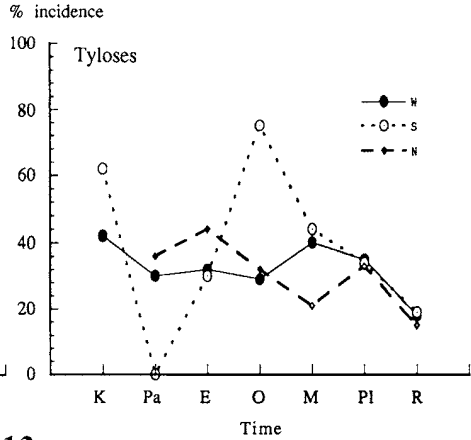
the Tertiary their occurrence fluctuates or changes slightly. A few features (Figs. 21, 22, 23, 24, 35) gradually increase or decrease in incidence throughout geologic time. Often there are marked differences between data for Laurasia (N: today largely temperate to subtropical) and the Tropics and Southern Hemi-







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Figs. 6–8. Vessel element lengths. Short = 350  $\mu\text{m}$  or less; Medium = 350–800  $\mu\text{m}$ ; Long = 800  $\mu\text{m}$  or more. — Fig. 9. Fibres with distinctly bordered pits. — Figs. 10 & 11. Vessel diameter. — 10: Vessel diameter < 100  $\mu\text{m}$ . — 11: Vessel diameter > 200  $\mu\text{m}$ . — Fig. 12. Vessel-ray parenchyma pits. — Fig. 13. Tyloses. — See also legend Figs. 2–5.

sphere (S: largely tropical to subtropical). In the subsequent sections, the significance of these changes will be explored, first, for a reappraisal of the Baileyian trends, and second, in the context of our current understanding of ecological strategies in xylem structure, followed by an epoch by epoch summary of these climatic inferences.

**The fossil record and the Baileyian trends**

*Tracheary elements* (Figs. 2–13; Tables 1–7)

The fossil record supports the Baileyian syndrome of tracheary element specialisation – changes from scalariformly perforated vessel elements with scalariform to opposite intervesel pits to simply perforated vessel elements with alternate pits; from solitary vessels to grouped vessels, and from fibres with distinctly bordered pits (fibre-tracheids) to libriform fibres, concomitant with a shortening of the cambial initials (about equal to vessel element length).

Incidences of scalariform perforations (Fig. 2; Tables 1, 2), scalariform pits (Fig. 4; Table 3), long vessel elements (Figs. 6, 8; Table 4), and fibres with distinctly bordered pits (Fig. 9; Table 5) all peaked in the Creta-

ceous, and show a sharp decline in the early Tertiary, to stay more or less constant throughout the Tertiary. Conversely, Baileyian specialisations such as exclusively simple perforations (Fig. 3; Table 1), alternate pits (Fig. 5; Table 3), and short vessel elements (Figs. 6, 8; Table 4) are relatively rare in the Cretaceous, and occur in ‘normal’ frequencies from the early Tertiary onwards.

The keystone to the Baileyian trends of specialisation is the shortening of vessel elements. There is a distinct trend in the fossil record for the percentage of taxa with long elements or elements of intermediate length to decrease (especially from the early Tertiary onwards; Figs. 6, 8; Table 4) and for taxa with short elements to become more frequent. This trend supports the major Baileyian evolutionary specialisation of reduction of vessel element length. However, it is somewhat surprising that the incidence of long vessel elements is similar in the Cretaceous and Recent, and that in the Cretaceous there is a relatively high percentage of medium-length vessel elements. We offer two explanations for this.

First, making vessel element measurements from sections can lead to grossly underestimating actual length. Element length is

properly determined from macerations and includes tails or ligules (Chalk & Chattaway 1934; Page 1979). Probably a majority of the early 20th century (and no doubt more recent ones) paleobotanists and wood anatomists measured element length from the midpoint of one perforation plate to the midpoint of the next. Moll and Janssonius apparently did this in their study of extant Javanese woods; measurements of complete vessel elements of the woods studied by Moll and Janssonius showed element length could be underestimated by 60% (cf. Baas *et al.* 1983). Therefore, the percentages for the Recent flora and only available for the world as a whole (based on Metcalfe & Chalk 1950; Fig. 6; Table 4; data derived from macerations) are not comparable with those for the fossil record. It is likely that vessel element lengths of fossil woods are recorded as shorter than they truly are.

Secondly, vessel element length is correlated with habit, in general, shrubs have shorter elements than trees. Another possible explanation for the relatively low percentage of woods with long vessel elements in the Cretaceous is that relatively few angiosperms were large trees.

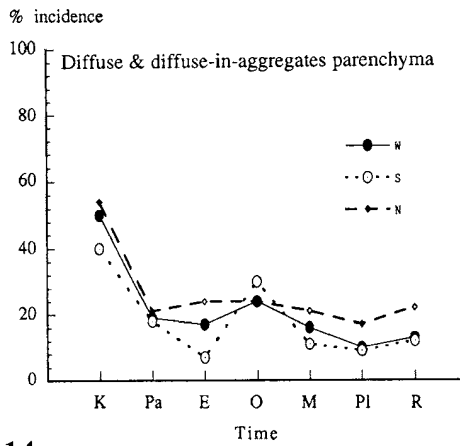
There is an unequivocal agreement of the fossil record with Baileyan trends, yet many specialised tracheary features are already present in the Cretaceous, albeit in relatively low percentages relative to the present day. For instance, woods with exclusively simple perforations, alternate intervessel pits, and fibres with minutely bordered pits occur in the mid-Cretaceous (the Aptian/Albian *Paraphyllanthoxylon utahense* from the Cedar Mountain Formation of Utah, Thayne *et al.* 1983, and a *Paraphyllanthoxylon* from the Albian Potomac Group, P. Herendeen, pers. comm., 1991). Another presumed specialisation, septate fibres (almost always associated with minutely bordered to simple pits) (Tippo 1938), even shows a peak occurrence in the Cretaceous (48% as contrasted to 14–26% for later periods, including the Present, Fig. 20), because of the numerous occurrences of *Paraphyllanthoxylon* (Thayne & Tidwell 1984) and putative Monimiaceae (Mädel 1960). These occurrences of 'derived' features in the Baileyan sense, support the view

that the major specialisations in xylem evolution already existed in the Cretaceous (Gottwald 1977; Baas 1982). Changes in percentage occurrence of derived features may be interpreted as either the success of lineages with these features, or, alternatively, parallel origins of similar specialisations (without excluding the possibility of reversals). At this time, the fossil wood record by itself cannot shed light on these alternatives.

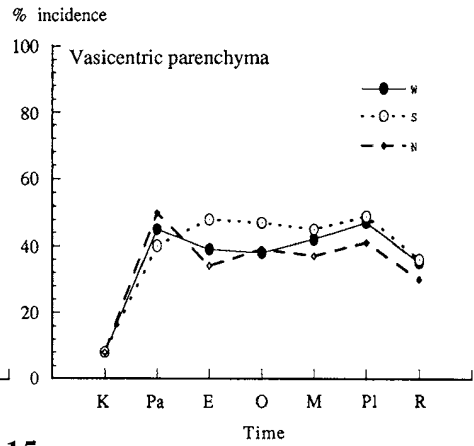
Two distinct structural patterns co-exist in the Albian (*Paraphyllanthoxylon* with simple perforation plates and septate fibres and *Icacinoxylon* with scalariform perforation plates and fibres with distinctly bordered pits, Thayne *et al.* 1983, 1985; P. Herendeen, pers. comm.), this suggests there were at least two major lineages of woody dicotyledons among the early angiosperms, and this in turn suggests either a biphyletic origin for woody dicotyledons or a very early divergence leading to these two types.

The Baileyan trends in specialisation of the tracheary elements have been hypothesised to be highly synchronised, and highly correlated (Frost 1930a, 1930b, 1931; Bailey 1944). This synchrony and correlation is evident in the fossil record. There is a nearly identical pattern of change for the incidence of scalariform perforation plates (Fig. 2) and the incidence of scalariform and opposite intervessel pits (Fig. 4), and for the incidence of simple perforation plates (Fig. 3) and alternate intervessel pitting (Fig. 5). Frost (1931) believed that intervessel pitting specialised more rapidly than perforation plate type. The data summarised here do not support that hypothesis, but more data are needed to assess its validity. Specialisation of perforation type is highly correlated with an increase in vessel element diameter and a decrease in element length (Bailey 1944); the fossil record shows a clear synchrony (Figs. 2, 3, 6–8, 10, 11; Tables 1, 3, 4, 6).

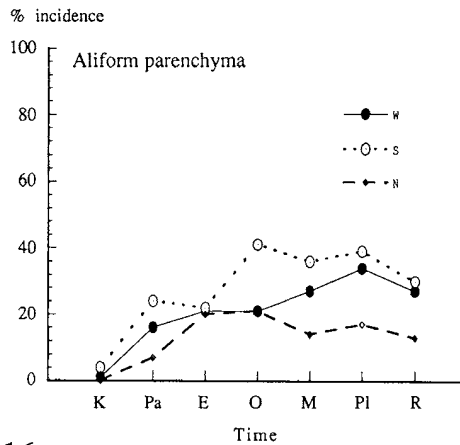
The data for vessel-ray parenchyma pits (Fig. 12; Table 7) suggest that simple vessel-ray parenchyma pits preceded half-bordered vessel-ray parenchyma pits in the history of woody angiosperms. This contradicts Frost's (1931) suggestion that fully bordered vessel-ray parenchyma pits are primitive and gave rise to the half-bordered and the non-bordered



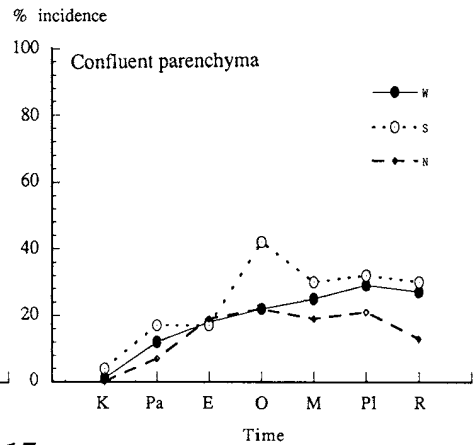
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Figs. 14–17. Parenchyma distribution. — 14: Diffuse and diffuse-in-aggregates. — 15: Vascentric. — 16: Aliform. — 17: Confluent. — See also legend Figs. 2–5.

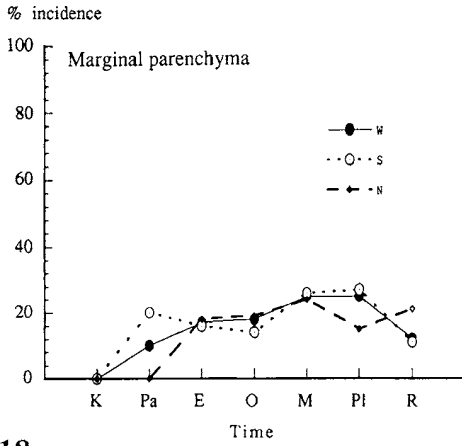
(simple) type. The fossil record (Fig. 13; Table 7) may be cited in support of Bonsen and Kučera's hypothesis (1990) that tyloses formation is the original mode of vessel occlusion in angiosperms and that gum occlusions are a later specialisation.

*Parenchyma distribution* (Figs. 14–19, 21; Tables 8, 9)

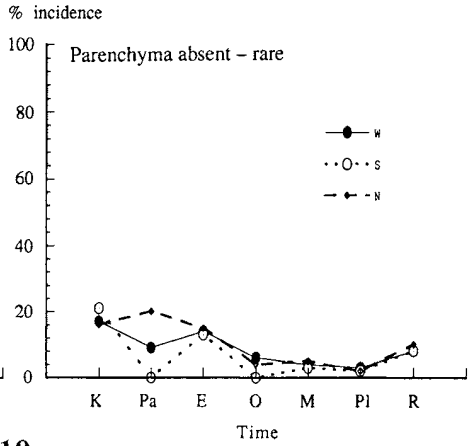
On the basis of statistical correlations of parenchyma distribution types with specialisation levels in the vessel element (in the

Baileyian sense), Kribs (1937) postulated that evolutionary specialisation proceeded from apotracheal (diffuse and diffuse-in-aggregates) to various paratracheal or banded types. Both Kribs and Chalk (1937) viewed marginal parenchyma as a separate specialisation which could be associated with either apotracheal or paratracheal parenchyma.

