GROWTH RINGS IN CRETACEOUS AND TERTIARY WOOD FROM ANTARCTICA AND THEIR PALAEOCLIMATIC IMPLICATIONS

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ABSTRACT. Although the Antarctic Peninsula now has a glacial climate, during the Cretaceous and early Tertiary it was sufficiently warm for forests to thrive, even at palaeolatitudes of 59°-62° S. The forests grew on an emergent volcanic arc and the wood was subsequently buried in fluvial and basinal sediments on the margins of the back-arc basin. The forests were composed mainly of podocarp and araucarian conifers. By the late Cretaceous, angiosperm trees were also present, particularly *Nothofagus*, forming the characteristic forest association of the southern hemisphere today. The growth rings in the fossil wood are wide and extremely uniform, indicating that the environment was very favourable for tree growth. By comparison with living forest trees with similar growth characteristics, a warm to cool-temperate climate is proposed for the Antarctic Peninsula in the Cretaceous and early Tertiary. Features of fossil floral assemblages and sedimentary rocks are also indicative of this type of climate. An increase in the level of atmospheric carbon dioxide is considered the most likely cause of the warm polar climate at this stage.
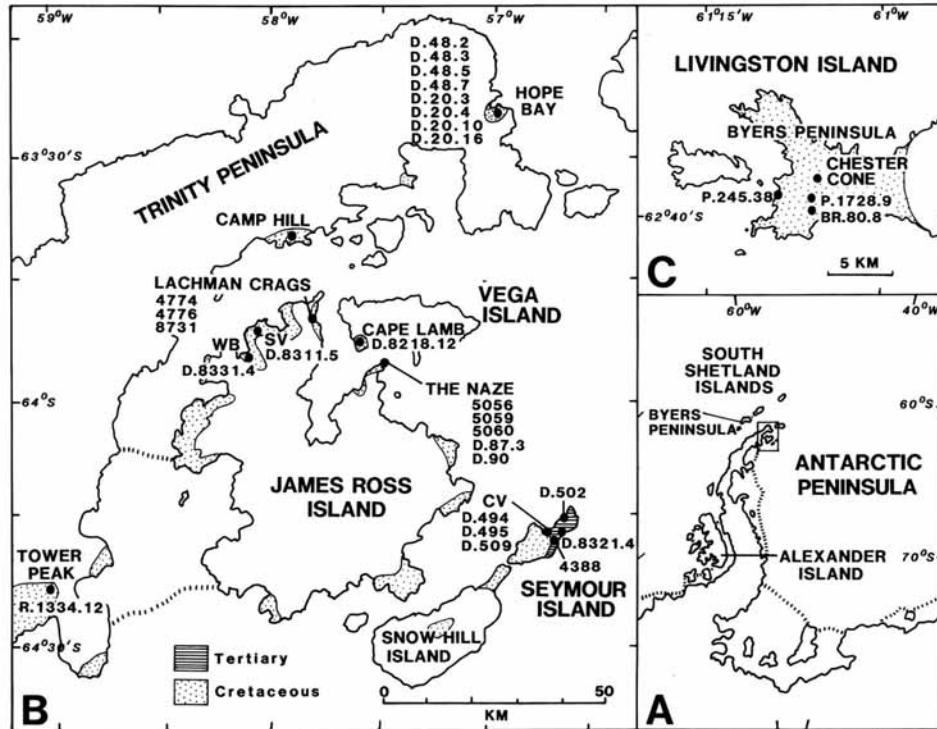
ALTHOUGH the Antarctic Peninsula (text-fig. 1) now has a glacial climate during the Cretaceous and early Tertiary it was sufficiently warm and temperate to allow the growth of fairly diverse plant communities. These were principally composed of conifers, cycadophytes, and ferns, with angiosperms appearing in the late Cretaceous (Dusen 1908; Gothan 1908; Halle 1913; Plumstead 1962; Jefferson 1982, 1983). Structurally preserved wood is not only an important component of these floral assemblages (Gothan 1908; Jefferson 1982) but is also present in both marine and non-marine sediments in which other plant material is absent.

Certain aspects of the flora, such as the overall composition, leaf morphology and size, can give some indication of the tolerance of the plants to climatic extremes, particularly temperatures. However, the growth rings in the fossil wood preserve a more detailed record of the environment from which not only temperature constraints but also seasonal variations in rainfall can be determined in greater detail.

Growth ring analyses have been used to evaluate changing geological climates on a broad scale (Chaloner and Creber 1973; Creber and Chaloner 1984a, b) and to investigate individual fossil forest environments, e.g. Cretaceous forests of Antarctica (Jefferson 1982) and the Upper Jurassic/Lower Cretaceous forests of southern England (Francis 1984, in press). In this project a collection of Cretaceous and early Tertiary fossil wood from various localities around the northern part of the Antarctic Peninsula was studied to determine the botanical composition of the fossil forests and the nature of the palaeoclimate. The results of the growth ring analyses are presented and their palaeoenvironmental significance discussed. This complements a similar study by Jefferson (1982, 1983) on higher latitude early Cretaceous fossil forests from Alexander Island.

FOSSIL FORESTS AT HIGH LATITUDES

The fossil remains of plant assemblages that grew very near to both the North and South poles in the Cretaceous and early Tertiary provide some of the main evidence that polar climates were then much warmer than at present. Their presence has provoked much discussion since plant growth at

TEXT-FIG. 1. Map of the northern Antarctic Peninsula region showing localities. A, location of Byers Peninsula, Livingston Island (see inset C) and the northern part of the Antarctic Peninsula, enlarged in inset B. B, fossil wood localities in the northern Antarctic Peninsula region. CV = Cross Valley, SV = Sharp Valley, WB = Whisky Bay. ● D.8218.12 = fossil locality and number. C, location of fossil localities on Byers Peninsula, western Livingston Island, South Shetland Islands.

such high latitudes today is restricted by very low temperatures (Billings 1964; Grime 1979) and to some extent the low angle of the sunlight of the polar light regime (Wolfe 1980).

To provide a more even annual distribution of light, a reduction in the tilt of the earth's axis of rotation has been proposed for Cretaceous and early Tertiary times (Wolfe 1978, 1980; Douglas and Williams 1982; Jefferson 1982, 1983). There are, however, several arguments against such a proposal (Donn 1982; Axelrod 1984; Creber and Chaloner 1985). In particular, the clearly marked growth rings in fossil wood from the south polar region (Jefferson 1982; Douglas and Williams 1982; this study) and the Arctic region (Smiley 1967; Schweitzer 1980) are evidence that the climate had well-defined seasons, whereas the reduced axial tilt would produce a seasonless, more uniform environment. Furthermore, no plausible physical mechanism for actually changing the axial tilt has been proposed (Creber and Chaloner 1985). The climate model simulations of Barron (1984) have shown that a reduced obliquity would in fact result in lower polar temperatures due to a decrease in mean annual insolation at high latitudes.

