

Under the microscope: plant anatomy and systematics.
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Fossil angiosperm wood: its role in the reconstruction of biodiversity and palaeoenvironment

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Fossil wood is subject to different taphonomic, sampling and recognition biases in the palaeobotanical record when compared with leaves and palynomorphs. Wood therefore provides a systematically independent source of information that can increase our knowledge of past biodiversity and environments. Increase in fossil wood records from Cretaceous and Tertiary sediments helps further the understanding of trends in anatomical specialization through geological time. These data can then be used to distinguish such specialization from anatomical response to environmental change. Two case studies, a Late Cretaceous early Tertiary wood flora from Antarctica and a lower Tertiary wood flora from southern England, have been used to exemplify the importance of studying the fossil wood component of palaeofloras.

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ADDITIONAL KEY WORDS:—anatomy – Cretaceous – palaeobotany – Tertiary – xylem.

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INTRODUCTION

The evolution, diversification and radiation of angiosperms in conjunction with their adaptations to the environment is becoming increasingly understood through complementary studies of fossil organs and their modern counterparts (see Crane, Friis & Pedersen, 1995). Inasmuch as vegetation is an accurate indicator of climate

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and other environmental factors on land adjacent to the basin of deposition (Traverse, 1999), fossil remains can be used to interpret environmental and systematic trends. The fossil record for any one organ has limitations. Different organ types are subject to diverse taphonomic, sampling and recognition biases; different environments and taxa have dissimilar preservation potentials. Each organ type is an independent entity from which complementary information can be gathered and which together help in the understanding of ecology through the geological past.

Different taphonomic factors govern the occurrence of different plant organs such that biases are built into all fossil floras. The fossil record for leaves, pollen, fruits and seeds is often well represented and well used, although any organ not found with source sediments can give problems with age determinations (Wheeler & Baas, 1991). Fruits, seeds and leaves tend to be biased in favour of larger, more robust, specimens and also those whose parent plants were in close proximity to water channels (i.e. representing a localized, and possibly more riparian, vegetation). The pollen component can be biased in favour of wind pollinated, rather than insect pollinated, parent plants (Wodehouse, 1935) and is likely to represent a more regional flora than the associated leaf, fruit or seed flora (Chaloner, 1968). Moreover, not all taxa in a flora are represented in the dispersed pollen assemblage, and not all assemblages contain pollen taxa (Traverse, 1994). Therefore, one particular organ type will not necessarily accurately reflect the source of vegetation.

Superimposed upon the taphonomic bias there is a preservational bias. The preservation potential of different organs can vary from family to family. Some organs are more likely to undergo petrification; leaves *per se* are very rarely permineralized whereas wood often is. All organ types can be subject to loss of diagnostic characters through poor preservation (e.g. Page, 1979). Some sedimentary settings are better for organ preservation than others. A preserved flora therefore might be interpreted as indicating a substantial change in, for example, palaeoatmospheric composition or abundance of certain taxa when it may simply be reflecting preservational bias.

Wood is a resistant material that fossilizes by permineralization, petrification, charcoalification and incorporation into peats and lignites (Creber & Chaloner, 1984). Fossil wood is abundant but often under-utilized as a source of information (Wheeler & Baas, 1991). As wood is not a means for dispersal, the representation of such specimens in a fossil flora is somewhat more opportunistic than for other organs. The wood component of a fossil flora is likely to be biased in favour of trees and shrubs that grew relatively locally and near water courses. The abundance of wood in many fossil floras world-wide has potential to provide information concerning the biodiversity and palaeoenvironment of a region. Conifer wood is relatively simple with a single axial cell type, the longitudinal tracheid, for support and water conduction. Growth ring characteristics of fossil conifer wood have been used extensively as a source of information about seasonality, lengths of growing season, limiting temperatures and forest productivity in the geological past (Creber, 1977; Creber & Francis, 1999). Dicotyledonous angiosperm wood exhibits a division of labour with perforate vessel elements for water conduction and imperforate fibres for support (Wilson & White, 1986). Unlike conifer wood, fossil dicotyledonous wood characters have not been used extensively in reconstructing climate and climate change in the geological past (Wheeler & Baas, 1993). Nevertheless the potential to do so is great. Recently, dicotyledonous wood anatomical features have been used to determine climate variables such as temperature, growing conditions,

water availability and, to a lesser extent, precipitation (e.g. Woodcock & Ignas, 1994; Wiemann *et al.*, 1998). This has highlighted the potential of using wood physiognomy to determine terrestrial palaeoclimatic signals from fossil floras (e.g. Woodcock & Ignas, 1994; Wiemann, Manchester & Wheeler, 1999). Identification of the wood from thorough comparisons with modern material (such comparisons are essential and cannot be over-emphasized) provides detailed information on biodiversity and vegetational composition of fossil floras. If extrapolation of a fossil organ or assemblage to its closest living analogue is possible, then the climatic requirements of that fossil organ or assemblage can be assumed to be close to those of the nearest living relative. This Nearest Living Relative (NLR) approach provides one of the best methods for palaeoclimatic reconstructions especially for the late Palaeogene and Neogene (Mosbrugger, 1999) but further back into the geological past, relationships between modern and fossil taxa become more tentative and render this technique less effective. A similar technique, the Coexistence Approach, developed by Mosbrugger & Utescher (1997), uses nearest living relatives and their climatic requirements to determine the reconstruction of up to ten different climatic parameters for a given fossil flora with a minimum of *c.* 10 taxa. The anatomical approach coupled with the Coexistence Approach and Nearest Living Relative techniques can provide important palaeoecological data which supplement those obtained from leaves and pollen when other organ types are present.

