Cretaceous polar conifer forests: composition, leaf life-span and climate significance

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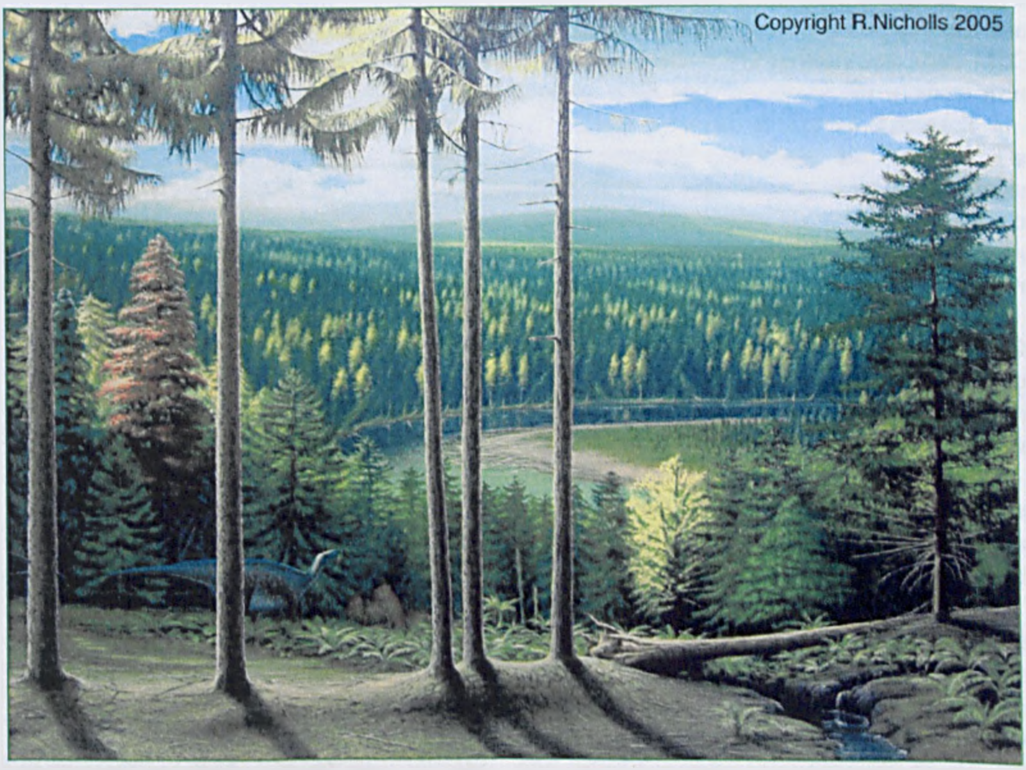

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Dedication

This thesis is dedicated to the memory of my father, Godfrey Harland

(24 May 1931-27 December 2003).

"The past seizes upon us with its shadowy hand
and holds us to listen to its tale"

A.C.Seward 1926

Abstract

Fossil wood is abundant in sediments that were deposited at high latitudes during the Cretaceous. The wood provides evidence for forests growing in high latitudes in the past, at times when climate was warmer during greenhouse periods. However, computer climate models that try to simulate past climates cannot reproduce the polar warmth necessary for the existence of forests but more commonly generate ice-covered polar regions. This may be due to the lack of a realistic vegetation component in the models.

The aim of this project is to determine the leaf habit and leaf life-spans (LLSs) of conifers growing at high latitudes during the mid-Cretaceous. The results will be used to test the outputs of the University of Sheffield Conifer Model (USCM), a model that will produce a new reconstruction of high latitude vegetation for coupling with computer climate models to determine the effects of high latitude vegetation on climate systems in the past.

Fossil conifer wood is studied from mid-Cretaceous sediments from the Canadian Arctic, Svalbard, Australia and Antarctica, all high latitude sites during the mid-Cretaceous. Identification of the woods indicates that Northern Hemisphere forests were composed of *Piceoxylon*, *Laricioxylon*, *Cedroxylon*, *Taxodioxylon*, *Pinuxylon*, *Palaepiceoxylon*, *Taxoxylon*, *Juniperoxylon*, *Protocedroxylon*, *Araucariopitys*, *Xenoxylon* and *Cupressinoxylon*. The Canadian Arctic was dominated by *Pinuxylon* and Svalbard by *Taxodioxylon*. In the Southern Hemisphere the conifers include *Podocarpoxylon*, *Taxodioxylon*, *Araucariopitys*, *Cupressinoxylon*, *Agathoxylon*, *Protophyllocladoxylon*, *Sciadopityoxylon* and *Circoporoxylon*. Antarctica was dominated by *Taxodioxylon* and in Australia the woods were dominated by *Podocarpoxylon*. Palaeoclimate analysis using nearest living relative and growth ring analyses indicate that the mid-Cretaceous climate in the Canadian Arctic was cool temperate and Svalbard was cool to warm temperate. In the Southern Hemisphere Australia appears to have been cool temperate whilst in Antarctica it is only possible to define the climate as temperate.

A new technique was developed to determine the leaf habit (evergreen or deciduousness) and LLSs of modern conifers using wood anatomy. This method quantitatively characterises cell patterns within growth rings as the Ring Markedness Index (RMI, a measure of the markedness of the ring boundaries). The RMI has been shown to have a strong logarithmic relationship to leaf life-span and can therefore be used to determine the leaf life-span of fossil woods.

Results of RMI analysis on fossil conifer woods provide an indication of the LLSs of mid-Cretaceous conifers for the first time. Both northern and southern hemisphere forests were dominated by evergreen conifers, with only a small component of deciduous conifer types. The dominant LLS in both Northern Hemisphere sites (the Canadian Arctic and Svalbard) was 33 months. In the Southern Hemisphere the dominant LLS in Australia was 63 months, on James Ross Island, Antarctica 48 months and on Alexander Island, Antarctica it was 151 months. Comparison with leaf habit and LLS predictions from USCM indicate a reasonable match, verifying model output. The Conifer Model will now be coupled with regional and global climate models to examine the magnitude of the effect of conifer forests in the polar regions during the mid-Cretaceous greenhouse climate.

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Chapter 1 Introduction

1.1. Introduction

During past greenhouse periods, such as the Cretaceous, the climate was warm enough at high latitudes to allow the growth of thriving conifer forests under an unusual light regime of up to six months of sunlight and six months darkness (Francis, 1986; Spicer and Parrish, 1986; Parrish and Spicer, 1988; Vakhrameev, 1991; Herman and Spicer, 1996; Parrish *et al.*, 1998; Falcon-Lang and Cantrill, 2001; Spicer and Herman, 2001; Francis and Poole, 2002; Howe, 2003). These polar forests are unique in that they have no modern analogues for direct study.

The physical characteristics of these forests, such as albedo, land-surface roughness, surface hydrology and the partitioning of sensible and latent heat (sensible heat being energy stored in a substance as a result of an increase in its temperature whilst latent heat flows to or from a material without a change to temperature), would have affected processes feeding back into the climate (such as vertical fluxes of radiation, heat and water vapour near to ground level) (Foley *et al.*, 1994; Deconto *et al.*, 2000a; Beringer *et al.*, 2005). Therefore these high latitude conifer forests would have contributed to global climates by significantly modifying climate dynamics. Forests also play an important role in atmospheric CO_2 and methane budgets, affecting the global biogeochemical cycle by providing a reservoir for carbon and aiding mineral weathering. The magnitude of these effects on palaeoclimates can be studied using numerical computer model simulations, which can be verified using proxy data such as sedimentary facies and the distribution of vegetation from the fossil record. However, in computer models of past climates high latitude vegetation has rarely been considered. Climate models generally simulate past polar regions as too cold in winter (Barron and Washington, 1982; 1984; Barron *et al.*, 1992; 1993). Recent studies suggest, however, that polar vegetation may have been a crucial factor that kept the high latitude regions warm (Foley *et al.*, 1994; Upchurch *et al.*, 1998; Deconto *et al.*, 2000a).

This research is part of a larger NERC-funded project undertaken at the University of Leeds (School of Earth and Environment) and the University of Sheffield (Department of Animal and Plant Sciences). It uses an interdisciplinary approach to bring together models of plant physiology and data about palaeobotany and palaeoclimatology. The aims of the main project are:

- To reconstruct the leaf life-spans of conifers (the length of time leaves remain on the tree) within high latitude forests during the mid-Cretaceous (100Ma) through new anatomical investigations of fossil conifer wood from several high latitude sites.
- To develop a conifer forest model structured around leaf life-span, to include coupled

above- and below-ground C and N cycles and competitive tree dynamics.

- To use the model to simulate evergreen and deciduous forest composition in the mid-Cretaceous and then to test model simulations with leaf habit data derived from fossil woods.
- To carry out sensitivity experiments to determine the role of climate and CO_2 on polar forest biogeography and undertake numerical modeling experiments to quantitatively characterize the magnitude and sign of polar forest feedback on regional high latitude climates in the northern and southern hemispheres.

This PhD is concerned with the analysis of mid-Cretaceous fossil wood from high latitude sites to determine forest composition, leaf habit (evergreen or deciduous habit) and leaf life-span.

This project involves:

- The determination of the composition of polar conifer forests during the mid-Cretaceous in both southern and northern hemispheres.
- Determination of the evergreen or deciduous habit of the conifer trees and their leaf life-spans, using a new method that relates growth ring characteristics to leaf life-span.
- Investigation of the palaeoclimatic conditions in the polar regions during the mid-Cretaceous from analysis of forest composition, geological setting and growth rings in the fossil wood.
- Comparison of the results of leaf habit and leaf life-span analysis with predictions of leaf life-span from the University of Sheffield Conifer Model to test the model predictions.

Fossil wood from the Canadian Arctic, Svalbard, Antarctica and Australia (all high latitude regions during the mid-Cretaceous) were studied and described for the first time in this project (for the purposes of this thesis high latitude is defined as regions above 60° palaeolatitude in order to incorporate samples from the southern latitudes e.g. the Antarctic Peninsula). The wood specimens were described and identified to determine forest composition and diversity (**Chapter 2**). Nearest Living Relative (NLR) analysis was used to gain an insight into the possible environmental settings and habitats of the trees.

A new method has been developed that uses characteristics of cells within growth rings in fossil wood to determine the leaf habit (evergreen or deciduousness) and the leaf life-span of fossil conifers. This new method, called Ring Markedness Index, was developed by analysis of a large set of modern wood (**Chapter 3**).

The relationship between Ring Markedness Index and leaf life-span was quantitatively derived from modern woods and then applied to the fossil wood, in order to determine leaf habit and life-span of Cretaceous polar conifers for the first time (**Chapter 4**).

The palaeoclimate significance of the growth rings in the fossil wood was determined and high latitude palaeoenvironments reconstructed. Comparisons were made with climate simulations from palaeoclimate models for the Cretaceous (**Chapter 5**).

The results of leaf habit and leaf life-span were then compared to the outputs of the University of Sheffield Conifer Model in order to test the accuracy and relevance of the model (**Chapter 6**). The polar conifer model, verified by fossil data, will be an important component in climate models used to simulate past greenhouse climates.

Chapter 7 discusses the implications of this research on our understanding of past polar climates and high latitude vegetation, and the interactions between the two.

1.2. Mid-Cretaceous polar forests: a review

This section introduces the fossil record of mid-Cretaceous high latitude forests in both northern and southern hemispheres (Section 1.2.1). This review was carried out in order to gain an overview of what is already known about the composition and distribution of these forests. It also provided details of the composition of forests in areas where specimens were not studied (e.g. Russia and New Zealand). A review of published ideas on how the vegetation survived in the high latitudes is presented in order to investigate how the trees may have adapted their growth patterns to survive the unusual high latitude conditions, what the growth forms tell us about these conditions and to provide a context for the leaf life-span analysis carried out in this study (Section 1.2.2). The deciduous or evergreen leaf habit of modern vegetation is then discussed to gain an understanding of why plants employ the habits they do now (Section 1.3). A review of mid-Cretaceous climates from geological evidence is presented in order to establish what is already known about the habitats in which these forests grew and what climatic stresses they may have had to endure (Section 1.4.1). This provided proxy data that could be compared to previous computer climate models and the results of this study. Climate models were examined to explore their development and determine what they have included in the past in terms of vegetation, whether the fossil evidence corresponds to model outputs and what effect incorporating vegetation has had on previous climate predictions (Section 1.4.2).

1.2.1. Composition of mid-Cretaceous polar forests

During the Cretaceous (Figure 1.1) forests covered vast areas of both the northern and southern hemisphere high latitude regions. The distribution of high latitude vegetation that represents the remains of Cretaceous forests (some *in situ*) is shown in Figure 1.2 and Table 1.1, compiled from previous publications. The fossil material includes wood, leaves, cones and cone scales, pollen, roots and rhizomes, seeds, flowers, fruits and spores. Both the north and south polar regions are considered in order to provide a context into which the current research can be placed and to provide a regional picture where fossil material was not included in this study (e.g. Russia). Elevations shown on the polar projection maps (Figure 1.2) were derived from the compilation of lithological and environmental data that constrain the depositional areas for the time-slice considered (personal communication P.Markwick). Highlands were positioned over areas of known tectonic activity whether rift-related, mantle plume/hot spot, collisional or arc related and used the modern range of elevations of such tectonic regimes as a guide to past elevations (personal communication. P.Markwick).

Era	Period	Stage	Tie Point ●	Age	Intervals m.y.	
			●	65.0		
Mesozoic	Cretaceous	Maastrichtian	●	74.0	9.0	81
		Campanian	●	83.0	9.0	
		Santonian	●	86.6	3.6	
		Coniacian	●	88.5	1.9	
		Turonian	●	90.4	1.9	
		Cenomanian	●	97.0	6.6	
		Albian	●	112.0	15.0	
		Aptian	●	124.5	12.5	
		Barremian	●	131.8	7.3	
		Hauterivian	●	135.0	3.2	
		Valanginian	●	140.7	5.7	
		Berriasian		145.6	4.9	

Figure 1.1. Geological time scale for the Cretaceous (after GTS89 definitive time scale, the black dots mark tie points, pseudo tie points or age modified by incorporating ocean floor spreading data (Harland *et al.*, 1989)).

Antarctic floras

In the Southern Hemisphere Antarctica contains fossil evidence for thriving vegetation during the mid-Cretaceous (Birkenmajer and Zastawniak, 1989; Truswell, 1991; Cantrill, 1996; Cantrill and Nichols, 1996; Falcon-Lang and Cantrill, 2000, 2001a, 2001b, 2002; Cantrill and Falcon-Lang, 2001; Howe and Cantrill, 2001; Riding and Crame, 2002; Cantrill and Poole, 2004). The Albian floras from the South Shetland Islands (Snow, Livingston and King George islands) and Alexander Island were dominated by conifers such as the Araucariaceae and

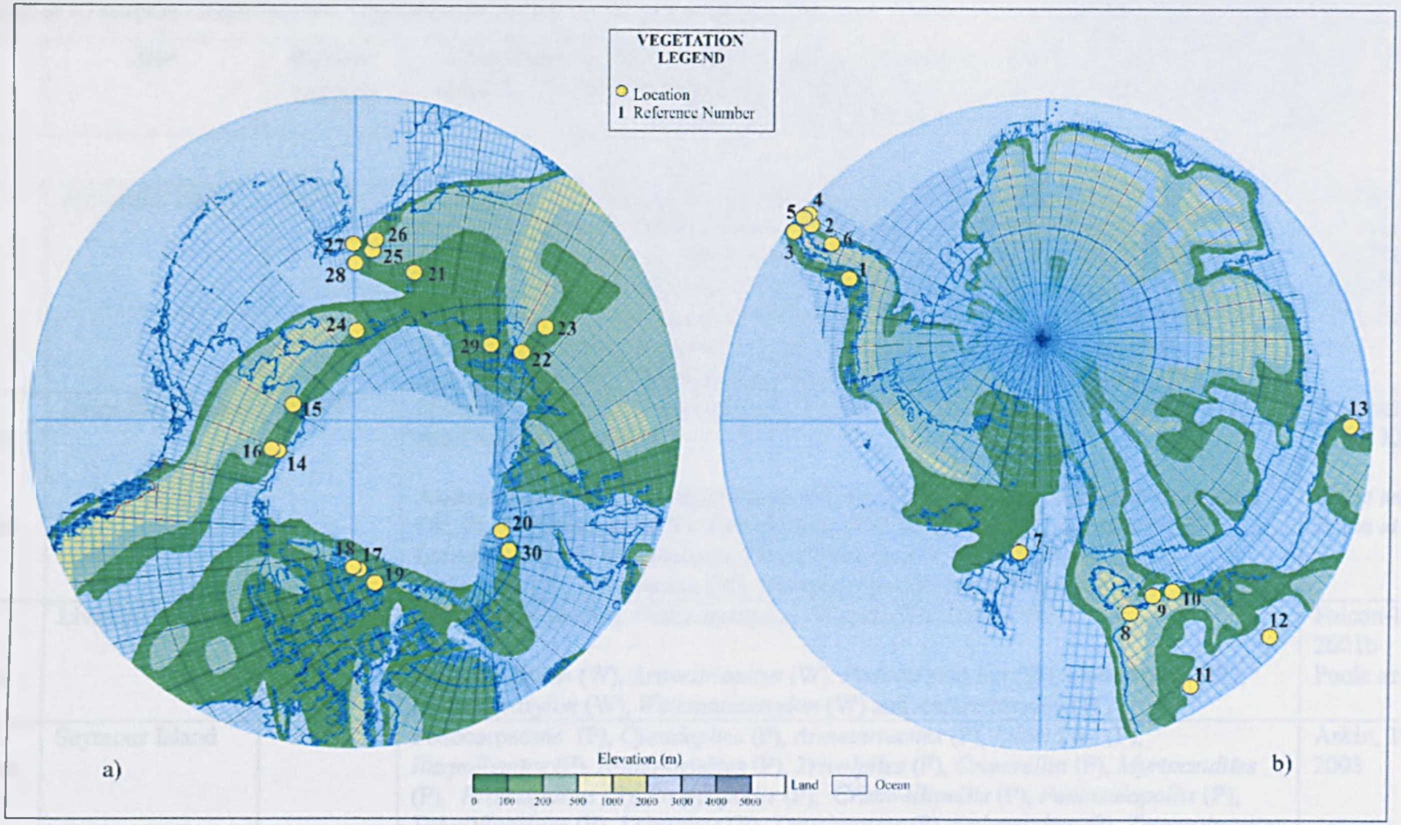

Figure 1.2. Polar projection maps (Albian 105Ma) showing only areas above 60° latitude with present day coastlines also added for reference. a) North polar region. b) South polar region. Both maps show the distribution of high latitude vegetation during the Cretaceous (see also Table 1.1 (Markwick *et al.*, 2000)). The numbers on the maps correspond to references listed within Table 1.1., note some references include descriptions of the same flora from several localities.

Table 1.1. The distribution of Cretaceous high-latitude vegetation as shown on the palaeogeography map (Figure 1.1). Palaeolatitudes are taken from references sited.

