# Cretaceous and early Tertiary climates of Antarctica: evidence from fossil wood

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## Abstract

Fossil wood is abundant in Cretaceous and early Tertiary sediments of the northern Antarctic Peninsula region. The wood represents the remains of vegetation that once grew in high palaeolatitudes when the polar regions were warmer, during former greenhouse climates. Fossil wood is a unique data store of palaeoclimate information. Analyses of growth rings and anatomical characters in fossil wood provide important information about temperature, rainfall, seasonality and climate trends for this time period in Antarctica. Climate signals from fossil wood, supported by sedimentary and geochemical evidence, indicate a trend of cool climates during the Early Cretaceous, followed by peak warmth during the Coniacian to early Campanian. Narrower growth rings suggest that the climate cooled during the Maastrichtian and Palaeocene. Cool, wet and possibly seasonal climates prevailed at this time, with tentatively estimated mean annual temperatures (MATs) falling from 7°C to 4–8°C respectively, determined from dicotyledonous (dicot) wood anatomy. The Late Palaeocene/Early Eocene was once again warm, with estimated MATs of 7–15°C from dicot wood analysis, but conditions subsequently deteriorated through the latter part of the Eocene, when cold seasonal climates developed, ultimately leading to the onset of Cenozoic ice sheets and the elimination of vegetation from most of Antarctica. © 2002 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

An important feature of greenhouse climates during the geological past is the presence of vegetation at high latitudes (Creber and Chaloner, 1985). The fossil remains of this vegetation are a primary source of evidence for high latitude warmth and the absence of major ice sheets. The polar forests represent a unique ecological niche that has no living analogue on Earth today because they grew in an environment where light was the dominating factor, requiring adaptation to the polar light regime with summers consisting of months of continuous sunlight and dark winters.

High latitude fossil forests have been reported from the Permian to the Neogene and from both the Southern Hemisphere (e.g. Jefferson, 1982; Francis, 1986; Taylor et al., 1992; Francis et al., 1994; Pole, 1999) and the Northern Hemisphere

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(e.g. Parrish and Spicer, 1988; McIver and Basinger, 1999; Francis, 1991a). Although fossil leaves and pollen are known from high latitude sediments, it is the fossil wood remains, especially as in situ stumps or trunks, that can provide a more detailed picture of forest density and productivity, as well as floral composition. In addition, fossil wood is a unique data store of palaeoclimate information and proxies for climates on land. This can be determined from analyses of growth rings in fossil wood (palaeodendroclimatology) (see review in Creber and Francis, 1999; Falcon-Lang, 2000a) and from investigation of specific anatomical characters that are associated with certain aspects of climate (Wheeler and Baas, 1993; Wiemann et al., 1998).

Fossil wood is an important component of Cretaceous and early Tertiary floras from the Antarctic Peninsula region and in many formations is the only plant material preserved. Studies of fossil wood have produced much information about the floral composition of Antarctic vegetation for this time interval (e.g. Torres and Lemoigne, 1989; Falcon-Lang and Cantrill, 2000; Francis, 2000; Poole and Francis, 1999, 2000; Poole et al., 2000a,b,c) but much less is known about the palaeoclimate signals stored within the fossil wood. This paper presents new information about Cretaceous and Palaeogene climates based on analyses of growth rings of conifer wood and the use of anatomical characters in fossil dicotyledonous angiosperm (dicot) wood.

## 2. Geological setting

During the Cretaceous and early Tertiary the northern tip of the Antarctic Peninsula was situated at about 59–62°S, according to the palaeogeographic reconstructions of Lawver et al. (1985). An uplifted and periodically active volcanic arc, adjacent to a subduction zone, occupied the peninsula region. The fore-arc regions were emergent land areas that were forested, as indicated by the remains of in situ fossil trees (e.g. Alexander Island, South Shetland Islands, Fig. 1). Fossil plant assemblages are also present in non-marine fluvial sediments on the arc itself

(the Botany Bay Group, Farquharson, 1984). To the east of the arc Cretaceous–Tertiary sediments were deposited in a large back-arc basin, the James Ross Basin, with sediment supply from the active magmatic arc to the west-northwest, now represented by the Antarctic Peninsula land mass (Pirrie et al., 1997). Plants that were growing on the arc itself were subsequently washed into this basin and preserved within marine sediments (Francis, 1986).

The James Ross Basin was initially filled with deep marine strata during the early part of the Cretaceous (Gustav Group), consisting mostly of coarse-grained submarine fan deposits (Ineson, 1989). Fossil plants are rare in this coarse clastic sequence. As the basin filled, shallow marine environments developed during deposition of the overlying Marambio Group. The Santa Marta Formation, the lower part of this group, is dominated by volcanogenic sandstones and mudstones deposited in a mid- to outer shelf environment at the base but overlain by a sandstone-dominated sequence representing a shallower inner shelf environment (Crame et al., 1991). The overlying Lopez de Bertodano Formation records the shallowing trend with mostly bioturbated mudstones and siltstones formed in a shallow marine setting or shallow shelf/shoreface environments. During the Tertiary the basin continued to fill and a range of shallow shelf and deltaic environments formed (Elliot and Trautman, 1982; Askin, 1997). Fossil plants are more common in these shallow sequences and fossil wood in particular is abundant throughout.

## 3. Materials

The fossil wood used in this study was collected from the South Shetland Islands and from islands in the James Ross Basin, Antarctic Peninsula (Fig. 1). Most wood samples have numbers relating to the British Antarctic Survey (BAS) record system and are housed in the BAS collections.

The wood is petrified and mostly preserved by calcite mineralisation, although some samples from the volcanogenic sediments of the terrestrial arc setting are silicified (Francis, 1986, 1991b).
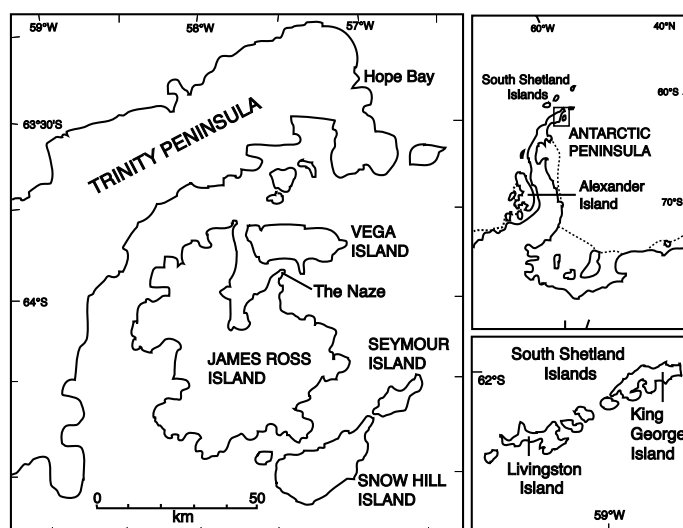
Fig. 1. Map of the Antarctic Peninsula region showing localities mentioned in the text.

Anatomical details are generally well preserved (e.g. Poole and Francis, 1999, 2000; Poole et al., 2000a,b,c). The fossil specimens range in size from a few cm to over 40 cm in diameter, and represent the remains of twigs, trunks and branches. Both angiosperm and conifer woods are represented, the angiosperm woods appearing in the Late Cretaceous.

## 4. Methods

### 4.1. Growth ring analysis

Tree rings in fossil conifer wood provide a variety of measurements that can be used as proxy climate records (Creber and Francis, 1999; Parrish, 1999). Parameters which have climate significance include the presence or absence of growth rings (indicative of seasonal or non-seasonal climates respectively), ring width as an indicator of growing conditions (Fritts, 1976; Schweingruber, 1988), the presence of false rings (interruptions in growth during a growing season caused by drought, fire or insect attack), and mean sensitivity (MS), a measure of the variability of growth from year to year (Fritts, 1976). Although there are limitations to the use of fossil growth ring analysis for climate study (see below), several

case studies have shown that significant palaeoclimate information can be determined from fossil tree rings (e.g. Jefferson, 1982; Francis, 1984, 1986; Keller and Hendrix, 1997; Parrish and Spicer, 1988; Kumagai et al., 1995).