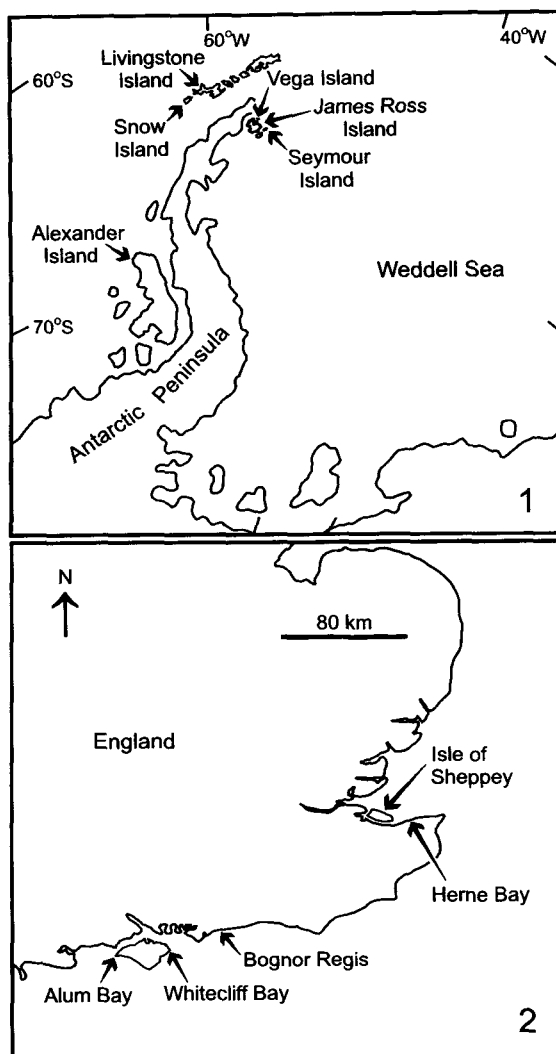
Two examples of wood floras: (i) the high latitude Late Cretaceous–early Tertiary silicified and calcified wood flora from the northern Peninsula region of Antarctica (Fig. 1) and (ii) the Lower Tertiary London Clay pyritized and calcified wood flora from south-east England, (Fig. 2) have been used to demonstrate the importance of studying fossil wood to form a more complete picture of past biodiversity and ecology.

CASE STUDIES

Late Cretaceous–early Tertiary wood flora from the northern peninsula region of Antarctica

Plant fossils preserved in the Cretaceous and Tertiary rocks of Antarctica provide information on the vegetation that covered this continent at a palaeolatitude of between 60 and 65°S. This was a crucial stage in the evolution, diversification and radiation of angiosperms throughout the Southern Hemisphere at a time when the Gondwanan supercontinent was gradually breaking up.

Antarctica is the only major isolated land mass on which there is no reasonably diverse extant terrestrial vegetation. Palaeobotanical data, therefore, are critical for evaluating the biotic relationships of this land mass and for the full understanding of austral biogeography (Drinnan & Crane, 1990). Leaves from the Antarctic Peninsula are often preserved as impressions with no cuticle to help in the systematic identification. The permineralized wood from this region appears to be more abundant than the leaves. Generally, the wood has undergone relatively little compression and the fine anatomical details needed for identification have been excellently preserved (Figs 3–11). The palaeobotanical record of Cretaceous angiosperm wood is relatively poor (Herendeen, 1991) especially in the Southern Hemisphere. Further collections of angiosperm wood from Antarctica will help to



Figures 1, 2. Locality maps of (1) the northern Antarctic Peninsula region showing the major fossil wood localities; (2) the south-east of England indicating the major fossil localities where the London Clay outcrops.

redress the Northern- *versus* Southern Hemisphere bias, increase our understanding of high latitude Southern Hemisphere Cretaceous floras, and enable comparisons with other wood floras in other regions. Studies of this wood flora provide an opportunity to increase the existing knowledge of the biodiversity and palaeoclimate at high (southern) latitudes where there is no modern analogue.

Angiosperm spread to southern Gondwana was probably via Africa and South America, during the latest Barremian-Aptian, with herbaceous or shrubby taxa in the first wave (Dettman, 1994) followed by a second wave during Middle Albian–Cenomanian (Brenner, 1976). Migration into southern Gondwana (Australia, Antarctica, southern South America) continued via southern South America

to the Austro-Antarctic region during the remainder of the Cretaceous (Turonian–Maastrichtian) with differentiation from Northern Gondwanan lineages in the southern high latitudes (Dettman, 1992). Such diversification was concurrent with volcanic and tectonic activity. The Antarctic Peninsula region (Fig. 1) where Cretaceous and Tertiary floras are mainly found today was an active volcanic arc covered in forests. Wood, leaves, pollen and other organic remains would have been carried into the eastern back-arc basin (James Ross Basin) and deposited within shallow marine sediment (e.g. James Ross Island, Late Cretaceous–Albian to Early Tertiary–Palaeocene and Seymour Island, Late Cretaceous and Tertiary). Fossil wood also accumulated in inter-arc (e.g. Snow Island, Early–mid Cretaceous, Aptian and Livingston Island, Late Cretaceous) and fore-arc settings (e.g. Alexander Island, mid Cretaceous).

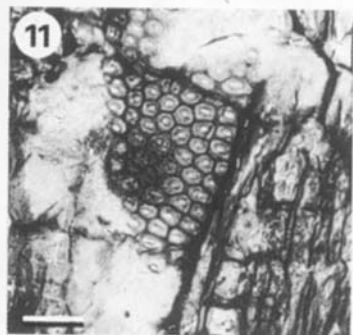
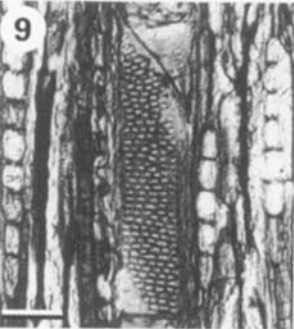
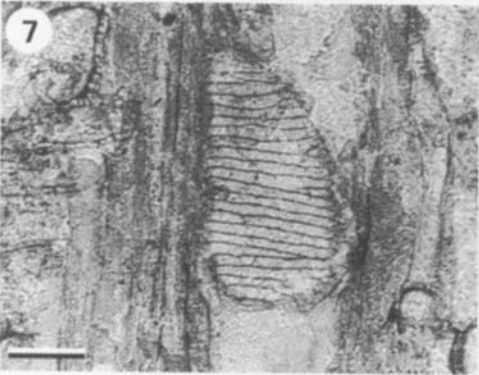
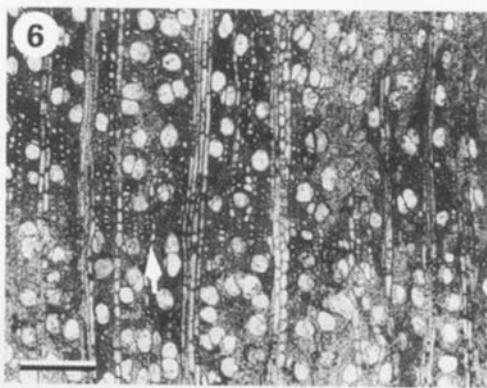
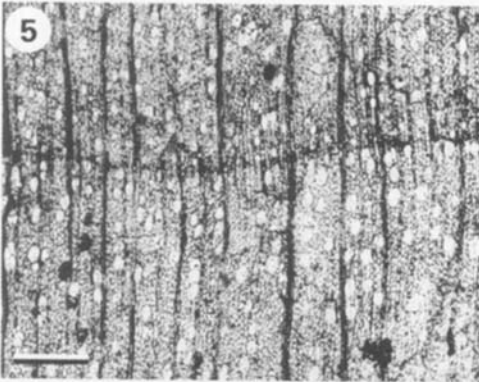
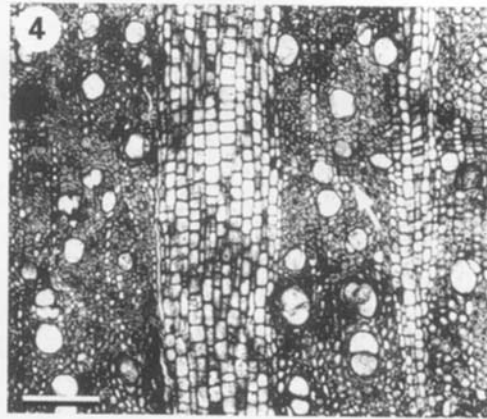
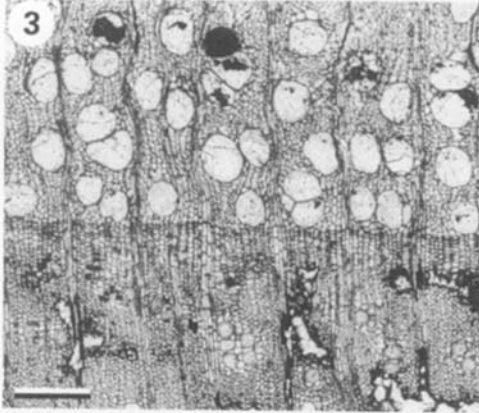
Table 1 summarizes the Late Cretaceous and early Tertiary angiosperm wood flora from the northern Peninsula region of Antarctica in conjunction with the modern distribution of the putative nearest living relative of each taxon. Although not all the woods listed in Table 1 represent the first record at family level in the Antarctic flora, systematic studies of the woods have provided earliest records of some known taxa.