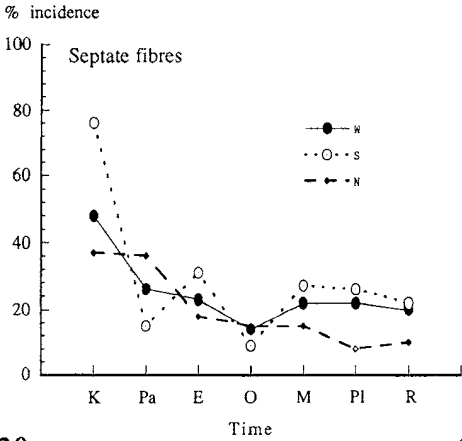
The fossil record provides unambiguous support for Kribs' hypothesis that diffuse parenchyma is 'primitive' and abundant paratracheal parenchyma is derived. Diffuse and



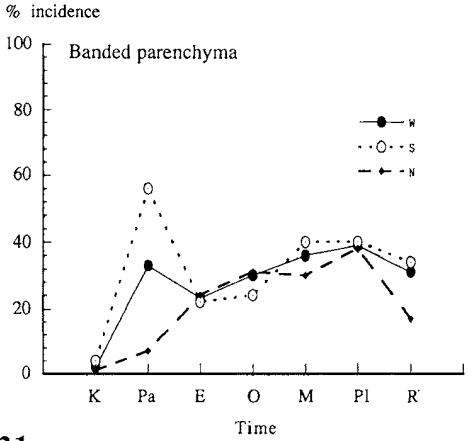
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Fig. 18. Marginal parenchyma. — Fig. 19. Parenchyma absent-rare. — Fig. 20. Septate fibres. — Fig. 21. Banded parenchyma. — See also legend Figs. 2-5.

diffuse-in-aggregate parenchyma is the most common in the Cretaceous and shows an abrupt drop in occurrence in the early Tertiary (Fig. 14; Table 8). Vasicentric and aliform or confluent parenchyma (Figs. 15-17; Table 9) do not occur or are extremely rare among Cretaceous woods (one specimen reported from Africa, *Cassinium dongolense* Giraud & Lejal-Nicol, 1989), but are already fairly well represented in the few known Paleocene woods. Vasicentric parenchyma (Fig. 15) has a peak incidence as early as the Paleocene,

while the incidence of aliform and confluent parenchyma (Figs. 16, 17) reaches modern levels in the Oligocene in the northern and southern hemisphere. Marginal parenchyma (Fig. 18) also is not reported from the Cretaceous and its incidence gradually increases up to the Miocene.

Kribs (1937) considered absence or extreme paucity of axial parenchyma a primitive condition, albeit derived from diffuse, which he considered "the primitive type." Absence or extreme paucity of parenchyma (Fig. 19;

Table 8) is relatively common in the Cretaceous and gradually decreases over time. However, absence or extreme paucity of parenchyma often is associated with septate libriform fibres (septate fibres functionally replace axial parenchyma; Wolkinger 1969). One interpretation would be that loss of diffuse apotracheal parenchyma and the development of septate fibres (Fig. 20) occurred as very early specialisations in woody angiosperms. In the Tertiary, woods with diffuse parenchyma or septate fibres either were lost or the lineages in which they occurred were less successful than they had been in the Cretaceous. An alternative interpretation is to consider septate fibres as not specialised, but as 'primitive' as fibres with bordered pits. Woods with septate fibres and woods with fibres with distinctly bordered pits co-occur in the mid-Cretaceous and are among the earliest known dicotyledonous woods. The evolutionary status of septate fibres is not unequivocal. Tippe (1938), on the basis of a study of the Moraceae and its allies, considered septate fibres advanced. However, because septate fibres are more common in woods with scalariform perforation plates (a 'primitive' feature) than in woods with storied structure (an 'advanced' feature), Chalk (1937) considered septate fibres primitive and "more or less on a level with fibre-tracheids and ... not ... part of the series tracheid-fibre-tracheid-libriform fibre."

Broad parenchyma bands can be either apotracheal or paratracheal. In some extant families (e.g. Lythraceae, Melastomataceae) there is fibre dimorphism with short, thin-walled septate fibres arranged in parenchyma-like bands, and in these same families there is a morphological series from 'normal' septate fibres, to short (and often thin-walled) fibres, to fusiform (septate) parenchyma to 'normal' parenchyma strands. It has been suggested that within these families parenchyma bands were phylogenetically derived from fibres via dimorphism (Baas & Zweypfennig 1979; Carlquist 1958, 1978, 1988; Ter Welle & Koek-Noorman 1978; Van Vliet *et al.* 1981). However, in other families (e.g., Leguminosae, Moraceae), there is a sequence from paratracheal confluent to banded parenchyma. Broad parenchyma bands (Fig. 21) peak in incidence in the Paleocene of the 'southern

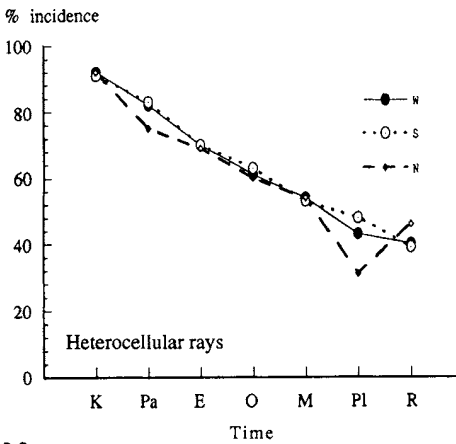
grouping', and are somewhat more common in the Miocene and Pliocene than they are in the Eocene and Oligocene.

Kribs was unsure of how the transformation from apotracheal diffuse parenchyma to elaborate paratracheal patterns (aliform-confluent) would occur. One hypothesis for the origin of paratracheal parenchyma suggested by the fossil record and by the distribution of septate fibres in the extant flora is that paratracheal parenchyma is derived from septate fibres. In some extant woods with both septate fibres and non-septate fibres (e.g., some Meliaceae), the septate fibres generally are near the vessels, i.e. a paratracheal distribution, and so it may be hypothesised that in at least some families paratracheal parenchyma is derived from septate fibres. This latter suggestion is in agreement with Chalk's (1937) suggestion that apotracheal and paratracheal parenchyma are independent lines of development.

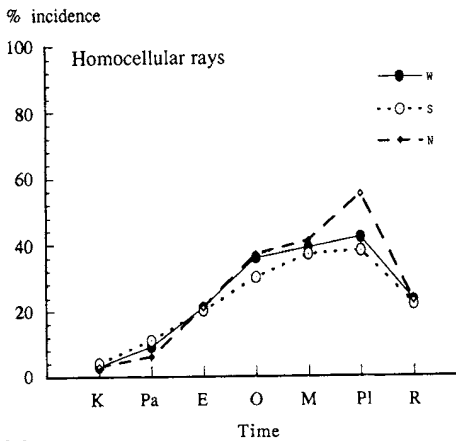
#### *Ray composition and size* (Figs. 22, 23; Tables 10–12)

Homocellular rays composed of procumbent cells only are considered derived from heterocellular rays with procumbent body ray cells and marginal rows of upright and/or square cells; markedly heterocellular rays with many rows of marginal cells were considered more primitive than heterocellular rays with one or but a few marginal rows (Kribs 1935). The incidence of exclusively heterocellular rays (Fig. 22; Table 10) is highest in the Cretaceous and gradually declines through the Paleocene, Eocene and Oligocene to its lowest level in the Pliocene; the incidence of homocellular rays (Fig. 23) shows a mirror-wise increase. Throughout time the incidence of markedly heterocellular rays with many marginal rows of square and/or upright cells has decreased (Table 11).

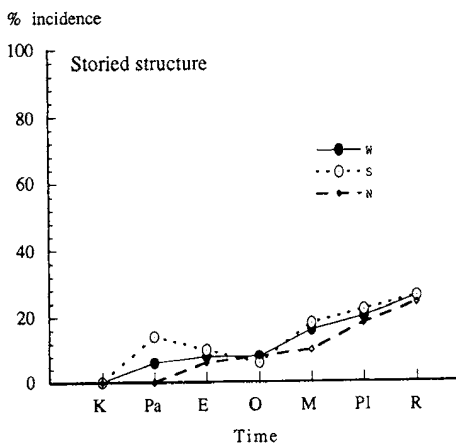
The present day levels of incidence of heterocellular and homocellular rays are more or less similar to that in the Oligocene. Strangely enough there is a somewhat higher incidence of 'specialised' rays in the Miocene and Pliocene than at present. The change in incidence of homocellular and heterocellular rays has been continuous throughout the fossil record, and the pattern of change is quite



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different from that for the tracheary elements. Rays of two size classes have also been speculated to precede rays of intergrading sizes or woods with either exclusively uniseriate rays or (almost) exclusively broad rays. The fossil record (Table 12) barely supports the speculation about rays of two size classes as they are very rare in the Cretaceous, and fluctuate around 'modern' levels from the Paleocene onwards. On the other hand, the increase in incidence of exclusively uniseriate rays throughout the Tertiary (Table 12) supports the hypothesis of Kribs.

*Storied structure* (Fig. 24; Table 13)

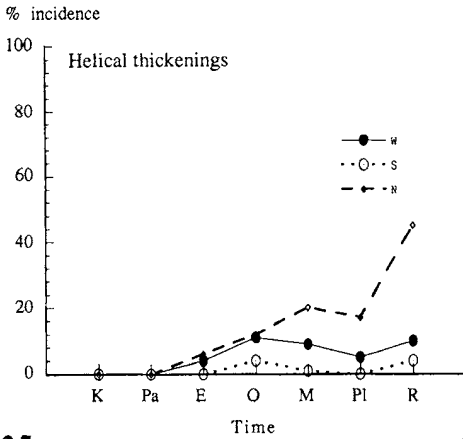
Because storied structure is associated with short cambial initials and a suite of other supposedly derived features, it is considered a highly specialised feature (Bailey 1923; Chalk & Chattaway 1935; Chalk 1937). Storied structure is not reported until the Paleocene in Laurasia, and the Eocene in the Southern Hemisphere. After these first reports, the incidence of storied structure gradually increases through the Pliocene. However, one cannot attach too much value to the differences in percentage occurrence of this feature which is at low frequencies throughout its known history.

*Other specialisations*

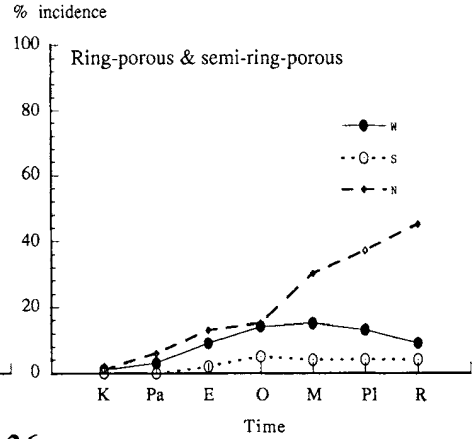
Helical thickenings are considered a specialised feature (cf. Tippo 1938; Frost 1931). The fossil record (Fig. 25; Table 14) supports this claim: distinct helical thickenings in vessel elements are not recorded until the Eocene and reach 'modern' levels in the Oligocene.

Ring-porosity (Fig. 26; Table 15): The earliest record of distinct ring-porosity is in the Eocene (2% only) and incidences of the feature comparable to those in the extant flora do not occur until the Oligocene. This supports the view that ring-porosity is a derived feature (Frost 1930a; Huber 1935; Gilbert 1940).