Growth ring analysis of a selection of wood samples from the Antarctic Peninsula and islands of the James Ross Basin was undertaken (see Table 1); procedures were undertaken in accordance with those outlined in Francis (1986). Samples with growth rings with a radius of curvature as large as possible were used, as these were assumed to be from the outer parts of large mature trees. The inner rings of a tree formed during the sapling stage are generally wider (but have small radii of curvature) than rings in the outer parts of a mature tree (with rings of large radii of curvature) (Fritts, 1976). Standardisation procedures to eliminate growth trends (such as that used by Kumagai et al., 1995) were not used because most of the ring series used here were considered too short to reflect significant growth trends and only rings from mature trees were measured.

For each sample mean ring width and MS were calculated, and minimum and maximum width recorded. MS is the mean variability in ring width over a series of rings (for formula see Fritts, 1976; Creber and Francis, 1999). Values can range from 0 (no variation) to a maximum of 2 (greatest var-

Table 1
Compilation of tree ring data from the Antarctic Peninsula (some data from Francis 1986)

| Locality | Sample number | Formation | No. of rings | MRW | MS | Min– max | Wood type |
|---|---|---|---|---|---|---|---|
| Seymour Island | DJ.1057.36 | La Meseta Formation | 22 | 1.85 | 0.209 | 0.9–2.8 | A |
| Seymour Island | DJ.1057.58 | La Meseta Formation | 29 | 2.08 | 0.297 | 0.9–3.6 | A |
| Seymour Island | DJ.1057.10 | La Meseta Formation | 8 | 3.25 | 0.269 | 1.9–5.5 | C |
| Seymour Island | DJ.1056.65 | La Meseta Formation | 18 | 1.77 | 0.274 | 0.7–2.9 | C |
| Seymour Island | DJ.1057.15 | La Meseta Formation | 18 | 2.09 | 0.298 | 0.7–3.5 | C |
| Seymour Island | D.502 | La Meseta Formation | 23 | 1.32 | 0.207 | 0.4–3.3 | A |
| Seymour Island | D.8321.4 | La Meseta Formation | 11 | 5.70 | 0.214 | 2.5–8.4 | A |
| Seymour Island | DJ.1057.56 | La Meseta Formation | 52 | 1.34 | 0.228 | 0.3–3.4 | C |
| Seymour Island | D.509 | Cross Valley Formation | 13 | 0.84 | 0.371 | 0.4–1.4 | C |
| Seymour Island | 4388 | Cross Valley Formation | 16 | 2.51 | 0.267 | 1.2–6.3 | C |
| Seymour Island | D.494 | Cross Valley Formation | 14 | 2.58 | 0.173 | 2.0–4.6 | A |
| Seymour Island | DJ.1047.1 | Cross Valley Formation | 22 | 3.03 | 0.243 | 1.5–4.4 | C |
| Seymour Island | DJ.1047.11 | Cross Valley Formation | 30 | 1.93 | 0.254 | 0.7–3.0 | C |
| Seymour Island | DJ.1047.22 | Cross Valley Formation | 12 | 1.76 | 0.209 | 1.0–2.2 | C |
| Seymour Island | DJ.1047.18 | Cross Valley Formation | 7 | 2.87 | 0.254 | 2.1–3.7 | C |
| Seymour Island | D.495 | Sobral Formation | 27 | 0.52 | 0.139 | 0.4–0.7 | C |
| Seymour Island | K126 | Sobral Formation | 44 | 0.56 | 0.442 | 0.2–1.2 | C |
| Seymour Island | DJ.1055.70 | Sobral Formation | 17 | 1.10 | 0.221 | 0.6–2.2 | C |
| Seymour Island | DJ.1055.25 | Sobral Formation | 119 | 0.37 | 0.240 | 0.2–0.9 | C |
| Seymour Island | DJ.1055.74 | Sobral Formation | 69 | 0.28 | 0.190 | 0.2–0.5 | C |
| Seymour Island | DJ.1055.56 | Lopez de Bertodano Formation | 18 | 2.63 | 0.233 | 1.0–4.2 | C |
| Seymour Island | DJ.1053.23 | Lopez de Bertodano Formation | 16 | 0.88 | 0.199 | 0.6–1.2 | C |
| Seymour Island | DJ.1015.2 | Lopez de Bertodano Formation | 49 | 1.51 | 0.244 | 0.7–2.4 | C |
| Seymour Island | 758 | Lopez de Bertodano Formation | 19 | 1.00 | 0.185 | 0.7–1.4 | A |
| Seymour Island | 754 | Lopez de Bertodano Formation | 62 | 0.40 | 0.132 | 0.3–0.7 | C |
| Seymour Island | K143 | Lopez de Bertodano Formation | 35 | 1.18 | 0.252 | 0.4–2.5 | C |
| Seymour Island | DJ.1029.1 | Lopez de Bertodano Formation | 40 | 0.68 | 0.307 | 0.2–1.6 | C |
| Seymour Island | DJ.1053.1 | Lopez de Bertodano Formation | 41 | 0.34 | 0.329 | 0.2–1.6 | C |
| Vega Island | DJ.396.08 | Snow Hill Island Formation | 13 | 2.45 | 0.158 | 1.9–3.0 | C |
| Vega Island | D.8218.12 | Snow Hill Island Formation | 6 | 7.50 | 0.123 | 6.2–9.0 | A |
| The Naze, JRI | 5056 | Snow Hill Island Formation | 19 | 1.37 | 0.177 | 0.7–2.4 | A |
| The Naze, JRI | 5059 | Snow Hill Island Formation | 31 | 0.78 | 0.188 | 0.4–1.6 | C |
| The Naze, JRI | 5060 | Snow Hill Island Formation | 8 | 2.29 | 0.205 | 1.2–2.9 | C |
| The Naze, JRI | D.87.3 | Snow Hill Island Formation | 26 | 0.80 | 0.192 | 0.4–1.4 | C |
| The Naze, JRI | D.90 | Snow Hill Island Formation | 19 | 1.82 | 0.284 | 1.1–3.8 | A |
| James Ross Island | DJ.144.3 | Santa Marta Formation | 36 | 1.05 | 0.226 | 0.3–1.9 | C |
| James Ross Island | DJ.455.3 | Santa Marta Formation | 24 | 2.41 | 0.244 | 1.5–4.9 | C |
| James Ross Island | DJ.462.2 | Santa Marta Formation | 22 | 2.04 | 0.231 | 1.0–3.0 | C |
| James Ross Island | DJ.452.4 | Santa Marta Formation | 84 | 0.62 | 0.284 | 0.3–1.5 | C |
| James Ross Island | DJ.451.3 | Santa Marta Formation | 14 | 3.70 | 0.373 | 1.7–5.5 | C |
| James Ross Island | D.421 | Santa Marta Formation | 56 | 0.61 | 0.357 | 0.1–1.7 | C |
| James Ross Island | 4774 | Santa Marta Formation | 60 | 1.45 | 0.187 | 0.8–2.5 | C |
| James Ross Island | 4776 | Santa Marta Formation | 11 | 2.33 | 0.146 | 1.9–3.6 | C |
| James Ross Island | 8731 | Santa Marta Formation | 9 | 5.28 | 0.181 | 3.6–7.8 | C |
| James Ross Island | DJ.455.1 | Santa Marta Formation | 12 | 2.68 | 0.255 | 0.8–4.5 | C |
| James Ross Island | DJ.451.4 | Santa Marta Formation | 8 | 2.88 | 0.315 | 1.6–3.7 | C |
| James Ross Island | DJ.464.1 | Kotick Point Formation | 18 | 1.56 | 0.142 | 1.1–2.2 | C |
| James Ross Island | D.8311.5 | Kotick Point Formation | 12 | 1.17 | 0.125 | 1.0–1.4 | C |
| James Ross Island | D.8331.4 | Kotick Point Formation | 17 | 1.84 | 0.199 | 1.1–2.4 | C |
| James Ross Island | DJ.464.1b | Kotick Point Formation | 20 | 1.55 | 0.135 | 1.1–2.0 | C |
| Hope Bay | D.20.3 | Mount Flora Formation | 15 | 2.71 | 0.146 | 1.9–3.4 | C |
| Hope Bay | D.20.4 | Mount Flora Formation | 12 | 4.92 | 0.178 | 3.6–6.7 | C |