That the plants (and animals) were able to adapt physiologically to long periods of winter darkness was presented as an alternative solution by Axelrod (1984) and Creber and Chaloner

(1984*a*, *b*, 1985). Although the annual distribution is not uniform, the total light energy flux for polar regions today is equivalent to that at more temperate latitudes. Thus the high-latitude trees may well have been photoperiodic ecotypes (as some are today), specifically adapted to growing at faster rates in short seasons with long hours of daylight (Vaartaja 1962; Axelrod 1984; Creber and Chaloner 1985). Other adaptions include suitable tree densities and conical growth habits to intercept the maximum amount of solar radiation with minimum mutual shading (Creber and Chaloner 1984*a*, *b*; Creber, in press). Axelrod (1984, p. 128) suggests that the trees 'survived the winter darkness in polar regions by a general metabolic shutdown'.

The warm Cretaceous/Tertiary polar temperatures, as indicated by the plants and animals, were part of the warm equable climate with a low global temperature gradient that was characteristic of the Mesozoic (Frakes 1979; Hallam 1985). The cause of the polar warming has been investigated using climatic simulation models based on Cretaceous continental distribution (Barron *et al.* 1981; Barron and Washington 1982, 1984; Barron 1983). Their results indicated that the proximity of the continental masses would result in an overall global warming with a warmer low latitude belt, correlating well with evidence from fossil tree-ring data collated by Creber and Chaloner (1984*a*, *b*, 1985). However, the polar regions would have remained cold. An increase in the CO_2 level of the atmosphere was proposed by Berner *et al.* (1983) and Barron and Washington (1984) to be the additional mechanism required to explain the palaeoclimatic data. Climate models based on modern palaeogeography illustrate that an increase in atmospheric CO_2 would result in an increase in the poleward transport of latent heat. This would cause a reduction in the equator-pole temperature gradient, much like that proposed for the Mesozoic (Manabe and Wetherald 1975, 1980). Furthermore, the temperatures at the poles would increase as would the rates of evaporation and precipitation.

Since CO_2 is important for photosynthesis, higher levels would have also raised photosynthetic rates and increased plant productivity. As shown by Creber and Chaloner (1985, tables IV and V), tree species in particular show large increases in productivity under higher levels of CO_2. Changes in growth rates exhibited by modern tree-rings were also attributed to recent changes in the level of atmospheric CO_2 by LaMarche *et al.* (1984). Thus higher levels of atmospheric CO_2 in the Cretaceous and early Tertiary would not only have raised temperatures at high latitudes to levels allowing plant growth, but plant productivity would also have been enhanced, possibly accounting for the wide growth rings in the fossil wood described here.

ANTARCTIC FOSSIL WOOD

Specimens used in this growth ring analysis are housed in the collections of the British Antarctic Survey, Cambridge and the British Museum (Natural History). The wood was collected in past field expeditions including Operation Tabarin (1943–1945), Falkland Islands Dependencies Survey 1945–1947 (collections mainly by W. N. Croft), and during more recent field surveys by the British Antarctic Survey.

The wood ranges from early Cretaceous (Barremian) from the South Shetland Islands (text-fig. 1) to Eocene/early Oligocene from Seymour Island. Specimen numbers, locality, and stratigraphic information are given in text-fig. 1 and Table 1.

Both conifer and angiosperm woods are represented, the angiosperms occurring in late Cretaceous (Campanian of the Naze) and younger rocks. The conifers are mainly of podocarp and araucarian affinities, forming assemblages similar to the typical southern hemisphere conifer forests of today. The most common fossil angiosperm wood is that of *Nothofagus* (southern beech), the living relatives of which are evergreen and deciduous broad-leaved beeches found today in South America and Australasia (Darlington 1965).

The fossil wood specimens range in size from small twigs to large sections over 25 cm in diameter. However, these represent both small branches with central pith and outer bark still attached and rings of small radius of curvature, and also sections of outer parts of large trunks. Most of the larger samples consist only of the heartwood (the inner secondary xylem) so the maximum size of the trunk is unknown.

An estimate of the size of the trees from which the samples originated can be obtained from the degree of curvature of the growth rings. Many of the specimens have almost 'flat' rings (Pl. 51, figs. 2, 5) indicating that they came from outer parts of large trees. In particular, most angiosperm woods have rings of large radius of curvature from trees with trunks or branches at least 30–40 cm in diameter. These were clearly

TABLE 1. Locality and stratigraphic information for fossil wood samples used for tree-ring analysis. Localities are shown in text-fig. 1.

Locality and sample information	Lithology/Environment of deposition	Probable age
INTRA-ARC: Byers Peninsula, western Livingston Island, South Shetland Islands: P.1728.9 (Crame and Farquharson 1984) and BR.80.8 from tuff of Volcanic Member south of Chester Cone. P.245.38 from surface on west coast, probably from Volcanic Member.	Intra-arc sequence of deep marine mudstones (Mudstone Member), marine volcaniclastics (Mixed Marine Member), and terrestrial pyroclastic rocks (Volcanic Member), forming the Byers Formation. A basinal environment envisaged by Smellie et al. (1980), with pyroclastic material from local vents being deposited in small lakes and over forested land. Main wood-bearing strata belong to Volcanic Member, which also contains leaf impressions. Fossil tree stump preserved in growth position.	Volcanic Member flora considered 'Wealden' in age (Araya and Hervé 1966), possibly Barremian (Hernandez and Azcarate 1971). A ?Valanginian–Barremian–Hauterivian age was proposed by Askin (1983a) on palynological evidence. (K–Ar dating of intrusive rocks gives a minimum age of Cenomanian, Smellie et al. 1984.)
Mount Flora, Hope Bay, Trinity Peninsula: D.20.3, D.20.4, D.20.10, D.20.16, D.48.2, D.48.3, D.48.5, D.48.7.	An extensive flora preserved within the Mount Flora Formation, Botany Bay Group (Farquharson, 1984). Non-marine conglomerates and mudstones deposited on alluvial fans and braided river plains on emergent arc. Plant remains buried in fine sediment in ephemeral lakes but grew locally, as shown by coals, rootlet horizons, and an in situ tree stump at Camp Hill (text-fig. 1) (Farquharson 1982, 1984).	Flora of ferns, cycadophytes and conifers originally considered of Middle Jurassic age (Nathorst 1904; Halle 1913) or early Jurassic (Rao 1953). Latest floral and stratigraphic evidence suggests early Cretaceous age (Stipanicic and Bonetti 1970; Taylor et al. 1979; Farquharson 1983, 1984).
Tower Peak, Trinity Peninsula: R.1334.12	Tower Peak Formation, Botany Bay Group. Sedimentary setting and age similar to that at Hope Bay (Farquharson 1984).	
BACK-ARC: Western James Ross Island: D.8311.5 from Sharp Valley. D.8331.4 from south of Whisky Bay.	Lower Cretaceous rocks originated as dominantly coarse-grained volcaniclastic detritus deposited across faulted margins of back-arc basin (Bibby 1966; Farquharson 1984; Ineson 1985). Divided by Ineson et al. (1986) into Gustav Group for lower coarser units and Marambio Group for upper finer units (≡ Snow Hill Island Series of Bibby 1966). Calcified wood present throughout Gustav Group, having originated from forests on volcanic arc to the west.	D.8311.5. Upper part of Kotick Point Formation of Aptian/Albian age (Ineson et al. 1986). D.8331.4. Base of Marambio Group (lower part of Snow Hill Island Series) of late Cretaceous age, probably post Santonian.
Lachman Crags and the Naze, James Ross Island: Lachman Crags. D.421, 4774, 4776, 8731. The Naze. D.90, D.87.3, 5056, 5059, 5060.	Sedimentary strata consist of poorly lithified sands with intercalated clays and nodules of calcareous, glauconitic sandstone (Bibby 1966). Much fossil wood collected from within sandy clays and nodules at both localities by Croft (1947). Angiosperm leaves also found at Lachman Crags. Strata belong to lower part of Snow Hill Island Series (Bibby 1966) ≡ Lopez de Bertodano Formation, Marambio Group of Rinaldi (1982).	Ammonite faunas from both localities considered to be upper Lower to Middle Campanian in age (Spath 1953; Howarth 1958, 1966), even possibly Maastrichtian (Henderson and McNamara 1985). Crame (1983) proposed pre-Campanian age for lower part on basis of Inoceramus. Palynological evidence suggests a ?Senonian–Campanian age for the Naze (Askin 1983b).