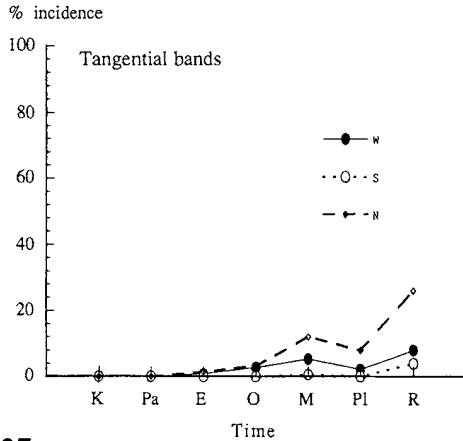
Figs. 22 & 23. Ray composition. — 22: Heterocellular rays. — 23: Homocellular rays. — Fig. 24. Storied structure, includes both ray and/or axial parenchyma storied. — See also legend Figs. 2–5.



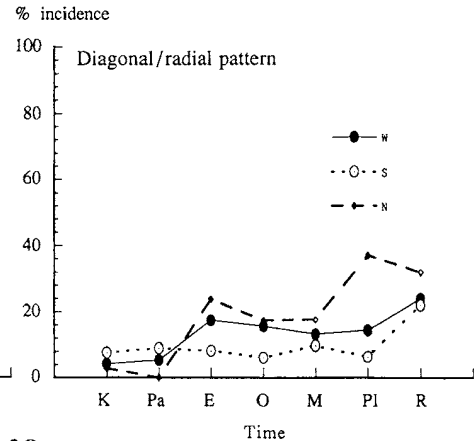
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Fig. 25. Helical thickenings in vessel elements. — Fig. 26. Ring-porous and semi-ring-porous. — Figs. 27 & 28. Vessel patterns. — 27: Tangential bands. — 28: Diagonal or radial pattern. — See also legend Figs. 2–5.

*Special patterns of vessel arrangements:*

Woods with randomly distributed or diffuse vessels are considered primitive in the Baileyian sense, and woods with a deviating non-random pattern have been considered specialised (Tippo 1938). Tangential vessel arrangements (Fig. 27; Table 16) have not been reported in the fossil record until the Eocene and can thus be considered derived. Radial/diagonal patterns (Fig. 28; Table 16) occur in the Cretaceous and Paleocene, but in

appreciably lower frequency (2–3%) than in the late Tertiary and Recent floras (6–15%). This can also be interpreted in favour of the hypothesised Baileyian trends.

**Ecological trends and functional interpretations**

There apparently is a great deal of parallelism and convergence (homoplasy) in wood anatomy, as the incidences of certain wood anatomical features are highly characteristic

of certain ecological categories, regardless of which families (lineages) are dominant. The tropical rain forests of Southeast Asia, West Africa and the Neotropics are all characterised by similarly high percentages of woods with wide vessels, low vessel frequencies, simple perforation plates, and paratracheal or banded parenchyma. Cool temperate floras of both the Northern and Southern Hemisphere are all characterised by relatively high percentages of scalariform perforations, narrow vessels, high vessel frequencies, helical vessel wall thickenings, fibres with distinctly bordered pits and apotracheal parenchyma (Baas 1976, 1986; OPCN data; Carlquist 1988). Thus, the predictive value of incidences of wood anatomical features and feature combinations may be considered to be as great as that of the widely applied correlates of leaf physiognomy and climate (Bailey & Sinnott 1915; Wolfe 1971, Wolfe & Upchurch 1987b).

Before beginning our very generalised climatic inferences we wish to reiterate that these inferences are based on samples that are widely dispersed, both spatially and temporally. Obviously, any interpretation of the incidence of wood anatomical features within very large geographical areas ignores the great ecological diversity within each area as well as the diversity in depositional settings and modes of preservation (e.g., silicified woods preserved in volcanics vs. lignites).

#### *Distinct growth rings* (Fig. 29; Table 17))

Cretaceous woods show a much lower percentage of distinct growth rings than the Tertiary or Recent woody flora, indicating a largely tropical nonseasonal environment (for both Northern and Southern Hemisphere provenances). For the world and the Southern Hemisphere, the percentage of woods with distinct growth rings is higher throughout the Tertiary than in the Recent flora. In view of the well documented larger extent of tropical to subtropical conditions throughout most of the Tertiary (Wolfe 1978) this seems to indicate that there is a bias in the fossil record towards temperate elements or habitats with some sort of seasonal variation (e.g., variation in water availability, temperature). This, however, is contradictory to trends for other

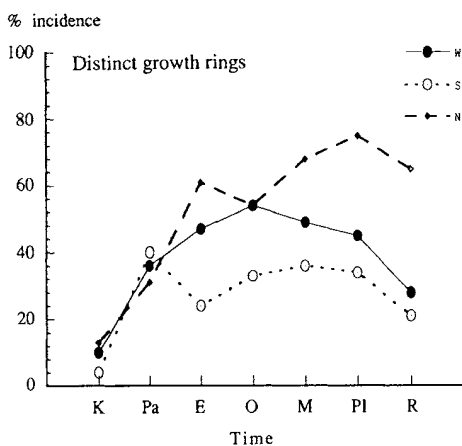


Fig. 29. Distinct growth rings. — See also legend Figs. 2–5.

features (see below – vessel diameter and frequency) which point to a higher incidence of tropical elements in the early Tertiary.

It is likely that the data for growth rings in fossil woods are not comparable with those for modern woods as recorded in the OPCN database. For fossil woods, all microscopic indications for growth rings have been coded positive for growth rings distinct. For extant woods, the 'requirements' for what constitutes a distinct growth ring have no doubt been higher. The interpretation of what constitutes a distinct growth ring varies from individual to individual. Growth ring boundaries are marked in a variety of ways, and some of the boundaries that occur in trees of seasonal tropical forests (cf. Worbes 1989) do not occur in temperate trees. Consequently, the incidence of microscopically distinct growth rings probably is underestimated in the extant flora.

The pronounced increase in incidence of distinct growth rings in both the Southern and Northern Hemisphere in the Paleocene indicates a seasonal climate for about 40% of the records. From the Eocene onwards Laurasia shows a distinct increase of seasonal elements (up to 77% in the Pliocene), oddly there is no marked increase in distinct growth rings at the Eocene–Oligocene transition, but



rather a decrease in the Northern Hemisphere. During the Tertiary, the tropical and Southern Hemisphere fossil floras contain a high degree of non-seasonal elements with only about one-third of the taxa showing distinct growth rings; in this region nonseasonal elements are particularly abundant in the Eocene.

#### *Porosity* (Fig. 26; Table 15)

Distinct ring-porosity is not known until the Eocene, and is more common throughout the late Tertiary and modern times in Laurasia than in the tropics and Southern Hemisphere. It is usually, but not always, associated with temperate climates and deciduousness [NB: most deciduous species are diffuse-porous; some tropical species from seasonally dry forests are ring-porous or semi-ring-porous and some of these are deciduous, some are not (Chowdhury 1964)].

Assuming similar correlations between climate and incidence of ring-porosity in past and present, the fossil record would indicate a much lower degree of seasonality and/or deciduousness up to and through the Oligocene. In the tropics and Southern Hemisphere, ring-porosity is rare throughout the fossil record, as it still is today. In Laurasia the incidence of ring-porosity and semi-ring-porosity remained well below modern levels up to the Pliocene which suggests the proportion of tropical elements was higher up to the Miocene. There is no marked change in the incidence of ring-porosity from the Eocene to the Oligocene as might be expected because of the late Eocene climatic deterioration, and the changes in leaf physiognomy (Wolfe 1978).

#### *Vessel arrangement* (Figs. 27, 28; Table 16)

Tangential (Fig. 27) or dendritic vessel arrangements are of rare occurrence in the modern flora and largely restricted to temperate or subtropical regions. Exceptionally high incidences of this character state have been recorded in the Mediterranean flora (up to 35%, cf. Baas *et al.* 1983). In the fossil record absence of these 'elaborate' vessel arrangements in the Cretaceous and early Tertiary cannot be used to infer tropical conditions for the angiosperm flora, because these arrangements likely had not yet evolved.

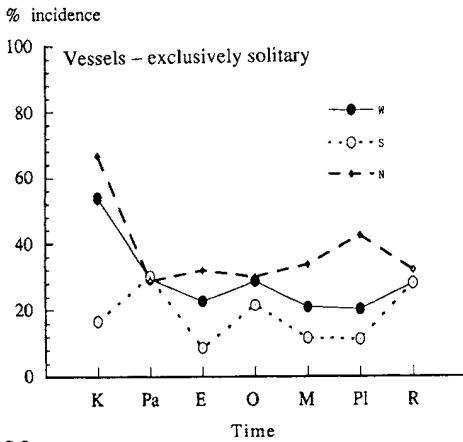
It would be inappropriate to attach any significance to the slight fluctuations in their incidence in the late Tertiary because very small fluctuations in characters of such rare occurrence are likely due to chance.

Radial and diagonal patterns of vessel arrangement occur in both tropical and temperate floras, although they are somewhat more common in temperate regions. Radial and diagonal patterns are characteristic of *Quercus* and some other genera of the Fagaceae, but also occur commonly in largely tropical families such as Myrtaceae and Guttiferae (Clusiaceae). In the fossil record (Fig. 28) the feature is very rare in the Cretaceous and Paleocene (restricted to some records from the tropics and Southern Hemisphere), and remains below modern levels, with the exception of the Pliocene of Laurasia (with many reports of *Quercoxylon*). In view of the poor correlation of radial/oblique vessel patterns with climatic conditions in the modern flora, no ecological inferences can be drawn from the fossil record occurrence of this feature.

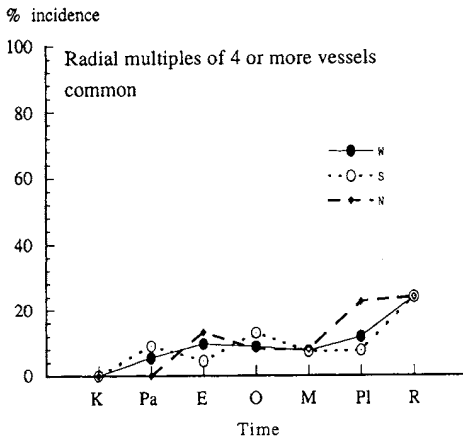
#### *Vessel groupings* (Figs. 30–32; Table 18)

Woods with (almost) exclusively solitary vessels occur throughout the world flora at fairly low percentages (11–17%; usually somewhat less frequently in the tropics than in North temperate to subtropical regions). Baas and Schweingruber (1987) found that, within the European flora, cool temperate to boreal elements showed this feature much more frequently than the warm temperate and Mediterranean flora. In the flora of the Middle East, this feature was in turn more common among Mediterranean elements than in the desert flora (Baas *et al.* 1983). With the exception of the Paleocene (Fig. 30), there is throughout the fossil record a higher incidence of solitary vessels in Laurasia than in the tropics and Southern Hemisphere, more or less in agreement with extant trends. There is a decrease in the incidence of exclusively solitary vessels from the Cretaceous to the Paleocene for the Northern Hemisphere.

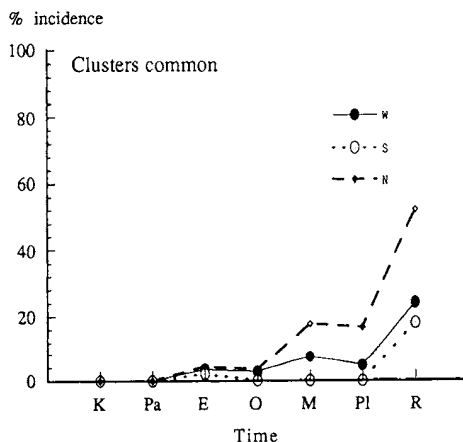
According to current knowledge of ecological trends in the modern flora, the relatively high incidence of solitary vessels in most of the Cretaceous implies a more tem-



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perate (less equable) ecology for Cretaceous angiosperms than for Tertiary and Recent angiosperms – a notion which is clearly in conflict with data on growth rings and with current knowledge on climatic conditions during the Cretaceous and Tertiary (Wolfe & Upchurch 1987b; Upchurch & Wolfe 1987). The higher incidence of woods with (almost) exclusively solitary vessels in the Cretaceous relative to the Tertiary and present is better explained by accepting the Baileyan concept that the primitive angiosperm xylem was characterised by solitary vessels and fibres with distinctly bordered pits. In Carlquist's interpretation (1984) such a ground tissue would make vessel grouping functionally redundant.