Reference Number	Age	Site	Palaeo-latitude	Genus/Species (W = wood, P = pollen or spores, L = leaves, R = rhizomes or roots, C = cones or cone scales, S = shoots, Se = seeds, St = stem F = flowers or fruits and ? = non defined fragments)	References
Antarctica					
1	Albian	Alexander Island	70-75°S	*Podozamites* (L), *Pentoxylon* (L), *Brachyphylum* (W, L), *Araucariopitys* (W), Araucariaceae (L,C), *Araucarioxylon* (W), *Elatocladus* (L,W), Podocarpaceae (L,C,W), Taxodiaceae (L,W,C), *Ginkgoites* (L), *Phyllopteroides* (L), *Cladophlebis* (L), *Ptilophyllum* (?), *Gleinchenites* (L), *Taeniopteris* (L), *Equisetales* (L), *Sphenopteris* (L), *Alamatus* (L), *Aculea* (L), *Marchantites* (?), *Hausmannia* (?), *Nilssonia* (L), *Pagiophyllum* (S, L), *Hydrocotylophyllum* (L), *Gnafalea* (L), *Araliaephyllum* (L), *Timothyia* (L), *Ficophyllum* (L) and *Dicotylophyllum* (L)	Cantrill, 1996; Cantrill and Nichols, 1996; Falcon-Lang and Cantrill, 2000; 2001a Cantrill and Falcon-Lang, 2001; Howe and Cantrill, 2001
2	Albian-Cenomanian	James Ross Island	~60 °S	Podocarpaceae sp (P), Araucariaceae (P), *Clavatipollenites* (P), *Brachyphyllum* (P) and *Cheirolepidaceae* (P)	Dettman and Thomson, 1987; Keating *et al.*, 1992
	Coniacian-Maastrichtian			Araucariaceae (W, P), Podocarpaceae (W, P), Cycadales (St), Atherospermataceae (W, P), Chloranthaceae (P), Cunoniaceae (W), Illiciaceae (W), Lauraceae (W), Loranthaceae (P), Monimiaceae (W), Myrtaceae (P), Nothofagaceae (P, W), Proteaceae (P), Winteraceae (W), *Dacrycarpites* (P) and *Phyllocladites* (P)	Poole and Francis, 2000; Poole *et al*, 2005
3	Aptian	Livingston Island	~62°S	*Araucarioxylon* (W), *Podocarpoxylon* (W) and *Sahnioxylon* (W)	Falcon-Lang and Cantrill, 2001b
	Cenomanian-Campanian			*Araucarioxylon* (W), *Araucariopitys* (W), *Podocarpoxylon* (W), *Sahnioxylon* (W), *Hedycaryoxylon* (W), *Weinmannioxylon* (W) and *Antarctioxylon* (W)	Poole and Cantrill, 2001
4	Campanian-Maastrichtian	Seymour Island	~60 °S	Podocarpaceae (P), *Cycadopites* (P), *Araucariacites* (P), *Lilacidites* (P), *Ilexpollenites* (P), *Nothofagidites* (P), *Tricolpites* (P), *Cranwellia* (P), *Myrtaceidites* (P), *Proteacidites* (P), *Propylipollis* (P), *Cranwellipollis* (P), *Peninsulapollis* (P), *Tubulifloridites* (P), *Forcipites* (P), *Tricolporites* (P), *Polycolpites* (P), *Tetracolporites* (P), *Myreugenelloxylon* (W) and *Gambierina* (P)	Askin, 1990; Poole *et al.*, 2003

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Reference Number	Age	Site	Palaeo-latitude	Genus/Species (W = wood, P = pollen or spores, L = leaves, R = rhizomes or roots, C = cones or cone scales, S = shoots, Se = seeds, St = Stem, F = flowers or fruits and ? = non defined fragments)	References
5	Coniacian-Maastrichtian	King George Island	~65 °S	*Nothofagoxylon* (W), *Nothofagus* sp (P, L, R, S), Myrtaceae (L), Araucariaceae (S), Podocarpus (P, L), Cyatheaceae (P), Gleicheniaceae (P), Proteaceae (P), *Podozamites* (L), *Araucariacites* (P), *Dacrydiumites* (P) and *Phyllocladidites* (P)	Birkenmajer and Zastawniak, 1989; Dutra and Batten, 2000
6	Santonian	Table Nunatak Eastern	~65 °S	*Erlansonisporites* (P), *Hugesisporites* (P), *Podocarpoxylon* (W), *Phyllocladoxylon* (W), Angiosperms (General) (F, Se), *Lycophytes* (P) and *Pteridophytes* (P)	Eklund *et al.*, 2004
New Zealand					
7	Albian – Cenomanian	Middle Clarence Valley, South Island	~70 °S (? 85-90°S)	*Agathis* (L), *Phyllopteroides* (L), *Coniopteris* (L), *Cladophlebis* (L), *Sphenopteris* (L), *Equisetium* (L), *Nilssonia* (L), Bennettitaleans (L), *Ginkgo* (L), *Araucaria* (L,W), Podocarps (L), *Archaepetala* (L) and *Carpolithus* (L)	Parrish *et al.*, 1998
	Campanian-Maastrichtian			Proteaceae (?), Araucariaceae (?) and Podocarpaceae (?)	Specht, 1992
Australia					
8	Albian-Aptian	Gippsland Basin, Victoria	70-85°S	Araucarians (L), Podocarps sp (L), *Pachypters* (L, Se), *Rienitsa* (L, Se), Ginkgoites (L), Lycophites e.g. *Bacutriletes* (P) and Filicopsids (P)	Douglas and Williams, 1982; Tosolini *et al.*, 2002
9	Albian-Aptian	Otway Basin, Victoria	70-85°S	Araucarians (L), Podocarps sp (L), *Pachypters* (L, Se), *Rienitsa* (L, Se) Ginkgoites (L), Lycophites e.g. *Bacutriletes* (P) and Filicopsids (P)	Douglas and Williams, 1982; Tosolini *et al.*, 2002
	Santonian-Maastrichtian			*Podocarpus* (P), *Dacrydium* (P), *Dacrycarpus* (P), *Araucaria* (P), *Ilex* (P), *Lagarostrobus* (P), *Microcachrys* (P), Proteacea (P), Winteracea (P), Trimeniaceae (P), *Nothofagus* (P), *Adenanthos* (P), *Stirlingia* (P), and Epacridaceae (P)	Specht *et al.*, 1992
10	Albian-Aptian	Casterton, Otway Basin, Victoria	70-85°S	Araucarians (L), Podocarps sp (L), *Pachypters* (L, Se), *Rienitsa* (L, Se), Ginkgoites (L), Lycophites e.g. *Bacutriletes* (P) and Filicopsids (P)	Douglas and Williams, 1982; Tosolini *et al.*, 2002
11	Barremian-Cenomanian	Surat Basin	Various	Podocarps (P), *Ginkgo* (P), *Araucaria* (P) and Cheirolepidaceae (P)	Dettman, 1994

Continued ....

Reference Number	Age	Site	Palaeo-latitude	Genus/Species (W = wood, P = pollen or spores, L = leaves, R = rhizomes or roots, C = cones or cone scales, S = shoots, Se = seeds, St = stem, F = flowers or fruits and ? = non defined fragments)	References
12	Barremian-Cenomanian	Eromanga Basin	Various	Podocarps (P), *Ginkgo* (P), *Araucaria* (P) and Cheirolepidaceae (P)	Dettman, 1994; Frakes and Francis, 1990
13	Barremian-Cenomanian	Perth Basin	Various	Podocarps (P), *Ginkgo* (P), *Araucaria* (P) and Cheirolepidaceae (P)	Dettman, 1994
Alaska					
14	Albian-Turonian	North Slope of Alaska, Colville River Region	85 °N	*Ginkgo* (L), ?*Cephalotaxopsis* (L, S), *Pityophyllum* (L, S), *Sphenolepis* (L, S), *Podozamites* (L, R, S), *Abieites* (S, C), *Taiwania* (W), *Amenotaxus* (L), ?*Juniperites* (L), *Sequoia* (L), *Torreya* (L), *Araucarites* (L), *Equisetites* (W, R), *Taxites* (L), *Elatocladus* (L), *Sphenobaeria* (L), *Xenoxylon* (W) and *Cedrus* (W)	Arnold, 1953; Smiley, 1969; Spicer and Parrish, 1986; Parrish and Spicer, 1988
15	Albian-Cenomanian	North Slope of Alaska, Kukpowruk region	~75-86 °N	*Ginkgo* (L), *Pityophyllum* (L), *Podozamites* (L,W), *Cephalotaxopsis* (L,C, S), *Juniperus* (L), *Sequoia* (L,C), *Pinus* (L,C, P), *Torreya* (L,S,C), *Taxodium* (L,S,C), ?*Larix* (L), *Equisetites* (R), *Birisia* (L, R), Cycadophytes including *Nilssonia* (L), *Parataxodium* (L), *Arctopteris* (L), *Desmiophyllum* (L), *Czekanowskialeans* (L), *Thallites* (?), *Pityostrobus* (C), *Pagiophyllum* (S, L) and *Picea* (C, P)	Smiley, 1966; Spicer and Parrish, 1990; Herman and Spicer, 1996; Spicer and Herman, 2001; Spicer, 2003
16	Coniacian-Campanian	North Slope of Alaska, Chandler-Colville region	~75 °N	*Ginkgo* (L), *Platanus* (L), *Trochodendroides* (L) and *Dalembia* (L)	Smiley, 1969; Herman and Spicer, 1997
Canadian Arctic					
17	Albian	Strand Fiord Peninsula, Axel Heiberg Island	~72 °N	*Cedroxylon* (W)	Bannan and Fry, 1957
18	Albian	Amund Rigness Island	~71 °N	*Piceoxylon* (W)	Bannan and Fry, 1957
19	Campanian-Maastrichtian	Ellesmere Island	~75 °N	*Ginkgo* (L), Taxodiaceae (L, P, S) including *Taxodioxylon* wood, *Parataxodium* (S, L), *Trochodendroides* (L), Ferns including *Baculatisporites* (P) and *Piceoxylon* (W)	Falcon-Lang *et al.*, 2004

Continued .....

Reference Number	Age	Site	Palaeo-latitude	Genus/Species (W = wood, P = pollen or spores, L = leaves, R = rhizomes or roots, C = cones or cone scales, S = shoots, Se = seeds, St = stem, F = flowers or fruits and ? = non defined fragments)	References
Russia					
20	Neocomian	Franz Joseph Land	~74 °N	Ginkgoales (?), Czekanowskiales (?), *Pityophyllum* (?), *Nilssoniopteris* (?), *Florinia* (?), *Tyrmia* (?), *Parataxodium* (?), *Araucariopitys* (W), *Pinoxylon* (W), *Palaeopiceoxylon* (W), *Cedroxylon* (W), *Cupressionoxylon* (W) and *Xenoxylon* (W)	Shilkina, 1967; Vakhrameev, 1991
21	early Cretaceous up to Albian	Zyryansk Basin	~78 °N	*Arctopteris* (?), Abundant angiosperms including *Cinnamonomoides* (?), *Ranunculicarpus* (?), *Mirella* (?) and *Cercidiphyllum* (?)	Vakhrameev, 1991; Spicer and Herman, 2001
22	Neocomian-Albian	Northern Lena Province	~80 °N	*Aomozamites* (?), *Nilssonia* (?), *Sequoia* (?), *Parataxodium* (?), *Pseudolarix* (S), *Hausmannia* (?), *Osmundaiopsis* (?), *Birisia* (?), *Coniopteris* (?), *Ginkgo* (L), *Baiera* (?), *Eremaphyllum* (?), *Sphenobaiera* (?), *Podozamites* (L), *Pitycladus* (S, L, Se), *Cephalotaxis* (S), *Adiantopteris* (?), *Arctopteris* (?), *Asplenium* (?), *Scloropteris* (?), *Neozamites* (?),*Czekanowskia* (L), *Parataxodium* (Se), *Prototrochondendroides* (L), *Cyparissidium* (?) and *Elatocladus* (S)	Vakhrameev, 1991
23	Neocomian - Albian	Southern Lena Province	~75 °N	*Aomozamites* (?), *Nilssonia* (?), *Sequoia* (?), *Parataxodium* (?), *Pseudolarix* (S), *Hausmannia* (?), *Osmundaiopsis* (?), *Birisia* (?), *Coniopteris* (?), *Ginkgo* (L), *Baiera* (?), *Eremaphyllum* (?), *Sphenobaiera* (?), *Podozamites* (L), *Pitycladus* (S, L, Se), *Cephalotaxis* (S), *Adiantopteris* (?), *Arctopteris* (?), *Asplenium* (?), *Scloropteris* (?), *Neozamites* (?), *Czekanowskia* (L), *Parataxodium* (Se), *Prototrochondendroides* (L), *Cyparissidium* (?) and *Elatocladus* (S)	Vakhrameev, 1991
24	Turonian-Campanian	Okhotsk-Chukotka Volcanic Belt , North East Russia	79 °N	*Coniopteris, Kolymelia* (L),, *Heilungia* (L),, *Tchaunia* (L),, *Cladophlebis* (L), *Phoenicopsis* (L), *Ctenis* (L), *Pagiophyllum*(L), *Araucarites* (L), *Taxus* (L), *Metasequoia* (L), *Quereuxia* (L), *Zizyphoides* (L), *Trochodendroides* (L) and *Menispermites* (L)	Spicer, 2003
25	early-middle Albian	Bol'shoi Anui River Basin	~72 °N	*Thallites* (?), *Coniopteris* (L), *Onychiopsis* (L), *Ginkgo* (L), *Taeniopteris*? (L), *Elatocladus* (S) and *Anomozamites* (L)	Spicer and Herman, 2001

Continued .....

Reference Number	Age	Site	Palaeo-latitude	Genus/Species (W = wood, P = pollen or spores, L = leaves, R = rhizomes or roots, C = cones or cone scales, S = shoots, Se = seeds, St = stem, F = flowers or fruits and ? = non defined fragments)	References
26	early-middle Albian	Yeropol River Basin	~72 °N	*Thallites* (?), *Coniopteris* (L), *Onychiopsis* (L), *Ginkgo* (L), *Taeniopteris?* (L), *Elatocladus* (S) and *Anomozamites* (L)	Spicer and Herman, 2001
27	latest Albian-early Cenomanian	Grebenka River	~72 °N	*Araucarites* (L), *Scheffleraephyllum* (L), *Platanus* (L), *Araliaphyllum* (L), *Menispermites* (L), *Dalembia* (L), *Magnoliaephyllum* (?), *Grebenka* (L), *Trochodendroides* (L), *Equisetites* (?), *Birisia* (?), *Coniopteris* (?), *Arctopteris* (?), *Asplenium* (?), *Nilssonia* (L, S), *Hausmannia* (L), *Elatocladus* (L), *Cephalotaxopsis* (L), *Pseudolarix?* (?), *Zizyphus* (?), *Pityophyllum* (?), *Pityospermum* (?), *Thallites* (?), *Ginkgo* (?), *Pagiophyllum* (L, S), *Sequoia* (C), *Sorbites* (?), *Myrtophyllum* (L), *Cladophlebis* (?), *Phyllites* (?), *Sphenopteris* (?), *Sapindophyllum* (L), *Sagenopteris* (?), *Dicotylophyllum* (L) and *Gleichenites* (L)	Spicer and Herman, 2001; Spicer, 2003; Spicer *et al.*, 2002; Herman 1994
28	Lower Coniacian	Northern Pekulney (Pekul'nei) Range	~78 °N	*Coniopteris* (?), *Osmunda* (?), *Ochotopteris* (?), *Hausmannia* (?), *Ginkgo* (?), *Nilssonia* (?), *Ctenis* (?), *Cephalotaxopsis* (?), *Thuja* (?), *Elatocladus* (?), *Pityophllum* (?), *Metasequoia* (?), *Quereuxia* (?), *Phoenicopsis* (?), *Dicotylophyllum* (?) *Desmiophyllum* (L), *Arthollia* (?), *Psedoprotophyllum* (?), *Paraprotophyllum* (?), *Trochodendroides* (L), *Zizyphus* (L), *Menispermites* (L), *Araliaephyllum* (L), *Leguminosites* (?), *Dalbergites* (?), *Celastrinites* (?), *Viburniphyllum* (L), *Grewiopsis* (?), *Terechovia* (?), *Platanus* (L), *Sciadopitys* (?) and *Sequoia* (?)	Craggs, 2005; Herman 1994
29	Turonian	Novaya Sibilr' Island	~82 °N	*Hausmannia* (?), *Cladophlebis* (?), *Sphenobaiera* (?), *Podozamites* (?), *Pityophyllum* (?), *Cephalotaxopsis* (?), Sequoia (?), *Parataxodium* (?), *Trochodendroides* (L), *Platanus* (L), *Pseudoprotophyllum* (?), *Macclintockia* (?), *Cissites* (?) and *Dalembia* (L)	Herman and Spicer, 1997
Svalbard					
30	Barremian-Aptian	Spitsbergen	~72 °N	*Ginkgoales* (?), *Czekanowskiales* (?), *Nilssonia* (?), *Ginkgo* (?), *Elatides* (?), *Podozamites* (?), *Pitycladus* (?), *Pseudotorellia* (?), *Cycadophytes* (?) and *Osmundacidites* (L)	Vakhrameev, 1991; Harland, 1997

Podocarpaceae, with Cheirolepideacean conifers (now extinct) represented in small numbers (Cantrill, 1996; Francis, 1996). The understorey contained cycadophytes, ginkgoes and diverse ferns, including *Alamatus* and *Aculea* (Cantrill, 1996; Francis, 1996). Rare taxodiaceous conifers were also present (Falcon-Lang and Cantrill, 2000). Falcon-Lang and Cantrill (2001a) suggested that the presence of Araucariaceae and Podocarpaceae conifers during the Albian of Alexander Island indicated that the canopy was dominantly evergreen, although they indicate that the presence of angiosperm fossils (e.g. *Araliaephyllum* and *Gnafalea*) suggests there was also a deciduous element (Cantrill and Nichols, 1996). The integration of detailed sedimentary information with the distribution of *in situ* leaf litter layers resting on palaeosol surfaces indicate that the conifers grew in a variety of environments Cantrill and Falcon-Lang, 2001). These environments included dense stands in back swamps, stands of 5 or 6 trees in upper coastal plain meander belts, and in braided and meandering fluvial settings (Cantrill and Falcon-Lang, 2001).

In the late Albian the forests of the islands off the northern Antarctic Peninsula included angiosperms for the first time, especially types of *Nothofagus*, although magnoliid leaves are also reported (Francis, 1986; Howe and Cantrill, 2001; Eklund, 2003). The diversity of the angiosperms became richer by the Late Cretaceous (late Santonian, ca 85 Ma) and included monocots, magnoliids and eudicots (Eklund, 2003). From the Coniacian to the Campanian James Ross Island still maintained the Araucariaceae and Podocarpaceae that had been present in the Albian but now the flora also contained Lauraceae, Myrtaceae, Proteaceae, Loranthaceae and Nothofagaceae (Dettman and Thomson, 1987; Cantrill and Poole, 2004; Poole *et al.*, 2005). Livingston Island also contained a mixed conifer-dicotyledonous angiosperm forest with an understorey of a bennettitalean gymnosperm *Sahnioxylon* (Chapman and Smellie, 1992). However, during the Santonian to Maastrichtian angiosperms gained prominence over the conifers on King George Island, represented by abundant fossil leaves (*Nothofagus* and Myrtaceae) associated with the Araucariaceae and Podocarpaceae (Birkenmajer and Zastawniak, 1989; Falcon-Lang and Cantrill, 2001a). Dutra and Batten (2000) indicated that *Podocarpus fildesensis* was the dominant conifer species within this flora. On James Ross Island the vegetation was still dominated by conifers (*Araucarioxylon, Phyllocladoxylon* and *Podocaproxylon*) with subordinate angiosperms including Winteraceae, Nothofagaceae, Myrtaceae and Gunneraceae (Dettman and Thomson, 1987; Keating, 1992; Cantrill and Poole, 2004; Poole *et al.*, 2005).

On the eastern side of the Antarctic Peninsula Santonian age sediments from Table Nunatak contain a flora preserved as charcoalified fossils, probably due to the intense volcanic activity on Antarctica at that time (Eklund *et al.*, 2004). This flora appears to have been much more diverse than on the islands further north. However the high diversity may also be a result of the charcoalification process allowing the preservation of fine detail whilst, once produced, the charcoal remains chemically highly inert (Eklund *et al.*,2004). The flora contained lycopods

(*Cabochonicus, Erlansonisporites* and *Hughesisporites*), ferns (*Arcellites*), conifers (*Podocarpoxylon* and *Phyllocladoxylon*) and angiosperms (unidentified) and shows that, although conifers were probably dominant, the angiosperms were by then an important component (Eklund *et al.*, 2004). The oldest flowers on the Antarctic Peninsula were found in these Santonian sediments and are related to extant Siparunaceae, Winteraceae and Myrtaceae (Eklund, 2003). This suggests that either the conditions in this area were particularly favourable for angiosperms or it was among the first areas to be colonized.

New Zealand

In Albian-Cenomanian times New Zealand's forest structure was similar to that of Antarctica, consisting of emergent Araucariaceae, Podocarpaceae and ginkgoales occurring as widely spaced trees on floodplains and in upland areas (Parrish *et al.*, 1998). These forests would have also had a canopy of shrubby Osmundaceous ferns, seed ferns, cycads, Bennettites, Pentoxylalean plants and angiosperms including the Proteaceae (Parrish *et al.*, 1998). Ferns and horsetails were probably the first colonizers before becoming an integral part of the understorey. The angiosperms appear to have formed an important part of the vegetation near to channels, but swampy interludes were dominated by *Agathis*. Parrish *et al.* (1998) suggested that *Agathis* was deciduous in habit due to the presence of leaf mats (see Chapter 7). Several evergreen trees were also present and it is also possible that some of the small thick leaved angiosperms were evergreen (Parrish *et al.*, 1998). Angiosperm reproductive structures (*Archaepetala* and *Carpolithus*) and leaves are also found in these sediments (Parrish *et al.*, 1998). In the Campanian to Maastrichtian the composition of these New Zealand forests differed slightly from those of Antarctica, being dominated by a canopy of Podocarpaceae, Araucariaceae and Proteaceae and lacking the abundant *Nothofagus* present on Antarctica (Specht *et al.*, 1992).

Australia

In Victoria, Australia, from the Neocomian to the Albian the landscape was also occupied by forests, the tree elements of which were principally conifers (Araucariaceae, Cheirolepidiaceae and Podocarpaceae) and to a lesser extent Ginkgoales, with a wide variety of associated plants (ferns, lycophytes, equisetaleans and bryophytes) forming ground cover and understorey (Douglas and Williams, 1982; Tosolini *et al.*, 2002). Further to the north in the Eromanga Basin in the Aptian/Albian, the forests were mainly composed of Araucariaceae and Podocarpaceae conifers, probably representing two populations (Frakes and Francis, 1990). Population A displayed restricted growth in its wood structure and may have represented a cool highland area whilst Population B may have represented faster growth in a warm climate at lower altitudes near the basin shoreline (Frakes and Francis, 1990). There is also evidence of an understorey of ferns, seed-ferns and cycadophtyes, suggesting that this flora was very similar to that further south in the Gippsland Basin, Victoria (Douglas and Williams, 1982; Frakes and Francis, 1990). During the Santonian-Maastrichtian the Otway Basin contained diverse and structurally complex forests similar to present day perhumid tall open-forest (very wet rainforest climate with humidity index of equal to or >100 (Gluckmann, 1999)) consisting of *Araucaria, Dacrydium* and *Podocarpus* with an understorey of Proteaceae, Winteraceae, Trimeniaceae and cryptogams (Specht *et al.*, 1992).

