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RECONSTRUCTION OF ANTARCTIC PALAEOCLIMATES USING ANGIOSPERM WOOD ANATOMY

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ABSTRACT. Fossil angiosperm wood is abundant within Cretaceous and Tertiary sediments on the Antarctic Peninsula. The wood, which represents the trunks and branches of large forest trees that once grew on an emergent volcanic arc, is exquisitely preserved by petrifaction with calcite and silica. Microscopic anatomical details of the angiosperm wood, such as the intervessel and vessel- ray pitting, are present which has permitted comparison with the anatomy of modern woods and identification of the fossil wood taxa plus investigation of the climate significance of certain anatomical features. The families Nothofagaceae, Monimiaceae, Winteraceae, Illiciaceae and Atherospermataceae have been identified so far. Growth ring analysis indicates that these trees grew well under a favourable temperate climate during both the Late Cretaceous and Early Tertiary. Studies of anatomical features show that some characters, such as vessel diameter and distinctness of growth rings, correlate with changing temperatures and water availability.

KEY WORDS: angiosperm wood, palaeoclimate, Cretaceous, Antarctica

INTRODUCTION

Cretaceous and Tertiary fossil floras from the northern Antarctic Peninsula region are important because they record the first appearance of angiosperms in this area and document the evolution of the Southern Hemisphere floras (Francis 1996). Since the middle of the 19th century when Hooker (1847) first recognised floristic similarity across South America, southern Australia and New Zealand, Antarctica has been considered a key continent in the reconstruction of the vegetation in the Southern Hemisphere. In addition, many novel taxa have originated in Antarctica and subsequently migrated to become a significant part of the low-latitude biota (Dettman 1989, Truswell 1991, Hill & Scriven 1995). Today the rarity of vascular plants on Antarctica testifies to the major extinctions which were probably a consequence of climate change. Therefore the plant fossils from Antarctica play a major role in developing concepts of the biogeographical history of the Southern Hemisphere. The evolutionary record of the angiosperm component of the floras is particularly important, since angiosperms are a dominant, and economically important, feature of the living Southern Hemisphere vegetation. This paper presents the preliminary findings of the first comprehensive study undertaken on dicotyledonous wood from Antarctica and its use for reconstructing the palaeoclimate of Gondwana during the Late Cretaceous and Early Tertiary.

Fossil plants are important palaeoclimatic indicators because terrestrial plants, being sedentary in habit, are influenced to a certain extent by the prevailing climate. Estimates of palaeoclimate derived from the composition of plant fossil assemblages are usually based on comparison with the climates in which the nearest living relative (NLR) of the fossils concerned live today. Huntley (1993) outlined a number of assumptions which underlie such an approach. These have been summarized by Chaloner and McElwain (1997) as: (1) climate largely controls the abundance and distribution of a plant species, (2) the modern relatives are in equilibrium with the present day climate, (3) the fossil species was in equilibrium with the palaeoclimate, and (4) a sufficiently close biological analogue exists today from which can be deduced a palaeoclimate from a fossil assemblage. Such assumptions must be acknowledged when using this taxon-dependent approach. This method can provide qualitative (e.g. Jordan *et al*. 1995) or quantitative (e.g. Sluiter *et al*. 1995) results. However, alternative, taxon-independent, techniques have been designed to circumvent the problems of assuming tolerance and evolutionary stasis. For example, leaf floras can be analysed by using the leaf characters of the dicotyledonous angiosperm component (e.g. Wolfe 1993, 1995, Herman & Spicer 1997), wood anatomy reflects seasonally-controlled growth through the production of growth rings in temperate environments (Creber & Chaloner 1985), and characteristics of dicotyledonous wood anatomy have been correlated with temperature variables such as mean annual temperature, mean annual range in temperature, cold month mean temperature and length of the dry season (Weimann *et al*. 1998). Determining specific climatic variables from dicotyledonous wood however relies on large sample sizes (Weimann *et al*. 1998) and an understanding of the evolutionary processes involved in wood structure (Wheeler & Baas 1993).

The fossil angiosperm wood used in this study represents forest trees which once grew on an emergent and active volcanic arc in the northern Antarctic Peninsula region during the Late Cretaceous and Early Tertiary. The trees were washed into a back arc basin (the James Ross Basin) to the east as driftwood and were subsequently waterlogged and buried within marine clastic sediments that gradually filled the basin (Francis 1986, Pirrie *et al.* 1991, Pirrie 1994). The woody material was then infiltrated by silica and calcite-rich solutions that later petrified the wood such that the preservation state of the wood is excellent (Plate 1).