Table 1 (*Continued*).

| Locality | Sample number | Formation | No. of rings | MRW | MS | Min–max | Wood type |
|----------|---------------|-----------|--------------|-----|-----|---------|-----------|
| Hope Bay | D.20.10 | Mount Flora Formation | 20 | 3.26 | 0.137 | 1.9–4.3 | C |
| Hope Bay | D.20.16 | Mount Flora Formation | 35 | 1.47 | 0.146 | 0.9–2.7 | C |
| Hope Bay | D.48.2 | Mount Flora Formation | 17 | 3.77 | 0.145 | 1.6–4.8 | C |
| Hope Bay | D.48.3 | Mount Flora Formation | 7 | 3.23 | 0.146 | 2.6–3.8 | C |
| Hope Bay | D.48.5 | Mount Flora Formation | 20 | 1.48 | 0.148 | 1.0–1.9 | C |
| Hope Bay | D.48.7 | Mount Flora Formation | 20 | 1.46 | 0.152 | 1.0–2.0 | C |
| Hope Bay | D8754.15 | Mount Flora Formation | 11 | 2.21 | 0.157 | 1.3–2.8 | C |

MRW = mean ring width per wood sample, MS = mean sensitivity, min–max = minimum and maximum growth ring values, wood type C = conifer, A = angiosperm, JRI = James Ross Island.

iation). An arbitrary value of 0.3 is taken to separate 'complacent' trees that grow evenly under a favourable and uniform climate (MS < 0.3) from those that are 'sensitive' to fluctuating climate parameters (MS > 0.3).

For fossil growth analysis several assumptions were made. It was assumed here that there was no taxonomic bias in tree ring formation and that external factors exerted a much greater influence than internal ones, such as taxonomic bias or competition amongst trees (as discussed by Creber and Chaloner, 1984). Falcon-Lang (2000b) found

that the markedness of the ring boundary (distinct or indistinct boundaries) in conifers was related to taxon but not related to the actual width of the ring. This study is, however, able to check for this: if the climate signal is stronger than taxonomic or other internal factors then the final tree ring curve (Fig. 2) should match other climate curves (as it does, see below).

The response of angiosperm woods to climate is less well understood than that of conifers due to their more complex anatomical structure (Hughes et al., 1982; see below). However, some angio-

Table 2

Stratigraphic information for fossil wood collections used for growth ring analysis

| Formation | Age | Conifers+angios | | | Conifers only | | |
|-----------|-----|-----|------|-----|-----|------|-----|
| | | MRW | S.D. | MS | MRW | S.D. | MS |
| La Meseta Formation, Seymour Island Group | Early–Late Eocene, Elliot and Trautman, 1982; Dingle et al., 1998 | 2.42 | 1.45 | 0.250 | 2.11 | 0.82 | 0.267 |
| Cross Valley Formation, Seymour Island Group | Late Palaeocene, Elliot and Trautman, 1982 | 2.22 | 0.76 | 0.253 | 2.16 | 0.82 | 0.266 |
| Sobral Formation, Marambio Group | Palaeocene, Crame et al., 1991 | 0.57 | 0.32 | 0.246 | 0.57 | 0.32 | 0.246 |
| Lopez de Bertodano Formation, Marambio Group | Late Maastrichtian to Early Palaeocene, Pirrie et al., 1997 | 1.08 | 0.74 | 0.235 | 1.09 | 0.80 | 0.242 |
| Snow Hill Island Formation, Marambio Group | Late Campanian to ?late Maastrichtian, Pirrie et al., 1997 | 2.43 | 2.33 | 0.190 | 1.58 | 0.91 | 0.186 |
| Santa Marta Formation, Marambio Group | Late Coniacian–latest Campanian, McArthur et al., 2000 | 2.28 | 1.39 | 0.254 | 2.28 | 1.39 | 0.254 |
| Kotick Point Formation, Gustav Group | Early Albian, Riding et al., 1998 | 1.53 | 0.28 | 0.150 | 1.53 | 0.28 | 0.150 |
| Mount Flora Formation, Botany Bay Group | Early–Mid-Jurassic, Cantrill, 2000 | 2.72 | 1.20 | 0.151 | 2.72 | 1.20 | 0.151 |
| Fossil Bluff Formation, Alexander Island | Late Albian, Jefferson, 1982; Kelly and Montcrieff, 1992 | 1.38 | 0.73 | 0.424 | 1.38 | 0.73 | 0.424 |

MRW = mean ring width, S.D. = standard deviation, MS = mean sensitivity. Summary of tree ring data for the Alexander Island forests from Jefferson (1982) is also included. The Mount Flora Formation is difficult to date and has been considered as Early Cretaceous in the past (Farquharson, 1984) but recent work by Cantrill (2000) considers it Early–Middle Jurassic in age.
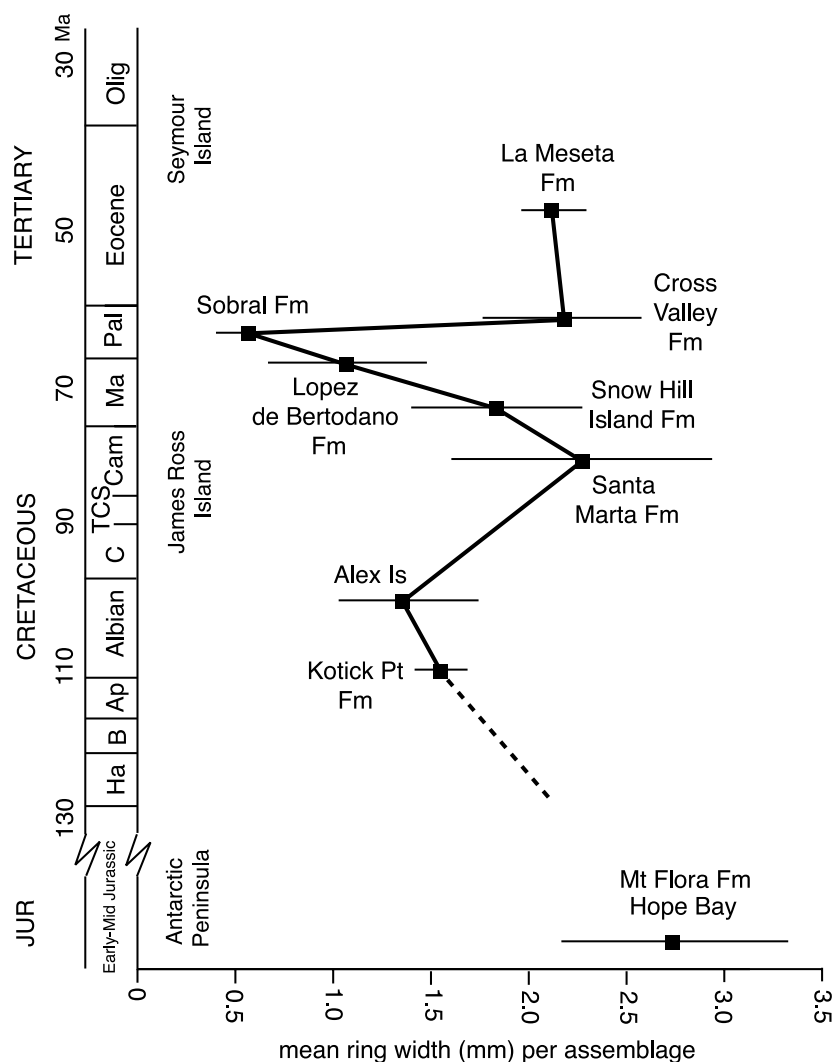
Fig. 2. Plot of conifer growth ring data for the Antarctic Peninsula region. Each square represents the mean ring width value for the conifer wood assemblage for that formation (see Table 2). That point is plotted in the mid-point of the time interval for that formation. Standard deviation per point represented by a horizontal line. Alex IS = Alexander Island, Ha = Hauterivian, B = Barremian, Ap = Aptian, C = Cenomanian, T = Turonion, C = Coniacian, S = Santonian, Cam = Campanian, Ma = Maastrichtian, Pal = Palaeocene, Olig = Oligocene.

sperm woods with well defined ring boundaries that were easy to measure were included in this study to compare the data with those of the conifers. These data are included in Tables 1 and 2. However, due to the less well established climate response of dicot wood as shown in their growth rings, only ring data for conifers were plotted in Figs. 2 and 5.