High degrees of vessel grouping as manifested in the features 'radial multiples of four or more vessels common' (Fig. 31) or 'clusters common' (Fig. 32) are of fairly rare occurrence in the modern flora. Vessel grouping has been considered a device for hydraulic safety (Carlquist 1984, 1988). Radial multiples of 4 or more are as common in tropical as in temperate floras. Clusters are far more common in subtropical to temperate floras than in tropical floras, and frequently are associated with dendritic or tangential vessel arrangements in semi-ring-porous to ring-porous woods (e.g., *Ulmus*, *Morus*, several Papilionoideae).

Since the two features of extreme vessel grouping are an innovation of early Tertiary origin (Paleocene for radial multiples of four or more common; Eocene for clusters common) they cannot be used for climatic inferences about the Cretaceous.

The clear differences between the incidence of vessel clusters in the Tertiary fossil record of Laurasia (relatively high) and the Tropics and Southern Hemisphere (absent) are in agreement with the ecological trends in the modern flora. However, there is a much

Figs. 30–32. Vessel groupings. – 30: Vessels 'exclusively solitary', more than 90% solitary. – 31: Radial multiples of 4 or more vessels common. – 32: Clusters common. — See also legend Figs. 2–5.

higher incidence of clusters in the Recent flora than in the Miocene and Pliocene. This increase in incidence from the late Tertiary to the Recent flora may be the result of either 1) a response to climatic deterioration of the Quaternary, and an increase in Mediterranean and xeric climates, or 2) underrepresentation in the fossil record of the environments in which woods with clusters are common.

#### *Vessel diameter* (Figs. 10, 11; Table 6)

Vessel diameter is probably one of the most significant parameters for hydraulic efficiency of angiosperm wood because of the relationship of conductive capacity with the fourth power of the radius of the conduit (Zimmermann 1983). Vessel diameter has been used extensively in ecological analyses (Carlquist 1977 1988; Baas 1973; Van der Graaff & Baas 1974; Van den Oever *et al.* 1981; Wolfe & Upchurch 1987). Although tropical lowland taxa tend to have wide vessels and cool temperate or high montane tropical species tend to have narrow vessels, the relationships between mean tangential diameter and climate in seasonally cool or dry, or permanently arid floras can be obscured by the simultaneous incidence of vessels of two or more size classes in the same growth ring (Baas *et al.* 1983; Baas & Schweingruber 1987). Ring-porosity is but one of the manifestations of this syndrome. There is also a general trend for vessel diameter to be positively related to plant size.

The frequencies of diffuse-porous woods with mean tangential diameters of less than 100  $\mu\text{m}$  and more than 200  $\mu\text{m}$  are shown in Figures 10 and 11. In the extant flora, the Northern Hemisphere, which is largely temperate, and Southern Hemisphere, which is largely tropical, have different profiles, particularly from the Miocene onwards.

In the Cretaceous, woods with moderately narrow vessels are more common than in Tertiary floras (particularly for the 'Southern Hemisphere'); this generalisation applies even when excluding the Cretaceous woods known to be from small diameter axes. In terms of modern ecological trends this would indicate a cooler (or even more xeric) average climate for Cretaceous fossil woods. In combination with data on absence of growth

rings which clearly indicates aseasonal conditions, this suggests a tropical high montane provenance for the Cretaceous angiosperms, a view reminiscent of earlier suggestions for an upland origin of the Angiosperms (see Raven & Axelrod 1974). An alternative hypothesis would be to take into account the high number of 'primitive' woods with scalariform perforations in the Cretaceous. There evidently is some constraint on maximum vessel diameter in woods with scalariform perforation plates. Woods with scalariform perforation plates usually have small diameter vessels; the combination of large diameter vessels and scalariform perforation plates is extremely rare in the extant flora (some species of *Dillenia* and a few climbers, Wheeler *et al.* 1987).

In the Paleocene of both Laurasia and the more Southern floras the relatively high frequencies of vessel diameter classes of 100–200  $\mu\text{m}$  and over 200  $\mu\text{m}$  (Fig. 11) indicate a markedly more tropical environment the world over at this time. This agrees with the larger leaf sizes of Paleocene floras compared to late Cretaceous floras of middle palaeolatitudes in North America (Upchurch & Wolfe 1987). In the extant flora, large diameter vessels unaccompanied by vessels of distinctly smaller size classes are characteristic of tropical trees. It has been hypothesised that angiosperms were not commonly emergents or large trees until the Paleocene (Wing & Tiffney 1987; Wolfe & Upchurch 1987b). Differences between the Laurasian fossil record and the 'Southern' record indicate a higher percentage of tropical lowland elements in the latter (with average vessel diameter over 200  $\mu\text{m}$ ) than in Laurasia.

In the Eocene of Laurasia there is a marked shift towards more narrow vessels (less than 100  $\mu\text{m}$ ), suggesting either climatic deterioration or dispersal of angiosperms into less favourable climatic regions and cooler or drier sites (Fig. 10). This shift is consistent with interpretations of leaf physiognomy data that indicate that in southeastern North America and Eurasia major regions of seasonally dry climates had developed (Wolfe 1985; Upchurch & Wolfe 1987). There is a higher proportion of subtropical to warm temperate elements than in the modern flora.

In comparison with the modern flora the southern Eocene woods show vessel diameter frequency distributions that suggest a slightly higher incidence of nontropical elements.

The southern fossil floras of the late Tertiary have a higher incidence of large diameter vessels than in the Eocene or Oligocene, or at present. In Laurasia vessel diameter is suggestive of a warmer climate than at present, with a very low incidence of microporous woods (vessels less than 50  $\mu\text{m}$ ), and a slightly higher incidence of megaporous woods.

In summary, for vessel diameter: there are major shifts in size distributions between the Cretaceous and early Tertiary and between the Paleocene and Eocene. The first shift probably reflects a release from structural constraints and the development of simple perforations, and perhaps is associated with the emergence of angiosperms as dominants in multistratal forests, the Paleocene–Eocene shift may be a result of climatic change (but the Paleocene record is extremely scanty). There is no evidence of the late Eocene climatic deterioration in the vessel diameter data.

#### Vessel frequency (Figs. 33, 34; Table 19)

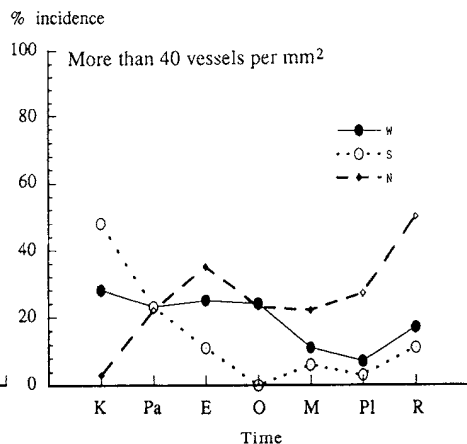
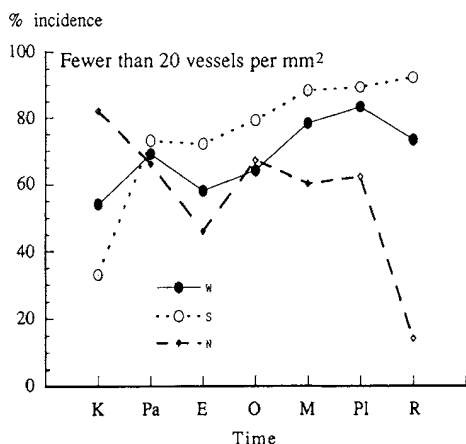
Vessel frequency is usually inversely proportional to vessel diameter and of some significance to water conducting capacity, although less so than diameter. Woods with

scalariform perforations usually have relatively high vessel frequencies because they have relatively narrow vessels. High vessel frequencies are typical of cool temperate to arctic or tropical high montane (to alpine) species and of xerophytes (Carlquist 1977; Baas 1973, 1986); low vessel frequencies are typical of lowland tropical species. Shrubs or branchwood of trees have much higher vessel frequencies than mature (bole)wood of trees. Interpretation of the data for vessel frequency is confounded because there have been two different procedures for counting vessels per sq. mm (Wheeler 1986).

Cretaceous woods show a wide range of vessel frequencies (Table 19), with a relatively high number of woods with very numerous vessels in the Southern floras indicating perhaps that these were from cooler provenances than those from Laurasia; many Southern Hemisphere Cretaceous woods are from high latitudes (Nishida & Nishida 1985, 1987).

In the Paleocene the incidence of woods with low vessel frequencies is similar throughout the world, thereby suggesting, as did the vessel diameter data, prevailing tropical conditions.

In Laurasia, the increase in the percentage of woods with vessels over 40 per sq. mm suggests an increase in temperate elements in the Eocene, again paralleling the changes in



Figs. 33 & 34. Vessel frequency. – 33: Fewer than 20 vessels per square mm. – 34: More than 40 vessels per square mm. — See also legend Figs. 2–5.

vessel diameter classes. In the Oligocene, Miocene, and Pliocene, the vessel frequencies suggest fewer temperate and xeric elements than at present. Incidences of low vessel frequencies drop dramatically and high vessel frequencies increase markedly from the Pliocene to the Recent in the Northern Hemisphere. Possible explanations for this marked post-Pleistocene change are similar to those offered for the marked post-Pleistocene increase in vessel clusters common — either post-Pleistocene there was an increase in cool, cold, and xeric habitats in the Northern Hemisphere or in the fossil record there is underrepresentation of the environments in which high vessel frequencies occur.

For the Southern Hemisphere/Tropical region, the Eocene decrease in woods with numerous vessels suggests more tropical conditions. The Oligocene increase in woods with low vessel frequencies and decrease in woods with high vessel frequencies suggest a continued increase in tropical elements. The incidence of woods with low vessel frequencies (characteristic of tropical trees) is similar in the Miocene, Pliocene, and Recent floras.

#### *Vessel element length* (Figs. 6–8; Table 4)

There is a distinct trend for the percentage of taxa with long elements or elements of intermediate length to decrease over time (especially from the early Tertiary onward), and for the percentage of taxa with short elements to increase. Current knowledge of ecological trends in vessel element length suggests that the increase in the incidence of short vessel elements from the early Tertiary onwards results from an increasing percentage of subtropical to temperate elements (cf. data on growth rings). Seasonality in temperature or in rainfall is correlated with significant reductions in element length (cf. Baas *et al.* 1983, where in the series from tropical rain forest, through tropical monsoon forest, temperate forests, mediterranean high maquis, to severely arid vegetations the average element length in trees is reduced according to the following series: c. 750–530–480–360–300  $\mu\text{m}$ ).

It is remarkable that in the Cretaceous and Paleocene vessel element lengths tend to be much shorter in the Southern/Tropical floras

(Fig. 7) than in Laurasia (Fig. 8), while in later epochs there is hardly any difference between these two very different climatic zones (Table 4). From modern trends one would expect woods of the Southern floras to have longer elements throughout the Cretaceous and Tertiary because of the higher proportion of tropical elements. This raises the question of whether the relatively small number of fossil wood records with information on element lengths really gives a representative picture of the actual range of variation at any given time. Also, it invites a critical re-evaluation of vessel element length in the modern tropical floras, because the example cited above (from Baas *et al.* 1983) was based on indirect estimates only for the tropical flora of Java.

#### *Perforations* (Figs. 2, 3; Tables 1, 2)

The incidence of scalariform perforations shows distinct ecological trends in the modern flora with peak values in cool temperate to arctic (23–53%) and tropical high montane floras (15–33%) and minima in tropical lowland forests (0–5–8%) and arid floras (Baas 1976, 1986; Baas & Schweingruber 1987; Carlquist & Hoekman 1985, OPCN database). For the very high incidence of scalariform perforations in the Cretaceous, one could only find a modern equivalent in arctic floras. In view of the tropical environment suggested by the lack of distinct growth rings, this high percentage of scalariform perforation plates clearly is much better accounted for by accepting the Baileyian transformation series.