MATERIALS AND METHODS

Specimens used in this study are fossilised dicotyledonous angiosperm woods from James Ross Island, Vega Island, Seymour Island and Snow Hill Island (see Francis 1986 for locality information). The wood ranges in age from Late Cretaceous (Coniacian) to Tertiary (Eocene). The material includes small branches with a central pith, pieces of branch or large diameter trunk wood (exact dimensions unknown). The wood is, in most cases, mature and thus overcomes the problem of juvenility when using the anatomical characters for identification (Poole 1994). The fossils were thin sectioned revealing the microscopic details of the ultrastructure of the wood thus allowing comparison with the wood anatomy of extant material. Identification involved comparisons with published literature (e.g. Weidenburg 1948, Metcalfe & Chalk 1950, Meylan & Butterfield 1978, Schweingruber 1978, Metcalfe 1987, Rancusi *et al*. 1987, Carlquist 1988, Ilic 1991) and slides of modern wood housed in the Jodrell Laboratory, Royal Botanic Gardens, Kew and in the Herbarium, Utrecht University.

The growth rings were analysed in terms of their Annual Sensitivity (AS), i.e. the difference in width between a pair of consecutive rings divided by their average width, and the average of these values for each specimen, i.e. the Mean Sensitivity (MS) (see Fritts 1976, Creber & Chaloner 1985, Francis 1996). The MS value gives an indication of the tree's response to variable factors of the climate that may have influenced its growth. The MS is calculated using the formula:

$$\text{Mean Sensitivity} = \frac{1}{n-1}\sum_{t=1}^{t=n-1}\left|2\,(X_{t-1} - X_t)/X_{t+1} + X_t\right|$$

where x is the ring width, n is the number of rings and t is the year number of each ring. MS values range from 0, where there is no variation from year to year and the trees are termed 'complacent', to a theoretical maximum of 2 which represents the greatest variation and the trees are termed 'sensitive'. An arbitrary value of 0.3 is taken to separate the complacent trees that have grown under favourable conditions from the sensitive trees which have responded to limiting factors in the climate. The width of each ring on a petrographic thin section of the specimen was measured along a radial line to obtain as long a ring series as possible although measurements were continued along adjacent radii to avoid poor preservation if necessary.

RESULTS

T a x o n - d e p e n d e n t a p p r o a c h. The size range of the fossils indicates that the material is from large trees rather than small shrubs which are often associated with plants found in subpolar regions today. The identification of the material has been successful due to the exceptional preservation of the majority of the material. It has been possible to determine taxonomic affinities at least the familial level for a number of specimens. The results from preliminary identifications are summarized in Table 1. The families are listed with the number of organ genera so far assigned to each family. Some of these families are already found in the pollen and/or leaf floras from the same region (Askin 1992) but there are some taxa belonging to the Winteraceae, Illiciaceae and Atherospermataceae which represent the first record of these families in Antarctica. The Monimiaceae represents the first record in the Antarctic wood flora. According to the distributions recorded by Mabberley (1990) these families are generally found in warm temperate to tropical parts of the world today. The Cretaceous angiosperm wood fossils (n=18) to date include the Atherospermataceae, Monimiaceae, Winteraceae, Nothofagaceae and Illiciaceae whereas the Tertiary wood (n=8) fossil taxa include the Monimiaceae and Nothofagaceae. The relatively small sample size to date prevents determination of conclusive palaeoclimatic changes through shifts in

Table 1. Table showing the families so far identified in the Antarctic dicotyledonous wood flora with the relative abundance in the Cretaceous (Kr) and Tertiary (T) and the modern day distribution. *Data from Mabberley 1990

Family	Fossils			Modern Distribution*
	number	age	taxa	
Monimiaceae	8	7Kr 1T	3	tropical
Winteraceae	1	1Kr	1	montane, cool temperate forests (S. Pacific)
Atherospermataceae	1	1Kr	1	warm temperate
Nothofagaceae	13	8Kr 5T	6	temperate
Illiciaceae	2	2Kr 1T	1	subtropical

relative proportions of taxa between the Late Cretaceous and Early Tertiary.

Taxon-independent approach. The presence of well marked growth rings in the Antarctic woods (Plate 1) indicates that the trees grew in an environment characterized by well-defined seasons (Francis 1986). The growth rings in the angiosperm woods are generally wide and uniform with average ring widths for the Cretaceous and Tertiary woods being 2.46 mm (standard deviation, sd, = 1.4) and 2.48 mm (sd = 0.1) respectively. These values indicate that growth rates were quite fast in a favourable environment. However the presence of very wide rings (i.e. greater than 6 mm) in a number of the Cretaceous specimens indicates that the tree had the potential for extremely high growth rates in a very favourable climate. Conversely very narrow growth rings (<1 mm) in other specimens suggest that the climate was not consistently favourable. The mean MS values for the Late Cretaceous and Tertiary woods were 0.49 (sd = 0.3) and 0.35 (sd = 0.1) respectively, indicating slightly more variable growth in the Late Cretaceous.