Such records help further the understanding of angiosperm radiation. Examples of these earliest records include:

(1) *Winteraceae*. Fossil wood of the Winteraceae (Poole & Francis, 2000) has been found in mid-late Santonian to early Campanian sediments (Crame *et al.*, 1991; Keating, 1992). The existing pollen (Cranwell, 1959) and leaves (Dusén, 1908) document the Winteraceae as only having a Tertiary record in Antarctica. However, Winteraceae pollen is known also from the Upper Cretaceous (Lower Campanian) sediments of southeastern Australia and New Zealand in floras very similar to the palaeofloras found in Antarctica (Dettmann, 1989).

(2) *Cunoniaceae*. The identification of cunoniaceous material with anatomy similar to extant *Weinmannia* L. (Poole *et al.*, in press) is derived from Coniacian to Santonian and mid-late Santonian to early Campanian sediments on James Ross Island, and from Williams Point on Livingston Island (probably Cenomanian to Campanian in age; Chapman & Smellie, 1992). Leaf and pollen of the Cunoniaceae is known in the Antarctic Peninsula from the beginning of the Maastrichtian to the end of the Eocene (Askin, 1992). The recognition of Santonian to Campanian cunoniaceous-like wood may extend the fossil record of this family by *c.* 10 Ma.

(3) *Lauraceae*. Lauraceous pollen has a poor preservation potential due to little sporopollenin (Stone, 1987 and references therein) and does not have a Cretaceous record (Muller, 1981). The macrofossil record is better. Cantrill & Nichols (1996) reported leaves with lauraceous features from the Late Albian of Antarctica which is probably the oldest record of this family in the Southern Hemisphere. Wood may provide more reliable data for this family. Fossil lauraceous woods described early last century have been reviewed (e.g. Süss, 1958) and many of the early reports of fossil Lauraceae have dubious relationships with this family. One lauraceous wood from Antarctica has anatomy similar to the extant genus *Sassafras* Nees & Eberm. (Poole, Richter & Francis, in press). This wood morphotype found in Santonian to Campanian sediments from the James Ross Basin is ring porous with scalariform perforation plates in some latewood vessel elements, and has oil cells associated with



ray cells (Fig. 5). Today *Sassafras* is restricted to the Northern Hemisphere (East Asia and North America). This fossil wood suggests that the genus might have been more widespread in the geological past. Its presence in the Antarctic Peninsula represents the earliest occurrence of fossil wood with anatomical similarity closest to extant *Sassafras*.

(4) *Nothofagaceae*. Taxa in this family produce copious, distinctive pollen that is widespread and abundant within the fossil record of the Southern Hemisphere. The family is postulated to have originated in southern Gondwana during the Campanian (Dettman, 1992). This family is amply represented in the macro and microfloras from the Antarctic Peninsula (e.g. Hayes, 2000; Hill & Jordan, 1993 and the references therein; Torres & Lemoigne, 1988; Poole, in prep.). Further studies of the woods will help determine the timing of appearance of different sections/subgenera and the evolutionary history of *Nothofagus* Blume as different types of nothofagaceous-like wood have been recognized (e.g. Nishida, Nishida & Ohsawa, 1989; Torres & Lemoigne, 1988; Poole, in prep.).

Monimiaceae. Monimiaceous pollen is widespread in the Barremian and Aptian of Gondwana but the macrofossil record begins with leaves from the Palaeogene of Antarctica (Zastawniak, 1966). The wood flora contains monimiaceous material from the Coniacian/Santonian of James Ross Island that shows anatomical similarity to extant *Hedycarya* J.R. Forst. & G. Forst. and *Tambourissa* Sonn. (Poole & Gottwald, submitted). The wood may document the earliest occurrence of this family in Antarctica.

First records of families or ancestors to modern families have been identified from the wood flora. Such records increase our knowledge of the diversity of the high latitude palaeoflora of southern Gondwana during the Cretaceous. Examples of these records include:

Atherospermataceae. Atherospermataceous woods have been found in Coniacian/Santonian and Campanian sediments from James Ross Island (Poole & Francis, 1999). Other atherospermataceous fossils have been found in the Southern Hemisphere e.g. South America (Nishida, 1984; Nishida, Nishida & Nasa, 1988), Australia (Collinson, Boulter & Holmes, 1993; Hill & Macphail, 1985) and Antarctica (Dusén, 1908), but all are younger by at least *c.* 10 Myr than the Antarctic woods.