Alaska

On the North Slope of Alaska (Kukpowruk, Colville and Chandler River sections) deposits of Albian-Turonian age yielded assemblages of high diversity (e.g. 57 plant taxa from the Kukpowruk River Section), rich in ferns and conifers (Parrish and Spicer, 1988; Spicer and Parrish, 1990; Spicer and Herman, 2001). *Equisetites* were probably the initial colonizers of the succession, providing the ground cover with the fern *Birisia* growing over much of the floodplain to form marginal marine and early successional marsh/heath communities (Spicer and Parrish, 1986; Spicer and Herman, 2001; Spicer, 2003). The lower floodplain sediments were dominated by *Podozamites* leaves, associated with *in situ* trunks in fluvial, overbank and pond deposits (Spicer and Parrish, 1986; Spicer, 2003). Fluvial sandstones in the Chandler Colville Region also yielded *Ginkgo* fossils representing shrubby to forested river margin communities. Other *Ginkgophytes* were largely confined to overbank regions and were most abundant and diverse in Albian sediments, but became limited to a single genus by the end of the Cenomanian (Smiley, 1969; Spicer and Parrish, 1986; Herman and Spicer, 1996; 1997; Spicer and Herman, 2001; Spicer, 2003). The conifers present included *Cedrus*, *Xenoxylon, Parataxodium* and *Metasequoia,* with the latter two genera forming closed canopy forests in swamp environments. The conifers become more common and taxonomically diverse in the upper Albian (Arnold, 1953; Spicer and Parrish, 1986; Parrish and Spicer, 1988). The lower floodplain sediments were dominated by *Podozamites* leaves, associated with *in situ* trunks in fluvial, overbank and pond deposits (Spicer and Parrish, 1986; Spicer, 2003). This conifer-fern-Ginkgo-cycad flora across the North Slope of Alaska provided the background for angiosperm influx represented by tricolpate pollen in early Albian sediments, with the first leaves representing *Menispermites* and *Populophyllum* found in late Albian strata (Smiley, 1969; Spicer, 2003). Several angiosperm leaves have been described from the Kukpowruk River Section that have been assigned to *Schefferaephyllum*, *Platanus* and *Dicotylophyllum* although they were probably rare and restricted in ecological distribution (Spicer and Herman, 2001).

From a physiognomic standpoint, the modern vegetation type most similar to that of the mid-Cretaceous North Slope of Alaska is the low montane mixed coniferous forest (Spicer and Parrish, 1986; 1990). However, abundant coal beds present at Kukpowruk and Colville Rivers containing common *Xenoxylon*, *Podozamites*, *Pagiophyllum*, *Pityostrobus*, *Pityolepsis*, *Cephalotaxopsis*, *Parataxodium* and *Pityophyllum*, indicated the presence of low lying mire forest communities which, beside indicating the presence of abundant water, also suggest that the drainage was poor (Parrish and Spicer, 1988; Spicer and Herman, 2001; Spicer, 2003). Therefore there may have been several microhabitats present across this large area during the Cretaceous.

Canadian Arctic

The flora of the Canadian Arctic (Axel Heiberg and Amund Ringnes islands) appears to have been dominated by coniferous forests (*Cedroxylon* and *Piceoxylon*) during the Albian (Bannan and Fry, 1957). In the Campanian-Maastrichtian the flora on Ellesmere Island was low to medium diversity, dominated by taxodiaceous conifers (*Parataxodium*) with subordinate *Piceoxylon*, ginkgos, cycads, angiosperms, ferns, lycopsids and bryophytes growing in alluvial plain and peat mire environments (Falcon-Lang *et al.*, 2004). Some areas of the peat mire contain closely spaced *in situ* stumps suggesting the presence of dense coniferous forest stands (Falcon-Lang *et al.*, 2004). No other previously published work could be found on the Cretaceous palaeoenvironments of this region.

Russia

The north-eastern part of Russia contains a wealth of Cretaceous plant-bearing rocks and coals (Spicer, 2003). At the onset of the Albian the first angiosperms (*Prototrochodendroides*) were represented in the Lena Province by small leaf forms among a diverse flora including ferns (e.g. *Birisia*), cycadophytes (e.g. *Nilssonia*) and conifers (e.g. *Parataxodium* and *Elatocladus*) (Vakhrameev, 1991).

Another diverse flora, the Buor-kemuss Flora, was present at various locations in north-eastern Russia during most of the Albian, including in the Bol'shoi Anui River Basin (Ainakhkurgen Depression), the Yeropol River Basin (Umkuveem Depression) and the Zyrianka River (Figure 1.2, Spicer and Herman, 2001). This flora included conifers (*Elatocladus*), liverworts (*Thallites* and *Mirella*), ferns (*Coniopteris* and *Onychiopsis*), ginkgoaleans (*Ginkgo*) and cycadophytes (*Taeniopteris* and *Anomozamites*) and is very similar in composition to the less diverse flora found in the Albian of the Kukpowruk River area on the North Slope of Alaska (Spicer and Herman, 2001). This would suggest that there was a migration route (?the Bering Strait Land Bridge) linking Alaska and western Canada to north-eastern Russia (Herman, 1994).

In the late Albian the Taxodiaceae conifers increased in dominance in north-eastern Russia. The late Albian to early Cenomanian Grebenka flora from the Grebenka River region inhabited a floodplain with a fluvial system that was much more energetic than that seen on the North Slope of Alaska although the flora is very similar in composition to the third Kukpowruk River suite (known as the Corwin Flora) (Spicer and Herman, 2001; Spicer *et al.*, 2002; Spicer, 2003). This fossil flora is highly diverse and abundant enough to allow vegetation dynamics to be reconstructed: *Equisetites* and bryophytes were pioneering plants colonizing the bare substrate before being invaded by the fern *Birisia*. These areas were then colonized by angiosperms including *Platanus*, *Grebenkia* and *Scheffleraephyllum* with an understorey of *Birisia* and *Gleichenites* before being invaded by more diverse flora of *Araliaphyllum*, *Menispermites*, *Nilssonia* and the conifers *Elatocladus* and *Cephalotaxopsis* (Herman, 1994; Spicer *et al.*, 2002; Spicer, 2003). However, where there was standing water the aquatic fern *Hausmannia* formed a monodominant community (Spicer *et al.*, 2002). The conifers eventually became dominant in drier areas, including *Pagiophyllum*, *Araucarites* and *Sequoia* (Spicer *et al.*, 2002; Spicer, 2003). There are no coals present in the Grebenka area due to the past high energy nature of the area preventing the accumulation of organic matter in standing water (Spicer, 2003).

The high diversity of the north-east Russian floras persisted into the early Coniacian in the Northern Pekulney Range Flora with two large plant assemblages in the Tylpegyrgynai and the Poperechnaya Formations, containing sixty-eight different species of plants (Craggs, 2005). This flora was dominated by angiosperms although conifers, ferns, cycadophytes, ginkgophytes and sphenophytes were also present in a floodplain setting that was increasingly influenced by volcanic activity (Craggs, 2005).

Even in the highest northern sites in Russia the flora continued to be abundant and diverse in the Turonian as studies of Novaya Sibilr' Island have shown (Herman and Spicer, 1997). Little palaeoenvironmental data was found on this area other than that mean annual temperature was ~9.0°C with winter temperatures probably above freezing. The flora included *Hausmannia*, *Cladophlebis*, *Sphenobaiera*, *Podozamites*, *Pityophyllum*, *Cephalotaxopsis*, *Sequoia*, *Parataxodium*, *Trochodendroides*, *Platanus*, *Pseudoprotophyllum*, *Macclintockia*, *Cissites* and *Dalembia*, suggesting that it may have been growing in similar floodplain settings to those found in other north-eastern Russian sites (Herman and Spicer, 1997).

The Turonian to Campanian Chauna flora of the Okhotsk-Chukotka volcanogenic belt of north-eastern Russia is unlike any other flora in this area, representing a vegetation from higher elevations than those found on the coastal plains and also due to frequent ash falls from volcanic activity (Spicer, 2003). This flora includes endemic ferns (*Koymella* and *Tchaunia*), cycadophytes (*Heilugia* and *Ctenis*), *Phoenicopsis*, a group of uncertain affinity, and conifers (*Taxus*, *Metasequoia* and *Araucarites*).

Svalbard (Spitsbergen)

The forests of Spitsbergen (the main island of Svalbard) seem to have been dominated by *Ginkgo, Elatides, Podozamites, Pinites* and *Pseudotorellia* with rare cycadophytes in a warm equable climate during the early part of the Cretaceous (Harland, 1997).

Like the Canadian Arctic little work appears to have been carried out on the Cretaceous palaeoenvironments of Spitsbergen and no other references could be found for inclusion in this review.

1.2.2. Survival strategies of forests in high latitudes

The polar regions are currently characterized by either tundra vegetation or, at the very highest latitudes, glaciers. Therefore there are no modern analogues to the Cretaceous high latitude forests which grew under the unique conditions of high-latitude light regimes coupled with mid-latitude temperatures (Creber and Chaloner, 1984a; Read and Francis, 1992). This section reviews previously published ideas on how the vegetation may have adapted its growth patterns to survive in these unusual polar regions, what the growth forms tell us about the conditions prevailing at the time and also provides the context for the leaf life-span analysis carried out in this study. The types of strategies that the polar conifers employed have been investigated in the past using the fossil record and experimental and analytical research carried out on extant trees. All approaches are examined here for completeness and to gain an insight in to the current knowledge base.

The forests in the Cretaceous would have had to develop survival strategies in order to be able to tolerate the unique conditions such as long periods of darkness and extended periods of polar sunlight in summer (Figure 1.3, Herman and Spicer, 1997; Beerling and Osborne, 2002).

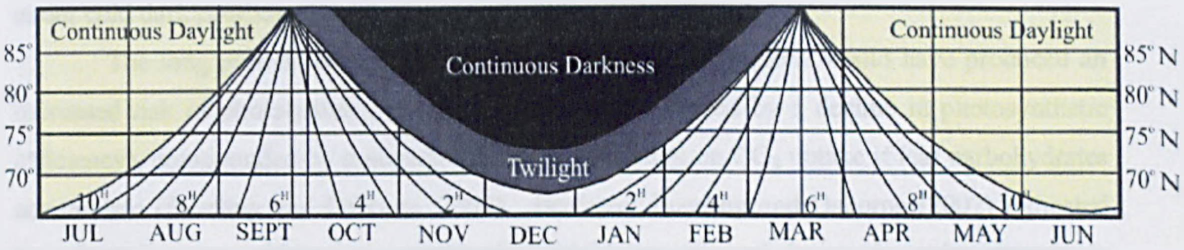


Figure 1.3. Duration of daylight in the modern Arctic. " = hours. (redrawn from Herman and Spicer, 1997)

It has been argued that polar vegetation in the past would have been deciduous because the winter darkness would have favoured respiration over photosynthesis. This would not have favoured evergreens because the trees would have used more carbon in respiration in the dark than they could have made up via photosynthesis during light periods (Chaney, 1947; Wolfe, 1980). In 1984 Axelrod suggested that trees with a deciduous habit would have been better adapted to warm polar darkness but evergreens would have been viable if their response to climate and photoperiod was the same as modern trees. The idea that deciduousness prevents carbon loss in trees during winter was therefore firmly established in the literature but no experimental evidence existed to support this claim (Osborne *et al.*, 2004).

Creber and Chaloner (1984b) indicated that the light regime would have been adequate for growth of forests at high latitudes and showed that cone-shaped trees would have had the most beneficial growth form. This shape, adopted by extant spruce-fir trees, is of benefit because at low angles of sunlight solar beams penetrate deep into the crown, with much of the back-scattering of reflected light being absorbed by trees on their otherwise shaded sides (Specht *et al.*, 1992). They also produce minimal shading of neighbouring trees (Francis, 1986; Crame, 1989). Herman (1994) also indicated that the diffuse quality of the summer sunlight at high latitudes, with no infrared rays to cause overheating of large leaves, is photosynthetically beneficial. Diffuse light is better utilized by plants than direct sunlight and is absorbed almost entirely. Temperature, rather than light, is thus the factor preventing modern floras from colonizing high latitude areas (Herman, 1994).

Given the lack of comparable modern analogues, greenhouse experiments have been carried out in order to determine likely past leaf habits. Read and Francis (1992) carried out experiments on extant plants to investigate their survival under the long dark polar winter periods. Their results showed that stored starch content and, at least in evergreen species, the rate of leaf respiration in the dark, may have been significant factors in determining plant survival in prolonged dark periods. This is because of the high cost of canopy replacement, compared to the alternative costs of leaf foliar dark respiration or stress tolerance. The plants, grown under experimental winter dark conditions for 10 weeks at either warm (15°C) or cold (4°C) temperatures by Read and Francis (1992) in Hobart, Tasmania had a higher survival rate under cold dark conditions rather than warm dark conditions.

The long periods of continuous sunlight in the polar regions would have produced an increased risk of photoinhibition (reduced CO_2 uptake caused by a decline in photosynthetic efficiency), compounded by a negative feedback operating on CO_2 uptake if leaf carbohydrates accumulate (Beerling and Osborne, 2002). However Beerling and Osborne (2002) indicated that there is scant evidence to suggest photoinhibition occurred during the polar summer in either evergreen or deciduous taxa. Indeed, experimental data indicate that higher rates of photosynthesis may have been possible (Beerling and Woodward, 1996).

During the Cretaceous period CO_2 levels in the atmosphere are believed to have been much higher than present (3 to 6x present levels, Harland *et al.*, 1989; Barron *et al.*, 1992; Kelley, 2003) therefore the polar conifer forests would have had to function under these conditions. It has been suggested that these high concentrations of atmospheric CO_2 may have decreased the respiratory costs of evergreen trees by suppressing leaf and root respiration rates by 25-50% during the mild polar winters, diminishing the need for deciduousness (Beerling and Osborne, 2002). Reich *et al.* (1995) found that under elevated CO_2 the leaf life-span of extant species *Taxus cuspidate*, *Picea jezoensis* and *Betula maximowicziana* is decreased, which is consistent with greater carbon gain being related to shorter leaf duration. However, using experimental data collected from six species of deciduous and evergreen trees, representing some taxa of ancient polar forests, Beerling and Osborne (2002) suggested that trees with long lived foliage show the greatest benefit from growth in an elevated CO_2 environment. This is because the growing season of plant organs is longer in evergreen than in deciduous trees (Woodward, 1995), leaving evergreen trees better placed to exploit the high CO_2 and warm spring and autumnal temperatures and therefore benefiting from a longer period of photosynthesis (Beerling and Osborne, 2002). Further experiments were carried out by Royer *et al.* (2003) on these same types of trees in environmentally-controlled growth rooms in order to confirm whether an evergreen or deciduous strategy would be of most benefit to trees growing at high latitudes. These experiments showed that respiration rates of evergreen plants during the winter dark period were higher than those for leafless deciduous plants, as would be expected. There was no difference in respiration related to elevated CO_2 treatments. Evergreens lost on average eight times more carbon through respiration costs (Royer *et al.*, 2003; Osborne *et al.*, 2004). This suggests that evergreen plants would have been disadvantaged in high latitude areas by being unable to retain as much carbon as deciduous plants. The production of leaf litter by deciduous plants is an additional carbon cost to be taken into account and this was significantly greater for deciduous plants than evergreens (Royer *et al.*, 2003; Osborne *et al.*, 2004). The deciduous trees lost, on average, twenty times more carbon through leaf shedding than the evergreen trees.

When these two effects, of carbon loss due to winter respiration and of leaf shedding, were added together the carbon cost of leaf production far outweighed that of respiration, with the combined cost for evergreens being only a ninth of the total cost for deciduous trees. These findings therefore overturn the carbon loss hypothesis and suggest that evergreen trees were far from being disadvantaged by the high latitude environment but appear to have had the competitive advantage over deciduous forms (Royer *et al.*, 2003; Osborne *et al.*, 2004). When scaled up to the whole forest level the difference in carbon cost between leaf habits diminished because the scaled calculations more completely account for carbon losses by leaf fall for an evergreen canopy but the deciduous habit still incurred a winter carbon cost that was 1.5 to 2 times greater than for evergreens. An additional surprising result of these experiments was that evergreen species appear not to capitalize on having foliage early and late in the growing season when deciduous trees are leafless, fixing only 1% of their annual carbon early in the season and 3.5% late in the season (early and late seasons as defined in Royer *et al.*, 2005).

The leaf type is also an important feature in survival at these high latitudes. Beerling (1994) suggested that evergreen gymnospermous trees with xerophytic needle leaf morphology, including sunken stomata, thick cuticle and epicuticular waxes, would have had an advantage over deciduous angiosperms growing under elevated CO_2 levels during the Cretaceous. This is for two reasons: firstly the evergreens could continue to exploit the high CO_2 levels as discussed above to fix carbon throughout the year without the cost of replacing their canopy in spring, and secondly, this leaf form would reduce transpiration water losses in the warm climate making the trees more resource-efficient (Beerling, 1994). The advantages of higher carbon gain and water use efficiency at mid-latitudes shown by angiosperms may have therefore been offset by the evergreen habit of conifers at high-latitudes.

When conditions are cold trees develop small, prostrate forms (Mitton, 1995) growing close to the ground to avoid freezing winds, as in extant Arctic and alpine willows and junipers (personal observation; Francis and Hill, 1996), forming narrow growth rings in a distinctly asymmetrical form due to slow growth along the ground. These signals are not seen in the Cretaceous woods. The evidence from the Cretaceous woods indicates the existence of large erect tree forms (Jefferson, 1982; Specht *et al.*, 1992; Francis, 1996; Falcon-Lang and Cantrill, 2000, 2002 ; Howe and Cantrill, 2001). Examples of these large *in situ* tree stumps are described by Jefferson (1982) with stumps up to 22cm diameter and 7m high from Alexander Island, Antarctica, although Falcon-Lang and Cantrill (2002) have reported even wider stumps of *Araucarioxylon* from the South Shetland Islands (>150cm in diameter). Falcon-Lang and Cantrill (2002) used architectural and phenological data to reconstruct the heights of the trees and predicted that, although most would have been between 20-30m high, at least one could have been >45m. Specht *et al.* (1992) used present day ecophysiological parameters and palaeotemperatures to predict stand heights for gymnosperms in the Cretaceous of up to 45m. In general the high latitude fossil trees also possessed wide evenly-spaced growth rings indicating warm, equable conditions of growth (Jefferson, 1982; Francis, 1986; Francis, 1996).

An important factor amongst these survival strategies at high-latitudes is leaf retention time because it is this that determines the effectiveness of a) the trees' ability to gain carbon throughout the year, and b) the resource efficiency under warm high CO_2 environmental conditions (Beerling, 1994; Woodward, 1995; Beerling and Osborne, 2002). It has been suggested that the leaf longevity and seasonal timing of leaf abscission is closely related to climate as it produces feedbacks to the climate through albedo, land surface roughness etc (Falcon-Lang and Cantrill, 2001a). Therefore analysis of leaf phenology of fossil plant communities has the potential to yield valuable palaeoclimatic data needed to test and refine numerical models of past global climates, vegetation and environments (Falcon-Lang and Cantrill, 2001b).

1.3. Deciduous or evergreen habits in modern vegetation

Deciduous plants are defined as those that keep their leaves for less than 12 months (usually between 6 and 9 months), shedding all of their foliage to leave bare branches each year. Evergreen trees keep their leaves for 12 months or more and shed only a small percentage of their leaves at one time, therefore sustaining a continuous leaf canopy. In general angiosperms are deciduous whilst conifers are evergreen but there are exceptions to this e.g. evergreen oak (*Quercus ithaburensis*, Ne'eman, 1993) and deciduous larch (*Larix decidua*, Reich *et al.*, 1999) (Reich *et al.*, 1995). There are advantages to both types of leaf habit, as outlined in Table 1.2.

Table 1.2. Table showing the advantages to trees (angiosperm and conifers) of having an evergreen or deciduous leaf habit.

Leaf Habit	Advantages	References
Evergreen	• Reduces the amount of energy trees have to divert to foliage production. • Adapted to reduce water loss in areas of poor water availability. • Efficient in terms of carbon gain in areas with short growing seasons. • Productive in low fertility areas.	Monk, 1966; Gower and Richards, 1990; Ne'eman, 1993; Ennos, 2001; Mediavilla and Escudero, 2003; Oleksyn *et al.*, 2003; Warren and Adams, 2004
Deciduous	• Efficient in terms of carbon gain in areas with long growing seasons, repaying the higher investment in foliage production. • Rapid photosynthesis leading to high CO_2 uptake. • Efficient where moisture and nutrient availability are high.	Monk, 1966; Gower and Richards, 1990; Ne'eman, 1993; Reich *et al.*, 1995; Ennos, 2001; Mediavilla and Escudero, 2003; Oleksyn *et al.*, 2003; Warren and Adams, 2004

As pointed out in Section 1.2.2, trees with the leaf habit best suited for the conditions under which they are growing will survive and thrive because they are the most cost effective in terms of carbon gain. Leaf life-span is the length of time a tree, angiosperm or conifer, keeps its leaves. There can be large natural variations between the length of time one genus of tree keeps its leaves compared to another. For instance, among the conifers *Larix* has a mean leaf life-span of 6 months (0.5 years, Reich *et al.*, 1999) whilst *Araucaria* has a mean leaf life-span of 108 months (9 years, Falcon-Lang, 2000a). Even within a species the leaf life-span can vary considerably. For example although *Araucaria araucana* has been reported to have a mean leaf life-span of 9 years (Falcon-Lang, 2000a) mean values in shaded and mountainous areas have been recorded as being as long as 26 or even 40 years (Lusk, 2001). Variations in leaf life-span in modern trees has been shown to correlate with genetics, physiology, growth, productivity, nutrient use and carbon allocation (Reich *et al.*, 1995; 1999; Ennos, 2001) and within all species of conifers observed leaf retention times seem to be greatest for individuals grown at higher elevations (Schweingruber, 1996; Oleksyn *et al.*, 2003). This is not just related to temperature but also factors such as soil fertility, length of growing season and drought and is reflected in the types and location of forests found across the globe (Table 1.3).

There are presently two zones of evergreen-dominated forests, one at low tropical latitudes and another at the Boreal high latitudes. This pattern has also been shown by outputs of cost-benefit analysis models based on the balance between photosynthetic rate (benefit) and producing and maintaining leaves (cost) (Reich *et al.*, 1995).

It is suggested that moisture and temperature combined are the limiting factors to the geographical distribution of plants. For example, in tundra areas water is held within the soil but because of the low temperatures freezing prevents it from being available for plant uptake (Krebs, 1972). Therefore many of the distributional effects attributed to temperature constraints may be combined with the water balance of plants (Krebs, 1972).

The determination of whether modern trees are deciduous or evergreen appears to be controlled by complex interactions between the genetics of the tree and the balance between the carbon costs (producing and maintaining leaves) and benefits (photosynthetic rate) of the leaf habit in the environment concerned. The genetics seem to be the dominant factor. If the tree is not genetically predisposed to grow in an environment it will not become established or if the climate changes to be unfavourable for the growth of that type of tree it will not survive.