It is also assumed that relative ring width re-

lates to growth rate and is a proxy for climate, i.e. relatively narrower rings record cooler climates and wider rings record warmer wet conditions favourable for tree growth (see discussion in Fritts, 1976). Absolute ring width has little meaning in terms of climate, but if used in a comparative sense, for example, comparison of two floras or of assemblages from different time intervals, relative climate changes can be determined.

To investigate the trend in ring widths over time the samples were grouped according to the stratigraphic formation in which they occurred and the mean ring width, standard deviation and MS calculated for each formation (Table 2). A simple plot was then constructed of mean ring width per formation against geological time to show the trend in ring width for conifers through time (Fig. 2). The mean ring width data point was plotted in the mid-point of the time interval for each formation. Growth ring data of Early–Middle Jurassic age from the Mount Flora Formation, Antarctic Peninsula, were added to extend the curve. In addition, a mean ring width from ring data from the Early Cretaceous Alexander Island forests published by Jefferson (1982) was calculated to add an extra data point.

## 4.2. Angiosperm anatomical analysis

Dicotyledonous wood anatomical characters have been shown to document a relationship with climate (e.g. Carlquist, 1966, 1975, 1977; Baas, 1982; Wheeler and Baas, 1991; February, 1993; Wiemann et al., 1998; Zimmerman, 1978, 1983). Carlquist (1966) was the first to observe that xylem vessel diameter decreases, and vessel density increases, with increasing aridity. Further

work (Carlquist, 1977) indicated that there was a positive correlation between xylem anatomy and habitat. Carlquist devised two formulae, the vulnerability index and mesomorphy ratio, as indicators of the plant's adaptation to the available water in its habitat and therefore, indirectly, to the habitat itself. His observations have been upheld by further studies such as those of Baas (1982), Baas and Schweingruber (1987), Wilkins and Papassotiriou (1989) and Wiemann et al. (1998), who all related anatomical trends to macroclimate, and February (1993) who related such trends to more local climate. Further studies have applied these concepts to fossil wood anatomy with the aim of reading the palaeoclimatic signal. Wheeler and Baas (1991) undertook a comprehensive review of angiosperm wood in an attempt to determine its significance for ecological and evolutionary studies. More quantitative approaches were developed, including that of Wiemann et al. (1999) who developed 16 formulae that relate anatomical characters of trees, shrubs and woody liana species from 42 sites in the Northern Hemisphere to reconstruct Cenozoic palaeotemperatures, and Terral and Mengüal (1999) who used olive wood anatomical characters to reconstruct Holocene palaeotemperatures and precipitation.

The formulae devised by Wiemann et al. (1999)

Table 3

This table shows the results for palaeotemperature and degree of wetness in the environment for the Maastrichtian through to the Eocene as devised from the formulae of [a]Wiemann et al. (1999) where formula $9 = -4.3 + 34.14$ (predominantly paratracheal parenchyma), formula $11 = 27.28 - 15.16$ ($<100$ μm) $+ 24.17$ (storied rays), and formula $13 = 14.8 - 16.89$ (exclusively homocellular rays) $+ 24.86$ (storied rays) $+ 14.92$ (predominantly paratracheal parenchyma), and [b]Carlquist (1977) where vulnerability index (VI) = mean vessel diameter (μm)/mean number of vessels per mm$^2$; mesomorphy ratio (MR) = VI × mean vessel element length (μm)

| Formulae | MAT (°C) | | | Relative degree of wetness | |
| | 9[a] | 11[a] | 13[a] | VI[b] | MR[b] |
|---|---|---|---|---|---|
| Eocene | 9.57 | 7.30 | 14.98 | 0.68 | 380 |
| Palaeocene | 6.68 | 4.00 | 8.04 | 0.60 | 175 |
| Maastrichtian | 7.30 | *8.11* | *9.94* | 0.88 | 279 |

Compare these VI and MR values with those of ca. 0.5 and 250–300 respectively for native trees from southeast England where the mean annual precipitation is ca. 600 mm (Poole, 1993). Temperatures in italics are only valid if storied nature of the rays can be shown to have evolved in the Southern Hemisphere by the Maastrichtian but have been included here for completeness. These results indicate that the environment was relatively warm and wet, i.e. cool–warm temperate (cf. Whittaker, 1975; Holdridge, 1967), in the Maastrichtian and Eocene but was relatively cooler and drier, i.e. cold–cool temperate (cf. Whittaker, 1975; Holdridge, 1967), in the Palaeocene.
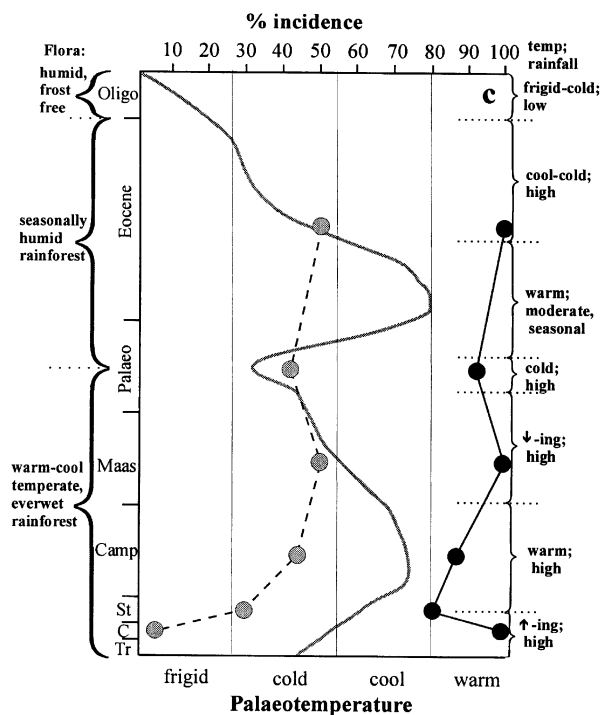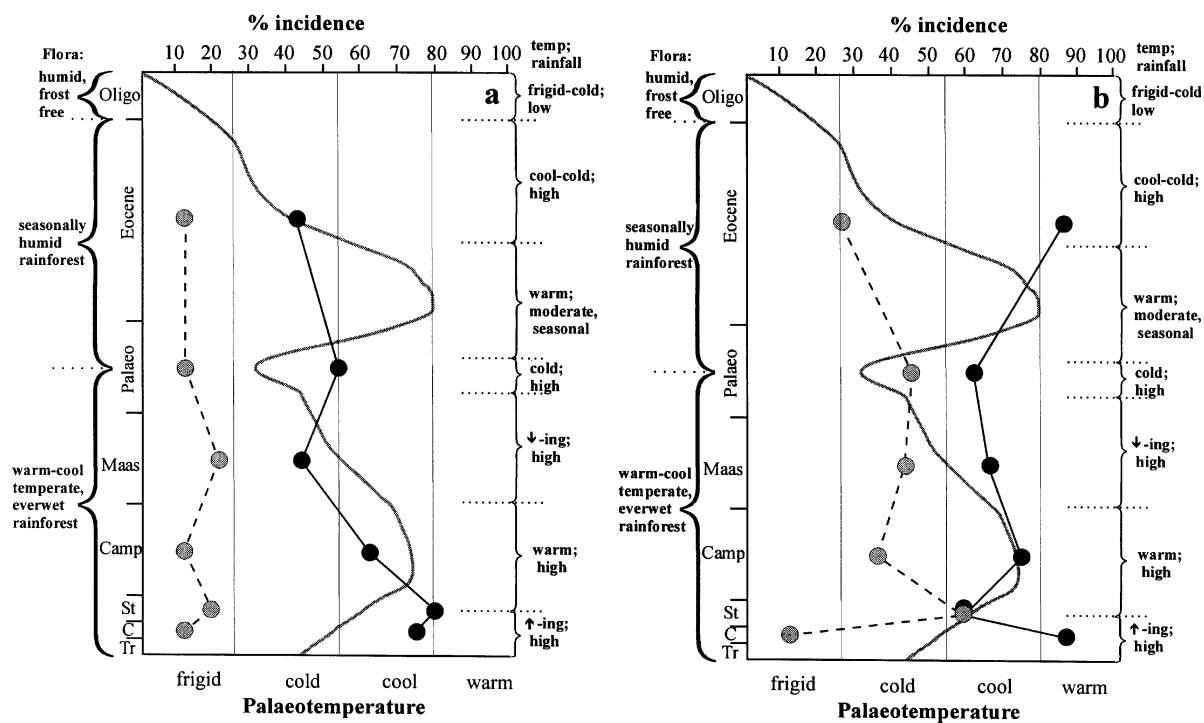
| | a) perforation plates | |
| --- | --- | --- |
| | simple | scalariform |
| **Eocene** | ±12 | ±19 |
| **Palaeo** | ±12 | ±14 |
| **Maas** | ±16 | ±16.5 |
| **Camp** | ±12 | ±17 |
| **Sant** | ±18 | ±18 |
| **Con** | ±12 | ±15 |
| | b) growth rings | |
| | distinct | indistinct |
| **Eocene** | ±17 | ±13 |
| **Palaeo** | ±14 | ±13 |
| **Maas** | ±16.5 | ±16 |
| **Camp** | ±17 | ±15 |
| **Sant** | ±22 | ±22 |
| **Con** | ±12 | ±12 |
| | c) porosity | |
| | semi-ring & ring | diffuse |
| **Eocene** | ±10 | ±17 |
| **Palaeo** | ±5 | ±13 |
| **Maas** | ±10 | ±16.5 |
| **Camp** | ±6 | ±15 |
| **Sant** | ±18 | ±18 |
| **Con** | ±6 | ±0 |