Locality and sample information	Lithology/Environment of deposition	Probable age
Cape Lamb, Vega Island: D.8212.12	Sedimentary sequence at Cape Lamb similar to that at Lachman Crags and on the Naze (Bibby 1966).	Askin (1983b) proposed a late Campanian–?early Maastrichtian age and suggests strata here slightly younger than those at the Naze.
Seymour Island: D.495 from Cross Valley (Sobral Formation). D.494, D.509, and 4388 from Cross Valley Formation. D.502 and D.8321.4 from northern part of island, in La Meseta Formation.	In the southern part of the island large logs and plant remains occur within concretionary sandstones and siltstones of the upper part of the Lopez de Bertodano Formation (≡ Older Seymour Island Beds of Andersson 1906). Many leaf assemblages and logs, some up to 1 metre diameter (Zinsmeister 1982) in the Tertiary Sobral and Cross Valley Formations in south-east and Cross Valley. Strata represent distributary channel fills and interdistributary flats of delta, with river systems draining vegetated highlands to west (Elliot et al. 1975). The overlying La Meseta Formation represents shallowing deltaic-lagoonal environment as back-arc basin gradually filled (Elliot and Trautman 1982).	Lopez de Bertodano Formation is late Campanian–Maastrichtian in age (Rinaldi et al. 1978; Elliot and Trautman 1982; Zinsmeister 1982); upper part may even be Danian (Askin 1985). A Palaeocene age given for Cross Valley Formation by microfossils (Hall 1977; Wrenn 1985). La Meseta Formation considered to be late Eocene–?early Oligocene age (Zinsmeister and Camacho 1982; Hall 1977).

well-grown trees rather than weedy shrubs, the habit proposed for some of the early angiosperms that colonized unstable floodplain environments (Retallack and Dilcher 1981).

Preservation. Fossil wood from the South Islands and Trinity Peninsula (including Hope Bay and Tower Peak) is preserved by chalcedony (text-fig. 1). The lignin retained within the cell walls is dark brown or black and displays only a homogeneous amorphous structure, suggesting that the wood has been subject to some degree of maturation or thermal metamorphism. At these localities the wood is buried within volcaniclastic sediments. Thus the most likely sources of the permineralizing silica is from weathered volcanic minerals, a common source for the silicification of wood (Murata 1940).

In contrast, fossil wood from James Ross, Vega, and Seymour Islands (text-fig. 1) is calcified. The state of preservation is excellent; the very fine ultrastructure of the cells is still apparent in most cases, particularly in the angiosperm wood. This calcified wood has been extensively bored by bivalves (boring type *Teredolites*; Kelly and Bromley 1984). The borings were subsequently filled with the surrounding sediment or crystalline calcite cement (Pl. 51, fig. 1; text-fig. 2). The wood was incorporated in the marine clastic and deltaic sediments of the back-arc basin so the calcite for permineralization most likely has a marine source.

These two types of mineralization show an interesting relationship to the palaeoenvironmental setting. The silicified material is associated with the terrestrial volcanic environment on the emergent arc and the calcified wood found in the marine back-arc basin. A more refined analysis of this distribution may prove that the study of mineral types in fossil wood could be a useful tool for locating the arc/basin margin.

GEOLOGICAL SETTING

During the Cretaceous and early Tertiary an emergent and periodically active volcanic arc was present in the region now occupied by the Antarctic Peninsula (Thomson et al. 1983; Farquharson 1983). Volcaniclastic sediments eroded from this arc gradually accumulated across the fault-controlled margins of a subsiding back-arc basin to the east (Farquharson 1983; Farquharson et al. 1984). The sedimentary environments range from a non-marine fluvial setting across the arc (the Botany Bay Group, Farquharson 1984) to deeper marine clastic sediments within the basin (the Gustav and Marambio Groups of Ineson et al. in press). As the basin progressively filled, a deltaic

a   b
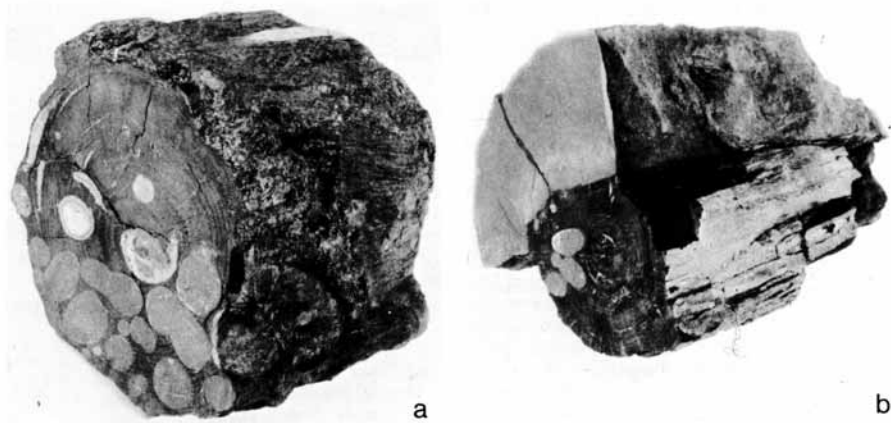
TEXT-FIG. 2. Calcified fossil wood from The Naze, James Ross Island. *a*, 5059. Wood with calcitized and sediment-filled borings, × 1·1. *b*, D.87.3. Wood with a portion of the surrounding volcaniclastic sedimentary concretion still attached on the upper surface, × 0·8.
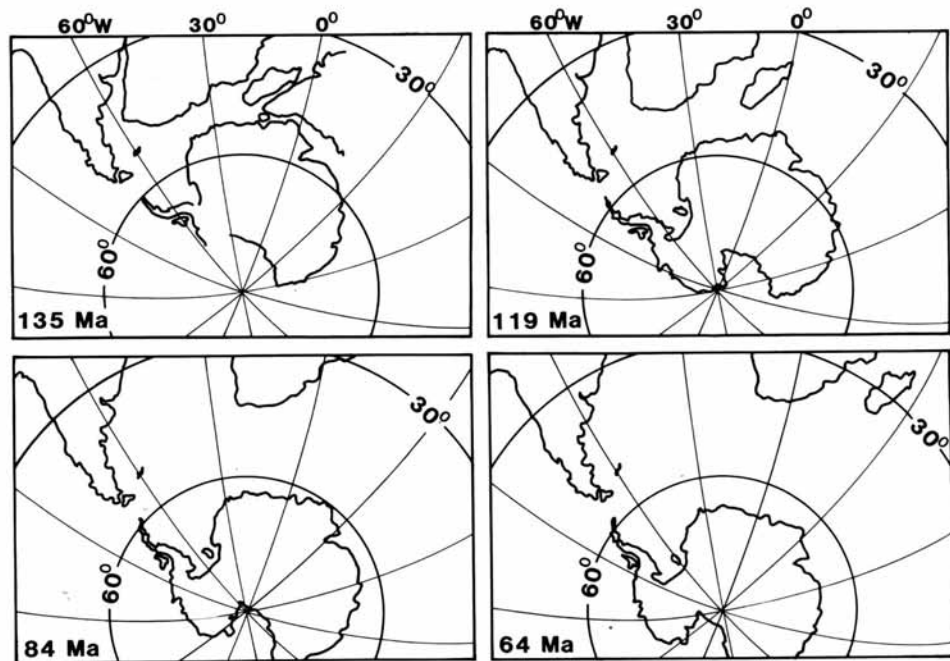
TEXT-FIG. 3. Position of Antarctica at selected times during the Cretaceous and early Tertiary, based on Lawver *et al.* 1985. 135 Ma = Valanginian, 119 Ma = Aptian, 84 Ma = Campanian, 64 Ma = Palaeocene.