Illiciaceae. Wood with very close anatomical similarity to extant *Illicium* L. (Poole, Gottwald & Francis, 2000) from Coniacian/Santonian sediments on James Ross Island may represent the earliest record of this family in the Southern Hemisphere

Figures 3–11. Examples of a selection of the anatomical characters discussed in text as illustrated by Antarctic fossil wood. Fig. 3. Small diameter latewood vessels and large diameter earlywood vessels in Cretaceous wood (DJ1051.5) of *Sassafrasoxylon* (Lauraceae). Fig. 4. Diffuse porosity in Cretaceous wood (DJ134.30) with growth ring boundary indicated. Fig. 5. Distinct growth ring in Cretaceous wood (DJ1053.31). Fig. 6. Indistinct growth ring (arrow) in Cretaceous wood (DJ463.3). Fig. 7. Scleriform perforation plate in Cretaceous wood (DJ458.4). Fig. 8. Simple perforation plate in Tertiary wood (D494.2). Fig. 9. Generally opposite intervessel pitting in Cretaceous wood (A197/2). Fig. 10. Opposite to transitional intervessel pitting in Cretaceous wood (A197/2). Fig. 11. Bordered alternate intervessel pitting in Cretaceous wood (51.8). Scale bars: Figs 3, 4 = 250 μ m; 5 = 400 μ m; 6 = 500 μ m; 7, 11 = 40 μ m; 8 = 20 μ m; 9, 10 = 60 μ m.

TABLE 1. Summary of the fossil wood taxa described from Cretaceous and Tertiary sediments of Antarctica. 'From Mabblerley (1997) and Heywood (1998)

Taxon	Affinity based on wood characters	Locality	Age	New record of family in the Antarctic flora	Modern distribution of closest modern taxa' (NLR)
<i>Laurelites jamesrossi</i> Poole & Francis, 1999	Atherospermataceae: <i>Laurelopsis</i> Schodde	James Ross Island	Cretaceous	✓	temperate South America to Australasia and in valleys with subtropical aspects
<i>Atherospermoxylon</i> sp. (Poole & Gottwald, submitted)	Atherospermataceae: <i>Daphnanandra</i> Benth., <i>Laurelia</i> Juss.	Seymour and Vega Islands	Cretaceous and Tertiary	(✓)	temperate South America to Australasia and in valleys with subtropical aspects
<i>Weinmannioxylon nordenskiöldii</i> Petriella (Poole <i>et al.</i> , 2000)	Cunoniaceae	James Ross and Livingston Islands	Cretaceous	×	warm temperate, some subtropical
<i>Illiciomylon</i> species (Poole, Gottwald & Francis, 2000)	Illiciaceae: <i>Illicium</i>	James Ross, Vega and Seymour Islands	Cretaceous and Tertiary	✓	subtropical and warm temperate
<i>Sassafrasoxylon gottwaldii</i> Poole, Richter & Francis, (2000)	Lauraceae: <i>Sassafras</i>	James Ross and Seymour Islands	Cretaceous	×	subtropical and temperate
<i>Hedycoxyxylon</i> sp. (Poole & Gottwald, submitted)	Monimiaceae: <i>Hedycoxya</i> , <i>Tambourissa</i>	James Ross and Livingston Islands	Cretaceous	×	subtropical and warm temperate
<i>Wintexylon jamesrossii</i> Poole & Francis, 2000	Winteraceae: <i>Bubbia</i> Teigh., <i>Tasmanium</i> DC.	James Ross Island	Cretaceous	×	tropics to cool temperate
<i>Nothofagoxylon</i> species (e.g. Nishida <i>et al.</i> , 1989, Torres & Lemoigne, 1988, Poole, work in progress)	Nothofagaceae	northern Antarctic Peninsula region	Cretaceous and Tertiary	×	subtropics and temperate

as only Cretaceous seeds and Tertiary wood from the Northern Hemisphere have been recorded to date (e.g. Frumin & Friis, 1999; Gottwald, 1992).

The wood flora has enhanced our understanding of the composition and development of a unique vegetation that existed in high latitude southern Gondwana from the Late Cretaceous, across the Cretaceous/Tertiary boundary and into the early Tertiary. Using the Nearest Living Relative approach, the presence of warm temperate/subtropical taxa, such as the Illiciaceae, Lauraceae, some Nothofagaceae and Monimiaceae alongside more cool temperate taxa such as Winteraceae, Athero-spermataceae and certain Nothofagaceae helps to confirm ideas of warm, humid climates and suggested mean annual temperatures ranging from 13–27°C in the Albian (Cantrill, 1995) to 8–15°C during the Maastrichtian (Askin, 1992) and 10–12°C in the early Tertiary (Li, 1992; Birkenmajer & Zastawniak, 1989; Dingle & Lavelle, 1998) before the onset of cooler and/or more seasonal climates during the Eocene (Askin, 1992).

Early Tertiary wood flora from southern England

After the Cretaceous-Tertiary boundary, the newly evolved taxa that had appeared during the Late Cretaceous spread rapidly across the Northern Hemisphere during a period of equable climate (Tiffney, 1985). The Northern Hemisphere flora consisted of a mixture of taxa, whose modern counterparts occur in widely separated habitats ranging from deciduous northern hardwood forests to paratropical and tropical rain forests, particularly southeastern Asia and Malaysia (Tiffney, 1985). This flora had a northern geography and thermophilic affinities and has been termed 'boreotropical' (Wolfe, 1975, 1977). The Eocene London Clay flora from southern England is a classic example of a boreotropical flora and represents one of the most varied, and the only diverse, flora from lower Eocene strata in Europe (Collinson, 1983). The London Clay flora, with approximately 145 extant and extinct genera placed in living families, shares similarities with smaller floras from this period in Europe and North America and suggests that a belt of similar vegetation may have extended across the Northern Hemisphere during the lower and early middle Eocene (Collinson, 1983).

The London Clay flora is thought to have been derived from the vegetation covering low lying land at least 80 km from the site of deposition at a palaeolatitude of 41°N (Wells & Kirkaldy, 1956; Dewey, 1958; Daley, 1972; Plaziat, 1981; Smith, Hurley & Briden, 1981). The organic matter was transported by river systems, from many different zones of the contemporaneous vegetation that existed within the catchment areas, and deposited in the London Basin which eventually gave rise to the London Clay deposits (Collinson, 1983).

The fruit and seed component has been the subject of considerable study over the last two centuries (e.g. Bowerbank, 1840; Reid & Chandler, 1933; Chandler, 1961, 1964, 1978; Collinson, 1983) and has provided a huge systematic database with over 500 plant types and some 350 named species (Collinson, 1983) mostly with Indo-Malaysian affinities. The pollen and spores component (Sein, 1961a, b; Machin, 1971) has, in turn, complemented and increased the diversity. The continual search for new taxa over such a long period of time might be supposed to have exhausted the riches of this flora (Chandler, 1978) but investigations of the wood component are beginning to reveal taxa as yet unknown in the fruit and seed flora.