and Carlquist (1975, 1977, 1988) were applied to the Antarctic wood in an attempt to further the understanding of the terrestrial palaeoclimate during the latest Cretaceous and Palaeogene (the formulae devised by Terral and Mengüal (1999) were not used as they relate specifically to olive wood). There are a number of problems, highlighted by Wheeler and Baas (1991), when using fossil angiosperm wood to interpret ecology that need to be clearly acknowledged: (1) it is not known whether the incidence of certain anatomical features and ecological factors was the same today as in the past; (2) correlations between anatomical features and ecology may not have been constant over time and so their incidence can be used only for inferences about past climatic conditions; (3) constraints imposed by different levels of specialisation at different geological ages may mask the ecological signal for that time interval, e.g. ring porosity (a derived feature) is considered to be an indicator for seasonal climate therefore the absence of ring porosity cannot be used to infer lack of seasonal climates (see Wheeler and Baas, 1991). Moreover, Wiemann et al. (1998) state that the formulae should not be used when the number of morphotypes is less than 25. If, through future research, the number of identified morphotypes per geological age in Antarctica reaches 25 or greater then the formulae can be reapplied and a more precise palaeoclimate signal will be published. With these considerations in mind, the use of the inferred palaeoclimatic data obtained herein should be used with extreme caution and reference to the associated problems outlined above fully acknowledged.

One hundred and seventy-five fossil angiosperm wood specimens from the South Shetland Islands (King George and Livingston islands) and the James Ross Basin, Antarctica, were studied to determine trends in characters through time and their environmental signal. Effort was made to ensure organ consistency (i.e. large branch/small trunk material) so that the anatomical data could be compared. Anatomical measurements were recorded according to the IAWA recommendations (IAWA Committee, 1989) wherever possible, apart from vessel element lengths which were measured from thin sections.

For the application of Wiemann et al.'s (1999) formulae and Carlquist's (1977) formulae only those specimens with the necessary anatomical characters preserved could be used. These fossils comprised 48 Eocene specimens, 26 Palaeocene specimens and 43 late Maastrichtian specimens. Using anatomical characters known to have evolved by the Maastrichtian, the Antarctic material enabled the use of Wiemann et al.'s (1999) arcsine transformation formulae numbers 9, 11 and 13 (see Table 3). Their recommended formulae 12 and 15 were not appropriate due to the ?evolutionary absence of spiral thickenings and marginal parenchyma in the Cretaceous and Palaeocene (personal observations which support the suggestion of Wheeler and Baas, 1991). Consequently, palaeotemperature signals using the formulae of Wiemann et al. and the degree of relative water availability with the vulnerability index and mesomorphy ratio were calculated (Table 3). Figs. 3 and 4 were constructed by plotting the relative abundance of a particular anatomical character of the Antarctic woods through the Late Cretaceous and Tertiary. The data points

Fig. 3. Dicotyledonous angiosperm anatomical characters. Incidence expressed as a percentage of wood feature through geological time (Palaeo = Palaeocene, Maas = Maastrichtian, Camp = Campanian, Sant/St = Santonian, Con/C = Coniacian, Tr = Turonian). Number of morphotypes: Eocene 7, Palaeocene 13, Maastrichtian 9, Campanian 8, Santonian 6, Coniacian 8. The lines joining the symbols merely serve to distinguish the data points and do not indicate statistically established trends. The estimated standard deviation, expressed as a percentage, for each data point has been calculated using the formula given by Wheeler and Baas (1993) and tabulated along with the total number of morphotypes per geological time. Palaeotemperature, rainfall and flora data adapted from Dingle and Lavelle (1998) and the references cited therein. ↓ decreasing; ↑ increasing. (a) Perforation plates through time where closed circles represent scalariform perforation plates and shaded circles represent simple perforation plates; (b) growth rings where shaded circles represent distinct growth rings and closed circles represent indistinct growth rings; (c) porosity where closed circles represent diffuse porosity, shaded circles represent semi-ring and ring porosity.

have been plotted in the middle of the geological age range for each stratigraphic formation and thus artificially constrains the data.

## 5. Results

### 5.1. Growth rings analysis

A total of 48 ring series were measured, ranging in length from 6 to 119 rings (Table 1). In the conifer rings the boundaries are marked by a distinct zone of narrow latewood cells, indicating that the trees were responding to a seasonal change in the environment. Mean ring width per tree ranged from 0.28 to 7.50 mm (including dicots) or from 0.28 to 5.28 mm for conifers only, which represents a considerable range in growth rates.

When the trees were grouped according to stratigraphic formation, however, it is apparent that there are clear trends in ring width over time (Fig. 2). Peaks in ring width are apparent in the Late Palaeocene (Cross Valley Formation) and Coniacian–Santonian (Santa Marta Formation). Wide growth rings are also present in trees of Jurassic age from the Mount Flora Formation. Narrower growth rings are more common during the Early Cretaceous and in an interval from the late Maastrichtian to the Early Palaeocene. There is also a slight decrease in ring widths in the Eocene.

If ring width is taken as a simple proxy for climate (i.e. narrower rings are indicative of cooler climates and wider rings of warmer climates) then an interesting climate trend is apparent from Fig. 2. The curve suggests warmer climates during the Jurassic followed by a cooling during the Early Cretaceous. Climates warmed again during the middle of the Late Cretaceous but then cooled dramatically. A distinct cooling is apparent in the late Maastrichtian and Early Palaeocene, across the Cretaceous–Tertiary boundary. By the Late Palaeocene the climate had warmed again and then cooled slightly through the Eocene. There are obvious limitations to this curve: more data points are desirable and the plot of data points mid-formation is a somewhat artificial constraint.

The ring data can, however, provide an indication of trends of climate change and this curve matches well other climate curves for the Antarctic region (see discussion below).

It is notable that, regardless of ring width, MS values for the whole assemblage are remarkably consistent. MSs per formation range from 0.15 to 0.32, with the majority of individual samples having MSs less than 0.3. This indicates that, regardless of growth rate, the growing environment was relatively uniform from year to year and there were no significant episodes of erratic climate that caused irregular growth rates.