environment developed during the early Tertiary in the region of Seymour Island to the east (text-fig. 1) (Elliot and Trautman 1982; Zinsmeister 1982). Stratigraphic details are given in Table 1.

The most recent palaeogeographic reconstructions by Lawver *et al.* (1985) for selected times during the Cretaceous and early Tertiary place the northern tip of the Antarctic Peninsula at palaeolatitudes ranging from approximately 59° to 62° S. (text-fig. 3). The actual position of the peninsula in the reconstruction of Gondwanaland is still uncertain, particularly in relation to east Antarctica, but it remains in approximately this latitudinal range in most models (Dalziel and Elliot 1982, and references therein).

GROWTH RING ANALYSIS

Growth rings in the fossil wood were measured from polished slabs in transverse section viewed under a dissecting microscope, from acetate peels of acid-etched surfaces, and from petrographic thin-sections. The rings were measured along a radial line to obtain as long a ring series as preservation permitted, although readings often had to be continued along adjacent radii to avoid patches of poor cellular preservation. If the

TABLE 2a. Results of growth ring analysis. (Wood types A = angiosperm, C = conifer.)

Locality	Specimen number	Number of rings	Mean ring width (mm)	Maximum ring width (mm)	Minimum ring width (mm)	Mean sensitivity	Wood type
TERTIARY							
Seymour Island:	D.502	23	1·32	3·3	0·4	0·207	A
	D.8321.4	11	5·70	8·4	2·5	0·214	A
	D.494	14	2·58	4·6	2·0	0·173	A
	D.495	27	0·52	0·7	0·4	0·139	C
	4388	16	2·51	6·3	1·2	0·267	C
	D.509	13	0·84	1·4	0·4	0·371	C
CRETACEOUS							
Vega Island:	D.8218.12	6	7·50	9·0	6·2	0·123	A
The Naze:	5056	19	1·37	2·4	0·7	0·177	A
	5059	31	0·78	1·6	0·4	0·188	C
	5060	8	2·29	2·9	1·2	0·205	C
	D.87.3	26	0·80	1·4	0·4	0·192	C
	D.90	19	1·82	3·8	1·1	0·284	A
Lachman Crags:	D.421	56	0·61	1·7	0·1	0·357	C
	4774	60	1·45	2·5	0·8	0·187	C
	4776	11	2·33	3·6	1·9	0·146	C
	8731	9	5·28	7·8	3·6	0·181	C
Sharp Valley:	D.8311.5	12	1·17	1·4	1·0	0·125	C
Whisky Bay:	D.8331.4	17	1·84	2·4	1·1	0·199	C
Hope Bay:	D.20.3	15	2·71	3·4	1·9	0·146	C
	D.20.4	12	4·92	6·7	3·6	0·178	C
	D.20.10	20	3·26	4·3	1·9	0·137	C
	D.20.16	35	1·47	2·7	0·9	0·146	C
	D.48.2	17	3·77	4·8	1·6	0·145	C
	D.48.3	7	3·23	3·8	2·6	0·146	C
	D.48.5	20	1·48	1·9	1·0	0·148	C
	D.48.7	20	1·46	2·0	1·0	0·152	C
Tower Peak:	R.1334.12	9	5·57	6·9	4·0	0·218	C
Byers Peninsula:	BR.80.8	12	1·35	1·8	1·0	0·204	C
	P.245.38	14	0·99	1·8	0·6	0·239	C
	P.1728.9	29	1·18	1·9	0·6	0·189	C

TABLE 2b. Summary of growth ring analyses.

	Number of ring series	Mean ring width	Range of mean ring widths	Mean sensitivity	Range of mean sensitivities
Total ring series	30	2·30	0·52–7·50	0·206	0·123–0·371
Tertiary	6	2·25	0·52–5·70	0·228	0·139–0·371
Cretaceous	24	2·35	0·61–7·50	0·184	0·123–0·357

centre of the branch was not present, the radius of curvature of the rings was noted to estimate whether the wood specimen was part of a small branch or from the outer part of a large trunk.

The absolute ring widths were measured as a record of annual growing conditions. From these some of the standard statistical parameters used to describe modern ring characteristics (Fritts 1976) were calculated, but also taking into account the problems associated with fossil wood, such as the preservation of only a limited number of rings from an unknown part of the tree.

The most imformative parameter was the variability in width of the rings from year to year. This was calculated in terms of the annual sensitivity (AS), i.e. the difference in width between a pair of consecutive rings divided by their average width (Creber 1977), which illustrates the degree of variability between years. The average of these values for each tree, the mean sensitivity (MS) (Fritts 1976), gives an indication of the tree's response to variable factors of the climate that may have influenced its growth. The mean sensitivity is calculated using the formula

$$\text{MS} = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2x_{t+1} - x_t}{x_{t+1} + x_t} \right|$$

where x is the ring width, n is the number of rings, and t is the year number of each ring. Values of mean sensitivity range from 0 where there is no variation from year to year, to a theoretical maximum of 2 representing the greatest variation. An arbitrary value of 0·3 is taken to separate 'complacent' trees that have grown under a favourable uniform climate (MS < 0·3) from those 'sensitive' to limiting factors of climate (MS > 0·3) (Fritts 1976).

In selected rings with good cellular preservation, individual cell diameters along radial files were measured in order to classify the rings according to the scheme proposed for fossil wood by Creber and Chaloner (1984b, p. 371).

Results

A total of 30 ring series were obtained ranging in length from 7–60 rings, though series of 15–20 rings were most common. Some wood samples had the central pith present surrounded by rings of small radius of curvature representing the initial growth of the trees. However, the large radius of curvature of the rings in most specimens (Pl. 51, fig. 2) illustrates that they are from the outer sections of large trunks, areas where environmental influences have a stronger signal than the inherent growth trends.