The wood forms a major constituent of this flora but has been studied comparatively little. Both mature and small diameter ('twig') axes are represented with the latter constituting the major fossil type. More studies focusing on the wood component will help in elucidating the composition of this boreotropical vegetation.

Table 2 presents a summary of the published angiosperm wood taxa described from *c.* 30 wood and twig morphotypes known from the Eocene London Clay (Poole, 1993a; Crawley, in press; references cited in legend to Table 2). Modern distributions of the nearest living relative of each taxon have also been included for palaeoclimatic inferences. Although not all the woods listed in Table 2 represent the first record at family level in the London Clay flora, some (e.g. Vitaceae, Sapindaceae elements) are new additions below family level. All the records provide significant information concerning the diversity of the vegetation that covered southern England during the lower Eocene. Using the Nearest Living Relative approach, evidence from the wood flora supports a postulated paratropical environment. Based on oxygen isotope measurements a temperature of between 20° and 27°C has been suggested (Buchardt, 1978). Forty-two percent of the elements from the total flora are temperate (e.g. *Pinus*, *Myrica*, *Rubus*), which implies that a tropical, frostless climate with high non-seasonal rainfall and a mean annual temperature above 25°C is an overestimation and that conditions were cooler (Collinson, 1983). Seasonality has been suggested from initial surveys of the wood flora (Scott & de Klerk, 1974; Collinson, 1983) although the log and angiosperm twig woods usually have growth rings that are indistinct or lacking (Poole, 1999; Crawley, in press) which may be indicative of a more tropical flora. However, growth ring data need careful analysis as growth rings can vary according to genera rather than climate (Détienne, 1989).

Using the floristic components of the London Clay flora it has been suggested that rainforest of paratropical regions today provide the closest modern analogue (Reid & Chandler, 1933; Collinson, 1983). The lack of dipterocarpaceous fruits and seeds in the London Clay flora was used to support the hypothesis that there was no exact living counterpart. The dipterocarps make up a significant proportion of the Southeast Asian rainforests and it is surprising that no record of this family had been found in the fruit and seed flora. Poole (1993b), however, described dipterocarpaceous wood from the London Clay flora thus strengthening the Indo-Malaysian affinity for this fossil flora (new, undescribed dipterocarpaceous material, has also been found on subsequent visits to the Isle of Sheppey). Elements found in the wood flora also serve to illustrate that certain taxa, such as the Cercidiphyllaceae, were once widespread across the Northern Hemisphere in the geological past (Crane, 1984 and references therein). Inclusion of the data that can be obtained from the abundant wood component of the London Clay flora will contribute to a greater understanding of the biodiversity and prevailing climate in southern England and increase our knowledge concerning Lower Eocene boreotropical floras.

Both the case studies serve to illustrate the importance of the wood component of fossil floras by providing a more complete understanding of the vegetational composition in addition to an indirect palaeoclimatic signal via the Nearest Living Relative technique. The Coexistence Approach (Mosbrugger & Utescher, 1997) and other techniques employing dicotyledonous wood anatomy (e.g. Wiemann *et al.*, 1998) will be used to determine palaeoclimate when the number of distinct morphotypes per flora has increased, to at least 10 and 35 taxa respectively, with more than one specimen per morphotype. Small numbers of specimens assigned to taxa are

TABLE 2. Summary of the fossil wood taxa described from the Eocene London Clay flora of southeast England. ¹From Mabberley (1997) and Heywood (1998)

Taxon	Affinity based on wood [and pith in the case of twig (T) material] characters	New record of family in London Clay flora	modern distribution of closest modern taxa ¹ (NLR)
<i>Edenoxylon acutulum</i> Brett (1966), ? <i>Edenoxylon atkinsoniae</i> Crawley (1989)	Anacardiaceae	×	pan-tropical, subtropical and temperate
<i>Celastraxylois ramanualiformis</i> Poole & Wilkinson (1999); (T)	Celastraceae: <i>Calha</i> Forssk. ex Schreb.	×	tropical and warm temperate
<i>Cercidiphyllaxylon spenceri</i> (Brett) Pearson 1989, (Brett 1956)	Cercidiphyllaceae: <i>Cercidiphyllum</i> Sieb. & Zucc.	✓	temperate East Asia
<i>Dipterocarpylois ramanualiformis</i> <i>Quercinum jusanoides</i> Brett (1964)	Dipterocarpaceae: <i>Anisoptera</i> Korthals Fagaceae: <i>Lithocarpus</i> Blume	✓ ✓	tropical Indo-Malaysia Indo-Malaysia
<i>Meliaceoxylon collinsonae</i> Crawley (in press)	Meliaceae	×	tropical and subtropical
<i>Menispermoxylon</i> sp. (Poole & Wilkinson 2000); (T)	Menispermaceae: <i>Coscinium</i> Colebr.	×	Indo-Malaysia and Southeast Asia
<i>Plataninum decipiens</i> Brett 1972 (Crawley in press)	?Platanaceae: <i>Platanus</i>	✓	temperate Southeast Asia, Southeast Europe to north Iran
<i>Fagoxylon atkinsoniae</i> (Crawley in press)	Rutaceae: <i>Balfouridendron</i> Corr. Mello ex Oliv., <i>Chloroxylon</i> DC, <i>Esenberkia</i> Kunth., <i>Tetlea</i> Delle	×	tropical Africa
<i>Sapindoxylon guianoides</i> Poole & Wilkinson (1992); (T)	Sapindaceae: <i>Gaia</i> Cav.	×	mainly tropical, few warm temperate; Thailand to Samoa and China to Taiwan
<i>Sapindoxylon koelbrenoides</i> Poole & Wilkinson (1992); (T)	Sapindaceae: <i>Koelbertia</i> Laxmann		
<i>Hiaceoxylon ramanualiformis</i> Poole & Wilkinson (2000); (T)	Viaceae: <i>Rhoicissus</i> Planch	×	tropical, and South Africa

insufficient to assess the range of variation essential not only for species-to-species comparisons, comparisons between assemblages (Collinson, 1983) but also anatomical variation upon which modern palaeoclimatic interpretation rests. The values that can be gained from wood will be compared with palaeoclimatic values inferred from other sources (e.g. Reid & Chandler, 1933; Buchardt, 1978 for the London Clay material, and Dingle & Lavelle, 1998 and references cited therein for the Antarctic material).