1.4. Mid-Cretaceous polar climates: a review

The Cretaceous Period is considered to have been a time of transition, with temperatures rising from the early Cretaceous (Aptian-Albian) until the mid to early Late Cretaceous (Coniacian-early Campanian), after which the climate gradually cooled (Stanley, 1993; Herman, 1994; Dingle and Lavelle, 1998; Francis and Poole, 2002; Skelton, 2003). Thus the mid-Cretaceous was probably the warmest period of the Mesozoic with temperatures estimated to be 6-14°C higher than the present (Gerard and Dols, 1990; Barron *et al.* 1992; Valdes and Sellwood, 1992; Deconto *et al.*, 2000a, b). This section reviews the geological indicators of climate in order to establish what is already known about the habitats these forests grew in and what climatic stresses they may have had to endure. Computer climate models were then examined to explore their development and determine what they have included in the past in terms of vegetation, whether the fossil and geological evidence corresponds to their outputs and what effect incorporating vegetation has had on previous model results. This provides a context into which the current research can be placed and highlights the importance of incorporating realistic vegetation, verifiable using fossil assemblages, in computer climate models.

Table 1.3. Table showing the reasons for trees having evergreen or deciduous habits in different forest types and locations.

Leaf Habit	Forest Type/Location	Reason for Leaf Habit	References
Evergreen	Tropical Forests. Amazonia, central Africa, south east Asia	Little seasonal variation, high water availability making net photosynthesis possible in winter and replacement of canopy unprofitable.	Moore, 1982; Gower and Richards, 1990; Wang *et al.*, 1992; Ne'eman, 1993; Reich *et al.*, 1995; Ennos, 2001
	Temperate Forests. North America, Europe and Russia	Ability to withstand cold and drought.	
	Mediterranean Forests. Southern Europe, north Africa, north western USA, southern Australia	Due to summer drought and short damp winters on nutrient poor soils	
	Boreal Forests. North America, northern Europe, Russia, northern Asia	Nutrient conservation mechanism on nutrient-poor soils. Low embolism in cold winters and frost tolerant needle leaves. On northern slopes of mountains leaf life-span increases due to reduced potential for carbon gain and the cost of constructing thick leaves to resist cold.	
	Northern Montane Forests. North America, Europe	Low soil fertility, short growing season and drought	
Deciduous	Monsoon Forests. northern South America, Mexico, India, South East Asia	Pressures imposed by dry season prevent water loss at the cost of producing new foliage.	Gower *et al.*, 1987; Gower and Richards, 1990; Ne'eman, 1993; Ennos, 2001
	Mediterranean Forests. Israel	Deciduousness probably triggered by low temperature.	
	Temperate Broadleaved Forests. North America, Europe, east Asia, south east Australia, central South America	Due to long wet productive summers and mild winters with MAT's of 10°C.	
	Boreal Forests. North America, northern Europe, Russia, northern Asia	Larch trees are present in large stands in lowlands probably because they are extremely nutrient efficient and able to compete with evergreen conifers.	

1.4.1. Geological evidence

Geological evidence for past climates comes from various proxies. One source is the distribution of distinctive sedimentary rock types including tillites and dropstones (glacial deposits), coals and evaporites (humidity and aridity) (Skelton, 2003). Geologists can also use the distribution of climate-sensitive fossil plants and animals, and geochemistry to determine palaeotemperatures e.g. from oxygen isotope ratios (in calcite cements (Pirrie *et al.*, 1998) and fossiliferous remains of sea creatures e.g. belemnites, ammonites and foraminifera (Frakes and Francis, 1990; Ditchfield *et al.*, 1994; Dingle and Lavelle, 1998)) and foliar physiognomy, and rainfall (from clay mineral assemblages and foliar physiognomy) (Skelton, 2003).

A useful review of global geological data for the Cretaceous was published in 1995 by the Geological Institute of the Russian Academy of Science (Chumakov *et al.*, 1995; translated in Spicer and Skelton, 2003). This group combined palaeontological, sedimentological and mineralogical data to produce detailed biotic and palaeoclimatic patterns (Chumakov *et al.*, 1995) (Figure 1.4).

Figure 1.4 shows the Albian time slice and mid-Cretaceous palaeoclimate zonation. Although no palaeotemperatures are quantified this gives a good first impression of climatic conditions in high latitude regions, showing the Arctic region (dark green) as a Northern High-latitude Temperate Humid (NHT) zone with abundant coal-bearing beds and moderately thermophilic (warmth-loving) plants (Vakhrameev, 1991; Herman and Spicer, 1996). South of this is the Northern Mid-latitude Warm Humid zone (NMW) (light green). This climate zone is distinct from the NHT as it incorporates thermophilic insects and vegetation with abundant bauxites and kaolin weathering crusts or deposits (formed under warm and moist climates). The evidence of more arid conditions increase equatorwards with the presence of gypsum, anhydrite and other evaporite deposits. Bauxites and coals formed along the Equator suggest widespread equatorial moisture. This pattern is reflected in the Southern Hemisphere with a Southern High-latitude Temperate Humid (SHT) belt including evidence from moderately thermophilic vegetation, dinosaur remains and rare coals.

Northern Hemisphere terrestrial palaeoclimates

More detailed information about temperatures in the Northern Hemisphere during the Cretaceous has been obtained from various geological sources (Table 1.4).

During the Neocomian (earliest Cretaceous) the Northern Hemisphere Siberian Cretaceous region contained widespread Pinaceae species which displayed wide annual growth rings, indicating that the climate was humid, moderately warm and seasonal (Vakhrameev, 1991). Although the evidence suggests that warm temperatures continued throughout the Cretaceous, in

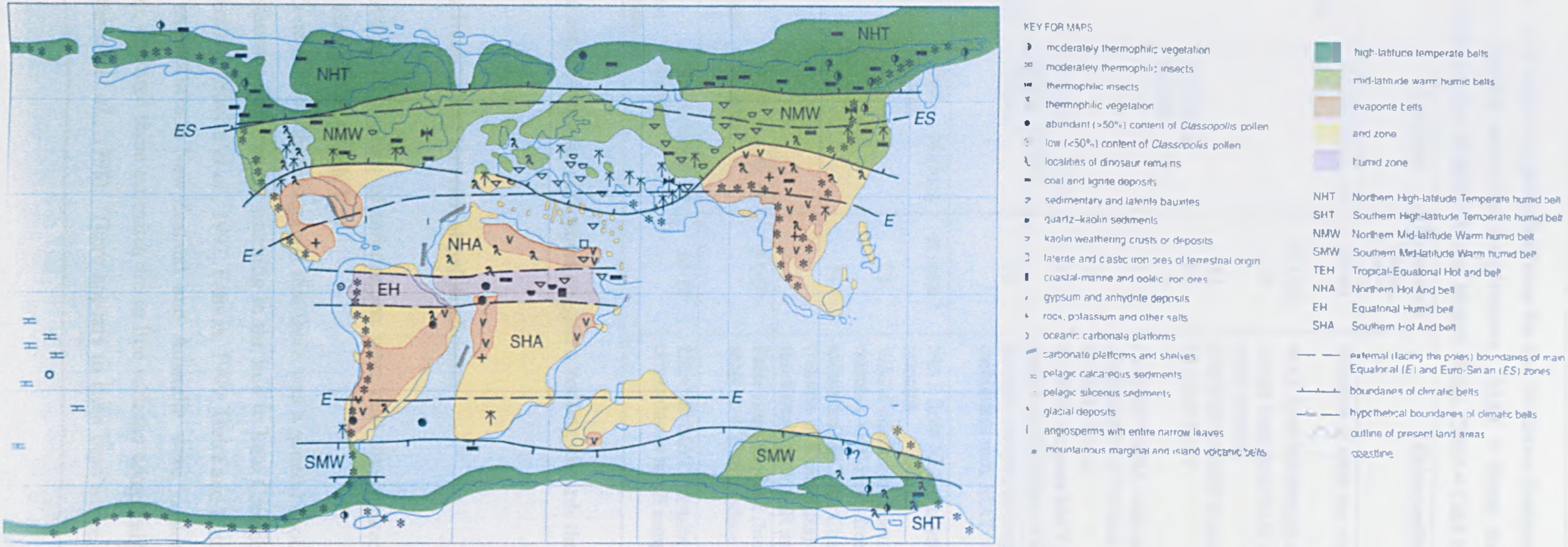


Figure 1.4. Global map of the Albian showing geological data that indicate palaeoclimate (Chumakov *et al.*, 1995; Translated in Spicer and Skelton, 2003).

Table 1.4. Table showing geological data for the Northern Hemisphere indicating mid- to Late Cretaceous estimated terrestrial temperatures. MAT = Mean Annual Temperature, NLR = Nearest Living Relative, WMM = Warm Month Mean, CMM = Cold Month Mean.

Age	Location	Estimated Temp. (°C)	Evidence/Notes	References
Albian-Cenomanian	North Slope of Alaska	10-40	Presence of wide tree rings	Spicer and Parrish, 1986 and 1990; Spicer *et al.*, 1994; Spicer, 2003
		10 (±3)	MAT from leaf margin analysis	
		-14	Lower limit from NLR analysis of turtle remains	
		-11	CMM lower limit from vegetation	
	Grebenka Russia	13	CLAMP MAT	Herman, 1994
		21	CLAMP WMM, with growing season precipitation of 741mm	
		6	CLAMP CMM	
	Central Vilui Basin, Russia	13	CLAMP analysis MAT with growing season precipitation of 827mm	
Cenomanian-Turonian boundary	Siberia	15	Isotopic analysis of biogenic carbonates min. MAT	Herman, 1994
Turonian-Coniacian	Axel Heiberg Island	at least 2	MAT from NLR analysis of turtle remains	Tarduno *et al.*, 1998
		25	WMM maximum from NLR of turtle remains,>100 frost- free days per year	
		14	minimum MAT for Champsosaurs (relative of Crocodiles) to remain functional from NLR anaylsis	
Campanian-Maastrichtian	North Slope of Alaska	5 (±3)	False rings in wood (biotic activity stops at 4 °C to produce these)	Spicer and Parrish, 1990; Spicer *et al.*, 1994
Late Campanian-Maastrichtian	North Slope of Alaska	10-12	CLAMP MAT, possibly subject to errors due to small sample set	Herman, 1994

the Siberian region biogenic carbonates suggest a cooling towards the end of the period (Herman, 1994).

Southern Hemisphere terrestrial palaeoclimates

Geological sources of information were also investigated for the Cretaceous of the Southern Hemisphere (Table 1.5).

Combined evidence suggests that there was a general cooling on Antarctica during the Early Cretaceous followed by warming in the mid to Late Cretaceous but dramatic cooling in the Maastrictian (Specht *et al.*, 1992; Francis, 1999; Dutra and Batten, 2000; Francis and Poole, 2002). Temperatures in New Zealand and Australia were cooler than for Antarctica during the Albian, although these estimates are in line with the comparable site on the North Slope of Alaska (Parrish *et al.*, 1998). There appears to have been a rise in mean annual temperature during the Campanian followed by a drop in temperatures during the Maastrichtian (Specht *et al.*, 1992).

Table 1.5. Table showing geological data for the Southern Hemisphere indicating estimated terrestrial temperatures. MAT = Mean Annual Temperature, NLR = Nearest Living Relative, WMM = Warm Month Mean, CMM = Cold Month Mean.

Age	Location	Estimated Temp.(°C)	Evidence/Notes	References
Aptian	Australia	10-30	NLR analysis of *Ceratus* (the lungfish), also precludes sea ice	Douglas and Williams, 1982
Albian	South Shetland & Alexander Islands	13-27	MAT from NLR analysis of *Hausmannia*	Cantrill, 1996; Francis, 1996; Francis and Poole, 2002
Albian-Cenomanian	New Zealand	10	MAT from CLAMP	Parrish *et al.*, 1998
Albian	Australia	5-8	MAT from vegetation	Spicer *et al.*, 1994
Coniacian	Antarctica	15-20	Leaf physiognomic analysis	Hayes, 2000
Coniacian-Early Campanian	Antarctica	16-23	MAT from tree ring analysis, leaf characters and geochemical indicators	Specht *et al.*, 1992; Francis, 1999; Dutra and Batten, 2000; Francis and Poole, 2002
Santonian	Otway Basin Australia	16.5	From plant community structure, species richness and productivity	Specht *et al.*, 1992
Campanian	Otway Basin Australia New Zealand	22 15.4	From plant community structure, species richness and productivity MAT from plant community structure, species richness and productivity	Specht *et al.*, 1992
Maastrichtian	New Zealand Australia	14.3 8-15	MAT from plant community structure, species richness and productivity MAT from plant cuticle analysis, with occasional frosts	Specht *et al.*, 1992; Francis 1996
Late Maastrichtian	Antarctica	7-11.7	MAT from tree ring analysis, leaf characters and geochemical indicators	Specht *et al.*, 1992; Francis, 1999; Dutra and Batten, 2000; Francis and Poole, 2002

1.4.2. Climate modelling

Climate models were developed as a means of understanding the mechanisms, interactions and feedbacks which control global climate (Beerling and Woodward, 2001). The earliest models were simple Energy Balance Models (EBM's) which had the advantage of using little computational power to represent the Earth as a single, non-dimensional entity, without representations of the dynamics of general circulation (Deconto *et al.*, 2000a). However with the advent of more powerful computer technology three-dimensional General Circulation

Models (GCM's) are now more widely used to produce more complex and detailed simulations of climate (Deconto *et al.*, 2000a).

The Cretaceous has been the focus of many palaeoclimate modeling projects since the 1980's to investigate the climate during warm greenhouse periods (Barron and Washington, 1982; 1984; Oglesby and Park, 1989; Gerard and Dols, 1990; Barron *et al.*, 1992; 1993; Schmidt and Mysak, 1996; Valdes *et al.*, 1996; Otto-Bliesner and Upchurch, 1997; Price *et al.*, 1998; Upchurch *et al.*, 1998; Beerling *et al.*, 1999; Deconto *et al.*, 2000).

Some of the first computer model results indicated that the change in continental configuration alone could have produced global warming of between 3 to 4.8°C (Barron and Washington, 1982; 1984). Barron and Washington's (1982) National Centre for Atmospheric Research (NCAR) General Circulation Model (GCM) predicted that the Northern Hemisphere polar temperatures were 5-10°C higher than at present and Antarctica just a few degrees higher, with Cretaceous continental geography. However with minimum allowed sea surface temperatures set at 10°C, the increased polar ocean temperatures did not result in warm continental interiors. The model results indicated that some areas of Antarctica were below freezing all year round, with only a narrow coastal zone of warmth in July of ~6°C. This suggests that the lack of a coupled ocean (therefore no stored heat) and use of mean annual insolation in early models were unlikely to give a realistic estimate of climate and were inadequate for comparison with geological observations (Barron *et al.*, 1992).

Although continental configuration has often been cited as a possible cause for the palaeoclimate warming, Hay *et al.* (1990) used the NCAR Community Climate Model GCM to show that a single continent at the tropics was substantially warmer (~5°C) than when the continents were symmetrically distributed (extending from 45°N and S to the poles). This suggests that as the continents were splitting apart and moving towards their modern configuration during the Cretaceous, the interiors should have been cooling if continental configuration was the only factor involved.

Gerard and Dols (1990) used a simple Energy Balance Model (EBM) with the inclusion of the long term carbon cycle to investigate several factors that may have been responsible for Cretaceous warming, citing CO_2 levels as being the major contributing factor. The change in continental palaeogeography raised the global surface temperature by only 1.6°C compared to the present, but when combined with the CO_2 cycle, the increase was 3.3°C. Sea floor spreading rates are thought to have been higher during the Cretaceous, increasing the levels of CO_2 degassed by volcanoes (Crowley, 1993). Therefore the level of volcanism was increased by 1.8x the present value in the model and the temperature difference then increased to 7.3°C. The warming predicted was within palaeoindicator limits, probably due to the combined factors of the different distribution of the continents, higher tectonic activity and possibly increased productivity of vegetation in the CO_2 rich atmosphere lowering albedo.

In 1992 Barron *et al*. used an extensively modified version of the GCM (GENESIS version 1.02), which incorporates basic vegetation types (mixed trees and ground cover) and a six-layer soil model (medium texture and colour). It also incorporated a mixed layer ocean (50m slab) in which heat transport and seasonal insolation values were included. Cretaceous continental configuration produced a slight global cooling of 0.2°C, in direct conflict with earlier models that produced warming. Antarctica showed a small increase in snow cover (trace amounts in winter) and a central region temperature increase, as much as 27°C higher than present in the austral summer (Figure 1.5). Sea-ice was also produced by the model in surrounding embayments and seaways. In northern high-latitudes Alaska had permanent snow cover and the North Pole had trace snow cover even in summer.

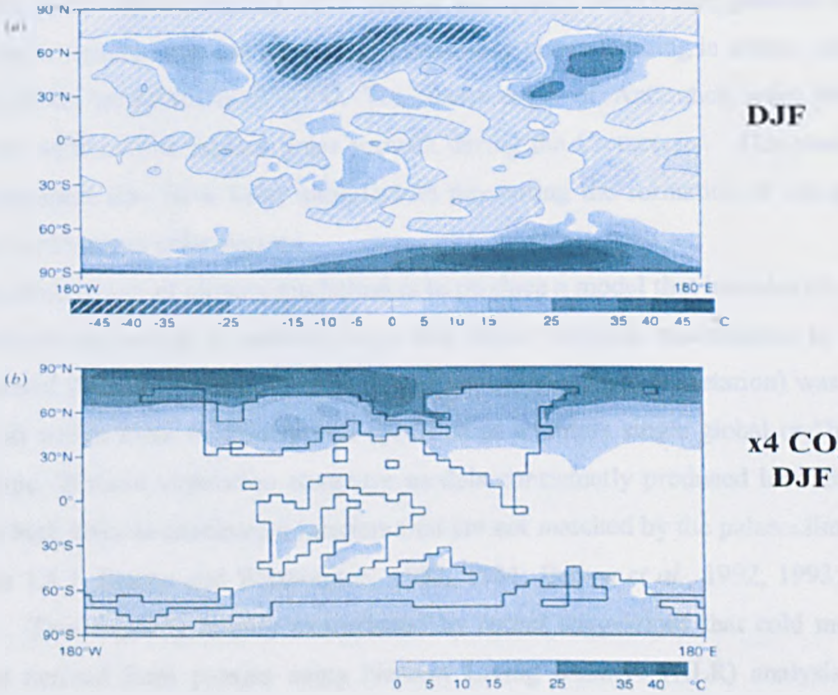


Figure 1.5. Difference between Barron *et al* (1992) model experiments for the Northern Hemisphere winter period (5°C contour interval); (*a*) Cretaceous minus Present day indicating Antarctica was warmer than present austral summer but the Arctic was cooler in the boreal winter (*b*) Cretaceous 4 x CO$_2$ minus Cretaceous; DJF = December, January, February averages therefore indicating the effect of the rise in CO$_2$ (Barron *et al.*, 1992).

The same model (Barron *et al.*, 1992) was then used with CO$_2$ levels set at 4 times present values (1,360ppm), which produced a global average surface temperature increase of 5.5°C. Mid latitude continental regions showed warming of 5.25°C in winter and the tropics a small but significant warming. Interior Antarctica had permanent snow cover with coastal regions showing the greatest changes, warming by >30°C in winter and ~9°C in summer. The

Arctic was nearly above freezing in winter, with the central region having temperatures of -5 to -10°C, whilst in summer the temperatures were near freezing but largely ice-free. This indicates that increased CO_2 had a much greater impact on warming than any other forcing factor, with the maximum temperature increase occurring at high latitudes, although interior continental areas were still too cold in winter to match the geological data.

Crowley (1993) suggested that ocean heat transport may have also been an important factor for Cretaceous climate warmth. Barron *et al.* (1993) used the GENESIS (version 1.02) GCM to test changes in ocean heat transport using CO_2 levels at present values and incorporated the same simple land surface model as Barron and Washington (1982). They found that with Cretaceous continental geography and ocean heat transport set to represent modern values, a global cooling of 0.2°C occurred. When the ocean heat transport was doubled the tropics became cooler, polar regions warmed and a weaker meridional temperature gradient developed. The interior polar regions were not ice-free, nor were they above freezing in winter, with Siberia experiencing winter temperatures of -47°C. The coastal areas of Antarctica were warmer but this is still not sufficient to explain polar warmth during the Cretaceous. However, doubled ocean heat transport may have been important in preventing the formation of ice around the edges of the continents in polar regions.

The ultimate aim of climate modelling is to produce a model that includes all aspects of the Earth system interacting in realistic ways that allow feedback mechanisms to affect the climate produced (Deconto *et al.*, 2000b). In the past the biosphere (vegetation) was either not included at all within these models or was specified as a simple single global or "best guess" vegetation type. Without vegetation computer models consistently produced low temperatures (freezing) in high-latitude continental interiors that are not matched by the palaeoclimatic proxy data (Section 1.4.1, Barron and Washington, 1982, 1984; Barron *et al.*, 1992; 1993; Valdes *et al.*, 1996). This disparity is only exacerbated by recent suggestions that cold month mean temperatures derived from proxies using Nearest Living Relative (NLR) analysis of plants should be raised by 1.5 to 3°C (Royer *et al.*, 2002). In addition, the early vegetation models were equilibrium or static models where disturbance and vegetation dynamics were not included, limiting their value when considering transient changes in climate and the response of the vegetation to these changes (Beerling and Woodward, 2001). It has been demonstrated that biosphere-atmosphere interactions can affect palaeoclimate by changing albedo and atmospheric moisture associated with changing the distributions of evergreen, deciduous and tundra ecosystems, therefore the inclusion of realistic vegetation may be vitally important (Bonan and Thompson, 1992; Otto-Bliesner and Upchurch, 1997; Deconto *et al.*, 2000b). It has also been suggested that increasing the areal extent of high-latitude forests has temperature effects comparable to doubling orbital forcing (Foley *et al.*, 1994) and may have initiated climate feedbacks that extended to lower latitudes (Bonan and Thompson, 1992).