Individual rings in the conifers are characterized by a relatively wide zone of large, thin-walled earlywood cells terminated by only four to five thick-walled cells of the latewood (text-fig. 4). The angiosperms also exhibit clear ring boundaries, marked by a decrease in fibre diameter and termi-nated by two to three very narrow fibres. The position of the largest vessels at the beginning of each ring in the ring-porous angiosperms also makes the rings very conspicuous (Pl. 51, fig. 3). Plots of


EXPLANATION OF PLATE 51

Figs. 1–6. Growth rings in Antarctic fossil wood. 1, D.8321.4 (angiosperm wood with borings), Seymour Island, × 1·7. 2, D.509 (conifer), Seymour Island, × 13·2. 3, D.90 (angiosperm), The Naze, James Ross Island, × 8·8. 4, D.8331.4 (conifer), South of Whisky Bay, James Ross Island, × 5·1. 5, D.48.5 (conifer), Hope Bay, Trinity Peninsula, × 4·0. 6, D.48.7 (conifer), Hope Bay, Trinity Peninsula, × 3·3.

PLATE 51
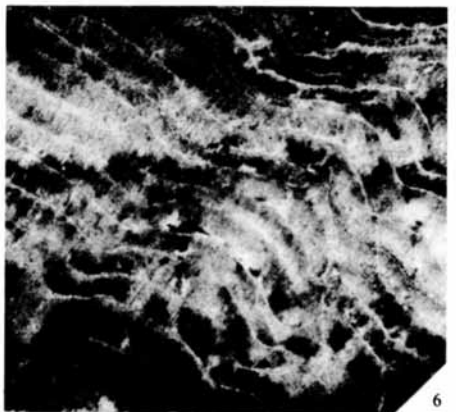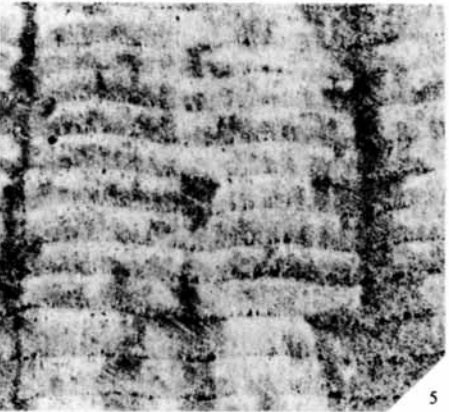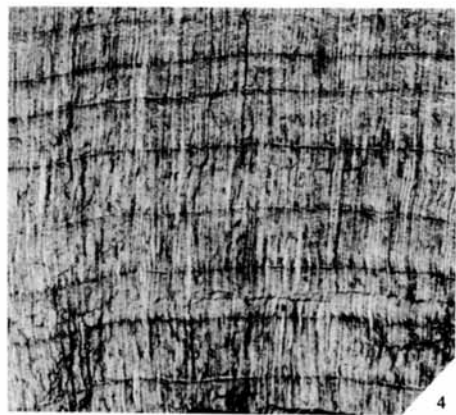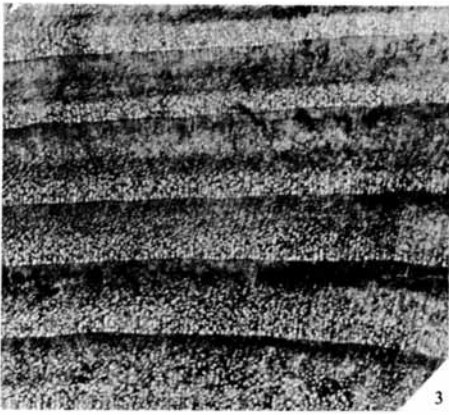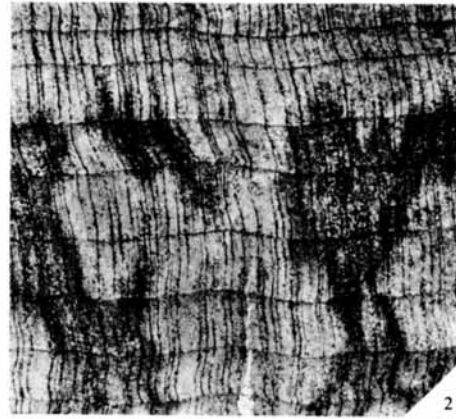
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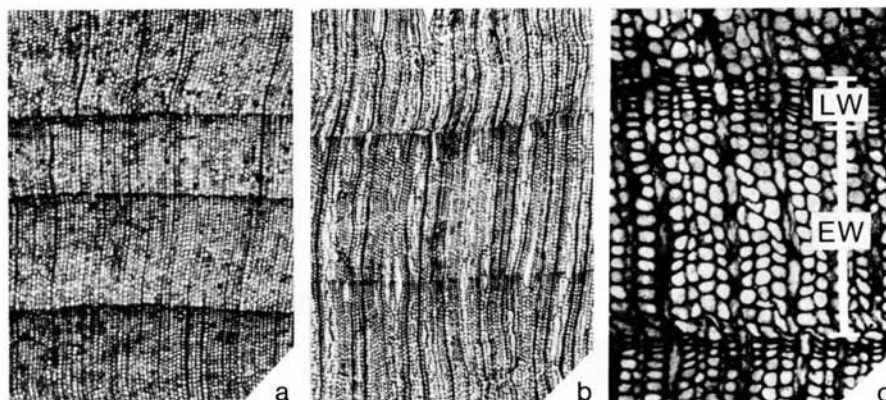
TEXT-FIG. 4. Growth rings in fossil conifer wood, showing well-defined ring boundaries (EW = early-wood, LW = latewood). *a*, 5059. The Naze, James Ross Island, ×28. *b*, D.8331.4. South of Whisky Bay, James Ross Island, ×22. *c*, D.509. Cross Valley, Seymour Island, ×80.

variations in cell dimensions throughout selected rings are shown in text-fig. 5. The curves show a very slight decrease in cell radial diameters throughout the earlywood portion of the ring followed by an abrupt transition to the narrow latewood cells at the end. These curves are characteristic of types D and E under the classification scheme for fossil growth rings proposed by Creber and Chaloner (1984*b*), interpreted as representing a relatively uniform growing season followed by a terminal event due to a cessation or retardation of cambial activity. False (intra-annual) rings, which can be caused by frost or drought (Fritts 1976), and scars due to insect attack or fire, were not observed.

The growth rings in the wood are very prominent (Pl. 51, figs. 1–6). The average ring widths were 2·25 mm for the Tertiary woods, 2·35 mm for the Cretaceous specimens, and 2·30 mm for the whole collection of wood (Table 2*b*). These values indicate that, on average, growth rates were quite fast. However, a notable feature is the presence of very wide rings (e.g. 9·00 mm in D.8218.12, 8·4 mm in D.8321.4) in a large number of specimens. This indicates that the trees had the potential for extremely high growth rates in a very favourable environment. Some of the widest rings occur in the angiosperms.

In contrast, a few specimens have consistently very narrow rings. Specimens 5059 and D.87.3 from the Naze, James Ross Island, consist of central portions of trunks so the narrow rings around the pith may simply represent initial development of the tree. However, specimens D.495 and D.509 (Cross Valley, Seymour Island) are parts of large trunks and their narrow rings may well be the result of a climatic change. These samples are Palaeocene in age and possibly reflect climatic deterioration at the Cretaceous/Tertiary boundary, although clearly many more samples are required to test this theory.