The pronounced decrease from the Cretaceous to the Tertiary in percentage of taxa with exclusively scalariform perforations may be related to selective pressures resulting from the development of: a) tropical lowland ecology and large tree stature; b) seasonal or permanent drought; c) changing phenology (deciduous habit) in response to b, or some combination thereof.

In the Paleocene, Laurasia still contains a relatively high percentage of woods with scalariform perforations, but in the Southern floras all fossil woods have exclusively simple perforations. This may be the result of preferential elimination of the scalariform perforation in tropical regions, as still wit-

nessed by their low incidence in modern tropical floras.

In the Eocene of Laurasia the percentage of woods with scalariform perforations is comparable to that of the modern flora, while in the Southern region it is much lower. In the Oligocene the high latitude Southern Hemisphere woods have a high percentage occurrence of woods with scalariform plates, while the 'tropical latitude' woods have exclusively simple perforations. The Miocene has percentages more or less identical to those of the Recent flora, but in the Pliocene there is a lower incidence of woods with scalariform plates than in the Recent flora. Scalariform perforations have been ascribed the function of trapping embolisms in thawing xylem sap (Zimmermann 1983; Carlquist 1988) and so may have been preferentially selected for under cool temperate to arctic conditions of the Pleistocene.

The elimination of scalariform perforations from arid and warm tropical regions makes sense functionally when considering high demands for efficient sap transport imposed by high peak transpiration rates, and the contribution of scalariform perforations to resistance to flow. We maintain this hypothesis despite evidence that the contribution to resistance to flow is probably quite small (Robson & Bolton 1986; Schulte *et al.* 1989).

From the Cretaceous to the Oligocene, there has been a decrease in the number of bars per perforation plate (Table 2). This decrease also can be viewed as an adaptation to more efficient water transport. Throughout time, there has been a fairly constant low incidence of woods with mixed simple and scalariform perforations.

#### *Intervessel pits* (Figs. 4, 5; Table 3)

Carlquist (1988) has proposed that alternate intervessel pitting creates a stronger vessel wall than scalariform or opposite intervessel pitting. Stronger vessel walls can be envisioned as adaptive with increased stature of woody dicotyledons, and the development of wider, longer vessels and higher tensions in the transpiration stream. The incidence of alternate intervessel pits (Fig. 5) increases markedly from the Cretaceous to the early Tertiary, coincident with the proposed time

for woody angiosperms commonly becoming large trees.

#### *Vessel-ray pits and tyloses* (Figs. 12, 13; Table 7)

In the modern flora the majority of woods have half-bordered vessel-ray-pits; i.e., the pit pairs are fully bordered on the vessel side and simple on the ray parenchyma side; in descriptions this feature is often referred to as 'vessel-ray pits similar to intervessel pits'. In approximately 35% of modern woods the vessel-ray pits are described as 'large and simple' when the pit borders on the vessel sides are apparently 'reduced'. Although no ecological trends previously have been suggested for these character states, the data from the OPCN database indicate that large and simple vessel-ray pits are more common in tropical (32–48%) than in North Temperate floras (23–25%). Large vessel-ray pits (at least pits exceeding a certain aperture diameter) have been associated with tyloses formation (Chattaway 1949; Bonsen & Kučera 1990); woods with pits below a certain aperture diameter occlude their vessels with gum in heartwood formation. All woods coded as having 'large and simple' vessel-ray pits are in the former category.

Figures 12 and 13 illustrate the incidence of tyloses and simple vessel-ray pits over time. There are fluctuations in both categories, but both features appear to be common in the Cretaceous, and in the Oligocene of the Southern Hemisphere. Tyloses appear to be more common throughout the fossil record than they are recorded for the modern flora in the OPCN database. This is perhaps because any wood that is well enough preserved to show tyloses will have this feature mentioned prominently in its description. For extant woods, tyloses are coded positive only when they are common. Also, some data for modern woods may be from sapwood samples in which tyloses had not developed, and it is likely that heartwood is preserved preferentially in the fossil record.

#### *Helical thickenings* (Fig. 25; Table 14)

Helical vessel wall thickenings show distinct correlations with ecological conditions in the modern flora. They are infrequent in

tropical floras (2–5% – OPCN data) and very common in temperate floras (39–42% – OPCN data), with peak occurrences in seasonally arid mediterranean type climates (Baas 1986; Carlquist 1988; Carlquist & Hoekman 1985). In the fossil record distinct helical thickenings are first reported for the Eocene of the Northern Hemisphere, and increase in frequency up to the Miocene. One mid-Cretaceous *Paraphyllanthoxylon* (a charcoalfied wood) that was studied with SEM showed faint spirals in parts of the vessel element (Herendeen, pers. comm.; 1991). Throughout the fossil record the incidence of helical thickenings is much lower than at the Present. Also, there is a distinct difference between the Laurasian and the largely tropical Southern fossil record, which agrees with modern ecological trends. The consistently lower incidence in the fossil record may be due to a combination of factors: 1) unless a wood is well-preserved, it is difficult to determine whether helical thickenings are present or absent; 2) if the fossil record shows a bias towards riparian trees, and if throughout time helical thickenings have been more common in more cool temperate or xeric species, then it is likely that this feature is underrepresented in the fossil record, and/or 3) the environments in which helical thickenings are common may not have been common until post-Pleistocene.

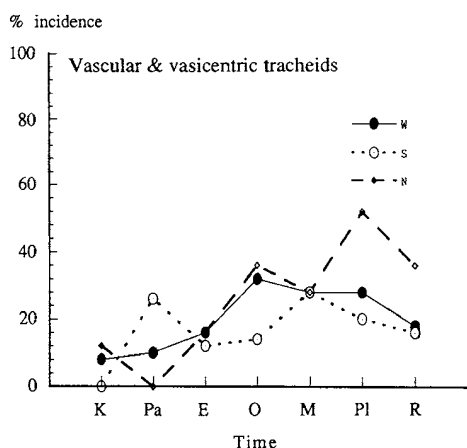


Fig. 35. Vascular and vascentric tracheids. — See also legend Figs. 2–5.

### Tracheids (Fig. 35; Table 20)

Vascentric and vascular tracheids are thought to provide additional safety in water transport and are especially common in taxa subject to (seasonally) arid conditions (Carlquist 1985, 1988; Baas & Schweingruber 1987). There are a number of hypothetical derivations of vascular and vascentric tracheids from ancestral conditions with narrow vessels or a ground tissue with distinctly bordered pits ('true tracheids' sensu Carlquist), thus tracheids can be considered as specialised modifications with different starting points. Due to vague definitions and difficulties in distinguishing these tracheids from narrow vessel elements or ground tissue fibres with bordered pits they have, unfortunately, not always been recorded reliably either for fossil or extant woods, invalidating any attempt at a detailed analysis of ecological correlation.

As shown in Figure 35 the incidence of vascular and vascentric tracheids fluctuates throughout time. The somewhat higher incidence in the late Tertiary than in the early Tertiary would coincide with the increase of seasonal climates in the late Tertiary. Tracheids are especially abundant in the Pliocene of Laurasia (with many species of *Quercoxylon*). From the Oligocene onward vascular and vascentric tracheids are more common in Laurasia than in the Southern floras, paralleling modern differences between North temperate to subtropical (incidence 11–17%) and tropical floras (incidence 7–10%).

### Fibres with distinctly bordered pits (Fig. 9; Table 5)

Fibres with distinctly bordered pits also have been hypothesised to provide the conductive system with additional safety (Braun 1961; Carlquist 1988; Baas & Schweingruber 1987). In modern floras they tend to be more common in temperate than in tropical floras (Baas 1982; OPCN data: Laurasia 39%; Tropical floras: 20% in Africa and Neotropics, 35% in Southeast Asia). The relatively high percent in Southeast Asia is probably due to a high proportion of montane elements, and a large number of Dipterocarpaceae, which have fibre-tracheids.

Throughout the fossil record this difference in tropical and subtropical to temperate prove-

nances is apparent (Fig. 9); fibres with distinctly bordered pits are consistently and significantly more common in the Laurasian fossil flora than in the Southern floras. Their very high incidence in the Cretaceous would indicate a cooler environment than exists at present if modern ecological trends would apply, but once again an explanation by accepting Baileyan evolutionary concepts is much more satisfactory (i.e., less in conflict with other facts). The incidence of fibres with distinctly bordered pits is nearly constant throughout the Tertiary, and is persistently lower than at the present. The difference in incidence between the Tertiary and the present may partly be an artefact of different conventions in applying the criterion 'fibres with distinctly bordered pits' for the OPCN database and for describing fossil woods or it may indicate more equable conditions in the Tertiary than at present. Given that the incidence of fibres with distinctly bordered pits fluctuates but slightly during the Tertiary, the incidence of this feature apparently is not a sensitive climatic marker.

#### *Septate fibres* (Fig. 20; Table 5)

In the modern flora septate fibres are more common in tropical floras (21–25%) than in temperate ones (8–10%). Extrapolating this trend to the fossil flora would indicate a tropical environment for the early angiosperms, an inference which also can be drawn from the general absence of growth rings.

Functionally, the early abundance of septate fibres makes sense. In the Cretaceous elaborate parenchyma distribution patterns such as aliform, confluent and banded are rare. The development of septate fibres which can remain living and metabolically functional as long as axial parenchyma was probably a good alternative to elaborate paratracheal or banded parenchyma patterns which became more common throughout the Tertiary (see below). Modern tropical floras are characterised by the common occurrence of either septate fibres or abundant parenchyma (Baas 1982).

#### *Parenchyma* (Figs. 14–19, 21; Tables 8, 9)

From the Cretaceous to the Tertiary there is a pronounced decrease in the number of woods with axial parenchyma exclusively

apotracheal diffuse or diffuse-in-aggregates (Fig. 14). Throughout the Tertiary there is only a slight fluctuation in the incidence of this 'primitive' type of parenchyma distribution. In the Recent flora there is a slight tendency for diffuse parenchyma to be more common in temperate than in tropical floras; this tendency also is present in the fossil record when comparing Laurasia with the Southern/tropical latitude floras.

Vasicentric parenchyma shows a dramatic increase in incidence post-Cretaceous, and its incidence fluctuates around modern values throughout the Tertiary (Fig. 15). Vasicentric parenchyma was and is somewhat more common in Southern/tropical than in temperate floras.

Abundant parenchyma (mostly aliform/confluent and/or banded) is much more common in the tropics than in temperate floras (Braun 1984; Baas 1982; OPCN data as presented in Figs. 16, 17, 21 & Table 9). Aliform and confluent parenchyma are present only in a very few Southern Hemisphere Cretaceous woods, and gradually increase in frequency throughout the Tertiary. Given that abundant axial parenchyma is today primarily a feature of tropical regions, the gradual increase in the incidence of abundant axial parenchyma runs counter to accepted trends for climatic change, and those inferred from growth ring data and vessel diameters. Throughout the fossil record, these elaborate types of parenchyma occur more frequently in the Southern floras than in Laurasia consistent with trends in the extant flora. The differences between the two regions become more pronounced post-Eocene attesting to the development of temperate and subtropical regimes in the Northern Hemisphere, and latitudinal gradations in climate. Nonetheless, there is still a higher incidence of aliform and confluent parenchyma in the late Tertiary than in the modern flora suggesting a higher proportion of tropical elements in the late Tertiary. For banded parenchyma there is a more or less similar trend to that for aliform and confluent parenchyma (Fig. 21).

Marginal parenchyma, a special form of banded parenchyma associated with growth ring boundaries, is reported first in the Paleocene and shows only very limited changes in



incidence from the Eocene onwards (Fig. 18). In the modern flora marginal parenchyma appears to be slightly less common than in the late Tertiary, but this may be due to different coding conventions (sometimes zonate parenchyma may have been reported as banded parenchyma, rather than marginal parenchyma). The absence of marginal parenchyma in Cretaceous supports other evidence of a tropical, nonseasonal environment. Chowdhury (1964) considered marginal parenchyma a character of ecological rather than of phylogenetic significance.