Upchurch *et al.* (1998) suggested that the inclusion of realistic distribution of palaeovegetation produced the best agreement between simulations and the geological record of palaeoclimate. They used the NCAR (GENESIS v1.02) model, including submodels of atmosphere, ocean and land surface over high latitude land. They incorporated a two layer model of vegetation with forests and shrubs in the upper layer and grass and bare soil in the lower layer. Vegetation biomes were prescribed based on best estimates (BESTGUESS) of the types of vegetation present from lithological and fossil evidence, including deciduous forests on Antarctica and northern high latitude sites (Figure 1.6). In areas where data were absent from the geological record outputs of a previous model simulation, EVERGREEN TREE-OHT, that prescribed broad-leaved evergreen trees (tropical rainforest) over all land surfaces at a fractional coverage of 98% with tripled ocean heat transport, were used to prescribe the vegetation.

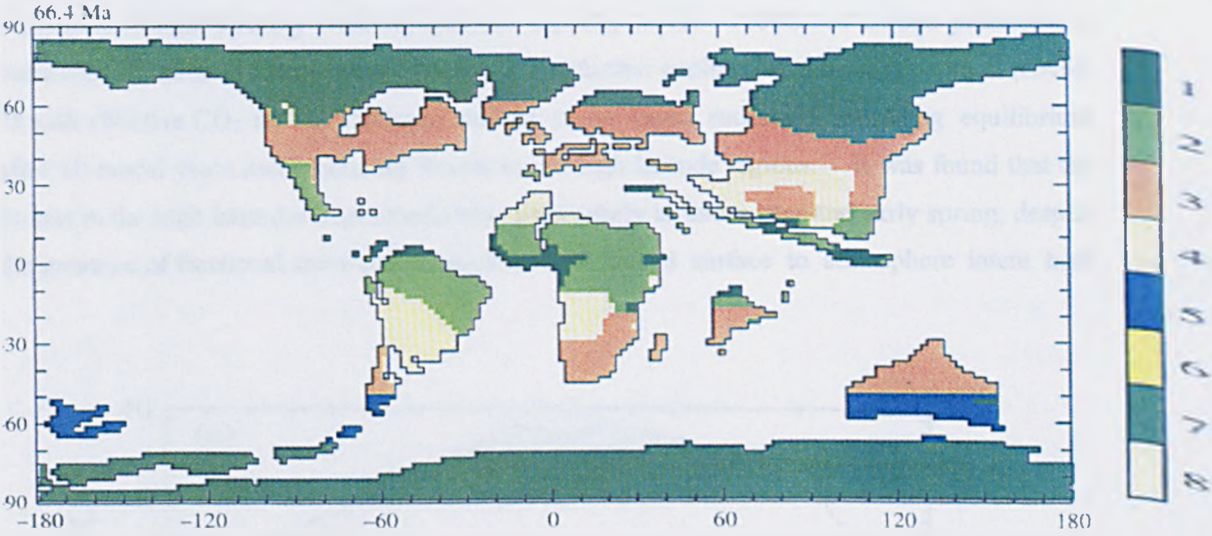


Figure 1.6. BESTGUESS estimate of Maastrichtian vegetation. Bare soil was used to code for cold deserts with extremely low floristic diversity. Subtropical woodlands have indicators of above-freezing winters such as palms. No Maastrictian equivalent of Mediterranean woodlands and chaparral is used in BESTGUESS simulations, although some model simulations predict the occurrence of such vegetation in restricted areas. Key 1 Tropical rainforest; 2 Tropical semi-deciduous forest; 3 Subtropical broad-leaved evergreen forest and woodland; 4 Desert and Semi-desert; 5 temperate evergreen broad-leaved and coniferous forest; 6 Tropical savanna (not used here); 7 Polar deciduous forest; 8 Bare soil (Upchurch *et al.*, 1998).

Vegetation was allowed to respond to climate physiologically but not by changing Leaf Area Index (LAI), fractional cover or other structural attributes, allowing first order climatic effects of vegetation to be observed. This resulted in net warming of the land surface year round of 2.2°C with realistic Maastrichtian vegetation. Ice-free conditions were also maintained and adjacent high latitude oceans were warmed by as much as 12°C (Figure 1.7) (Upchurch *et al.*, 1998).

This early research on the effect of including vegetation in climate models was followed by that of Deconto *et al.* in 2000(a) who used an updated version of GENESIS (v2.0) including a non-dynamical slab ocean model and multilayer models for soil, snow and sea ice to model Campanian climates. The vegetation represented a two layer canopy and used a new predictive Equilibrum Vegetation Ecology (EVE) model to allow the biomes to be predicted (rather than prescribed as in previous models) and the effects of the biomes allowed to feedback to the atmosphere. In an initial simulation (CASE 1) with CO_2 set at an effective concentration of 1230ppm the climate-vegetation never reached equilibrium with a tundra-cooling feedback, which led to collapse of the evergreen-dominated forests that initially formed at high latitudes. This did however highlight the huge effect that vegetation can have, showing that the tundra, analogous to peat-forming wetland, had the capacity to fix ~1100Gt of carbon producing a transient reduction in atmospheric CO_2 leading to further cooling. A second simulation (CASE 2) with effective CO_2 set at 1500ppm proved to be more successful, reaching equilibrium after 10 model years and producing forests in the high latitude regions. It was found that the forests in the high latitudes kept albedo low, particularly in late winter and early spring, despite the presence of fractional snow cover which, in turn, raised surface to atmosphere latent heat

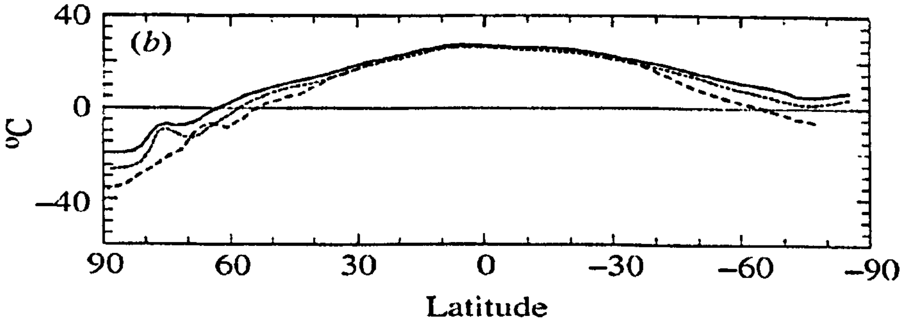


Figure 1.7. Zonally-averaged surface temperature (at a height of 2m) simulated by the GENESIS climate model in January for the Maastrichtian. (a) Land (b) Ocean. Solid line is the BESTGUESS simulation (including vegetation) and the dotted line is the BARESOIL simulation (with no vegetation). The dashed line is the present-day control simulation (Upchurch *et al.*, 1998).

flux by ~25W m^{-2} indicating the importance of vegetation in climate feedbacks. The forests also added moisture to the atmosphere, providing water vapor (a greenhouse gas) and increasing temperatures in the high latitude regions to produce a much better match to the proxy data than had been previously produced.

The development of these new Dynamic Global Vegetation Models (DGVMs) simulating the life, death and interactions of individual plants within a larger area of vegetation (e.g. a forest) means greater accuracy in models of forest-climate interactions with the overlying atmosphere (Deconto *et al.*, 2000b; Beerling and Woodward, 2001). The increased resolution possible within the latest computer models should allow better representation of terrestrial ecosystems on a regional scale, allowing the detailed, dynamic vegetation to be included (Deconto *et al.*, 2000b).

The current research in this project aims to enable the inclusion of a predictive vegetation model providing detailed, accurate vegetation types that can interact with all other elements (e.g. atmosphere, topography, oceans) of climate models. Leaf habit and leaf life-span have already been shown in Section 1.2.2 to be important strategies for the survival of high latitude vegetation (Beerling, 1994; Woodward, 1995; Beerling and Osborne, 2002) and in feedbacks to climate (Deconto *et al.*, 2000b) but have not previously been used as a dominant, accurately represented, parameter within vegetation models. Leaf life-spans are therefore used as input parameters in the prediction of vegetation distribution within the University of Sheffield Conifer Model (USCM) developed in this project to provide the most accurate representation of the high latitude Cretaceous forests produced to date. In order to verify the accuracy of the USCM, before coupling to climate models, fossil wood was analysed within this part of the project in order to provide a proxy for the model. The leaf habit and leaf life-spans of fossil conifer specimens from several high latitude locations were therefore determined and the results compared to the USCM outputs. It is hoped, based on the encouraging results of Upchurch *et al.* (1998) and Deconto *et al.* (2000a), that the USCM will provide a solution to the problem of cold high latitude continental interiors without warming the mid latitudes.

Chapter 2 Mid-Cretaceous polar conifers: fossil wood identification and forest composition

2.1. Introduction

In Chapter 1 the examination of previously published work on the high latitudes demonstrated that forests were present in the polar regions during the mid-Cretaceous. A major component of these forests were conifers (see Chapter 1, Section 1.2.1). On Alexander Island, Antarctica, for example, 100% of the wood collected (68 samples) from the Triton Point Formation by Falcon-Lang and Cantrill (2001a) represented conifers, of which 13% were Araucariaceae, 85% Podocarpaceae and 2% Taxodiaceae. As in Falcon-Lang and Cantrill's (2001a) study, the conifers are often represented as fossilized wood, the structural features of which can provide an important means of identifying the types of conifers present to allow the reconstruction of the forest diversity (Phillips, 1941; Kraüsel, 1949; Barefoot and Hankins, 1982). Not only can the wood hold information in its anatomical structure for identification purposes but, the growth rings are also an important source of information about the palaeoclimate. The internal structure of the growth rings can now be used to determine the leaf habit and leaf life-span of the tree, as will be demonstrated in Chapters 3 and 4.

This chapter presents detailed descriptions of the fossil conifer wood used in this study and their identification in order to determine the types of trees present and gain an indication of the composition and diversity of the conifer-dominated forests found in the high latitude regions during the mid-Cretaceous.

The chapter begins by introducing the reader to basic conifer wood anatomy and some of the specific features used in the identification of the specimens to form-genera level (Section 2.2). Preservation styles are discussed in Section 2.3 because the mode of preservation can distort features within the wood structure and is therefore important to consider if the samples are to be validly compared to the results of previous research projects. The material used and the specific methods of identification used in this research project are presented in Section 2.4. The geological setting of the sample locations, descriptions and identification of the fossil conifer wood and climatic inferences from comparison to modern wood are presented for both the northern and southern hemispheres in Sections 2.5 and 2.6. Finally, a summary of the findings of this chapter are given in Section 2.7.

2.2. Wood anatomy

The combination of features present or absent within a conifer wood specimen allow identification of the wood type that it represents (Phillips, 1941; Barefoot and Hankins, 1982). Keys that use wood anatomy originated within the timber production industry to allow the identification of commercially-important timber-producing trees but these often failed to account for natural variation within the trees and certainly did not incorporate fossil wood (Phillips, 1941; Greguss, 1955). Very few attempts have been made to produce wood anatomy keys for fossil samples and only two were found to be suitable for this study: Kraüsel's 1949 key specifically for fossil conifer wood and Barefoot and Hankins's 1982 key for the identification of modern and Tertiary woods. Therefore within palaeobotanical studies it is necessary to use a combination of all available keys, as well as previous detailed descriptions of fossil wood, in order to determine which features are preserved in fossil wood and are necessary for identification and comparison to previously published identifications. The features used to identify the specimens within this thesis are shown in Figure 2.1 and a glossary of the technical wood anatomy terms used is presented in Table 2.1.

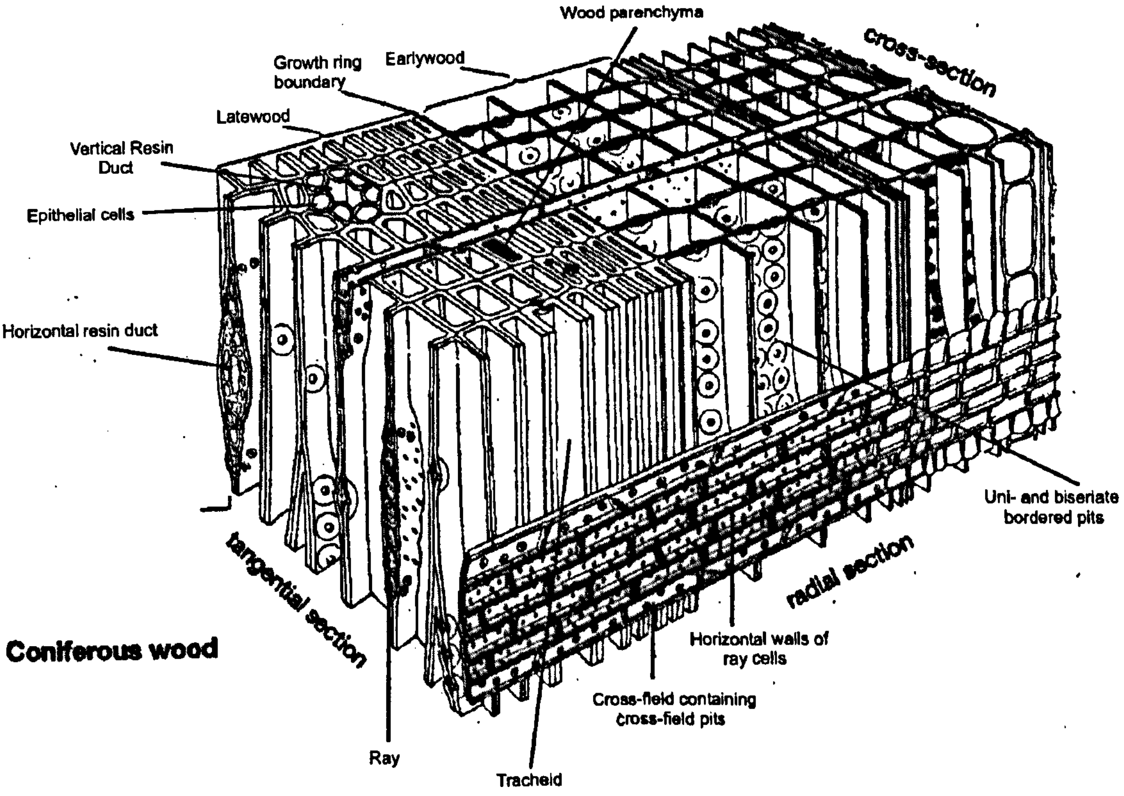


Figure 2.1. Diagrammatic representation of the key features present in conifer wood structure used for identification purposes in this thesis (modified from Schweingruber, 1996).

Table 2.1. Glossary of terms used to identify living conifer wood (modified from Greguss, 1955; Wilson and White, 1986)

Feature	Notes/Description
Bordered Pit	Observed in radial section. Thickening of the secondary wall giving rise to recesses with circular, rod-shaped, elliptic, or slit-like apertures in the middle. Allow water and nutrients to flow from one tracheid to the next.
Crassulae (Bars of Sanio)	Observed in radial section. Thickened intercellular layers above and below bordered pits.
Cross-field	Observed in radial section. Area of contact between an axial tracheid and a ray parenchyma cell, marked out by the axial walls of the tracheid and the horizontal walls of the parenchyma cell.
Cross-field pits	Observed in radial section. See below and Figure 2.2.
Earlywood	Observed in transverse and radial section. Wide inner portion of growth rings formed at the beginning of the growing season. Large, thin-walled cells.
Epithelial cells	Observed in transverse, radial and/or tangential section. The thick- or thin walled cells which line the resin ducts.
Growth rings	Observed in transverse section. Concentric layers representing seasonal growth increments.
Intercellular space	Observed in transverse section. A cavity resulting from the interwall space in a group of cells not being compactly arranged but more or less free from one another.
Latewood	Observed in transverse section. The outer portion of the growth ring consisting of elements produced during the latter part of the growing season. Small, thick-walled cells.
Longitudinal tracheids	Observed in tangential or radial section. Longitudinal vascular elements with walls displaying bordered pits and occasionally spiral thickenings. Usually prismatic or cylindrical in shape. Tubes connecting the various parts of the tree.
Parenchyma cells	Observed in transverse, tangential or radial section. Cells commonly with thin, simple-pitted, occasionally quite smooth walls. Longitudinal/wood parenchyma extend in the wood parallel with the axis of the stem and ray parenchyma at right angles to the stem. In transverse section longitudinal parenchyma cells are solitary, scattered, at times in rows or forming clusters. Ray parenchyma is seen as the horizontal walls of cross-field areas.
Rays	Observed in tangential section. Strands of one or more layers of cells, commonly parenchyma cells. Serve to transport food. Can be uni-, bi-or multiseriate around resin ducts.

Continued .....

Table 2.1. continued.

Feature	Notes/Description
Ray tracheids	Observed in radial section. In some genera the upper and lower margins of cross field areas are formed of ray cells; thin, radially elongated cells that can be smooth or have tooth like thickenings.
Resin ducts	Observed in all sections. Tubular cavities sheathed by resin-excreting cells.
Spiral thickenings	Observed in radial or tangential section. Delicate ridge-like thickenings in the form of a spiral.
Tracheids	Very long unicellular wood element extending parallel to the long axis of the organ with bordered pits and occasionally spirals. Allows water conduction and mechanical support.

Cross-field pits are apertures within the cross-field areas that allow the conduction of water and are an important feature in the identification of living coniferous woods. Where preservation allowed the cross-field pits were identified using the key shown in Figure 2.2. It should be noted that cupressoid and podocarpoid pits are very similar, as are dacrydioid and glyptostroboid pits, and should not be relied upon as the main feature for identification.

Although the botanical connection between fossil form-genera and modern taxa is not known, distinctive features within each fossil form-genus were characteristic enough to allow comparison to living taxa with a high degree of certainty. Where the geographic distribution of modern taxa is discussed for comparison it should be noted that these modern taxa have been affected by various events over geological time e.g. Quaternary glaciation where in some cases forests were overrun by ice leaving small isolated relict populations (e.g. *Cedrus*; Vidakovic, 1991), the change in the vegetation composition due to the radiation of angiosperms by the end of the Cretaceous, the distribution today in the polar regions limited by low temperature. Therefore this Nearest Living Relative approach is problematical and can only be used with caution.

2.3. Preservation

Understanding of the preservation style of wood is necessary to ensure validity, comparability and repeatability of results for studies involving palaeoclimate analysis and identification (Scott and Collinson, 2003). Therefore all fossil samples used in this thesis were examined to determine the nature of the preservation.

It is suggested that wood, particularly *in situ* stumps, provide a ready conduit for meteoric groundwater and for formation water released during compaction, allowing minerals

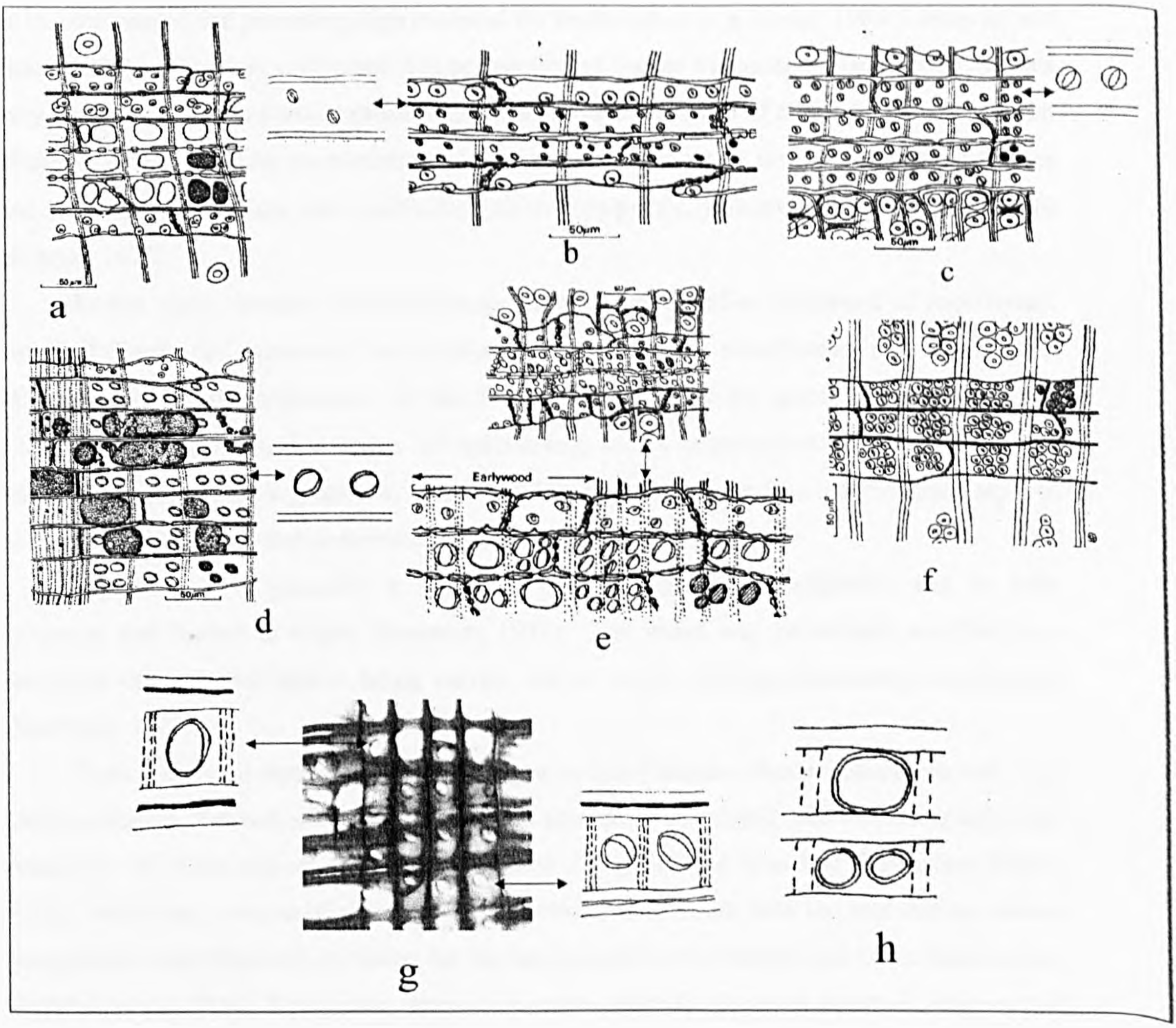


Figure 2.2. Variation in cross-field pits. a) 1-3 large, simple pits including window-like or primary pits (*Pinus*, *Phyllocladus*, *Dacrydium* and *Sciadopitys*). Illustration of *Pinus monticola* Dougl.ex D.Don. b) Piceoid pits having narrow and often slightly extended apertures (*Picea*, *Larix*, *Pseudotsuga* and *Cephalotaxus*). Illustration of *Larix laricina* (Du Roi) K.Koch. c) Cupressoid pits with aperture entirely within the limits of the border and rather narrower than the border (Cupressaceae (except *Thuja*), *Taiwania*, *Taxodium*, Araucariaceae, *Podocarpus* spp, *Taxus* spp and some *Cedrus* and *Tsuga*. Illustration of *Torreya californica* Torr. d) Taxodioid pits with large, ovoid to circular apertures wider than the border (*Pinus*, Taxodiaceae, *Abies*, *Cedrus*, many Podocarpaceae and *Thuja*. Illustration of *Sequoia sempervirens* (D.Don) Engl. e) Pinoid pits, fairly small, simple or with narrow borders and often irregular and variable in shape (*Pinus*). Illustration of *Pinus cembroides* Zucc. (top) and *Sula* (group of *Pinus*, bottom). f) Araucarioid pits, character is cupressoid but the arrangement is distinctive usually three or more pits wide and two to three pits high. Illustration of *Araucaria cunninghamii* D.Don. (Barefoot and Hankins, 1982). g) *Podocarpus imbricatus* Blume. x600 showing podocarpoid pits to the right with angle of aperture between vertical and oblique (45°) and dacrydioid to the left with very narrow or no border (Barefoot and Hankins, 1982). h) *Taxodioxylon drumhellerense* very narrow bordered glyptostroboid pits (reconstructed from Ramanujam and Stewart, 1969).

to be precipitated and providing high potential for fossilization (e.g. Hesse, 1989; Lindqvist and Isaac, 1991). The early infiltration and permeation of tissues by mineral-charged water in this way, known as cellular permineralization, produces the most detail of all modes of preservation (Schopf, 1975). Cellular perminerlization is the most informative for palaeobotanical studies and includes silicification and calcification as well as pyritic, limonitic and phosphatic forms (Schopf, 1975).