Whatever their width, the most conspicuous feature of the growth patterns in all the Cretaceous and Tertiary woods is the uniformity in width of the rings from year to year (Pl. 51; text-fig. 6). This is reflected in their consistent mean sensitivity values. The averages are 0·206 for all the trees, 0·228 for the Tertiary, and 0·184 for Cretaceous trees. Of the thirty samples, twenty-eight had MS values less than 0·3. Most were between 0·100 and 0·199 (75 %) and some were between 0·200 and 0·299 (21 %). These trees are thus overwhelmingly 'complacent' and their uniform growth reflects very constant and favourable growing environments in which no single climatic factor adversely affected tree growth. Histograms of the annual sensitivity values for each tree (text-fig. 7) also
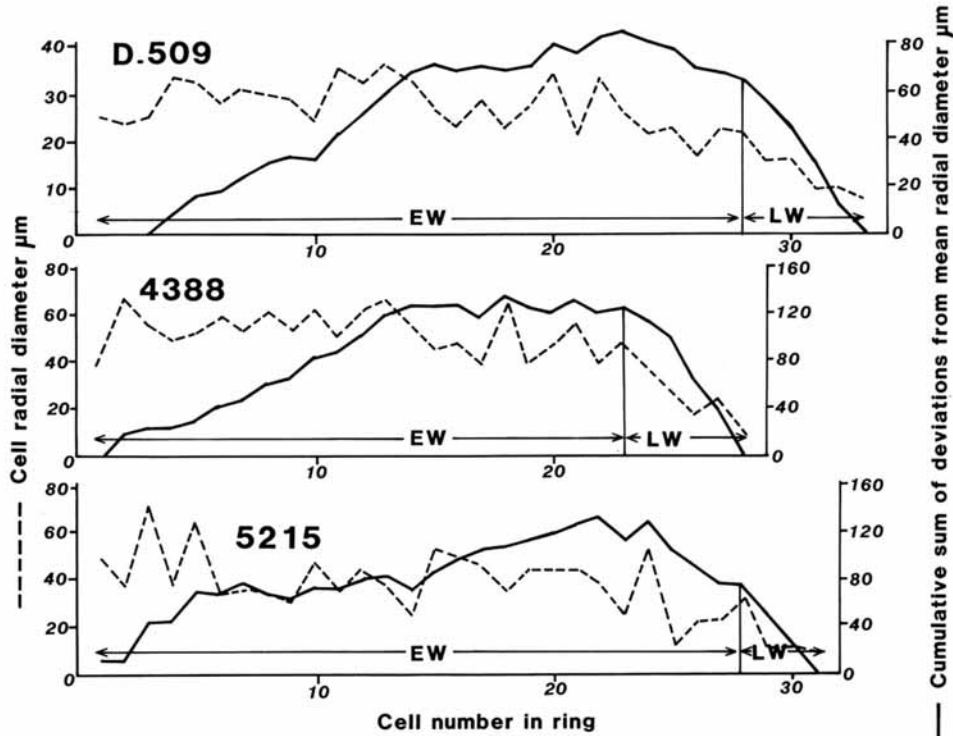
TEXT-FIG. 5. Graphs of variation in cell radial diameter across selected growth rings. The point at which the cumulative sum curve finally turns to zero is used to determine the earlywood (EW)/latewood (LW) boundary.

illustrate that the variation in growth was very low since a high proportion of the AS values are less than 0·3, the dominant values lying between 0 and 0·099. However, each tree has a few AS values of the 'sensitive' kind reflecting occasional periods of more marked climatic influence.

INTERPRETATION OF THE RINGS

The presence of well-marked growth rings in these Antarctic woods illustrates that their growth environment was characterized by well-defined seasons. The pattern of cell dimensions throughout the rings suggests that conditions during the growing season were very suitable for cell division and expansion (Creber and Chaloner 1984*b*), resulting in the large and numerous cells of the earlywood zones. However, conditions changed markedly at the end of the growing season and cell production was severely retarded. A narrow latewood zone within a ring can be the result of water shortage (Creber and Chaloner 1984*b*). However, this seems an unlikely cause in such a clastic-dominated sedimentary setting. Alternatively, the growing season may have been abruptly terminated by the low light levels during the onset of the winter season.

It is possible that the type of cell pattern in the rings seen here (text-fig. 5) may be a genetic
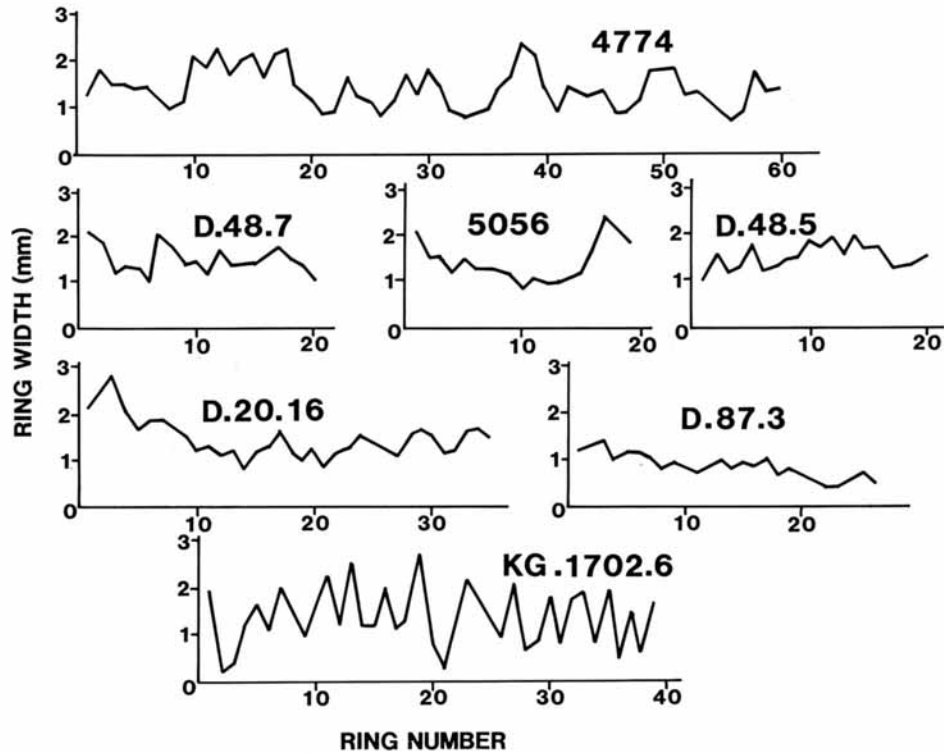
TEXT-FIG. 6. Plots of growth ring sequences. The first 6 graphs are of rings from the northern Antarctic Peninsula region showing fairly uniform growth. In contrast, the graph of KG.1702.6 from Alexander Island (Jefferson 1982) shows variable growth from year to year.

characteristic and not so significant in terms of climatic influence. A large number of the Antarctic fossil woods are conifers of araucarian or podocarpacean affinity; these types may have annual cell production somewhat independent of environmental influence (Creber and Chaloner 1984b). However, analyses of their ring series are still significant and living members of these families have been used for dendrochronological work in South America (LaMarche et al. 1979a, b; Hughes et al. 1982). However, the same ring types D and E are present in other types of Antarctic conifers and to some extent in the angiosperms, implying that these ring patterns truly reflect environmental influence.