### 5.2. Angiosperm anatomical analysis

Figs. 3 and 4 show the incidence of certain anatomical features in Antarctic dicot wood through the Late Cretaceous and Palaeogene. Fig. 3 shows the incidence of scalariform versus simple perforation plates (Fig. 3a), distinct versus indistinct growth rings (Fig. 3b) and diffuse porous versus ring porous/semi-ring porous woods (Fig. 3c). Fig. 4 shows the incidence of grouped versus predominantly solitary vessels (Fig. 4a), vessel diameter ($>$ 100 µm versus $<$ 100 µm) (Fig. 4b) and vessel abundance ($>$ 100 mm$^{-2}$ versus $<$ 100 mm$^{-2}$) (Fig. 4c). Climate information from Dingle and Lavelle (1998) is also shown on these graphs for comparison. This includes their climate curve, estimated temperatures and rainfall, plus the nature of the floras. In addition, Table 3 presents the tentatively estimated mean annual temperature (MAT) and degree of relative wetness from dicot wood anatomy for the Antarctic Peninsula from the Maastrichtian to Eocene.

By comparing the plot for anatomical features with the climatological trends described by Wheeler and Baas (1991, 1993) and the climate curve (Figs. 3 and 4), the value of the represented anatomical feature in the Antarctic woods as a climate proxy can be discussed. Vessel characters in modern plants are known to reflect environmental conditions; for example cool temperate and boreal woods have more frequent solitary vessels than warm temperate or desert floras (Baas and Schweingruber, 1987). In addition, narrow vessels (i.e. $<$ 100 µm) occur in cool temper-
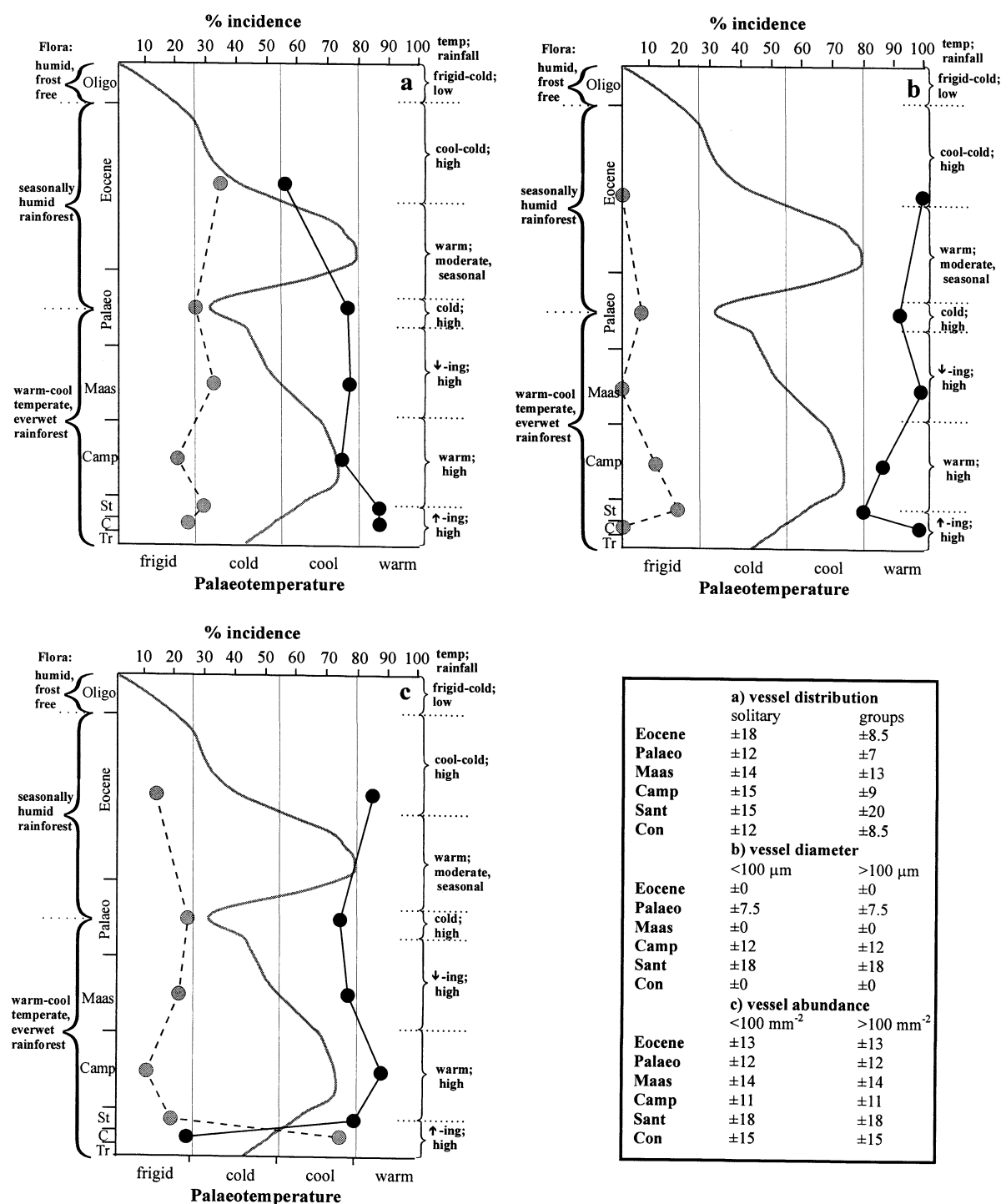
Fig. 4. Full details are given in the legend for Fig. 3. (a) Vessel distribution where shaded circles represent presence of grouped (i.e. clusters or radial multiples >4) vessels and closed circles represent mainly solitary vessels; (b) vessel diameter where shaded circles represent diameters >100 μm and closed circles represent diameters <100 μm; (c) vessel abundance where closed circles represent >100 mm⁻² and shaded circles represent abundances <100 mm⁻².
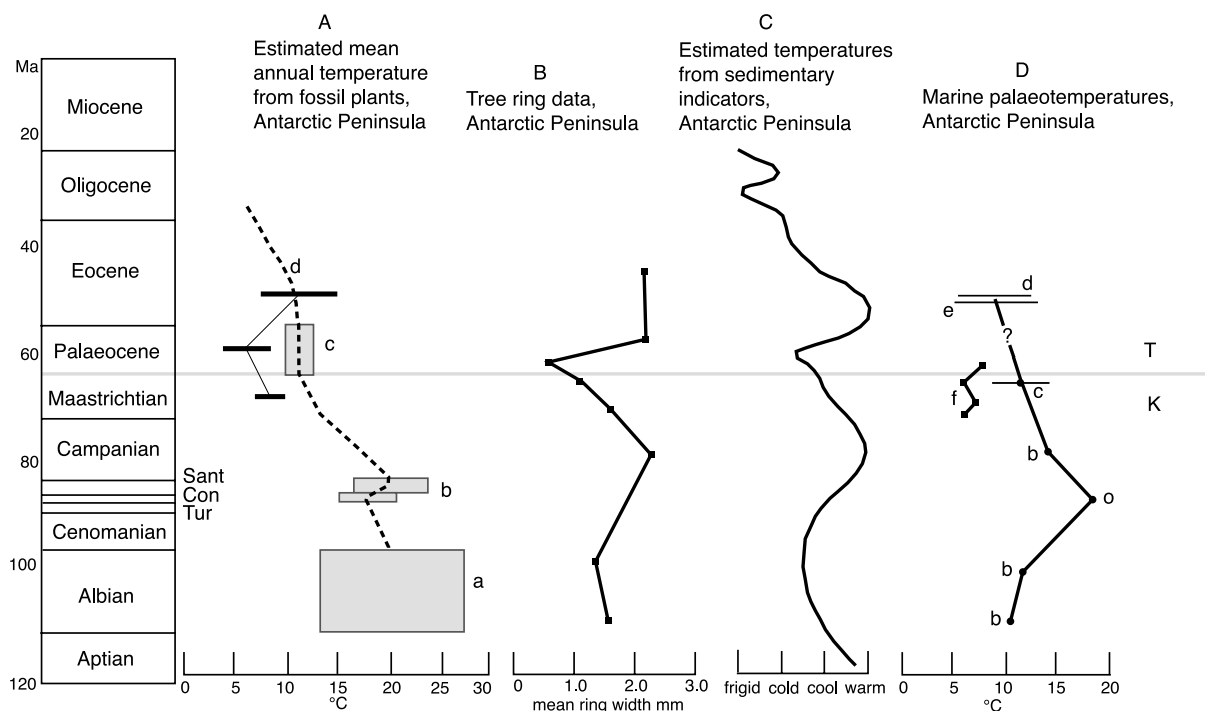
Fig. 5. Compilation of climate curves for the Cretaceous and Tertiary of the Southern Hemisphere. (A) Estimated MATs from fossil plant assemblages from the Antarctic Peninsula (updated from Francis, 1999). (a) Estimate for Alexander Island fossil forests 13–27°C from Cantrill (1995), (b) estimates from physiognomic analysis of two fossil leaf assemblages (Hayes, 2000); 15–20°C for the Hidden Lake Formation, Coniacian, and 16–23°C for the Santa Marta Formation, early Santonian–early Campanian, (c) nearest living relative estimate for leaf floras from the Palaeocene from the South Shetland Islands (10–12°C, Birkenmajer and Zastawniak, 1989), (d) climate trend of early and middle Eocene warmth followed by cooling in the Late Eocene and earliest Oligocene, deduced by Askin (1997) from palynological evidence. The three horizontal bars are the estimated MATs from dicot wood anatomical characters from Table 3. (B) Tree ring compilation from this study. (C) Estimated temperatures from a range of sedimentary indicators compiled by Dingle and Lavelle (1998). (D) Marine palaeotemperatures from oxygen isotope data. o = oysters, b = belemnites, c and d = range of temperatures from several invertebrate sources; all from Ditchfield et al. (1994). e = range of temperatures from infills of bivalve borings in fossil wood with $\partial_w$ −1.0‰ SMOW, Pirrie et al. (1998). f = temperatures from foraminifera, Barrera et al. (1987). Sant, Santonian; Con, Coniacian; Tur, Turonian.