In this study Northern Hemisphere specimens were silicified (Svalbard 12 specimens), calcified (Svalbard 1 specimen) or displayed a combination of silicification and calcification (Canadian Arctic 10 specimens). In the Southern Hemisphere the specimens were silicified (Australia 6 specimens, Antarctica 19 specimens), had a combination of silicification and calcification (Australia 1 specimen, Antarctica 17 specimens) or had an indeterminate style of preservation (Australia and Antarctica 1 specimen each).

Silicification is generally a terrestrial process where as calcification can be both terrestrial and marine in origin (Buurman, 1972). The wood may be initially silicified in a terrestrial environment before being carried out to sea to undergo secondary calcification (Buurman, 1972).

During the mid-Aptian rift activity began in the Canadian Arctic (Ellesmere and Axel Heiberg Islands; Patchett *et al.*, 2004). Basaltic volcanism associated with the rifting led to the deposition of thick coarse non-marine deposits thoughout the Sverdrup Basin (see Figure 2.6.b), providing a source of silica for the preservation of wood, with the mid-Aptian marine transgression that followed providing the marine sediments to produced calcite for calcification (Patchett *et al.*, 2004). Some plate tectonic reconstructions for the early Mesozoic suggest that Svalbard and Ellesmere Island were very close to each other with Svalbard forming an eastern extention to the Sverdrup Basin (Worsley *et al.*, 1986). The stable platform regimes of Svalbard were disrupted in the Early Cretaceous by significant faulting that was accompanied by large scale magmatic activity, particularly in eastern areas that could have been the main source of silica for wood preservation (Worsley *et al.*, 1986). In the south of the island there is a gradual transition from prodelta shales through delta front to fluvial dominated sequences but silica may also be liberated in fluvial settings by weathering and/or soil formation in the absence of volcanics (Buurman, 1972; Worsley *et al.*, 1986; Akahane *et al.*, 2004). Overlying the Svalbard sediments and partly laterally equivalent are marine sandstones, siltstones and shales suggesting a relatively open marine shelf setting that would have provided the carbonate for the formation of the concreations in which the wood was found as well as providing a preservation medium (Worsley *et al.*, 1986).

In the Southern Hemisphere during the Cretaceous the northern Antarctic Peninsula formed fore-arc and magmatic-arc terrains with the James Ross Island region evolving as a back-arc basin due to subduction of the Phoenix Plate. This would have provided the source of silica from volcanic deposits and carbonate from calcite-cemented sandstones in the marine basin setting (Elliot, 1988, see also Section 2.5.1 Geological setting).

Jefferson (1987) studied the silicification of conifer wood from the fore-arc basin on Alexander Island, Antarctica. He found that silicification depended on the early breakdown of volcanic components from the eroded Jurassic deposits in the volcanic arc to the east, abundant airfall detritus, and the mobility of the resultant mineralizing fluids. The most likely silicifying agent on Alexander Island is molecular silicic acid (H_4SiO_4), the form released from devitrification of volcanic glass and diagenesis of clay minerals (Jefferson, 1987). The potential for hydrogen bonding between silicic acid and holocellulosic complexes of the cell wall lead to exact replication of cell wall structure. However on Alexander Island it was proposed that the cell walls were permineralised (an impregnation and void filling process), leaving much of the original organic material there, rather than a replacement processes, the same as proposed for several other sites e.g. the Petrified Forest National Park in Arizona, USA (Schopf, 1975; Jefferson, 1987; Hesse, 1989; Akahane *et al.*, 2004). There then appears to have been further stages of chalcedony, cryptocrystalline quartz, euhedral-subhedral quartz (SiO_2) crystals and/or apatite and cellophane recrystallisation within cell lumen (Jefferson, 1982; Lindqvist and Isaac, 1991). It therefore appears from these previous studies that if well preserved rings (with non-ruptured or no excessively deformed cells) are used for analysis and the preservation type is consistent across the whole ring the cells may be used for analysis without incurring errors due to deformation during preservation by permineralising fluids.

Some wood has been found in calcareous concretions in the Eromanga Basin, Australia, suggesting that the marine setting provided an abundant source of calcite (Frakes and Francis, 1990, see also Section 2.6.1 Geological setting). Petrographic and chemical studies indicate a wide range of carbonate mineralization styles can occur dependent on the depositional and diagenetic environment and has been reported previously from Cretaceous woods (Higgins, 1960). Scott and Collinson (2003) discussed the nature of petrification in calcified wood and showed that if the preservation style is consistent across the rings with no rupturing or shrinkage observed, the cells may be used for analysis without incurring errors due to preservation.

Care was taken in selecting the specimens for study to ensure that only areas of the specimens where there was no rupturing or deformation of cells present were used for identification and where it appeared that the preservation style was consistent across the whole area.

2.4. Materials and methods of identification for this project

A total of fifty nine specimens of fossil conifer wood were examined for this project (see Appendix B, Table B1.1). These specimens included 13 from Svalbard (Spitsbergen), 10 from the Canadian Arctic (Ellesmere and Axel Heiberg islands), 8 from central Australia and 28 for Antarctica (James Ross Island). All of these samples are from the collection of Jane Francis and are held in the School of Earth and Environment at the University of Leeds, UK. Nine further specimens from Alexander Island, Antarctica, were examined from the collection held at the British Antarctic Survey, Cambridge, UK. Fossil wood of mid-Cretaceous age is rare on Antarctica, only occurring on Alexander Island therefore the samples were obtained from the British Antarctic Survery in order to have comparable aged samples to the other sites. The wood examined from the collection from James Ross Island was younger than the other specimens examined, being Turonian to Coniacian in age, however they were included in this study to ensure sufficient data from Antarctica.

Thin sections of the specimens had previously been prepared in tangential, radial and transverse orientations (Figure 2.3). All of the fossil specimens were cut to a standard thickness of ~30 μm.

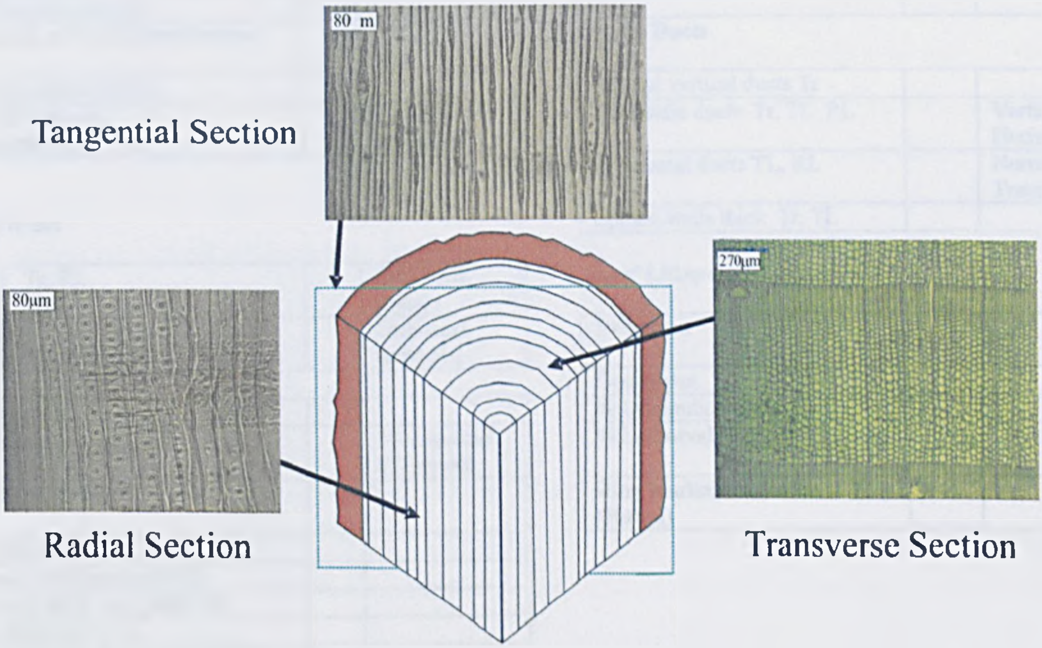


Figure 2.3. Diagrammatic representation of the orientation of thin sections taken from wood samples. The microscopic images are all of extant *Picea contorta.*

The combination of features present or absent within a conifer wood specimen allows identification to species level in some modern conifer genera (Phillips, 1941; Barefoot and Hankins, 1982). However the identifying features for species level identification are often very subtle and almost impossible to distinguish even in modern specimens (Phillips, 1941). Therefore, the fossil conifer wood in this project was only identified to form-genus level.

In order to identify the wood types present a wood identification sheet was prepared for each specimen, listing 37 microscopic structural characteristics that may or may not be present within fossil conifer wood (Figure 2.4).

WOOD IDENTIFICATION KEY FEATURE SHEET

Sample Number: **Location:** **Age:**

General

G.rings indistinct Tr		
Latewood Conspicuous Tr		Must cover ¼ of gr.ring

Tracheids

Pits alternate RL		
Pits >1-seriate, Opp. RL		
Uniseriate (%) RL		
Biseriate (%) RL		
Triseriate (%) RL		
Septa abundant		
% of Touching pits RL		
Pits spaced or >1 pit diameter apart RL		
Spirals in earlywood RL		
Dark cell contents Note distribution Tr		Ray Trach. Paren.

Parenchyma

Present Tr, RL		Latewood Zonate
Abundant Note Distribution Tr		Latewood Scattered

Rays

Ray tracheids RL		
R.T dentate (average) RL		17+ave.dent 17-smooth
R.T. reticulate RL		
R.P. horiz.walls thin RL		
R.P. horiz. walls unpitted RL		
R.P. horiz walls well pitted RL		
Ray height (cells) TL		
Rays cells often have resin spools		

Cross-field pits

Number of pits (pit size micrometers) RL		
Cross field pits circular (oopores) RL		
Cross field pits elliptical (oculipores) RL		
Cross field pits hexagonal RL		
Piceoid RL		
Cupressoid RL		
Taxodioid RL		
1-6 Pinoid RL		
Araucaroid RL		
Dacrydioid RL		
Podocarpoid RL		

Resin Ducts

Normal vertical ducts Tr		
Traumatic ducts Tr, TL, RL		Vertical Horizontal
Horizontal ducts TL, RL		Normal Traumatic
Epith.c.walls thick Tr, TL		

Leaf Lifespan

Evergreen		
Deciduous		
% Diminution (Range)		
% Latewood (Range)		
Ring Markedness Index (Range)		

Wood Identification:

Figure 2.4. Wood identification key feature sheet for use in the identification of fossil wood. Tr = Transverse Section, RL = Radial Longitudinal Section and TL = Tangential Longitudinal Section.

The sheet was compiled by identifying the features in modern wood keys that could be applied to fossil wood (Phillips, 1941; Greguss, 1955; Barefoot and Hankins, 1982), the key features from fossil wood schemes (Kraüsel, 1949; Barefoot and Hankins, 1982) and the features most commonly used in previous fossil wood identification papers (e.g.Ramanujam and Stewart, 1969; Greguss, 1970; Ramanujam, 1971; Roy, 1972; Meijer, 2000; Poole and Cantrill, 2001; Poole *et al.*, 2001, Falcon-Lang and Cantrill, 2001b) in order to be able to compare the samples used here with previously published descriptions. The specimens were identified by comparison with fossil wood schemes (Kraüsel, 1949; Barefoot and Hankins, 1982). This initial identification was then compared to previously published descriptions of the form-genus in question to verify the identification (Appendix B, Table B1.2). If initial identification was not possible or clear using the fossil schemes, modern conifer wood keys were used and the identification verified using a database of previously published conifer fossil wood descriptions (Appendix B, Table B1.2).

In order for comparisons to be made between the specimens used here and previous descriptions and to aid identification, it was necessary to calculate the percentage of certain features present within the wood structure. For example, bordered pits within a single specimen may be uniseriate, biseriate, triseriate and the percentage of each type can then help to identify the specimen to form-genus level. Therefore this quantitative data is given in a table within the description of each form-genus where more than one specimen was examined. Where only one specimen was examined the data is given within brackets within the text.

Chapman (1994) indicated that there are important differences in wood structure depending on from which part of the tree the sample came (branches or trunks and near the center or outer rings of the trunk). Therefore, in order to account for variations in structure it was necessary to determine whether the specimens were derived from branches or large trunks. Reaction/compression wood forms on the underside of conifer branches. This is deformation due to the strain of the branch supporting its own weight and can be used to identify branch wood in fossil material (Figure 2.5). Compression wood is expressed as rings that are asymmetrical, with the reaction wood making rings appear wider than in the normal wood and therefore producing an uneven width within any individual ring of the section (Figure 2.5).

In order to estimate where the wood came from within a trunk or branch a template was used showing concentric circles of 1cm spacing. The transverse thin sections were placed over the template on a light box and the growth rings aligned with the circles. If the specimen came from near to the centre of a trunk or originated from a branch the rings showed tight curvature and if they came from close to outer edge of a large trunk they had straight ring boundaries. The approximate distance from the centre could then be read directly off the template (Appendix B, Table B1.1).

Figure 2.5. Cross section through a *Pinus cembra* branch showing the asymmetric form of compression wood growth rings (photograph courtesy of Jan Esper, Swiss Federal Research Institute WSL, http://www.wsl.ch/staff/jan.esper accessed on 14 September 2005). Note that the growth rings on the compression wood side are also darker in colour in modern wood.

2.5. Northern Hemisphere fossil woods

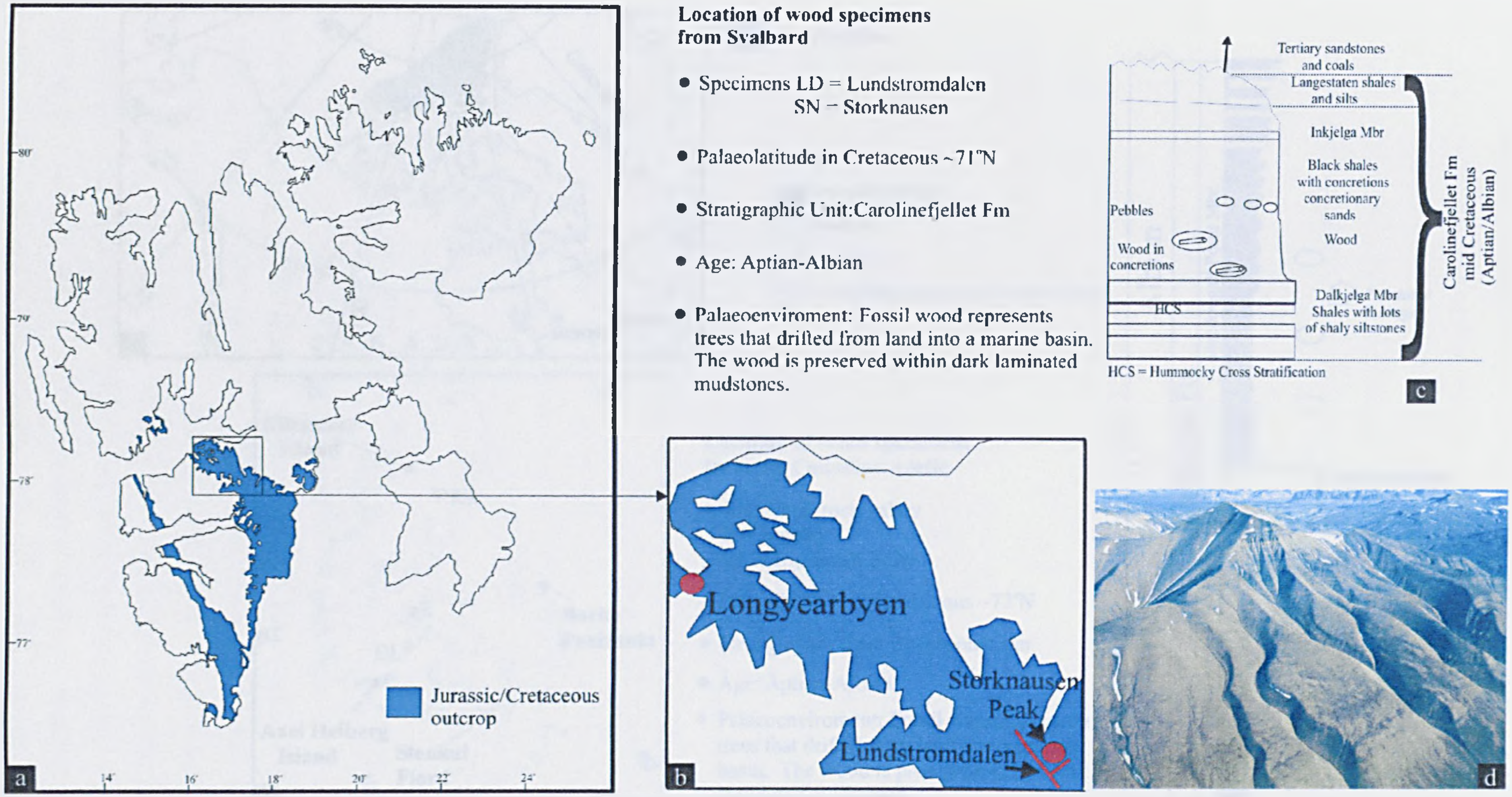
This section provides details of the geological setting in which the fossil wood was found, before presenting the descriptions of the specimens from the Northern Hemisphere sites.

2.5.1. Geological setting

Figures 2.6a and b provide details of the geological setting for the Northern Hemisphere fossil wood specimens.