The uniform width of the rings is the most revealing signal of the climate. Such trees with low mean sensitivity values of 'complacent' type grow today in stable forest environments where no single factor controls growth. Fritts et al. (1965), Fritts (1976), and LaMarche (1974) found that trees of this type grew in forest interiors where fairly uniform environments were established. This contrasts with trees growing nearer the forest borders and near the climatically determined limits of their distribution in which certain limiting factors, such as low temperatures at high altitudes or low rainfall at the lower forest border, have a very pronounced effect on the growth. This in turn is reflected in their growth patterns. The absence of false or partial rings in the Antarctic fossil wood
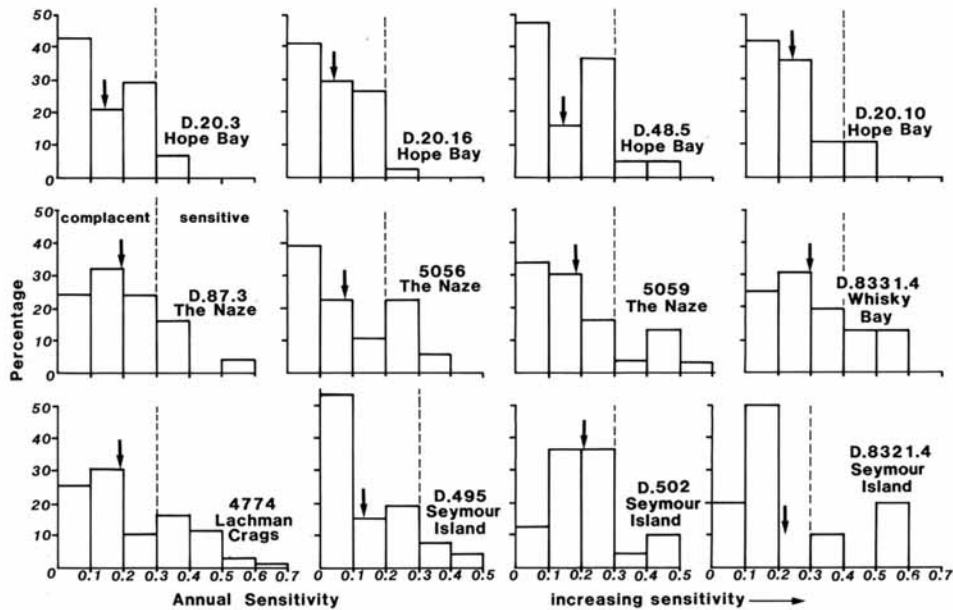
TEXT-FIG. 7. Histograms showing the amount of annual variation in the growth patterns of selected fossil trees. All these trees exhibit predominantly complacent growth. (Arrow indicates position of mean sensitivity.)

is consistent with the observations of Fritts *et al.* (1965) that these ring types are absent in forest interior trees.

DISCUSSION

Comparison with modern forest growth. The forest trees that grew in the Antarctic Peninsula region in the Cretaceous and early Tertiary clearly enjoyed very favourable growing conditions in a mild, temperate environment. Such growth is not apparent in trees at similar latitudes (59°–62° S.) today. In the southern hemisphere the most southerly forests grow in Magellanic (southernmost) Chile, up to about 56° S., approximately 500 miles north of the Antarctic Peninsula (Skottsberg 1960; Godley 1960; Darlington 1965; Young 1972; Crow 1975). The characteristic vegetation is very dense evergreen rainforest dominated by *Nothofagus betuloides*, and with only a few other conifer and angiosperm genera. This evergreen forest is limited to the fjord-like topography of the western slopes of the Andes where the rainfall is extremely high (up to 7500 mm/yr in the mountains; Young 1972) and distributed evely throughout the year. Both summers and winters are cool. The mean annual temperature is about 6 °C and the annual range only about 4 °C (Young 1972). The restriction to plants (and animals) is not therefore extreme cold but the lack of warmth for growth in summer, particularly for deciduous trees (Darlington 1965).

The *N. betuloides* rainforest trees grow to large sizes (up to 30 m in height and 2 m in trunk diameter) at slow rates. Some are estimated to be 1500–2000 years old (Young 1972). An average increase in trunk diameter of 1·42 mm/year (mean ring width of 0·71 mm) was recorded for a selection of these trees. Average ring widths of 0·37 mm and 1·00 mm were recorded from the conifer *Pilgerodendron uvifera* and the evergreen angiosperm *Drimys winteri* respectively (Young 1972). These trees grow at such slow rates due to the continuously cold and wet environment. To

the north and east of the rainforest region a more seasonal climate with lower rainfall prevails. A transitional type of drier, less dense forest becomes dominant, characterized by deciduous species of *Nothofagus* (e.g. *N. pumilio*, *N. antarctica*). LaMarche *et al.* (1979a) have obtained tree-ring chronologies mainly from *Araucaria araucana* in this area. Such trees from within latitudes 37°–43° S. in Argentina, have mean ring widths ranging from 0·38 to 3·33 mm, although the majority grow at rates of less than 1 mm/year. Values of mean sensitivity were also very low, ranging from 0·12 to 0·23, illustrating that growth was very uniform from year to year. In Chile, between latitudes 32° and 40° S., mean ring widths of between 0·40 to 1·75 mm were recorded (LaMarche *et al.* 1979b; Hughes *et al.* 1982).

The composition of these South American forests (and similar forests in Australasia, Godley 1960) is very similar to that of the Antarctic Peninsula fossil assemblages, as indicated by the fossil remains of *Nothofagus*, and members of the Podocarpaceae and Araucariaceae (Gothan 1908; Dusen 1908; Halle, 1913; Florin 1940; Cranwell 1959, 1969; Barton 1964; Orlando 1964; Plumstead 1962; Askin 1983a, b; Torres 1984). However, compared with the growth rings in the Antarctic fossil wood, those in the living trees are much narrower, recording considerably slower growth rates resulting from the lower temperatures of the cold temperate climate. However, most trees exhibit the same degree of ring uniformity as the fossils (Young 1972; LaMarche *et al.* 1979a, b), probably due to the constant rainfall throughout the year.

The present latitudinal limit of tree growth in the south is much lower than that in the northern hemisphere due to the influence of the extensive ice sheet over the Antarctic continent. In the north, the tree line lies at approximately 66° N., almost coincident with the 10 °C isotherm for July (Creber and Chaloner 1984a, b). The composition of the northern forests at latitudes corresponding to those in Chile differs in that they consist mainly of conifers, rather than evergreen angiosperms. The conifers grow under a more seasonal climate where growth is restricted to warmer summer months. Data compiled by Creber and Chaloner (1984b, Table XII, p. 429) illustrate that some angiosperms between 48°–61° N. have average growth rates of 0·5–1·6 mm/yr. At even higher latitudes, beyond 75°–70° N., the ring widths are exceedingly small (e.g. 0·032 mm) in trees from east Greenland, 73° N. However, conifers are still able to produce relatively wide rings up to about 70° N. Poleward of the tree-line, tree growth is limited by very low temperatures which adversely affect the metabolic processes, resulting in such low productivity that almost no wood is produced (Billings 1964; Grime 1979; Creber and Chaloner 1984a, b, 1985).