ate and high montane tropical species (Carlquist, 1988; Baas and Schweingruber, 1987) and may reflect relatively dry conditions.

When anatomical characters are taken together, ecological patterns become more evident. The relatively high incidence of low vessel abundance (Fig. 4c), large diameter vessels (Fig. 4b), indistinct growth rings (Fig. 3b) and diffuse porous woods (Fig. 4c) in the Coniacian suggests that growing conditions were more favourable than in the proceeding epochs. Throughout the remainder of the mid–Late Cretaceous through to the Eocene there is a general increase in semi-ring

and ring porous woods (Fig. 3c) with a corresponding increase in distinct growth rings (Fig. 3b) and a high incidence of predominantly solitary vessels (Fig. 4a) that suggest an increase in seasonality and/or temperate nature of the environment. An increase in semi-ring and ring porosity may be also reflecting increasing deciduousness. The predominance of woods with high vessel density (Fig. 4c) and scalariform perforation plates (Fig. 4a) at this time are also indicative of a cool temperate (or high montane) ecology. Relatively wet conditions are suggested by the prevalence of woods with large diameter vessels

(Fig. 4b). The general trend in postulated palaeoclimate from sedimentary indicators (Fig. 5C) over the Cretaceous–Tertiary boundary into the Early Eocene is reflected in the tentatively estimated palaeotemperatures derived from the dicot wood (Table 3, Fig. 5A). Moreover, dicot wood anatomy suggests relatively wetter phases in the Maastrichtian and Eocene and an intervening drier phase in the Palaeocene.

## 6. Discussion

### 6.1. Cretaceous and Tertiary climates of the Antarctic Peninsula region

Compilation of climate data from fossil plants, including those presented above, clearly illustrates changing climates through the Cretaceous and early Tertiary. Fig. 5A is a compilation of some MAT estimates from fossil plants from the Antarctic Peninsula. The data used here include (a) estimate for Alexander Island fossil forests 13–27°C from nearest living relatives from Cantrill (1995), (b) estimates from physiognomic analysis of two fossil leaf assemblages (Hayes, 2000); 15–20°C for the Hidden Lake Formation, Coniacian, and 16–23°C for the lower part of the Santa Marta Formation, late Coniacian–latest Campanian, (c) nearest living relative estimate for leaf floras from the Palaeocene from the South Shetland Islands (10–12°C, Birkenmajer and Zastawniak, 1989), (d) climate trend of Early and Middle Eocene warmth followed by cooling in the Late Eocene and earliest Oligocene, deduced by Askin (1997) from nearest living relative analysis of palynological evidence. The black bars in Fig. 5A represent the MAT estimates derived from dicot wood anatomy (this study). Other published climate estimates of pollen and leaf floral assemblages for the Cretaceous and Tertiary exist but they are expressed in terms of relative climate only and to some extent they have been included in the curve of Dingle and Lavelle (1998) (Fig. 5C).

Previous palaeoclimate information from the James Ross Basin is available from oxygen isotope analyses of marine macrofossils and foraminifera (Barrera et al., 1987; Pirrie and Marshall, 1990; Ditchfield et al., 1994) (Fig. 5D). These fossils were collected from the same sedimentary sequences as the fossil wood. They indicate cooler Early Cretaceous marine temperatures, a warming into the Coniacian to early Campanian followed by a gradual cooling through the Late Cretaceous and into the Palaeogene. Temperatures for the late Maastrichtian–Early Palaeocene Lopez de Bertodano Formation were determined as 12°C (Pirrie and Marshall, 1990) or 9–14°C (Ditchfield et al., 1994). The same peak warmth is apparent from fossil plant data, although the peak of warmth on land seems to have been during Santonian to Campanian times, rather than during the Coniacian (which could be accounted for by missing plant data prior to the Turonian).

The distinct cooling and warming trend across the Cretaceous–Tertiary boundary and into the Late Palaeocene, reflected by some of the plant data, is not apparent in the marine record. Barrera et al. (1987) analysed foraminifera from the Lopez de Bertodano Formation of Seymour Island; their data suggest a minor temperature rise in the early–middle Maastrichtian, followed by a cooling in the late Maastrichtian to Early Palaeocene (their palaeotemperatures are slightly cooler than those of Ditchfield et al. (1994) because they used a $\partial_w$ value of $-1.5\%o$ standard mean ocean water (SMOW); see discussion in Ditchfield et al., 1994). Oxygen isotope data were also obtained for the Eocene from calcite cements infilling borings in fossil wood, made by marine bivalves (Pirrie et al., 1998). Palaeotemperatures of 5–13°C ($\partial_w$ $-1.0\%o$ SMOW, normal salinity minimal glaciation) were obtained for the late Early to early Middle Eocene (La Meseta Formation) from the borings, similar to the range of 6–13°C from marine invertebrates (Ditchfield et al., 1994). These temperatures lie within the range estimated from the dicot wood (7–15°C).

A climate curve for the Antarctic Peninsula was compiled by Dingle and Lavelle (1998), using geochemical and sedimentological proxies for palaeoclimate (Fig. 5C). They were not able to predict absolute palaeotemperatures but more relative phases of warming and cooling. They used the chemical index of alteration (CIA), which quanti-

fies weathering processes of feldspars and clay minerals, and interpreted relative changes in CIA as a proxy for temperature change, having assumed humidity was constant. This assumption, that the presence of vegetation in Antarctica throughout this interval represents ever-wet conditions, is however questionable and the curve must be used with caution. In addition, in order to be an accurate proxy for climate, the provenance of the sediments must remain the same, but in this case the provenance changed through the Cretaceous and into the Tertiary. However, the climate trend shown by Dingle and Lavelle's (1998) curve is remarkably similar to others in Fig. 5 (see Dingle and Lavelle, 2000).

Taken together, a more detailed picture of Cretaceous and Tertiary climates is now presented for this high latitude site. Aptian–Albian climates are not well determined at present from fossil leaves but the tree ring data suggest relatively cooler climates during the Albian; this is consistent with evidence from marine oxygen isotope predictions from western Australia (Pirrie et al., 1995) and Antarctica (Ditchfield et al., 1994), and from weathering indices of Dingle and Lavelle which suggest cool temperate climates.