#### *Canals* (Table 21)

Axial and radial resin or gum ducts occur only in a restricted number of extant families, and often characterise natural lineages (e.g., Dipterocarpaceae, axial canals; Anacardiaceae, radial canals). They are more common in tropical than in temperate regions (5–10% vs. 1–2% for radial canals; 5–10% vs. 2–3% for axial canals, including traumatic ones). In the fossil record they are not reported until the Eocene, but from that period onward they are at least as common or more common than in the recent flora. This may be due to 1) preferential preservation of woods with secretory canals because the resins or other extractives which canals produce may act as wood preservatives (cf. Hillis 1987), or 2) preferential description, i.e., woods that are easy to assign to family are more likely to be described in print, and canals occur in but a few extant families. The geographical asymmetry of modern occurrence of axial canals (more common in the tropics) is also partly reflected in the fossil record.

#### *Miscellaneous features*

Ray composition and size (Tables 10–12) and storied structure (Table 13) have been left out of the discussion on ecological and functional significance because for these features interpretations of ecological and functional significance are particularly speculative.

#### **Epoch by epoch summary of the ecological inferences**

In the Cretaceous an integrated application of modern wood anatomical trends for deriving climatic inferences fails; there is considerable contradiction between the climatic infer-

ences based upon different features. Tropical, aseasonal conditions are suggested by a low incidence of distinct growth rings and high incidence of septate fibres, while temperate, cool, or xeric conditions are suggested by a high incidence of solitary vessels, narrow vessels, and scalariform perforations. Modern ecological correlations for the incidence of many features apparently do not apply in the Cretaceous, probably due to constraints imposed by the primitive structure prevalent at the time, and the predominance of shrubs and small trees. Upchurch and Wolfe (1987) similarly found it difficult to infer the mid-Cretaceous climate from leaf physiognomy.

For the early Tertiary, the most sensitive climatic markers probably are distinct growth rings, and vessel diameter and vessel frequency. Incidences of ring-porosity, elaborate vessel distribution patterns, high degrees of vessel groupings, distinct helical wall thickenings, and elaborate paratracheal parenchyma patterns cannot be used as reliable climatic markers for the early Tertiary, because these features are not reported until well into the Tertiary.

The Paleocene woods, although low in number, indicate tropical conditions on the basis of vessel diameter and frequency. The increase in incidence of wider vessels and a lower vessel frequency is also consistent with the proposed timing of the development of multistratal forests in the Paleocene (Wing & Tiffney 1987; Wolfe & Upchurch 1987b). In the Gondwana flora the absence of scalariform perforations is consistent with this inference, but in Laurasia the percentage of taxa with scalariform perforations indicates cooler climates than at present or the persistence of primitive elements. The fairly low percentage of woods with distinct growth rings favours an interpretation of a largely tropical flora. Distinct helical thickenings have not been reported for this era, but presumably still had to evolve in many clades, so their absence cannot be used as additional argumentation for a largely tropical, but partly seasonal ecology for the Paleocene.

The Eocene shows a marked increase in distinct growth rings (more strongly so in Laurasia than in the Southern floras). In Laurasia there is an increase in woods with

narrow vessels, a decrease in woods with exclusively scalariform perforations, and the first report of distinct helical thickenings. Apart from the decrease in scalariform plates these data point to a relative increase in seasonal, temperate (subtropical to warm temperate?) elements. The incidence of scalariform perforations is suggestive of a lowland tropical ecology in the Southern flora, and a mesic cool temperate one for Laurasia, respectively (in contradiction to the data for vessel diameter and frequency).

The Oligocene fossil woods show a slight tendency towards further increase of temperate elements in vessel diameter and frequency distribution, and in an increase in the incidence of helical vessel wall thickenings. In the Northern Hemisphere the incidence of scalariform perforations does not significantly change from the Eocene to the Oligocene. The late Eocene climatic deterioration that is recorded in changes in leaf physiognomy is not apparent in the fossil wood record as currently known; however, woods from continuous sequences across the Eocene–Oligocene transition and from a relatively restricted geographic region have not been studied to date.

The Miocene shows a small shift towards more tropical conditions in vessel frequency and vessel diameter distributions, consistent with a warming trend during the Miocene (Wolfe 1978). The incidence of distinct helical vessel wall thickenings increases in Laurasia, contradicting the above trend, but decreases in the Southern flora, reinforcing the impression of a largely tropical flora. The low frequency of distinct growth rings and scalariform perforations weakly reinforces this interpretation for the Southern flora.

The Pliocene shows a further increase in temperate aspects in the Laurasian flora (higher incidence of distinct growth rings and helical vessel wall thickenings; vessel frequency and vessel diameter distributions) and at least as tropical an environment for the Southern flora as we know it today (based on the low incidence of the same features). The low incidence of scalariform perforations in both Laurasia and the Southern continents is indicative of somewhat warmer conditions (on average) than exist at present.

## Conclusions

1. The fossil record supports the general validity of the Baileyan trends, and the synchrony and correlation of phylogenetic specialisation in tracheary elements.
  - a) The incidence of primitive features (scalariform perforations, opposite-scalariform intervessel pits, diffuse parenchyma) is much higher in the Cretaceous than in the Tertiary.
  - b) The incidence of advanced features (simple perforations, alternate intervessel pits, short vessel elements, aliform and confluent axial parenchyma) is much lower in the Cretaceous than in the Tertiary.
2. The tempo and timing of changes in ray composition, storied structure, and elaborate axial parenchyma patterns are not the same as those for the hydraulic system. The increase in incidence of homocellular rays, storied structure, and banded parenchyma is gradual throughout time, and there is no marked change between the Cretaceous and Tertiary as there is for incidences of perforation plate type and intervessel pitting arrangement.
3. Although there is a marked difference in the incidence of primitive and advanced wood features between the Cretaceous and Tertiary, the major Baileyan specialisations of tracheary elements are present by the end of the Cretaceous.
4. Septate fibres almost always have simple pits, and thus according to the Baileyan model would be considered as advanced compared to fibres with distinctly bordered pits. However, the fossil record supports Chalk's suggestion that septate fibres are primitive. Woods with septate fibres are among the earliest known, and the incidence of septate fibres is highest in the Cretaceous.
5. Data support the hypothesis that correlations of wood anatomical features with ecology have not been constant over time.
  - a) In the Cretaceous, different features provide conflicting information about the climate. The combinations of fea-

tures useful as climatic indicators in the extant flora cannot be applied in a general way to the Cretaceous, probably because of the 'constraints' imposed by phylogeny (the predominance of 'primitive' elements). Additionally, it is possible that in the Cretaceous a larger proportion of dicotyledons were shrubs or small trees than in the Tertiary.

- b) Some features, such as ring-porosity, tangential and dendritic vessel distribution patterns, high degrees of vessel groupings (clusters), helical vessel wall thickenings, and elaborate paratracheal parenchyma distribution patterns, apparently did not appear until the early Tertiary, and therefore should not be considered reliable ecological markers until the mid or late Tertiary.
6. In the Tertiary, modern ecological trends apparently do apply.
    - a) Throughout the Tertiary, the 'Southern Hemisphere/tropics' and the 'Northern Hemisphere/temperate' regions differ in the incidences of ecologically significant features. The nature of these differences is consistent with what would be expected based on data for Recent regional floras.
    - b) For many features, their percent occurrence in Tertiary and extant regional floras is similar. Thus, in spite of problems with defining 'wood species', making ecological inferences by comparing data for late Tertiary woods to data for extant woods would appear to be valid.
  7. The very similar profiles of tropical and temperate floras all over the world with respect to character state frequency indicates a high degree of parallel and convergent evolution of specialised wood anatomical features and provides substantiation for considering ecological adaptation to be a major force in directing xylem evolution (Carlquist 1988). Consequently, Bailey's (1957) and Dickison's (1989) cautions against relying solely on structural similarity as absolute proof of phylogenetic affinity warrant repeating. Whether the major Baileyan trends for tracheary elements (so impressively supported by the fossil record) are irreversible and unidirectional as claimed by Bailey (1944, 1957) or may instead be 'reversible' cannot be answered from the fossil record. Fluctuating percentages over time for 'primitive' features such as scalariform perforations or fibres with distinctly bordered pits only reflect the relative abundance of lineages with these features at any given time span. However, in our opinion one should keep an open mind for the possibility that increases in the incidence of a primitive feature in Tertiary or Quaternary times may also be caused by a reversal of the major evolutionary trend, dictated by adaptive value of the 'primitive' feature involved.
  8. On the basis of the available data, it appears that changes in the incidence of 'environmentally significant' features of wood and leaf structure are not always in concert.
    - a) For both leaves and wood, there is a marked difference between the Cretaceous and the Tertiary in the incidence of different features. Many of these changes in wood anatomy would increase conductive efficiency and coincide with the suggested timing for the development of multistratal forests and the emergence of angiosperms as large trees. However, there is no way of determining from the available data whether these changes in wood structure occurred over a very short time (a boundary event) or millions of years.
    - b) The late Eocene climatic deterioration is not noticeable in the available wood data; marked changes in the incidence of ring porosity, vessel groupings, narrow or wide vessels are not apparent until post-Oligocene. There are relationships between foliar and xylem morphogenesis. In some extant plants, modifications in leaf morphology and anatomy may act as buffers and permit 'primitive' xylem to survive in seasonally or permanently dry locations (Rury & Dickison 1984). Perhaps, on a large scale, the changes

in leaf physiognomy at the end of the Eocene preceded changes in wood anatomy, and 'delayed' changes in the incidence of ecologically significant wood anatomical features.

10. There is still a considerable need for primary data collection for well-dated fossil wood, if we are to better understand the relationships between wood anatomy and environmental change and evolution. There is a particular need for more information for woods from the mid-Cretaceous (the time of the initial radiation of angiosperms), from critical sequences across the Cretaceous-Tertiary boundary (especially for the Paleocene), and the mid-Eocene-early Oligocene (on the basis of other paleontological evidence, both times considered to be characterised by major climatic and vegetational change), and from relatively restricted geographic regions. Moreover, it would be helpful if descriptions of fossil woods followed the terminology and protocols for extant woods (IAWA Committee 1989).

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*Note* — Copies of the database as formatted for the GUESS program and the OPCN database (LaPasha 1986; LaPasha & Wheeler 1987; Wheeler *et al.* 1986) are available upon request (to the first author) and for a fee to cover postage and handling.

Tables 1–21. Percent incidence of wood anatomical features. W = World; S = 'Southern'/Gondwanan grouping; N = 'Northern'/Laurasian grouping. No. = total number of fossil records with presence or absence of feature reliably recorded.

Table 1. Perforations.

		All simple	Simple & scalariform	All scalariform	No.
Cretaceous	W	43 %	7 %	49 %	95
	S	42 %	21 %	38 %	24
	N	44 %	3 %	54 %	71
Paleocene	W	76 %	5 %	19 %	22
	S	100 %	0 %	0 %	8
	N	64 %	7 %	29 %	14
Eocene	W	80 %	5 %	15 %	216
	S	95 %	1 %	3 %	86
	N	69 %	8 %	23 %	130
Oligocene	W	79 %	4 %	17 %	193
	S	68 %	7 %	25 %	28
	S-trop	100 %	0 %	0 %	16
	S-temp	25 %	17 %	58 %	12
	N	81 %	4 %	16 %	165

(Table 1 continued)		All simple	Simple & scalariform	All scalariform	No.
Miocene	W	85 %	6 %	9 %	512
	S	93 %	3 %	3 %	296
	N	72 %	10 %	18 %	206
Pliocene	W	93 %	3 %	4 %	238
	S	98 %	2 %	1 %	184
	N	76 %	7 %	17 %	54
Recent	W	86 %	6 %	8 %	5260
	S	88 %	5 %	7 %	4469
	N	74 %	6 %	20 %	677

Table 2. Bars per perforation plate.