EVOLUTIONARY AND ECOLOGICAL TRENDS IN WOOD ANATOMICAL CHARACTERS

Vegetational and palaeoecological information are not the only data that can be obtained from wood anatomy. The model of trends in specialization within dicotyledonous angiosperms, introduced by Bailey and Tupper (1918), can be tested using anatomical characters of fossil wood. Such data can then be used to determine trends in anatomical specialization *versus* environmental adaptation. Wheeler & Baas (1991, 1993) surveyed the fossil record of dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. They suggested that: (i) the fossil record generally supports the Baileyan model for xylem evolution; (ii) the incidence of features believed to be associated with conductive efficiency changes through geological time; (iii) there are differences between the 'Northern'/Laurasian and 'Southern'/Gondwana regions in the incidence of wood features, and (iv) there is a need for more information on well-dated woods of Palaeocene age (<40 known world wide) and from continuous sequences across the K-T boundary, both critical times in the change in floral composition and development of modern vegetation. During the Cretaceous in southern Gondwana the radiation and diversification of angiosperms took place along with major tectonic activity and volcanism associated with the break up of the Gondwanan supercontinent. In the Northern Hemisphere during the Early Eocene, floras were having to cope with increased temperatures during the Eocene thermal maximum. Adaptation, diversification and radiation may be affected by the degree of xylem specialization and the external environment.

Unfortunately the anatomy of the axes of small diameter London Clay cannot be considered as their mature anatomy is not certain. The anatomical data from the few samples of mature London Clay wood were included in the study by Wheeler & Baas (1991, 1993). However Crawley (in press) has re-evaluated existing specimens and described new woods from the mature angiosperm wood floras from the lower Cretaceous and Palaeogene of Britain. For completeness, therefore, some data from Crawley's paper have been included (Figs 12 & 13) to enable comparisons with the general Laurasian trend. Crawley's conclusions have been included where appropriate and the trend in the British woods discussed when notably different from the general Laurasian trend. These variations also illustrate the problems of using small datasets.

The dataset for the 'Northern'/Laurasian grouping (based mainly on subtropical, temperate and boreal floras) and the 'Southern'/Gondwanan grouping (based mainly on temperate and tropical floras) have been replotted from the data tabulated in Wheeler & Baas (1991) along with the Antarctic data (which probably represent a relatively temperate flora) taken from all dicotyledonous angiosperm morphotypes, sectioned to date, collected from the northern Antarctic Peninsula region by the

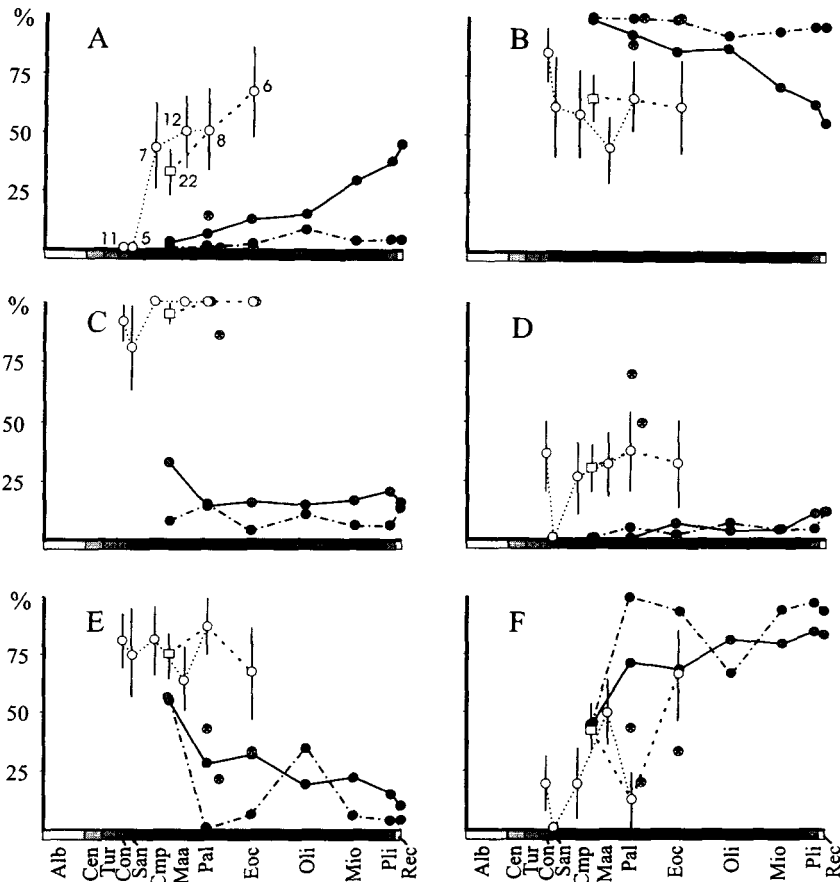


Figure 12. Incidence (%) of anatomical character against geological time: (A) semi-ring and ring porosity, (B) diffuse porosity, (C) solitary vessels dominate, (D) radial multiples >4 distinctly present, (E) intervessel pitting scalariform and opposite, (F) intervessel pitting alternate. Abbreviations: Alb = Albian, Cen = Cenomanian, Tur = Turonian, Con = Coniacian, San = Santonian, Cmp = Campanian, Maa = Maastrichtian, Pal = Palaeocene, Eoc = Eocene, Oli = Oligocene, Mio = Miocene, Pli = Pliocene, Rec = Recent. (○) Data for the different floras from Antarctica with the total number of morphotypes per flora as indicated on 'A'. (●) Data from Northern 'Laurasian' Hemisphere (Wheeler & Baas, 1991). (●) Data from the Southern 'Gondwanan' Hemisphere (Wheeler & Baas, 1991). (□) The Antarctic Cretaceous data which have been summarized to enable comparison with 'Cretaceous' data point plotted from Wheeler & Baas (1991). Vertical, solid lines represent estimated standard deviations (cf. Wheeler & Baas, 1993) and have been shown only for the Antarctic data to ensure clarity. Spotted circles represent the Lower Tertiary floras, data from Crawley (in press). Estimated standard deviations are $\pm 13\%$, $\pm 0\%$, $\pm 0\%$ for Palaeocene (sample size, $n = 7$), upper Palaeocene/lowermost Eocene ($n = 14$) and Eocene ($n = 3$; London Clay) data respectively on graphs A and B, $\pm 9\%$, $\pm 0\%$, $\pm 0\%$ on C; $\pm 17\%$, $\pm 13\%$, $\pm 0\%$ on D; $\pm 19\%$, $\pm 7\%$, $\pm 27\%$ on E; $\pm 19\%$, $\pm 0\%$, $\pm 27\%$ on F.