2.5.2. Descriptions of the fossil woods

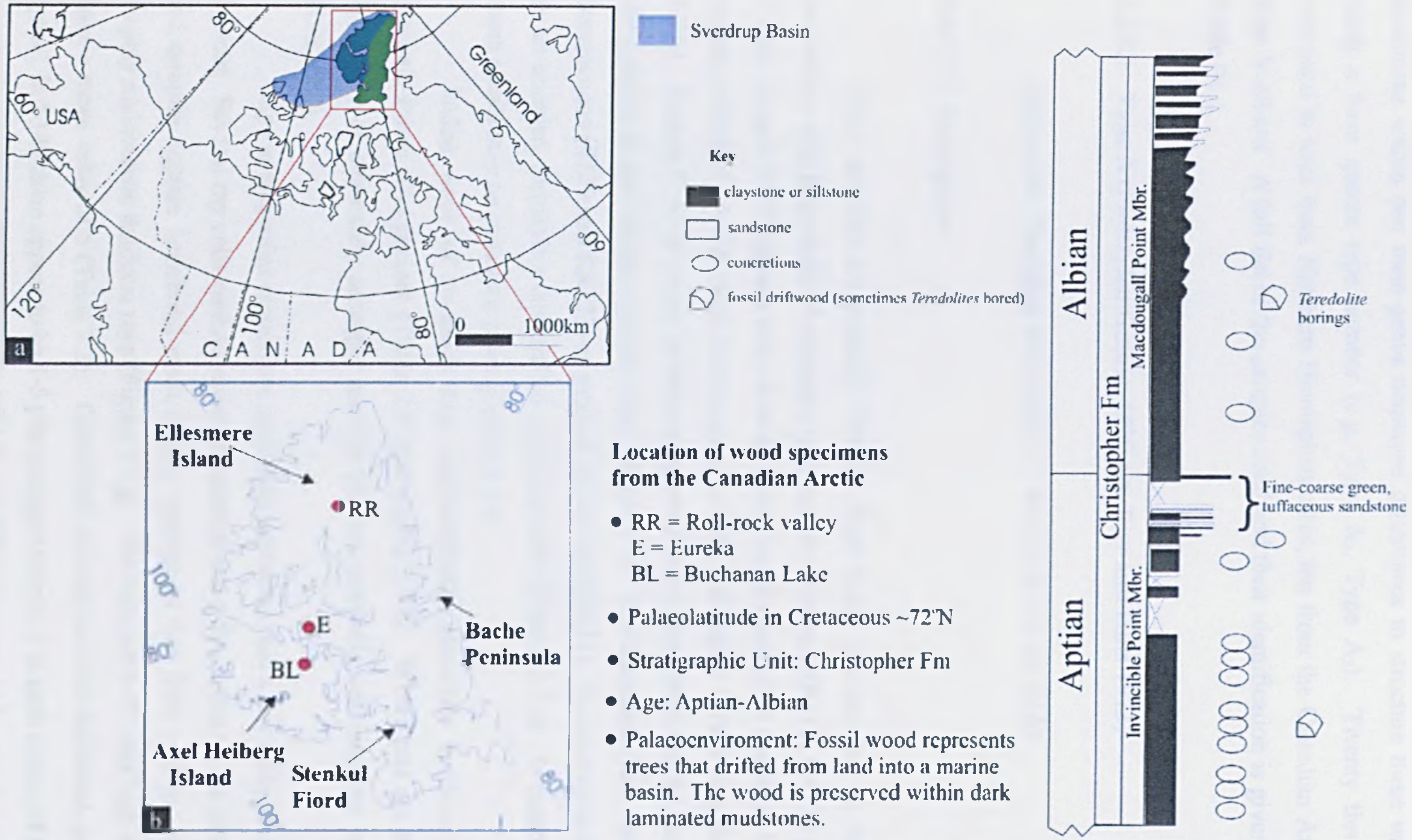
This section presents descriptions and identification of the fossil woods. Initially all woods were grouped as types with similar features e.g. Type A, Type B, etc. Subsequently each type was identified as a previously published form-genus (e.g. *Taxodioxylon*, *Piceoxylon*, etc). No attempt was made to identify the wood to species level as it was felt that



Location of wood specimens from Svalbard

- Specimens LD = Lundstromdalen
  SN = Storknausen
- Palaeolatitude in Cretaceous ~71°N
- Stratigraphic Unit:Carolinefjellet Fm
- Age: Aptian-Albian
- Palaeoenviroment: Fossil wood represents trees that drifted from land into a marine basin. The wood is preserved within dark laminated mudstones.

Figure 2.6.a. Geological setting of the Svalbard specimens. a) Present day map of Svalbard, blue area is Jurassic/Cretaceous sediments (modified from Worsley *et al.*, 1986). b) Enlarged map showing location of the specimen collection areas near Lundstromdalen and Storknausen. c) Generalised section log for Lundstromdalen (J. Francis, unpublished data). d) Photograph showing typical form of the shales in which the wood was found (J. Francis, unpublished).



Location of wood specimens from the Canadian Arctic

- RR = Roll-rock valley
  E = Eureka
  BL = Buchanan Lake
- Palaeolatitude in Cretaceous ~72°N
- Stratigraphic Unit: Christopher Fm
- Age: Aptian-Albian
- Palaeoenviroment: Fossil wood represents trees that drifted from land into a marine basin. The wood is preserved within dark laminated mudstones.

Figure 2.6.b. Geological setting of the Canadian Arctic specimens. a) Present day map of Canada showing location of Ellesmere and Axel Heiberg Islands (After Basinger, 1991) b) Enlarged map showing location of the specimen collection areas, marked with red dot. Sedimentary log of Aptian-Albian Christopher Fm, X = no exposure (compiled from Patchett *et al.*, 2004; Hall *et al.*, 2005)

this was not possible in several genera where there is very little difference in the wood structure between species even in modern wood (Phillips, 1941; Greguss, 1955). However where several specimens within one form-genus displayed differences in structure these were separated by using a form genera type number (e.g. Type A_1, Type A_2). Twenty three samples were examined in total from Northern Hemisphere sites, ten from the Canadian Arctic and thirteen from Svalbard. A full list of the samples used and their identification is given in Appendix B, Table B1.1.

2.5.2.1. Type A (*Pinuxylon* Gothan 1905 em. Roy and Hills 1972)

Specimens: Canadian Arctic RR111, RR122, E139 and E140

2.5.2.1.1. Description

Three samples are probably derived from trunk material due to their straight ring boundaries with large radii of curvature in transverse section (RR111, RR122 and E140, Figure 2.7.a). Sample E139 appears to be derived from branch material as indicated by uneven widths within individual growth rings (compression wood) and highly curved ring boundaries (Figure 2.7.b). Sample E140 is poorly preserved however some fine detail can be seen in all samples. All samples display distinct growth rings (Table 2.2). The transition from early to latewood is conspicuous (E139 and RR122) or gradual (E140 and RR111). Vertical resin canals are present in all samples, displaying thin walled epithelial cells (Figure 2.7.c). In sample E139 some of these canals may be traumatic pairs (Figure 2.7.d).

Radial walls of tracheids bear predominantly uniseriate bordered pits with some biseriate forms also present (Table 2.2 and Figure 2.7.e). Where pits are biseriate they are oppositely or alternately arranged and the pits are generally touching but with some spaced (Table 2.2).

Rays in tangential section are commonly uniseriate but a few multiseriate forms are also present. Several ray cells contain resinous material and a few appear to be pitted (Figure 2.7.f). All samples contain horizontal resin canals, varying in size from ~18 to ~42μm wide, most display multiseriate fusiform rays (Figure 2.7.g). The rays are 1-15 cells high and all specimens have a mean value of 5 (Table 2.2). Cross-field pits appear to be taxodioid, piceoid and pinoid types. In E140 there appear to be 1-5 pits arranged singly, 1 in each corner of the cross-field, or randomly arranged. Samples E139, RR111 and RR122 appear to have 1-6 pits arranged singly, side-by-side, 1 in each corner of the cross-field or randomly. Ray tracheids are present in samples E140, E139 and RR122 (Figure 2.7.h). The horizontal walls of ray cells are thin (compared to the vertical walls of tracheids) to slightly thickened (RR111) with smooth walls, although some pitting also present in places (RR111, RR122 and E139). Spiral thickenings and septa are absent.

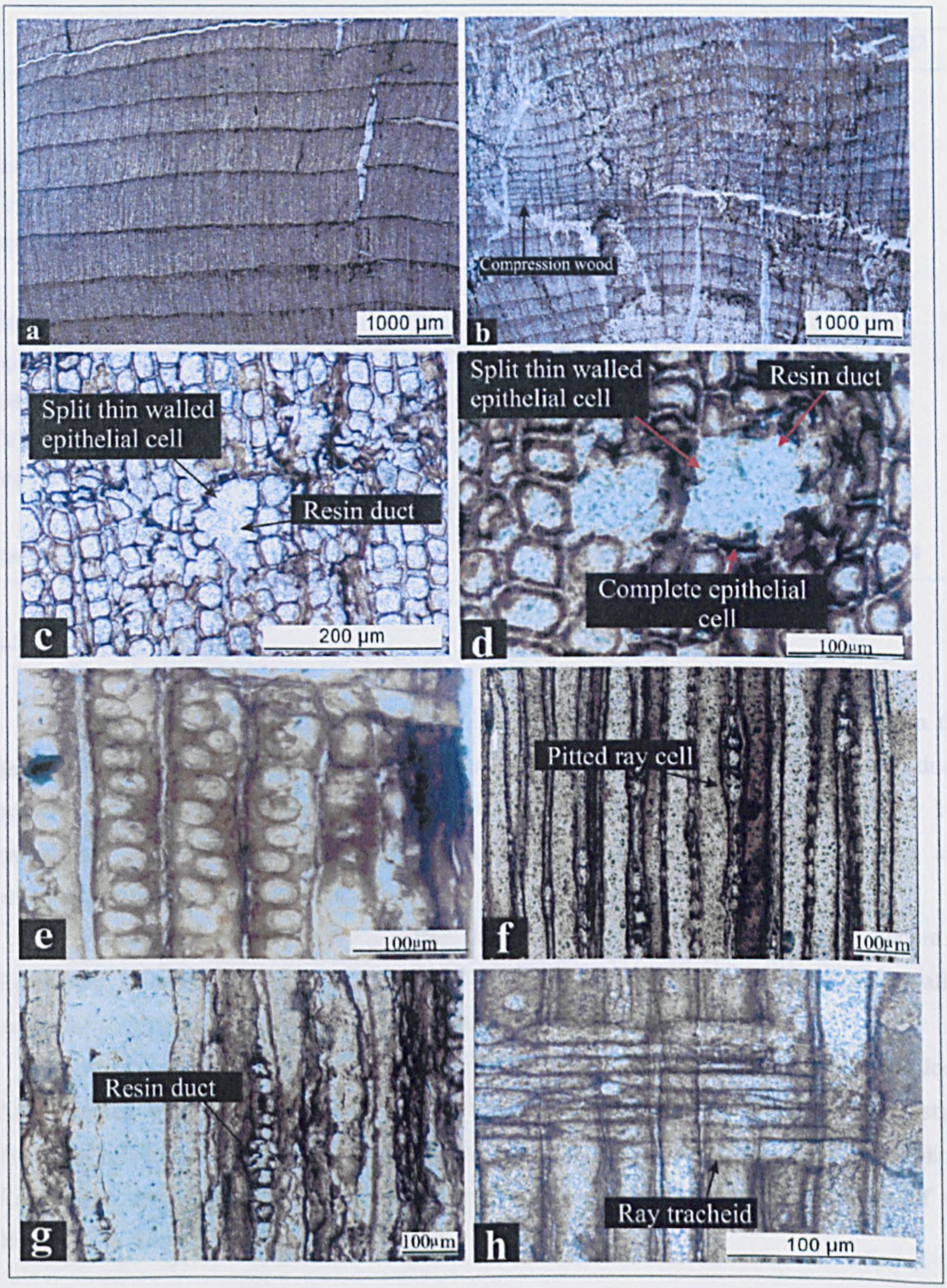


Figure 2.7. Type A (*Pinuxylon*). a) Transverse section showing straight, evenly-spaced ring boundaries (RR111). b) Transverse section showing rings pinching out towards the left hand side (compression wood) (E139). c) Vertical resin canal showing thin-walled epithelial cells (E140) d) Paired vertical resin canals, possibly traumatic (E139). e) Radial section showing uni- and biseriate bordered pits (RR111). f) Tangential section showing uniseriate rays (E140). g) Tangential section showing horizontal resin duct (E140). h) Radial section showing ray tracheids (E139).

Table 2.2. Table showing data collected for identification of samples E139, E140, RR111 and RR122.

	E139	E140	RR111	RR122
N° of rings present	49	29	63	49
Bordered pit type (%)				
Uniseriate	75	66	90	90
Biseriate	25	34	10	10
Bordered pit arrangement (%)				
Opposite	93	97	74	68
Alternate	7	3	26	32
Touching	82	61	80	70
Spaced	18	39	20	30
Ray height	1-12	1-15	1-15	1-14

2.5.2.1.2. Identification

These samples were identified as having affinities with the family *Pinuxylon* on the basis of displaying the following characteristics: growth rings invariably distinct, resin ducts present, walls of epithelial cells lining resin ducts thin or thick, in cross-field 1-6 pinoid or 1-4 piceoid or taxodioid pits, wood parenchyma present or absent, rays 1-45 cells high and uniseriate (Phillips, 1941; Greguss, 1955).

Pinus stands alone within the subdivision Pinoideae as it differs from other genera of Pinaceae in being the only genus with typically "pinoid" cross-field pits and having thin-walled epithelial cells surrounding resin ducts (Phillips, 1941; Roy and Hills, 1972).

Pinuxylon has previously been reported from Early Cretaceous sediments of Franz Josef Land, Russian High Arctic, confirming the presence of this genus within high latitude forests at this time (Shilkina, 1967). A possible pine cone (*Pityostrobus milleri* sp.nov.) from Hokodz River Basin, northwestern Caucasus of Russia of Aptian age may confirm the presence of the Pinoideae in this region (Falder *et al.*, 1998).

2.5.2.1.3. Comparison with extant wood

The fossil wood of Type A has similarities to wood of the family Pinaceae, which consists of *Abies*, *Keteleeria*, *Pseudotsuga*, *Tsuga*, *Picea*, *Pseudolarix*, *Larix*, *Cedrus* and *Pinus* (Phillips, 1941; Greguss, 1955; Roy and Hills, 1972). All fossil samples contain normal vertical and horizontal resin ducts, therefore *Cedrus*, *Abies*, *Keteleeria* and *Pseudolarix* may be discounted as these all lack resin canals or only produce occasional traumatic ducts. *Pseudotsuga* may also be discounted as this genus always displays well developed, closely spaced spiral thickenings in longitudinal and transverse tracheids. *Picea* and *Larix* do produce normal vertical and horizontal resin canals but are surrounded by thick-walled epithelial cells.

Only in *Pinus* are these cells thin-walled similar to samples described here.

Pinus is mainly distributed over temperate zones of the Northern Hemisphere (Vidakovic, 1991; Meijer, 2000). Only one species (*P. merkusii*) crosses the Equator into Sumatra. *Pinus*' range stretches from the polar regions to Guatemala, north Africa and Indonesia. In tropical regions of central America and southeast Asia *Pinus* are restricted to higher altitudes (Vidakovic, 1991; Meijer, 2000). The typical habitat of this genus is at elevations from near to sea level to 3650m, usually on dry rocky terrains and thin or poor sandy soils. It forms pure or mixed stands (Vidakovic, 1991).

2.5.2.2. Type B (*Piceoxylon* Gothan 1905 em. Roy and Hills 1972)

Specimens: Canadian Arctic RR102 and RR113
Svalbard LD105

2.5.2.2.1. Description

Two specimens are derived from mature stem material (LD105 and RR102, Figure 2.8.a) and one specimen branch material due to the presence of compression wood (RR113 Figure 2.8.b). Growth rings are distinct (Table 2.3). The transition from early to latewood is abrupt (LD105, RR113) or gradual (RR102). Vertical resin canals are present in all samples with thick-walled epithelial cells (Figure 2.8.c).

The radial walls of tracheids bear uniseriate, biseriate or rarely triseriate bordered pits (Table 2.3 and Figure 2.8.d). Where the bordered pits are multiseriate they are oppositely or alternately arranged with crassulae present (Table 2.3 and Figure 2.8.e). The bordered pits are generally circular but occasionally flattened along the contact when biseriate and they are spaced or touching (Table 2.3). Resin canals were observed in radial section in sample LD105 (Figure 2.8.f).

Rays seen in tangential section are generally uniseriate although some are biseriate (RR102; RR113) or triseriate (RR102). Rays are 1-19 cell high with mean values between 6 and 11 cells (Table 2.3). Where rays contain resin ducts they have fusiform multiseriate cells around the duct (Figure 2.8.g). Horizontal resin ducts have thick-walled epithelial cells.

Table 2.3.Table showing data collected for identification of samples RR102, RR113 and LD105.

	RR102	RR113	LD105
N° of rings present	6	43	13
Bordered pit type (%)			
Uniseriate	49	45	78
Biseriate	47	50	22
Triseriate	4	5	0
Bordered pit arrangement (%)			
Opposite	86	69	100
Alternate	14	31	0
Touching	80	73	36
Spaced	20	27	64
Ray height	1-28	1-19	1-31
Mean ray height	9	6	11

Cross-fields contain 1-6 (RR113; LD105) or possibly up to 8 (RR102) pits. Pits in all samples appear to be piceoid and taxodioid (Figure 2.8.h), mostly arranged 2 or 4 side-by-side or 4 in the corners. The horizontal walls of rays cells are thin and well pitted (Figure 2.8.d). Ray tracheids are present with dentate walls occasionally displaying minute projections (Figure 2.8.d).

Xylem parenchyma is present in latewood at ring boundaries (LD105) or scattered (RR102; RR113). Spiral thickenings were observed in sample RR113. Septa were absent in all samples.

2.5.2.2.2. Identification

These samples were identified as having affinities with the Abietoideae form of Pinaceae (having highly pitted horizontal walls) due to the lack of typically "pinoid" cross-field pits and thin-walled epithelial cells distinctive of *Pinus*. In erecting the genus *Piceoxylon* Gothan 1905 included characteristics of extant genera *Picea, Larix* and *Pseudotsuga*. Kraüsel (1949) continued to use the genus in this sense, as have authors such as Bannan and Fry (1957). As *Pseudotsuga* may be readily distinguished from *Picea* and *Larix* by the presence of well developed spiral thickenings it is felt that Roy and Hill's (1972) emended diagnosis

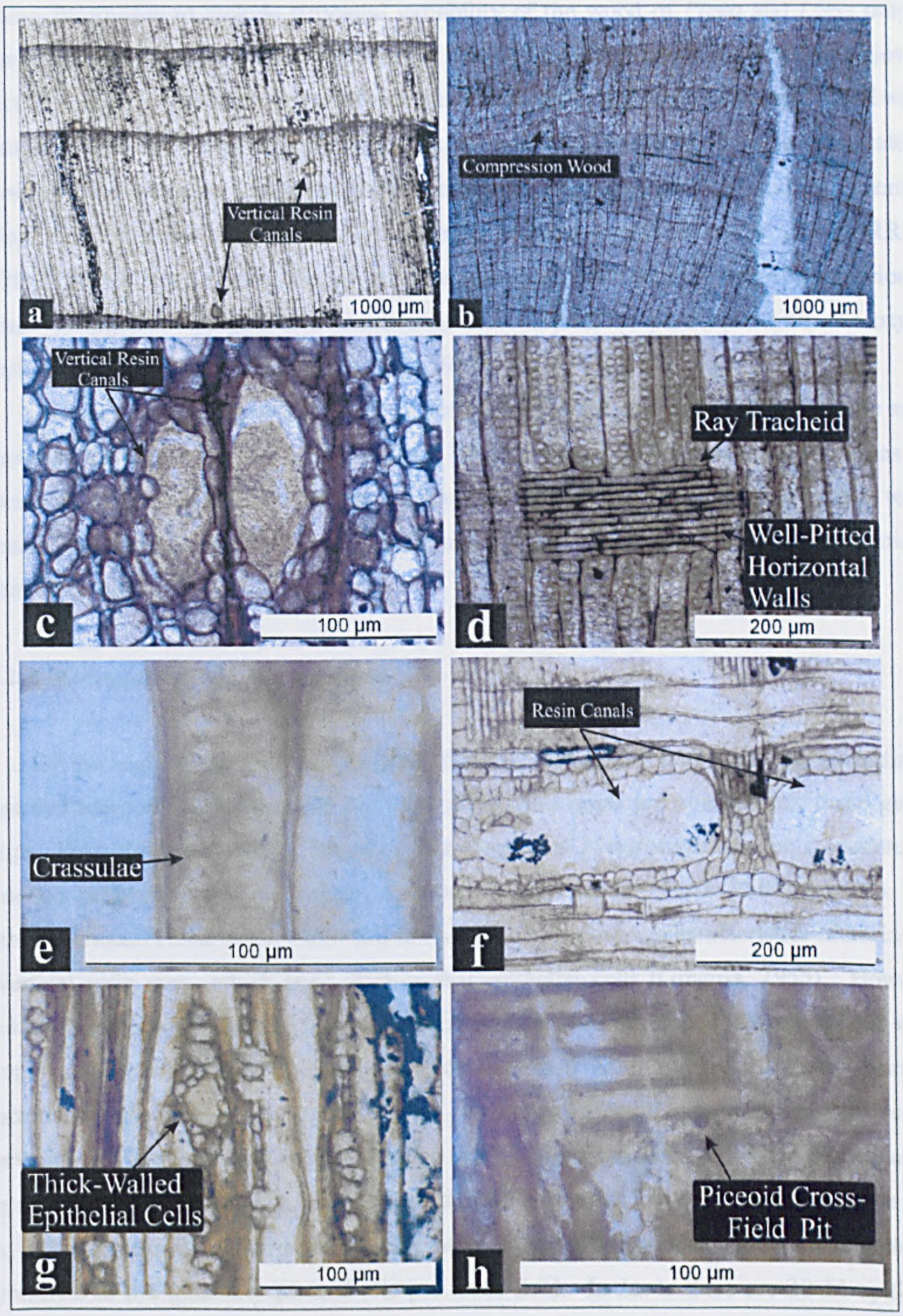


Figure 2.8. Type B (*Piceoxylon*) a) Transverse section of trunk wood showing straight evenly spaced ring boundaries and resin canals (LD105). b) Transverse section of branch material showing compression wood (RR113). c) Thick-walled vertical resin canals in transverse section (LD105). d) Radial section showing uni- and biseriate bordered pits, ray tracheids and well-pitted horizontal walls of ray cells (LD105). e) Radial section showing opposite and alternately arranged biseriate bordered pits with crassulae (LD105). f) Resin canals in radial section of sample LD105. g) Thick-walled horizontal resin canal in tangential section (LD105). h) Radial section showing piceoid pit (RR102).

restricting *Piceoxylon* to include structural variability of the wood of *Picea* and *Larix* only is more appropriate to use here. The presence of distinct growth rings with abrupt transition of early to latewood, vertical and horizontal resin ducts with thick walls, tangential and radial walls of vertical tracheids without spiral thickenings or checkings, radial walls with uniseriate or biseriate and opposite pits, crassulae present, cross-field pits generally piceoid, occasionally taxodioid and xylem parenchyma restricted to ring boundaries place samples LD105, RR102 and RR113 within this amended diagnosis. These samples were compared to other previously described *Piceoxylon* samples and similarities were noted, in particular with *Piceoxylon chrisopheri* and *P. thomsoni* (Bannan and Fry, 1957).