		< 10	No.	10–20	No.	20–40	No.	> 40	No.
Cretaceous	W	17 %	84	25 %	85	28 %	88	13 %	88
	S	24 %	20	30 %	20	27 %	22	0 %	20
	N	14 %	63	23 %	65	29 %	66	16 %	68
Paleocene	W	0 %	23	17 %	23	13 %	23	4 %	23
	S	0 %	10	0 %	10	0 %	10	0 %	10
	N	0 %	13	31 %	13	23 %	13	8 %	13
Eocene	W	10 %	230	10 %	230	10 %	231	3 %	232
	S	2 %	85	2 %	86	1 %	86	0 %	86
	N	14 %	145	14 %	144	15 %	145	6 %	146
Oligocene	W	6 %	189	10 %	184	9 %	185	3 %	185
	S	8 %	26	23 %	26	15 %	27	8 %	26
	N	6 %	163	8 %	158	8 %	158	2 %	159
Miocene	W	6 %	511	7 %	505	4 %	512	3 %	515
	S	2 %	290	3 %	290	2 %	293	2 %	293
	N	11 %	221	12 %	215	7 %	219	3 %	222
Pliocene	W	4 %	249	4 %	248	0 %	248	0 %	250
	S	2 %	183	0 %	182	0 %	183	0 %	183
	N	9 %	66	14 %	66	2 %	65	0 %	67

Table 3. Intervessel pits.

		Alternate	Opposite	Scalariform	No.
Cretaceous	W	44 %	36 %	20 %	98
	S	44 %	22 %	33 %	25
	N	44 %	41 %	15 %	73
Paleocene	W	86 %	11 %	4 %	28
	S	100 %	0 %	0 %	14
	N	71 %	21 %	7 %	14
Eocene	W	78 %	15 %	7 %	245
	S	93 %	5 %	2 %	95
	N	68 %	21 %	11 %	150
Oligocene	W	78 %	14 %	8 %	185
	S	66 %	19 %	16 %	32
	S - trop	100 %	0 %	0 %	17
	S - temp	27 %	40 %	33 %	15
	N	81 %	13 %	6 %	153

(Table 3 continued)		Alternate	Opposite	Scalariform	No.
Miocene	W	87 %	7 %	6 %	502
	S	94 %	4 %	2 %	288
	N	79 %	12 %	10 %	214
Pliocene	W	93 %	5 %	2 %	241
	S	97 %	2 %	2 %	179
	N	84 %	13 %	3 %	62
Recent	W	91 %	5 %	2 %	5260
	S	93 %	2 %	2 %	4469
	N	83 %	8 %	2 %	677

Table 4. Vessel element lengths.

		Short < 350 µm	Medium 350–800 µm	Long > 800 µm	No.
Cretaceous	W	8 %	69 %	23 %	77
	Small axes	3 %	68 %	29 %	31
	'Mixed sizes'	13 %	67 %	20 %	46
	S	18 %	82 %	0 %	11
	N	7 %	67 %	27 %	66
Paleocene	W	43 %	46 %	11 %	24
	S	70 %	30 %	0 %	10
	N	25 %	57 %	18 %	14
Eocene	W	49 %	43 %	8 %	200
	S	59 %	36 %	5 %	74
	N	43 %	48 %	10 %	126
Oligocene	W	57 %	39 %	4 %	113
	S	39 %	55 %	5 %	19
	S-trop	44 %	56 %	0 %	17
	S-temp	50 %	0 %	50 %	2
	N	60 %	36 %	4 %	94
Miocene	W	50 %	46 %	4 %	365
	S	44 %	52 %	4 %	205
	N	58 %	38 %	4 %	160
Pliocene	W	58 %	40 %	2 %	165
	S	58 %	40 %	2 %	134
	N	57 %	40 %	3 %	31
Recent *		< 400	400–800	> 800	No.
	W	32 %	43 %	25 %	600

\* For Recent woods, data for vessel element lengths are from Metcalfe & Chalk (1950: 1361), and are for the dicotyledons as a group, not by region, and the categories for short and medium are slightly different.

Table 5. Fibres.

		Pit borders		No.	Septate	No.
		Minute	Distinct			
Cretaceous	W	48 %	52 %	46	48 %	63
	S	90 %	10 %	10	76 %	17
	N	36 %	64 %	36	37 %	46
Paleocene	W	72 %	28 %	25	26 %	27
	S	85 %	15 %	13	15 %	13
	N	58 %	42 %	12	36 %	14
Eocene	W	77 %	23 %	155	23 %	212
	S	90 %	10 %	52	31 %	83
	N	70 %	30 %	103	18 %	129
Oligocene	W	74 %	26 %	107	14 %	158
	S	73 %	27 %	15	9 %	23
	S-trop	83 %	17 %	12	9 %	23
	S-temp	33 %	66 %	3	14 %	7
	N	74 %	26 %	92	15 %	135
Miocene	W	80 %	20 %	301	22 %	475
	S	89 %	11 %	171	27 %	281
	N	67 %	33 %	130	15 %	194
Pliocene	W	83 %	17 %	150	22 %	215
	S	88 %	12 %	114	26 %	165
	N	67 %	33 %	36	8 %	50
Recent	W	72 %	28 %	5260	20 %	5260
	S	74 %	26 %	4469	22 %	4469
	N	61 %	39 %	677	10 %	677

Table 6. Vessel diameter ( $\mu\text{m}$ ).

		$\leq 50$	50–100	100–200	$\geq 200$	No.
Cretaceous	W	7 %	62 %	27 %	4 %	91
	Small axes	16 %	71 %	13 %	0 %	31
	'Mixed sizes'	2 %	56 %	35 %	6 %	60
	S	5 %	63 %	21 %	11 %	19
	N	7 %	61 %	29 %	3 %	72
Paleocene	W	6 %	19 %	46 %	30 %	35
	S	5 %	17 %	33 %	45 %	21
	N	7 %	21 %	64 %	7 %	14
Eocene	W	12 %	40 %	38 %	10 %	221
	S	5 %	45 %	38 %	12 %	72
	N	15 %	38 %	38 %	9 %	149
Oligocene	W	9 %	30 %	47 %	13 %	170
	S	16 %	24 %	55 %	5 %	31
	S-trop	0 %	5 %	86 %	9 %	21
	S-temp	42 %	50 %	8 %	0 %	12
	N	8 %	32 %	46 %	15 %	139
Miocene	W	8 %	26 %	47 %	20 %	462
	S	4 %	16 %	57 %	22 %	239
	N	11 %	36 %	36 %	17 %	223

(Table 6 continued)		≤ 50	50-100	100-200	≥ 200	No.
Pliocene	W	3 %	24 %	52 %	21 %	198
	S	1 %	20 %	57 %	22 %	140
	N	8 %	34 %	39 %	19 %	58
Recent	W	16 %	39 %	64 %	9 %	5260
	S	12 %	35 %	43 %	10 %	4469
	N	34 %	62 %	3 %	1 %	677

Table 7. Vessel-ray parenchyma pits &amp; tyloses.

		Similar to intervessel	Simple	No.	Tyloses	No.
Cretaceous	W	34 %	66 %	68	42 %	92
	S	19 %	81 %	21	62 %	21
	N	40 %	60 %	47	36 %	72
Paleocene	W	38 %	62 %	13	30 %	23
	S	67 %	33 %	3	0 %	8
	N	36 %	64 %	11	47 %	15
Eocene	W	62 %	38 %	87	32 %	222
	S	71 %	29 %	17	30 %	83
	N	60 %	40 %	70	32 %	139
Oligocene	W	46 %	54 %	63	29 %	193
	S	25 %	75 %	16	75 %	24
	S-trop	57 %	43 %	7	67 %	12
	N	53 %	47 %	47	21 %	181
Miocene	W	62 %	38 %	173	40 %	504
	S	66 %	34 %	80	44 %	289
	N	59 %	41 %	93	35 %	215
Pliocene	W	56 %	44 %	75	35 %	249
	S	68 %	32 %	34	34 %	180
	N	46 %	54 %	41	36 %	69
Recent	W	65 %	35 %		18 %	5260
	S	53 %	37 %		19 %	4469
	N	63 %	27 %		15 %	677

Table 8. Apotracheal diffuse &amp; absent/rare parenchyma.

		Diffuse	No.	Absent/Rare	No.
Cretaceous	W	50 %	96	17 %	94
	S	40 %	25	21 %	24
	N	54 %	71	6 %	70
Paleocene	W	19 %	31	9 %	34
	S	18 %	17	0 %	19
	N	21 %	14	20 %	15
Eocene	W	17 %	232	14 %	232
	S	7 %	90	3 %	93
	N	24 %	142	5 %	139
Oligocene	W	24 %	197	6 %	194
	S	30 %	27	5 %	27
	N	24 %	170	4 %	167



(Table 8 continued)		Diffuse	No.	Absent/Rare	No.
Miocene	W	16 %	534	4 %	529
	S	11 %	314	3 %	310
	N	21 %	220	5 %	219
Pliocene	W	10 %	248	3 %	247
	S	9 %	190	2 %	188
	N	17 %	58	7 %	59
Recent	W	13 %	5260	8 %	5260
	S	12 %	4469	8 %	4469
	N	22 %	677	10 %	677

Table 9. Marginal & paratracheal parenchyma.

	Mrg	No.	Vc.	No.	Alif.	No.	Cf	No.	Bd	No.	
Cretaceous	W	0%	99	8%	92	1%	100	1%	100	2%	98
	S	0%	26	8%	26	4%	27	4%	27	4%	25
	N	0%	73	8%	66	0%	73	0%	73	1%	73
Paleocene	W	10%	29	45%	29	16%	32	12%	33	33%	33
	S	20%	15	40%	15	24%	17	17%	18	56%	18
	N	0%	14	50%	14	7%	15	7%	15	7%	15
Eocene	W	17%	237	39%	229	21%	238	18%	233	23%	240
	S	16%	92	48%	90	22%	90	17%	88	22%	95
	N	18%	146	34%	140	20%	148	19%	145	24%	145
Oligocene	W	18%	207	38%	202	21%	201	22%	199	30%	206
	S	14%	29	34%	29	24%	29	18%	28	26%	31
	S-trop	47%	17	41%	17	31%	16	32%	61	24%	17
	S-temp	17%	12	0%	12	0%	28	17%	12	0%	29
	N	19%	178	39%	173	21%	172	22%	171	31%	175
Miocene	W	25%	531	42%	514	27%	509	25%	502	36%	519
	S	26%	313	45%	303	36%	293	30%	285	40%	301
	N	24%	218	37%	211	14%	216	19%	217	30%	219
Pliocene	W	25%	236	47%	236	34%	231	29%	222	39%	236
	S	27%	180	49%	180	39%	177	32%	169	40%	182
	N	15%	53	41%	56	17%	54	21%	53	38%	55
Recent	W	12%*		35%		27%*		*		31%	
	S	11%		36%		30%		*		34%	
	N	21%		30%		13%		*		17%	

\* Mrg = marginal, Vc = vasicentric, Alif. = aliform, Cf = confluent, Bd = banded.  
 For Recent woods % = combined percentage for aliform and confluent parenchyma.

Table 10. Ray structure.

	Heterocellular	Heterocellular + Homocellular	Homocellular	No.
Cretaceous	W	92 %	4 %	89
	S	91 %	4 %	23
	N	92 %	5 %	66
Paleocene	W	82 %	9 %	33
	S	83 %	6 %	18
	N	80 %	13 %	15

(Table 10 continued)		Heterocellular	Heterocellular + Homocellular	Homocellular	No.
Eocene	W	70 %	9 %	21 %	219
	S	70 %	10 %	20 %	84
	N	70 %	9 %	21 %	135
Oligocene	W	61 %	4 %	36 %	180
	S	63 %	7 %	30 %	27
	N	60 %	3 %	37 %	153
Miocene	W	54 %	8 %	39 %	496
	S	53 %	10 %	37 %	292
	N	54 %	5 %	41 %	204
Pliocene	W	43 %	14 %	42 %	222
	S	48 %	15 %	38 %	170
	N	31 %	14 %	55 %	52
Recent	W	72 %	6 %	22 %	5260
	S	73 %	5 %	22 %	4469
	N	68 %	9 %	23 %	677

Table 11. Number of upright/square marginal rows in heterocellular rays.