British Antarctic Survey. The incidence of features is given as a percentage, but the number on which this is based varies with time and feature. The Cretaceous Antarctic dataset has been subdivided into the relevant geological stage for each flora to determine the trend of anatomical change through the Cretaceous as well as being presented as one 'Cretaceous' record (in which each morphotype was

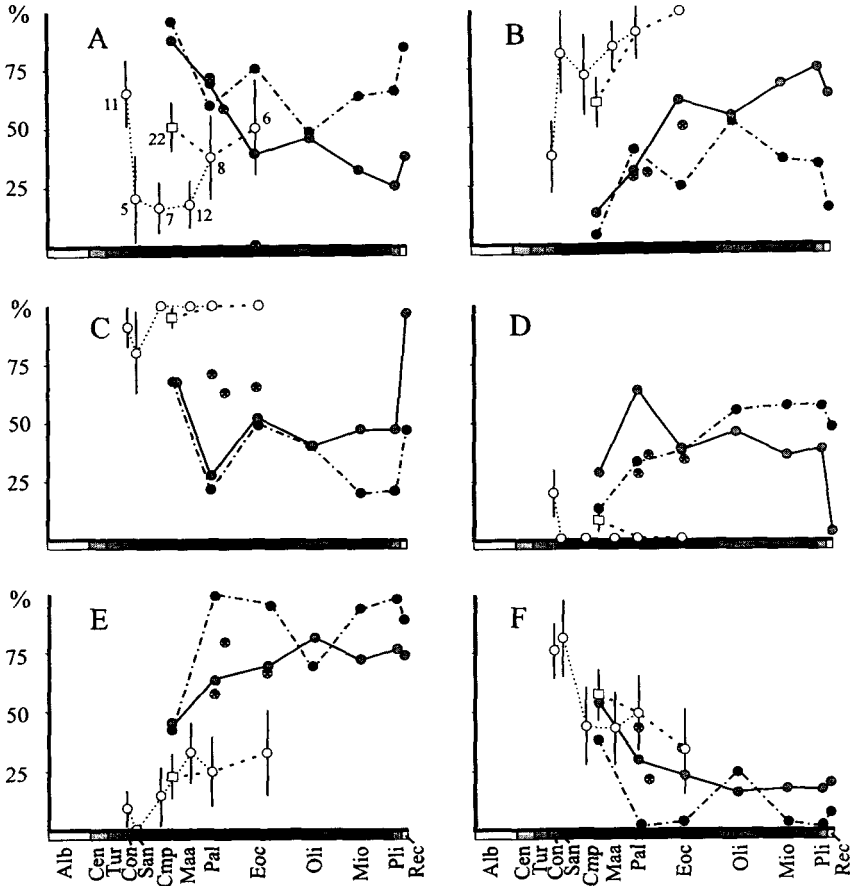


Figure 13. Incidence of anatomical character against geological time: (A) indistinct growth rings, (B) distinct growth rings, (C) vessel diameter $<100\ \mu\text{m}$, (D) vessel diameter $100\text{--}200\ \mu\text{m}$, (E) simple perforation plates, (F) scalariform perforation plates. Details as stated in Figure 3 except estimated standard deviations are $\pm 17\%$, $\pm 13\%$, $\pm 0\%$ for Palaeocene, Palaeocene/Eocene and Eocene data represented by spotted circles on graphs A; $\pm 17\%$, $\pm 12\%$, $\pm 29\%$ on B; $\pm 17\%$, $\pm 13\%$, $\pm 21\%$ on C; $\pm 17\%$, $\pm 13\%$, $\pm 27\%$ on D; $\pm 19\%$, $\pm 11\%$, $\pm 27\%$ on E; $\pm 19\%$, $\pm 11\%$, $\pm 27\%$ on F.

recorded once) to enable a direct comparison with the 'Cretaceous' data given by Wheeler & Baas (1991,1993). The characters illustrated in Figures 12 & 13 and discussed here are a subset of those used by Wheeler & Baas, as not all features are either preserved or readily identifiable in the Antarctic material.

Porosity (Fig. 12A, B)

Until now distinct ring porosity has not been documented until the Eocene (Wheeler & Baas, 1991) but the presence of this character is clearly defined within some of the Antarctic Cretaceous (e.g. *Sassafrasoxylon*, Fig. 3) and Tertiary morphotypes (Fig. 12A). This helps to confirm seasonality often associated with temperate climates and/or deciduousness (Chowdury, 1964) in the southern high latitudes during the Cretaceous. This is not unexpected considering that Antarctica

occupied a palaeolatitude within a few degrees of its present position and therefore experienced polar winters coupled with summers of long day lengths and warm temperatures. The incidence of diffuse porosity (Figs 4 & 12B) within the Antarctic woods generally decreases as semi-ring/ring porosity increases. This also suggests a higher degree of deciduousness and/or seasonality through time and reflects the general trend for woods from the 'Laurasian' and 'Gondwanan' regions (Wheeler & Baas, 1991). Ring porosity is considered to be a derived state in the Baileyan model and the data presented here would seem to confirm this.

Growth rings (Fig. 13A, B)

The Laurasian (including the woods from Britain; Crawley, in press) and Gondwanan regions show a relatively low percentage of distinct growth rings in the Cretaceous when compared with the Tertiary (Fig. 13B). The Antarctic floras meanwhile have a relatively high incidence of distinct growth rings (Fig. 5) which generally increases through the Cretaceous and into the Palaeocene possibly indicating a more seasonal climate. Indistinct growth rings (Fig. 6) are most frequent in the oldest-Cretaceous- and Eocene Antarctic floras (Fig. 13A) which may reflect the thermal maxima at these times. The effects of a strongly seasonal high latitudinal climate may be greater in these Antarctic woods than in woods from lower latitudes such as those represented by the Gondwanan dataset and the Tertiary woods from southeast England.