This was followed by a period of peak warmth during the mid–Late Cretaceous, during the Coniacian to early Campanian, from about 78 to 88 Ma. The climate was warm and wet, with MATs of 16–23°C, predicted from fossil leaf analysis (Hayes, 2000). The relative abundance of diffuse porous woods with indistinct growth rings supports a favourable environment.

From the late Campanian, through the Maastrichtian and across the Cretaceous–Tertiary boundary, the climate cooled considerably. Growth rings in the wood are much narrower in this interval and palaeotemperatures estimated from dicot wood anatomy suggest MATs of 7°C in the Maastrichtian and 4–8°C for the Palaeocene. The CIA ratios of Dingle and Lavelle are low enough to suggest glacial conditions but only cold conditions are proposed due to the present lack of sedimentary evidence for glaciation, and the lack of evidence for frost in the pollen flora (Askin, 1992). Although there is no evidence from plants for freezing conditions in the Peninsula re-

gion during the Maastrichtian and Early Palaeocene, the predicted MATs (7°C and 4–8°C) are low. Using a terrestrial climate gradient of −0.3°C for degree latitude (Wolfe and Upchurch, 1987) MATs of −2°C and −5°C to −1°C are estimated for the South Pole during the Maastrichtian and Early Palaeocene. This may have been cold enough to allow the formation of ice sheets, especially at high elevations on mountains that may have been present at that time (Stump and Fitzgerald, 1992).

A warming phase occurred from the Late Palaeocene into the Early Eocene. Dingle et al. (1998) found peak warming in the Early Eocene, co-incident with the global thermal maximum at this time (Röhl et al., 2000), although the extent of the Eocene warmth is unclear as yet from plant evidence. Some leaf floras of mixed broad-leaved angiosperms with conifers and ferns suggest relatively humid, warm temperate conditions with MATs of about 10–15°C (Askin, 1992; Birkenmajer and Zastawniak, 1989; Doktor et al., 1996) and growth rings indicate generally warmer climates during the Late Palaeocene but slightly cooler into the Eocene (Fig. 5B). Tentative estimates of MATs of 7–15°C were predicted from dicot wood anatomy for the Eocene. This is matched by marine oxygen isotope temperatures, measured from cements in marine borings in fossil wood, of ca. 5–13°C for the middle Middle–late Middle Eocene (Pirrie et al., 1998). The Middle Eocene climate seems to have been cold and wet, with strong seasonality of rainfall (Askin, 1997). Tree ring data for this time are not yet resolved well enough stratigraphically to provide a detailed climate analysis for the Eocene. By the latest Eocene the northern Antarctic Peninsula had a cold and relatively dry climate, possibly with snow and freezing temperatures (Dingle et al., 1998). The palynofloras become less diverse, which probably reflects the cooling temperatures (Askin, 1997) that ultimately led to the onset of the Cenozoic ice sheets and the elimination of vegetation from mainland Antarctica.

## 6.2. Global climate trends

The climate pattern seen in the Antarctic rec-

ord, of mid–Late Cretaceous warmth, cooling across the Cretaceous–Tertiary boundary and Late Palaeocene/Early Eocene warming, has been reported from a variety of sites globally, indicating that this is a global, rather than local, climate signal (Frakes et al., 1992). For example, mid–Late Cretaceous warmth was also determined from analysis of Coniacian–Turonian floras from the Arctic. MATs from fossil angiosperm leaf assemblages from Cretaceous high latitude sites in Alaska (about 75°N) (Parrish and Spicer, 1988; 1998) provided MAT estimates for the latest Albian–Cenomanian of $10 \pm 3$°C, warmer conditions during the Coniacian with MATs of 12–13°C, and a cooling phase during the Campanian and Maastrichtian to temperatures of about 2–8°C. Warm month mean temperatures were estimated to have ranged from 18 to 20°C during the Turonian and Coniacian, with cold month mean temperatures ranging from $-3.8$ to 5.7°C (Herman and Spicer, 1996). This peak warmth was also apparent in similar leaf analyses from lower latitude sites in North America (Wolfe and Upchurch, 1987). Cooler climates towards the end of the Cretaceous are also apparent from their data.

Ocean temperature records from outside the Antarctic Peninsula region also reflect Late Cretaceous warmth. A record of deep sea oxygen isotope data from foraminifera in the southern South Atlantic (DSDP Site 511, Falkland Plateau) reveals an abrupt warming during the Turonian with deep waters of 18°C and surface waters over 30°C at 59°S palaeolatitude. The warming continued through to the early Campanian, with deep waters ranging from 4 to 16°C and very warm surface water temperatures of between 20 and 27°C (Huber et al., 1995). This same trend is seen in other marine records (Huber, 2000).

Climate cooling across the Cretaceous–Tertiary boundary and into the Early Palaeocene is also now apparent globally (e.g. Barrera and Savin, 1999). Although there are no records of glacial sediments of this age, the presence of ice sheets has been proposed to account for large and rapid sea level drops during the Maastrichtian in the USA (Miller et al., 1999). Oxygen isotope records from foraminifera from Site 690 at 65°S indicate that deep water temperatures would have been about 5°C, which implies that ice sheets must have been present at higher latitudes (Miller et al., 1999).

The Late Palaeocene–Early Eocene thermal maximum is well established from many sites world wide (e.g. Zachos et al., 1993), and is believed to have been caused by a sudden input of methane into the atmosphere from dissociation of methane hydrates in continental margin sediments (see Röhl et al., 2000). According to the orbital chronology developed for ODP Site 690 (Weddell Sea, Southern Ocean), the warming phase lasted about 220 kyr. This warmth is apparent in Antarctic woods and marine sediments (Fig. 5), and nearest living relative analysis of pollen (Askin, 1992), although better stratigraphic resolution is required to fix the exact duration of the warm phase. Antarctic records show clearly that the climate cooled from the mid-Eocene onwards, ultimately resulting in the onset of major ice sheets (Barrett, 1996; Dingle et al., 1998).

## 7. Conclusions

(1) Fossil wood is abundant within Cretaceous and early Tertiary strata in the northern Antarctic Peninsula region and represents the remains of vegetation that was able to grow at high latitudes when the climate was much warmer. The wood provides important proxies for climate its anatomical structure.

(2) Analysis of growth rings in conifer woods has provided a record of climate trends for the Antarctic Peninsula through the Cretaceous and early Tertiary. The close similarity between the growth ring curves and those plotted from geochemical and sedimentary data indicates that, despite possible taxonomic and internal controls on growth ring formation, a strong external climate signal can be detected which matches global climate patterns.

(3) Analysis of anatomical characters in dicotyledonous angiosperm wood has provided important new information about general ecological conditions for this time period in Antarctica. These anatomical features in fossil wood may

not as yet provide a clear climate signal due to underlying constraints (see 4.2. Angiosperm anatomical analysis) but, when considered in association with other palaeoclimate data, may provide an important source of information about terrestrial environments in the past.

(4) Climate data determined from fossil plants, sediments and geochemical indicators for the Antarctic Peninsula region show a distinct pattern of warming and cooling through the Late Cretaceous into the early Tertiary. Cooler climates during the Early Cretaceous were followed by a warming phase which peaked during the Coniacian to early Campanian. MATs were in the range of 16–23°C on land and up to 17°C in the oceans. The climate cooled during the Maastrichtian and Early Palaeocene and cold wet and possibly seasonal environments prevailed. The Late Palaeocene/Early Eocene was once again warm but conditions subsequently deteriorated through the latter part of the Eocene, when cold seasonal climates developed.

(5) Although there is no evidence from plants or sediments for freezing conditions in the Peninsula region during the Maastrichtian to Early Palaeocene, low MATs are tentatively estimated from angiosperm wood (from 7°C to 4–8°C respectively). At higher latitudes MATs below freezing are thus estimated for the South Pole. This may have been cold enough to allow the formation of ice sheets, especially at high elevations on mountains.

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