Other anatomical characters of angiosperm wood, such as ray size, vessel diameter and abundance, and the presence of spiral thickening, can be used to determine palaeoclimate (e.g. Carlquist 1988, Wheeler & Baas 1991, Weiman *et al*. 1998). The results from the wood samples studied to date are tabulated in Table 2. They are compared with palaeoclimatic inferences for the Southern Hemisphere deduced from wood anatomy, published by Wheeler Baas (1991). The relative anatomical change in the Antarctic fossil woods agrees with that seen in other angiosperm woods which reflects the change in climate seen through the Late Cretaceous and Early Tertiary. However, one feature, vessel abundance does not agree with this trend. Instead of the vessels being abundant in the Cretaceous and then decreasing through the Tertiary the converse is seen (Plate 1). This discrepancy could be explained by either one or a combination of: (1) taphonomic bias whereby only taxa from a particular (possibly unrepresentative) habitat is preserved rather than a representative sample from the whole region, (2) specimen age (although most of the woods are generally from large diameter organs and thus mature), (3) an independent climatic signal. However, because the sample size is very small, further work with more fossils is necessary before any final conclusions can be drawn.

DISCUSSION

This fossil dicot wood material illustrates the point made by Jordan (1997) whereby a fossil assemblage often contains taxa whose NLRs do not overlap in their climatic range. This can be explained by: (1) changes in the ecological tolerances of the taxa with time, (2) extinct and extant species having similar anatomy or morphology, or (3) by the presence of a different climatic regime from those recognised today. In addition, plant growth of this type is not reflected in modern high-latitude environments because trees do not grow in similar latitudes today. Therefore there is no modern analogue with which to compare the fossil material and thus understand the strategies employed to overcome the problems associated with short-days and dark-induced dormancy. However, throughout the Late Cretaceous and Early Tertiary the Antarctic Peninsula obviously had a sufficiently warm and favourable climate to allow the growth of fairly diverse plant communities even at a palaeolatitude of approximately 65°C (Lawver *et al*. 1992).

Combining the results from this study with those previously undertaken on conifer wood (e.g. Francis 1986), leaves (P. Hayes pers. comm.) and palynomorphs (e.g. Dettman & Thomson 1987, Askin 1992, 1997) from the same area, the data presented here support the ideas regarding the palaeoclimate of Antarctica during the late Mesozoic and early Cenozoic. Taxon-dependent studies (see Askin 1992) suggest that during the Late Cretaceous

Table 2. A summary of the climatic change reflected in selected wood anatomical characters of Late Cretaceous and Tertiary fossils of the Southern Hemisphere (Wheeler & Baas 1991) compared with the Late Cretaceous (Kr) and Early Tertiary (T) dicotyledonous woods from Antarctica

Character	Southern Hemisphere trend (Wheeler & Baas 1991)	Antarctic fossils (this study)	
		Kr	T
Distinctness of growth rings	General increase from Kr to T (increase in seasonality) with decreases corresponding to the Late Kr and Eocene thermal maxima	+	+
Vessel diameter	Narrow vessels in Kr (xeric/cooler temps). Increasing into the Palaeocene (wetter/warmer). Decreasing from the Eocene (drier/cooler).	+	+
Vessels per mm^2	Abundant in Kr (cool temps). Fewer in Palaeocene/Eocene (more tropical). Decrease from the Eocene onwards (cooler).	x	x
Vessel element length	General decrease from Kr onwards (environment becoming less tropical and more temperate).	+	+
% rays heterocellular	Decrease from the Kr onwards (general decrease in temperature)	+	+

the northern Antarctic Peninsula was covered in rainforest vegetation dominated by podocarp and araucarian conifers with an understorey of ferns and angiosperms such as Proteaceae and Nothofagaceae. We have found evidence in the wood record for monimiaceous, atherospermataceous, illiciaceous, winteraceous and nothofagaceous elements in this flora. Moreover, from NLR comparisons, the fossil dicot wood may be indicating a somewhat warmer Tertiary climate than previously thought. At the end of the Cretaceous the mean annual temperature (based on dispersed plant cuticular evidence) is thought to have ranged between 8 and 15°C with a mean annual range in temperature <16°C and a coldest month mean temperature above 1°C (Askin 1992 and the references cited therein). The climate during Early Tertiary (from NLR studies, in Askin 1992), however, may have become cooler with a MAT of between 10° and 12°C and wetter with an annual rainfall of 1000–4000 mm. Askin (1998) interprets the Eocene palynofloras of Seymour Island (northern Antarctic Peninsula) as representing warm, frost-free conditions during the late Early-Middle Eocene followed by a cooling at the end of the Middle Eocene. From then on the floras indicate a cooling trend which is matched by other climate indicators in the geological record. (e.g. Birkenmajer & Zastawniak 1989, Hambrey & Barrett 1993, Birkenmajer 1997).