The tree-rings in the Antarctic fossil wood are more comparable with those in living trees in warm/cool-temperate forests in Australasia. The growth of selected examples of the podocarp *Phyllocladus* in southern New Zealand and Tasmania was considered analogous to that of the Cretaceous Alexander Island trees by Jefferson (1982, 1983); both have fairly large rings and high mean sensitivities. Some of these living trees also have low, complacent mean sensitivities more like the fossil trees from the northern Antarctic Peninsula. In Australia (25°–43° S.) LaMarche *et al.* (1979d) recorded mean ring widths of 0·31–1·22 mm and mean sensitivities of 0·12–0·47, mainly in trees of the Podocarpaceae and Cupressaceae. Further north, in Queensland (17° S.), *Callitris* conifers are able to produce very wide rings (3–5 mm, average 2·5 mm) (Ash 1983). The rings are also very uniform in width. The climate here is much warmer and has a more tropical aspect and, although the rainfall is very high (1700–2700 mm/yr), a distinct dry season causes the formation of growth rings. Compared to the wide and uniform growth rings in the northern Antarctic Peninsula fossil wood, the early Cretaceous trees on Alexander Island had wide but very variable ring widths. Jefferson (1982, 1983) recorded very high mean sensitivity values in his fossils, characteristic of trees growing at the limits of their ecological range in marginal environments where climate strongly influences growth. Since these trees were located at higher latitudes (65–75° KrS.) in the Cretaceous than those on the northern part of the peninsula, it may be that the Alexander Island forests represent the marginal limits of the Antarctic Peninsula forests.

The Cretaceous/early Tertiary climate of the Antarctic Peninsula. The growth patterns in fossil wood illustrate that the Antarctic climate was clearly not like that of today but was much warmer and

more comparable to warm temperate environments (Thomson 1982). Previous interpretations of
fossil plant collections have reached the same conclusions. The assemblage of conifers, ferns, and
cycadophytes of the early Cretaceous Hope Bay flora was considered by Halle (1913) to be part of
a global Mesozoic flora (although Florin (1940) and Plumstead (1962, 1964) argued that it was
rather more localized to the southern hemisphere) of warm temperate or subtropical nature. A
similar climate prevailed during the growth of the ferns, conifers, and angiosperms of the Seymour
Island flora (Dusen 1908). However, a rather cooler climate was envisaged by Askin (1983b) for
the Campanian palynomorphs from the Naze and Vega Island.

The size and morphology of angiosperm leaves have also been used as criteria for determining
climatic tolerance. Large leaves (> 10 cm long) of *Nothofagus* type from the Tertiary of Alexander
Island were considered to be indicative of warm-temperature conditions (Thomson and Burn 1977),
as were Tertiary leaves from Adelaide Island (Jefferson 1980). Mid-Tertiary plant assemblages from
King George Island, South Shetland Islands (Orlando 1964), which are composed primarily of
Nothofagus and Podocarpaceae, are comparable with cool/warm-temperate rainforests of Australia
on the basis of leaf morphology (Zastawniak *et al.* 1985). However, Barton (1964) considered that
the small size of the leaves was more like that of the trees in Chilean rainforests where the climate
is of cool-temperate type.

The early Cretaceous (Barremian–Albian) fossil forests of Alexander Island were also considered
analogous to Australian rainforests, with regard to both the wide but variable growth rings in the
wood and the floral characteristics. The leaves are exceptionally large and their margins entire,
typical of the 'tropical rainforest' types of Wolfe (1971) and those found in modern Australasian
temperate rainforests (Jefferson 1983). The large lamina size suggests that the leaves would not
have been tolerant of frosts. They do not exhibit xeromorphic adaptations so it would appear that
water was probably in plentiful supply.

Palaeoclimatic interpretations of the associated sedimentary strata support plant evidence. A
warm and periodically wet climate within a temperate environment was considered by Taylor *et al.*
(1979) to be necessary to produce the clastic sedimentation within the deltaic environments of the
late Jurassic/early Cretaceous rocks of Alexander Island. Similarly, the presence of braided stream,
debris flow, and sheet-flood deposits within the Botany Bay Group also implied a climate with
moderate to high rainfall causing periodic flooding (Farquharson 1984). Sea water temperatures
around the Antarctic were also much higher than today. Oxygen isotope data and palaeotempera-
tures from benthonic and planktonic Tertiary Foraminifera show a decline in temperatures through-
out the Tertiary. Bottom water temperatures of about 16 °C and surface water temperatures of
19 °C were recorded for the late Palaeocene (Shackleton and Kennett 1975; Kennett 1977). However,
stable isotope measurements and species distributional analysis of Foraminifera, which once in-
habited a mid-outer shelf environment and are now preserved within the Cretaceous sediments of
Seymour Island, indicate much cooler bottom water temperatures of 6°–8 °C and surface water
temperatures of approximately 12 °C at the Campanian/Maastrichtian boundary (Barrera and
Huber 1985). Records of the species diversity and their stratigraphic distribution demonstrate long-
term stability of cool-temperate conditions through the Campanian/Maastrichtian in this area.

The climate of the northern part of the Antarctic Peninsula region appears, therefore, to have
been of a warm/cool-temperate type during the Cretaceous and early Tertiary. Conditions for forest
growth were very favourable and no single climatic factor appeared to be limiting tree growth. By
comparison with warm/cool-temperate forests today, a heavy rainfall of perhaps 1000–2000 mm/yr
is envisaged for this area. The qualitative palaeoclimate models of Parrish *et al.* (1982) also predicted
a belt of high rainfall along the western margins of southern South America and the Antarctic
Peninsula during the late Mesozoic. The models show a slight decrease in rainfall (though still high)
from west to east across the peninsula region, presumably due to the oceanic influence to the west
and the orographic effect across the highland arc area. This region was also located within an area
of persistent low pressure, according to the models of Parrish and Curtis (1982). Enhanced rainfall
at high latitudes was also predicted in models of increased atmospheric CO_2 levels, the most
plausible mechanism for the elevated temperatures in the Mesozoic (Manabe and Wetherald 1980).

Organic productivity of the forests. Although the wood collection studied here consists only of isolated samples, it is apparent that fossil wood is preserved throughout Cretaceous and early Tertiary strata in the Antarctic Peninsula region, evidence that the emergent arc was extensively forested for the duration of this long period. Furthermore, some of the trees are preserved in their original growth positions (Smellie *et al.* 1980; Farquharson 1982) and it may be possible, with further field measurements, to obtain important information about forest density, tree habit, and forest productivity similar to that obtained by Jefferson (1982, 1983) and Creber and Chaloner (1984*a*, *b*, 1985) from the *in situ* Cretaceous forests on Alexander Island. The nature of the growth rings in the fossil wood from the Antarctic Peninsula suggests that these trees had the potential for high productivity (Creber, in press). Consequently, the trees may well have supplied a large quantity of organic material to the adjacent marine basins. During the same period in south-eastern Australia, cool-temperate rainforests were supplying organic debris to the Gippsland Basin, forming the Victorian Brown Coals, which later served as a source of hydrocarbons. In particular, coniferous vegetation (southern hemisphere types, principally Araucariaceae) provided large quantities of hydrogen-rich, exinite macerals (mainly from leaf cuticles and resin) for the generation of oil (Shanmugan 1985).

Although there are large quantities of wood and organic material within the Cretaceous and early Tertiary proximal marine sediments of the Antarctic Peninsula back-arc basin, they were buried within predominantly oxygen-rich environments. There may have been greater potential for the preservation of organic matter as a source for hydrocarbons under anoxic conditions in more distal facies to the east (J. R. Ineson, pers. comm.), although this area is as yet unexplored.

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