		1 row	No.	2-4	No.	> 4	No.
Cretaceous	W	50 %	52	54 %	54	35 %	60
	S	50 %	10	64 %	14	47 %	17
	N	50 %	42	50 %	40	30 %	43
Paleocene	W	64 %	22	53 %	17	10 %	21
	S	56 %	9	22 %	9	10 %	10
	N	69 %	13	88 %	8	9 %	11
Eocene	W	45 %	157	41 %	152	15 %	181
	S	40 %	43	41 %	46	12 %	60
	N	47 %	114	41 %	106	17 %	121
Oligocene	W	31 %	131	19 %	139	9 %	156
	S	20 %	20	26 %	23	22 %	27
	N	32 %	111	17 %	116	6 %	129
Miocene	W	43 %	429	29 %	414	9 %	464
	S	45 %	246	32 %	235	10 %	270
	N	39 %	183	26 %	179	7 %	194
Pliocene	W	39 %	201	23 %	199	7 %	227
	S	43 %	145	30 %	141	9 %	164
	N	29 %	56	7 %	58	3 %	63

Table 12. Ray sizes: exclusively uniseriate (1s) and of two distinct sizes.

		1s	No.	2 sizes	No.
Cretaceous	W	4 %	96	2 %	91
	S	4 %	25	0 %	22
	N	4 %	71	3 %	69
Paleocene	W	9 %	32	14 %	28
	S	18 %	17	7 %	15
	N	0 %	15	23 %	13

(Table 12 continued)		1 s	No.	2 sizes	No.
Eocene	W	14 %	249	9 %	222
	S	15 %	97	7 %	82
	N	13 %	152	10 %	140
Oligocene	W	6 %	207	13 %	205
	S	4 %	27	3 %	31
	S-trop	6 %	16	5 %	20
	S-temp	0 %	11	0 %	11
	N	7 %	180	14 %	174
Miocene	W	14 %	532	7 %	530
	S	18 %	299	3 %	314
	N	10 %	233	13 %	216
Pliocene	W	22 %	263	9 %	259
	S	23 %	187	4 %	188
	N	20 %	76	23 %	71
Recent	W	13 %	5260	11 %	5260
	S	14 %	4469	11 %	4469
	N	7 %	677	13 %	677

Table 13. Storied structure.

		Rays	Rays + Par.*	Par.	No.	Total storied
Cretaceous	W	0 %	0 %	0 %	93	0 %
	S	0 %	0 %	0 %	21	0 %
	N	0 %	0 %	0 %	72	0 %
Paleocene	W	0 %	3 %	0 %	29	3 %
	S	0 %	7 %	0 %	15	7 %
	N	0 %	0 %	0 %	14	0 %
Eocene	W	0 %	1 %	2 %	232	4 %
	S	1 %	1 %	3 %	91	5 %
	N	0 %	1 %	1 %	141	3 %
Oligocene	W	1 %	2 %	2 %	192	4 %
	S	0 %	3 %	0 %	34	3 %
	N	1 %	1 %	2 %	158	4 %
Miocene	W	2 %	4 %	2 %	525	8 %
	S	2 %	7 %	1 %	299	9 %
	N	1 %	1 %	3 %	226	5 %
Pliocene	W	2 %	5 %	3 %	240	10 %
	S	2 %	7 %	2 %	174	11 %
	N	2 %	0 %	8 %	66	9 %
Recent	W	2 %	6 %	6 %	5260	13 %
	S	2 %	7 %	5 %	4469	13 %
	N	1 %	1 %	10 %	677	12 %

\* Par. = Axial parenchyma.

Table 14. Distinct helical thickenings in vessel elements.

		No.				No.	
Cretaceous	W	0 %	94	Miocene	W	9 %	522
	S	0 %	24		S	1 %	307
	N	0 %	70		N	20 %	215
Paleocene	W	0 %	24	Pliocene	W	5 %	254
	S	0 %	9		S	0 %	184
	N	0 %	15		N	17 %	70
Eocene	W	4 %	230	Recent	W	9 %	5260
	S	0 %	87		S	4 %	4469
	N	6 %	143		N	45 %	677
Oligocene	W	11 %	177				
	S	4 %	28				
	N	12 %	149				

Table 15. Porosity.

		Ring	Semi-ring	Diffuse	No.
Cretaceous	W	0 %	1 %	99 %	98
	S	0 %	0 %	100 %	27
	N	0 %	1 %	99 %	71
Paleocene	W	0 %	3 %	97 %	36
	S	0 %	0 %	100 %	21
	N	0 %	7 %	93 %	15
Eocene	W	2 %	7 %	91 %	246
	S	0 %	2 %	98 %	98
	N	3 %	10 %	86 %	148
Oligocene	W	8 %	6 %	86 %	214
	S	3 %	6 %	91 %	32
	S-trop	0 %	9 %	91 %	21
	S-temp	8 %	8 %	83 %	11
	N	9 %	6 %	85 %	182
Miocene	W	8 %	7 %	85 %	551
	S	1 %	3 %	95 %	313
	N	17 %	13 %	71 %	238
Pliocene	W	9 %	4 %	87 %	260
	S	1 %	3 %	96 %	187
	N	29 %	8 %	64 %	73
Recent	W	4 %	5 %	91 %	5260
	S	1 %	3 %	96 %	4469
	N	24 %	21 %	55 %	677

Table 16. Vessel arrangement.

		Tangential		Diagonal		Dendritic	
		No.		No.		No.	
Cretaceous	W	0 %	98	2 %	96	0 %	98
	S	0 %	25	4 %	26	0 %	25
	N	0 %	73	1 %	70	0 %	73
Paleocene	W	0 %	35	3 %	37	0 %	37
	S	0 %	22	5 %	22	0 %	22
	N	0 %	13	0 %	15	0 %	15
Eocene	W	0 %	245	9 %	241	1 %	250
	S	0 %	98	4 %	98	0 %	99
	N	1 %	147	12 %	143	2 %	151
Oligocene	W	1 %	216	8 %	204	2 %	213
	S	0 %	31	3 %	32	0 %	31
	N	2 %	185	9 %	172	2 %	182
Miocene	W	3 %	551	7 %	533	3 %	552
	S	0 %	317	5 %	307	1 %	317
	N	6 %	234	9 %	226	5 %	235
Pliocene	W	1 %	264	7 %	251	1 %	259
	S	0 %	191	3 %	186	1 %	191
	N	4 %	73	19 %	65	3 %	68
Recent	W	4 %		12 %*			5260
	S	2 %		11 %*			4469
	N	13 %		16 %*			677

\* For Recent flora, diagonal and dendritic are recorded together, and not as separate character states.

Table 17. Growth rings.

		Distinct	Indistinct	No.			Distinct	Indistinct	No.
Cretaceous	W	10 %	90 %	79	Miocene	W	49 %	51 %	493
	S	4 %	96 %	23		S	36 %	64 %	297
	N	13 %	88 %	56		N	68 %	32 %	196
Paleocene	W	36 %	64 %	28	Pliocene	W	45 %	55 %	238
	S	40 %	60 %	15		S	34 %	66 %	174
	N	31 %	69 %	13		N	75 %	25 %	64
Eocene	E	47 %	53 %	219	Recent	W	22 %	78 %	5260
	S	24 %	76 %	83		S	15 %	85 %	4469
	N	61 %	39 %	136		N	62 %	38 %	677
Oligocene	W	54 %	46 %	187					
	S	52 %	48 %	23					
	S-trop.	33 %	66 %	12					
	S-temp.	73 %	27 %	11					
	N	54 %	46 %	164					

Table 18. Vessel groups.

		Exclusively solitary		Rm's 4+ *common		Clusters common	
		No.		No.		No.	
Cretaceous	W	27 %	93	0 %	96	0 %	93
	S	8 %	24	0 %	25	0 %	21
	N	33 %	69	0 %	71	0 %	72
Paleocene	W	15 %	34	3 %	37	0 %	37
	S	15 %	20	5 %	22	0 %	22
	N	14 %	14	0 %	15	0 %	15
Eocene	W	11 %	230	5 %	228	2 %	228
	S	4 %	92	2 %	91	1 %	91
	N	16 %	138	7 %	137	2 %	137
Oligocene	W	14 %	196	4 %	206	1 %	206
	S	11 %	28	7 %	31	0 %	31
	N	15 %	168	4 %	175	2 %	175
Miocene	W	10 %	508	4 %	535	4 %	535
	S	6 %	294	4 %	307	0 %	307
	N	17 %	214	4 %	228	9 %	228
Pliocene	W	10 %	248	6 %	255	2 %	260
	S	6 %	177	4 %	184	0 %	188
	N	21 %	71	11 %	71	8 %	72
Recent	W	14 %		12 %		12 %	
	S	14 %		12 %		9 %	
	N	16 %		12 %		26 %	

\* Rm's 4+ = radial multiples of 4 or more.

Table 19. Vessels per square mm.

		< 5	5-20	20-40	40-100	> 100	No.
Cretaceous	W	18 %	36 %	18 %	28 %	0 %	36
	S	18 %	15 %	20 %	48 %	0 %	20
	N	19 %	63 %	16 %	3 %	0 %	16
Paleocene	W	21 %	48 %	8 %	20 %	3 %	36
	S	20 %	53 %	5 %	23 %	0 %	20
	N	22 %	44 %	13 %	16 %	6 %	16
Eocene	W	16 %	42 %	17 %	17 %	8 %	206
	S	20 %	52 %	17 %	10 %	1 %	87
	N	14 %	35 %	17 %	22 %	13 %	120
Oligocene	W	24 %	40 %	12 %	11 %	13 %	149
	S	14 %	40 %	19 %	3 %	24 %	29
	S-trop	26 %	57 %	17 %	0 %	0 %	23
	S-temp	0 %	20 %	0 %	10 %	70 %	10
	N	27 %	40 %	11 %	13 %	10 %	120
Miocene	W	27 %	51 %	10 %	6 %	5 %	417
	S	31 %	57 %	6 %	2 %	4 %	281
	N	19 %	41 %	18 %	15 %	7 %	137
Pliocene	W	32 %	51 %	9 %	3 %	4 %	215
	S	34 %	55 %	8 %	2 %	1 %	174
	N	24 %	38 %	12 %	12 %	15 %	43

(Table 19 continued)		< 5	5–20	20–40	40–100	> 100	No.
Recent					≥ 40		
	W	24 %	49 %	10 %	17 %*		
	S	27 %	55 %	7 %	11 %*		
	N	4 %	10 %	36 %	50 %*		

\* For Recent woods this percentage is for wood with > 40 per sq. mm and includes both 40–100 and > 100 per sq. mm.

Table 20. Vasicentric and vascular tracheids.

		No.				No.	
Cretaceous	W	4%	92	Miocene	W	14%	487
	S	0%	24		S	14%	300
	N	6%	68		N	14%	187
Paleocene	W	5%	21	Pliocene	W	14%	242
	S	13%	8		S	10%	181
	N	0%	13		N	26%	61
Eocene	W	8%	226	Recent	W	9%	5260
	S	6%	85		S	8%	4469
	N	9%	141		N	18%	677
Oligocene	W	16%	165				
	S	7%	28				
	N	18%	137				

Table 21. Canals.

		Radial	No.	Axial	No.
Cretaceous	W	0 %	98	0 %	98
	S	0 %	25	0 %	25
	N	0 %	73	0 %	73
Paleocene	W	0 %	35	0 %	36
	S	0 %	20	0 %	21
	N	0 %	15	0 %	15
Eocene	W	2 %	247	4 %	251
	S	0 %	97	2 %	98
	N	3 %	150	5 %	153
Oligocene	W	5 %	204	1 %	206
	S	6 %	32	0 %	32
	N	5 %	172	1 %	174
Miocene	W	9 %	548	4 %	552
	S	13 %	315	7 %	318
	N	4 %	233	1 %	234
Pliocene	W	12 %	255	3 %	258
	S	15 %	189	4 %	191
	N	3 %	66	0 %	67
Recent	W	3 %	5260	6 %	5260
	S	4 %	4469	7 %	4469
	N	1 %	677	3 %	677

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## APPENDIX

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