Vessel groupings (Fig. 12C, D)

Wheeler & Baas (1991) showed a generally higher incidence of solitary vessels in Laurasia than in Gondwana (Fig. 12C). If the Antarctic data are considered along with the Gondwana flora (which would help to alleviate the tropical/warm temperate bias in the Gondwanan dataset) then this geographical distinction may be reversed with greater abundance of solitary vessels occurring in Gondwanan floras. From studies of modern wood, a high incidence of vessel grouping can be related to dryness of habitat although vessel groups can be absent in some families growing in very dry habitats (Carlquist, 1988). Wheeler and Baas (1991: 291–292) stated that "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 temperate (less equable) ecology...". The Antarctic morphotypes exhibit a high incidence of solitary vessels which may reflect a more temperate ecology. However, so do the Lower Tertiary floras from southeast England which is harder to explain in terms of environmental factors and is more likely to be the result of the small sized dataset. The earliest Cretaceous morphotypes give one of the highest incidences of radial multiples (Fig. 12D) in any Antarctic flora even though the incidence of vessel clusters in the Antarctic flora is greatest in the Tertiary (66% and 88% in the Eocene and Palaeocene respectively compared with a maximum of 58% during the Cretaceous, data not shown). In modern floras vessel clusters are far more common in subtropical to temperate floras than in tropical floras (Wheeler & Baas, 1991) and therefore the fossil wood from Antarctica might indicate that during the Tertiary, the southern high latitude was relatively more temperate than during the Cretaceous. However, Wheeler & Baas (1991) suggested that with lack of data on vessel grouping prior to the Tertiary this character cannot be used for climatic inferences about the Cretaceous. The woods from southeast England show a predominance of solitary

vessels with a sharp decline in vessels arranged in radial multiples (Crawley, in press). Wheeler & Baas explained the higher incidence of Cretaceous woods with solitary vessels, when compared with those of the Tertiary, by the Baileyan concept that primitive angiosperm xylem was characterized by solitary vessels. The woods from Antarctica and southeast England can shed no further light on this concept as the relative incidence of solitary vessels remains fairly constant through time. Vessel grouping in radial multiples of greater than four is rare in the modern floras and in the Laurasian and Gondwanan palaeofloras. The discrepancy between the incidence for the woods from both Antarctica and southern England when compared with the Gondwanan and Laurasian datasets might suggest an observer bias (which is an important consideration in all studies dealing with qualitative data) and/or the result of using small datasets.

Vessel diameter (Fig. 13C, D)

Vessel diameter is often considered to be one of the most significant parameters for hydraulic efficiency in angiosperm wood because of the relationship between conductive capacity with the fourth power of the radius of the conduit (Carlquist, 1975, 1977, 1988; Zimmermann, 1983; Wheeler & Baas, 1991). The abundance of Antarctic woods with vessels less than 100 μm in diameter (Fig. 13C) and the total absence of woods with vessels greater than 200 μm in diameter (data not shown), coupled with the relative incidence of distinctive growth rings and semi-ring to ring porous woods, suggest a cooler temperate or high montane climate. Alternatively this feature could be indicative of either a high latitudinal climate (although comparison with modern material is not possible due to the deficit in similar vegetation at equivalent high latitudes today) or the relative size of the parent plant.

Perforation plates (Fig. 13E, F)

Scalariform perforation plates (Fig. 7) show distinct ecological trends peaking in incidence in cool temperate, arctic and tropical high montane regions (Baas, 1976, 1986; Carlquist & Hoekman, 1985). The high incidence of distinct growth rings coupled with the abundant scalariform perforation plates through the Antarctic Cretaceous (Fig. 13F) suggests cool temperate/arctic/montane conditions. According to Wheeler & Baas (1991, 1993) the decrease in incidence of scalariform perforation plates and the increase in simple perforation plates (Figs 13E & 18) from the Cretaceous through to the Tertiary might be explained by: (i) the development of a warmer environment or the arboreal, as opposed to the shrub, habit; (ii) seasonal or permanent drought; (iii) changing phenology (deciduous habit) in response to (ii), or a combination of the above. The pattern within the Antarctic flora is similar to that shown in the Gondwanan and Laurasian floras and if the data from Gondwana and Antarctica are combined this helps reduce the geographical discrepancy. The 'localized' decrease in simple perforation plates and the increase in scalariform perforation plates from the Maastrichtian to Palaeocene of the Antarctic is more difficult to explain in terms of evolutionary trends and may be a reflection of absolute abundance of certain taxa at this time. When the relative incidence of simple versus scalariform perforation plates in both the Antarctic and British (Crawley, in press) floras are considered, the relative incidences generally comply with the trends for anatomical specialization put forward by Bailey and Tupper (1918) with simple perforations being the derived condition with respect to scalariform perforations.

Intervessel pitting (Fig. 12E, F)

Carlquist (1988) proposed that alternate intervessel pits (Fig. 11) increase the strength of a vessel wall when compared with scalariform or opposite pits (Figs 9 & 10) and thereby enable the development of wider, longer vessels which may in turn be related to an increase in overall plant stature. As in Gondwana and Laurasia, the decrease in incidence of scalariform and opposite intervessel pitting (Figs 12E & 10) from Cretaceous to Eocene and a corresponding increase in incidence of alternate pitting in woods from Antarctica (Fig. 12F) could be coincident with the proposed change in habit for woody angiosperms becoming large trees (Wheeler & Baas, 1991). The relative incidence of intervessel pitting through geological time in woods from Antarctica agrees with the Baileyan trend for xylem specialization. The reverse trend seen in the woods from southeast England probably reflects the small dataset. However, in the Palaeocene there is a decrease in alternate pitting and an increase in scalariform and opposite pitting. This is more difficult to explain in terms of ecological and/or environmental adaptation but might be a reflection of absolute abundance of certain taxa or perhaps a reflection of forest density which would offer protection from the elements and thus compensate for lack of structural adaptation. Once again, regional discrepancies may be reduced with the addition of these new data from Antarctic floras to the 'Southern'/Gondwanan dataset.

CONCLUSIONS

Although angiosperm fossil wood is subject to different taphonomic, sampling and recognition biases than leaves and palynomorphs, these two case studies demonstrate that wood is an important constituent of fossil floras. When datasets are large enough, wood can also reveal a great deal of information concerning diversification and establishment of angiosperm taxa, anatomical specializations and the environment in which these developments were taking place. The fossil record from these two wood floras to some extent supports the Baileyan trends of xylem specialization. The Antarctic data are generally concordant with data plotted by Wheeler & Baas (1991) for Cretaceous woods of the Southern Hemisphere, although geographical discrepancies may not be as great as previously suggested. Those wood features more keenly associated with ecology also help to support hypotheses put forward for palaeoclimate using the Nearest Living Relative approach through the Cretaceous and into the Tertiary. The data presented here are from ongoing studies focusing on biodiversity, palaeoclimate and wood anatomical specializations in southern high latitude Antarctica, from the Late Cretaceous and Palaeogene, and an early Tertiary flora from the southeast of England. Further work will help clarify uncertainties and enlarge our knowledge of characters and taxa in palaeofloras of the Northern and Southern Hemisphere.

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