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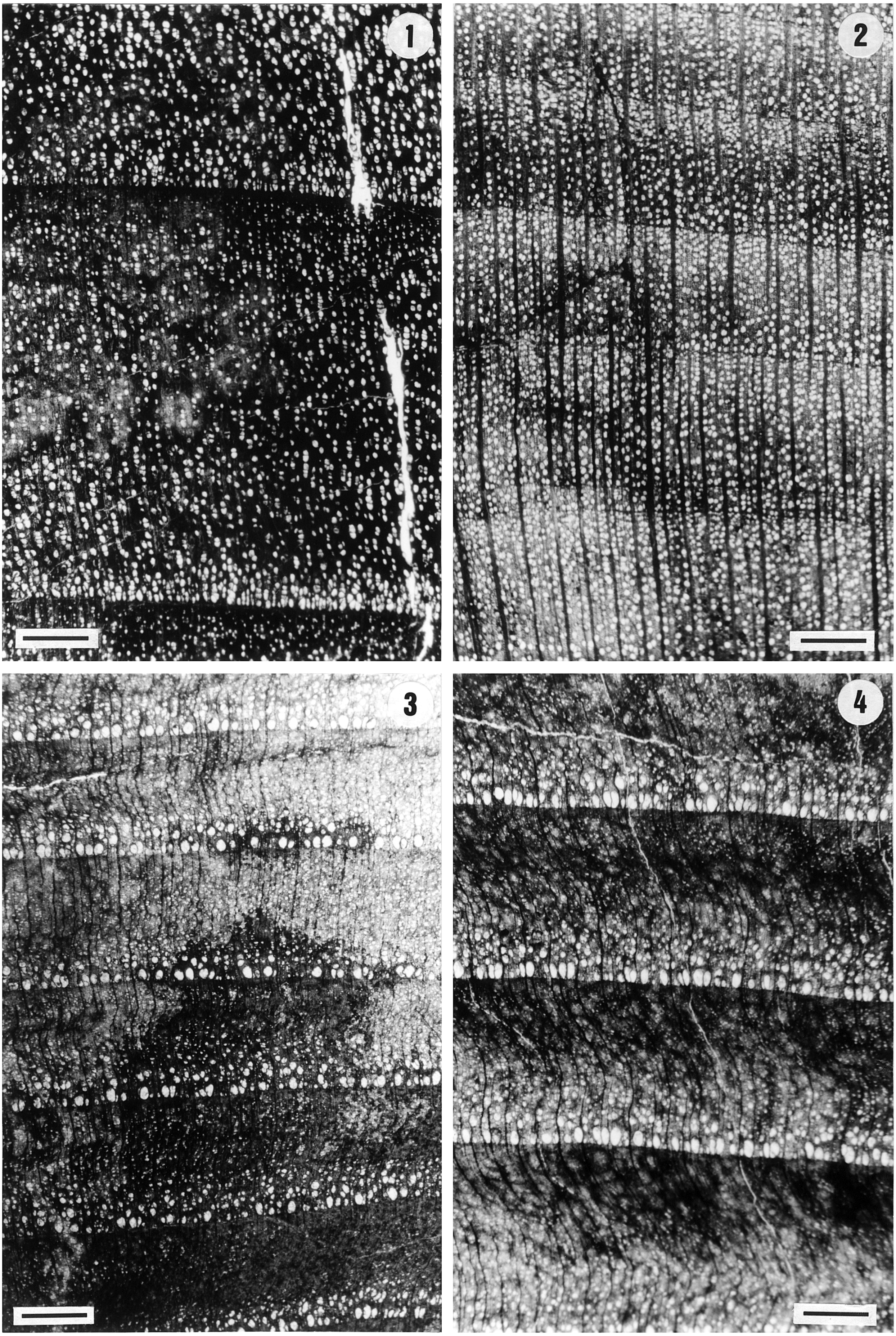
P L A T E

Plate 1

Photographs of transverse thin sections of fossil angiosperm wood from the Antarctic Peninsula region. 1 & 2 Cretaceous woods with vessels scattered throughout the growth ring (±diffuse porous), 3 & 4 concentration of vessels along ring boundaries (ring porous). 1 = DJ141.26, 2 = DJ455.2, 3 = D494.1, 4 = D494.2. Scale bars = 1 mm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