Piceoxylon of Albian age has been reported by Bannon and Fry (1957) from the same formation (Christopher Formation) on Amund Ringnes Island in the Canadian Arctic as the samples used in this project from Ellesmere Island. *Piceoxylon* continued to be present in to the Campanian-Maastrictian interval on Ellesmere Island when it appears to become more dominant (Falcon-Lang *et al.*, 2004).

2.5.2.2.3. Comparison with extant wood

Of the eight genera of Abietoideae, *Cedrus*, *Abies* and *Tsuga* can be immediately disregarded because normal vertical and horizontal resin ducts are absent from these genera (Phillips, 1941; Greguss, 1955). Likewise *Keteleeria* and *Pseudolarix* may be discounted as they do not produce normal resin ducts, only occasional traumatic cysts (Phillips, 1941). The remaining genera, *Pseudotsuga*, *Picea* and *Larix*, share the common characteristics of horizontal and vertical resin ducts which have thick-walled epithelial cells (Greguss, 1955). However, *Pseudotsuga* may be disregarded in this instance because well developed, closely spaced spiral thickenings were not observed in the samples described here. There are many common characteristics shared by *Larix* and *Picea*, making differentiation difficult unless the preservation is exceptional. However, Greguss (1955) suggested these genera may be separated using several diagnostic features. For *Picea* there are 8-10 epithelial cells surrounding the resin ducts, only occasionally paired bordered pits, walls of transverse tracheids minutely dentate and the presence of 2-6 generally piceoid pits per cross-field. In *Larix* there are 10-14 epithelial cells surrounding the resin ducts, fairly frequently paired bordered pits and crassulae, walls of transverse tracheids mostly smooth and 2-6 (8-10) piceoid or taxodioid cross-field pits. Taking all of these characteristics into account, plus the arrangement of the cross-field pits, these samples appear to have characteristics of both genera. However, the proportion of latewood in these samples is low and the resin ducts appear to be placed centrally within the rays, indicating a stronger affinity with *Picea* (Barefoot and Hankins, 1982).

Extant *Picea* occur in temperate and colder regions up to the Northern Hemisphere limit of the Arctic Circle and to the southern limits of Taiwan and Mexico, although most species occur in China (Vidakovic, 1991). In warmer regions (subtropical) *Picea* occurs in the high mountains e.g. Tibet and Assam in the Himalaya (Vidakovic, 1991). The typical habitat of this genus is in moist forests, mostly growing in shade with abundant atmospheric moisture on a light, acid, porous soil (Lanner, 2002). However the range of environments that *Picea* can tolerate is huge as suggested by its distribution between sea level (*P. sitchensis*) and ~4000m (*P. brachytyla*) depending on the species, local climatic conditions and latitude of growth.

2.5.2.3. Type C (*Laricioxylon* Greguss 1967)

Specimens: Svalbard LD123 and LD126

2.5.2.3.1. Description

Both specimens are probably derived from branch material as indicated by the presence of compression wood and the curvature of ring boundaries. The preservation is poor. Growth rings are distinct and the transition from early to latewood is conspicuous (Table 2.4 and Figure 2.9.a). Vertical resin canals with thick-walled epithelial cells are present (Figures 2.9.b). The canals sometimes contain resinous deposits also seen in the transverse tracheids (particularly in the latewood cells).

The radial walls of tracheids bear uniseriate or biseriate bordered pits (Table 2.4 and Figure 2.9.c). Where pits are biseriate they are mostly oppositely arranged but some are alternate with most touching but occasional spaced forms (Table 2.4).

Rays seen in tangential section are generally uniseriate with a few multiseriate. In sample LD123 multiseriate, fusiform rays occur around resin ducts (Figure 2.9.d). Rays are 1-30 cells high with means of 7 and 9 (Table 2.4). In radial section cross-field pits are cupressoid or piceoid with 1-4 pits per cross-field arranged either in 1 row side-by-side, singly or 1 pit in each corner (Figure 2.9.e). Ray tracheids may be present, though sparse (Figure 2.9.f). The horizontal walls of ray cells appear to be thick and whilst in some places they are smooth in others they are well pitted. Spiral thickeningsare present in LD126 but absent in LD123 and septa are absent in both samples.

2.5.2.3.2. Identification

As LD123 and LD126 show characteristics of both *Picea* and *Larix* they could be placed in the restricted genus *Piceoxylon* Gothan 1905 em. Bannon and Fry 1972. However, since they contain a high proportion of latewood cells and display characteristics most like extant *Larix* wood they are placed in the genus *Laricioxylon* Greguss 1967. The samples described here bear some resemblance to *Laricioxylon jarmolenkoi* (Blokhina, 1985) in the form of the bordered pits, the presence of thick-walled epithelial cells and having rays up to 30 cells high, however sample LD123 described here lacks the spiral thickenings observed by Blokhina (1985).

Table 2.4. Table showing data collected for identification of samples LD123 and LD126.

	LD123	**LD126**
N° of rings present	49	46
Bordered pit type (%)		
Uniseriate	63	64
Biseriate	37	36
Bordered pit arrangement (%)		
Opposite	85	69
Alternate	15	31
Touching	96	97
Spaced	4	3
Ray height	1-27	1-30
Mean ray height	7	9

The type specimen (holotype) of *Laricioxylon* is missing, although it was validly published but was not given the designation of "nov.gen.", therefore suggesting that any later diagnosis is doubtful (personal communication Philippe 2004). However, Philippe *et al.* (1999) suggest that this name can be used without problem.

No *Laricioxylon* appear to have been reported previously from the Cretaceous. However, it may be present but included with the generalised name *Piceoxylon*. This was a period of differentiation of the Abietoideae. A cone with affinities to extant *Larix* has been reported from the Lower Cretaceous, Shahai Formation, Yixian, Liaoning Province, China (Shang *et al.*, 2001), although this also has similarities to extant *Picea* and *Pseudotsuga*.

2.5.2.3.3. Comparison with extant wood

Sample LD123 contains both vertical and horizontal resin ducts which appear normal and not traumatic. Therefore *Cedrus*, *Abies*, *Keteleeria* and *Pseudolarix* may be discounted, as these all lack resin canals or only produce occasional traumatic ducts. *Pseudotsuga* may also be discounted as this genus always displays well developed, closely spaced spiral thickenings in its longitudinal and transverse tracheids which were not observed in these fossil samples.

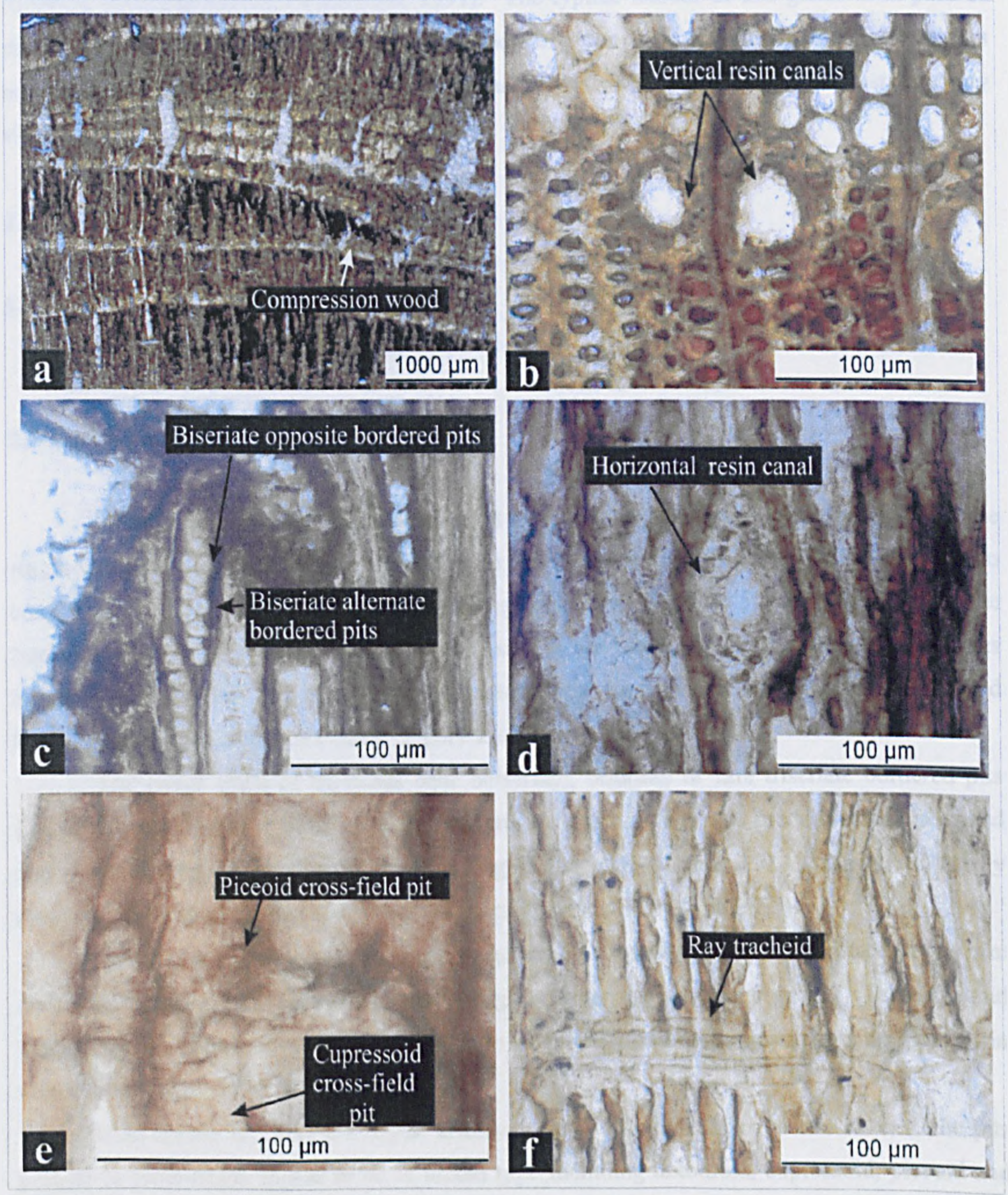


Figure 2.9. Type C (*Laricioxylon*) a) Transverse section of branch material showing compression wood (LD123). b) Transverse section showing vertical resin canals (LD126). c) Radial section showing uniseriate, biseriate (alternate and opposite) and triseriate bordered pits (LD126). d) Tangential section showing horizontal resin canal (LD123). e) Radial section showing piceoid and cupressoid cross-field pits (LD123). f) Radial section showing ray tracheids (LD123).

The difficulty of differentiating between *Picea* and *Larix* then arises. LD123 and LD126 show similarities to both, however, the large proportion of latewood and the frequent presence of paired bordered pits on radial walls of tracheids indicates a stronger affinity with *Larix* (Greguss, 1955).

Extant *Larix* is found in colder regions of the Northern Hemisphere; occurring in North America, Asia and Europe (Vidakovic, 1991). The typical habitat of this genus is in pure or mixed stands with free air circulation on moderately rich soils to light loam. *Larix* grows mainly in mountainous regions between 200 and 2400m although most prefer moist to boggy sites.

2.5.2.4. Type D (*Cedroxylon* Kraus 1872)

Specimens: Svalbard LD102
Canadian Arctic RR121 and RR123

2.5.2.4.1. Description

All three samples are probably derived from mature stem material as indicated by the ring boundaries with large radii of curvature in transverse section (Figure 2.10.a). There is no compression wood present. The number of rings present varies from 5 to 37 (Table 2.5). The transition from early to latewood is conspicuous. Tracheid cells appear to contain dark resinous material and in LD102 this seems to be restricted to the ring boundaries. Samples RR121 and RR123 contain traumatic resin ducts (Figure 2.10.b).

The radial walls of tracheids bear uniseriate, biseriate or rare triseriate bordered pits (Table 2.5 and Figure 2.10.c). Where pits are multiseriate they are predominantly arranged oppositely although a small number are arranged alternately (Table 2.5). The pits are mainly touching with some being spaced more than 1 pit diameter apart (Table 2.5).

Rays seen in tangential section are generally uniseriate with a few biseriate or rare multiseriate forms. The rays are generally high with means between 9 and 14 (Table 2.5 and Figure 2.10.d). Some ray cell walls appear to be pitted. Traumatic resin ducts are present in samples RR121 and RR123 (Figure 2.10.e).

Cross-fields appear to contain 1-8 pits arranged either side-by-side or in two rows. The pits present in cross-fields appear to be of mixed type including taxodioid, cupressoid, piceoid and pinoid types (Figures 2.10.f and g). Horizontal walls of ray cells are thin and well pitted (Abietoid) and ray tracheids are present (Figure 2.10.f and h). Xylem parenchyma is present but spiral thickenings and septa are absent.

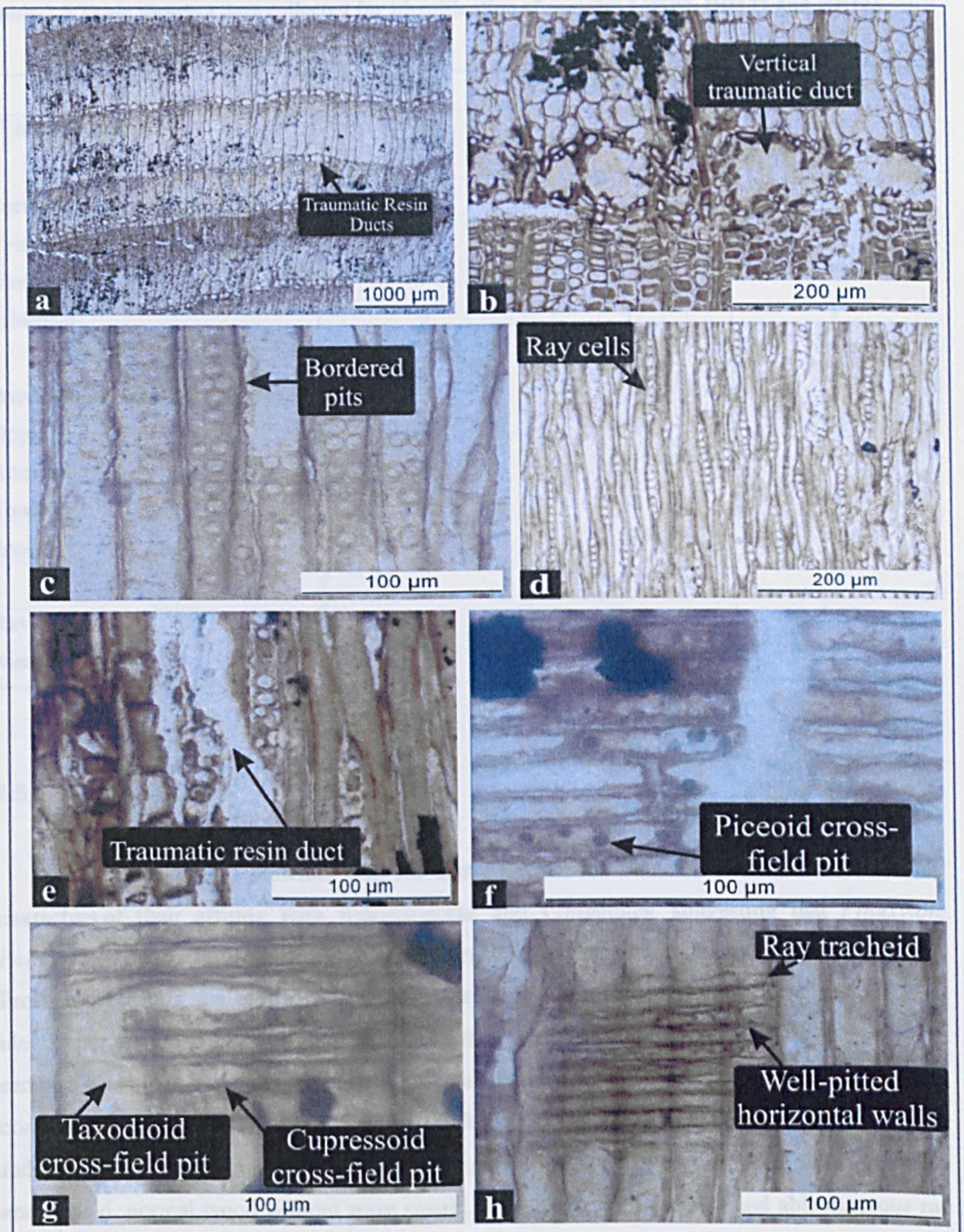


Figure 2.10. Type D (*Cedroxylon*). a) Transverse section showing the relatively straight ring boundaries and traumatic resin ducts (RR123). b) Transverse section showing detail of vertical traumatic resin ducts (RR121). c) Radial section showing uni- and biseriate opposite bordered pits (RR121). d) Tangential section showing ray cells (LD102). e) Tangential section showing poorly preserved horizontal traumatic duct (RR123). f) Radial section showing piceoid cross-field pit and well pitted horizontal walls (RR121). g) Radial section showing taxodioid and cupressoid cross-field pits (RR121). h) Radial section showing ray tracheids and well pitted horizontal walls (RR121).

Table 2.5.Table showing data collected for identification of samples LD102, RR121 and RR123.

	LD102	RR121	RR123
N° of rings present	5	37	22
Bordered pit type (%)			
Uniseriate	93	55	49
Biseriate	7	44	50
Triseriate	0	1	1
Bordered pit arrangement (%)			
Opposite	100	91	91
Alternate	0	9	9
Touching	85	64	60
Spaced	15	36	40
Ray height	2-26	1-49	1-37
Mean ray height	9	14	13

2.5.2.4.2. Identification

Shilkina (1967) indicates that the Early Cretaceous Pinaceae still retained structural characters of their affinity with Araucariaceae and Cordaitales, suggesting that *Pinuxylon, Palaeopiceoxylon*, *Cedroxylon* and probably *Keterleerioxylon* should be grouped together in the Protopinaceae. In the case of the samples described here it is felt that there are sufficient identifying factors available to place them firmly within the form genus *Cedroxylon.* The samples described here also provide a general match for the form genus *Cedroxylon* when compared to Kraüsel's (1949) scheme on the basis of the following characteristics: pits on radial walls of tracheids circular and, where multiseriate, oppositely arranged, never typically araucarioid, normal wood without resin canals, spiral thickenings absent and abietinaceous ray pitting present (Kraüsel, 1949). Samples RR121 and RR123 bear similarity to *Cedroxylon disjunctum* (Bannan and Fry, 1957) confirming their place within the genus. LD102 also bears some similarity to *C. disjunctum* however it is lacking the alternate radial pitting seen in this species.

It has been suggested that *Cedroxylon* is an illegitimate later synonym of *Tiloxylon*, even though it is widely used (Bannan and Fry, 1957; Philippe *et al.*, 1999; Bamford and Philippe, 2001). Bamford and Philippe (2001) further suggest that *Cedroxylon* is not represented in the Early Cretaceous of Gondwana and cannot be used for this time period. However the discussion below shows that it has been widely used for Early Cretaceous samples.

Cedroxylon of Albian age has been reported by Bannon and Fry (1957) from the Christopher Formation of Amund Ringnes Island, Canadian Arctic. *Cedroxylon* is also represented in the Lower Cretaceous of Franz-Josef Land (Shilkina, 1967). Seed cones of *Cedroxylon* have been found in the Albian-Cenomanian of the River Kiya, Chulym-Yenisei Basin, Siberia and various other remains of Upper Senonian age from the Sym Suite, Sym River, Yilyui Basin, Siberia (Vakhrameev, 1991).

2.5.2.4.3. Comparison with extant wood

Of the eight genera of Abietoideae, *Larix*, *Picea* and *Pseudotsuga* all contain normal vertical and horizontal resin canals therefore these genera can be disregarded because LD102 contains no resin canals and RR121 and RR123 contain only traumatic resin canals. Ray tracheids are present which discounts *Abies*, *Keteleeria* and *Pseudolarix* (Greguss, 1955; Stewart, 1983). *Cedrus* and *Tsuga* are very similar in anatomical characteristics however in *Cedrus* the torus is scalloped, rays are 2-30 cells high and wood parenchyma is present, whereas in *Tsuga* the torus is intact, rays are 1-18 cells high and parenchyma is not present (Greguss, 1955). All of the samples examined here are not well enough preserved to allow confirmation with certainty that the torus is scalloped or intact. However rays are high in all samples and wood parenchyma is present, indicating a closer affinity with *Cedrus*.

Cedrus is confined to temperate regions of the Northern Hemisphere, being widespread in North America, Northern Europe and North and East Asia (Phillips, 1941; Greguss, 1955). *Cedrus* however comprises four relict, closely allied species, found in north Africa, the mountains of the south and southeastern Mediterranean and the Western Himalaya (Greguss, 1955; Vidakovic, 1991). The typical habitat of this genus is in wet coastal sites or river terraces although it is also found in drier inland sites with well drained soil at elevations between 1000-3000m (Lanner, 2002). *Cedrus* usually grows in pure stands and prefer to have plenty of light. In mountainous areas young trees are prone to frost (Vidakovic, 1991).

2.5.2.5. Type E (*Palaepiceoxylon* Kraüsel 1949)

Specimen: Canadian Arctic BL125

2.5.2.5.1. Description

This sample is probably derived from a mature stem due to its straight ring boundaries with large radii of curvature in transverse section (Figure 2.11.a). The rings do not contain compression wood but are evenly spaced along their length. This sample has 59 distinct growth rings. The transition from early to latewood is gradual. Vertical resin canals are present with thick-walled epithelial cells (Figure 2.11.b).

The radial walls of tracheids bear uniseriate (58%), biseriate (40%) and rare triseriate (2%) bordered pits (Figure 2.11.c). There may be crassulae present but preservation is poor and this cannot be definitely confirmed. Where pits are multiseriate they are mainly arranged oppositely (76%) although some alternately arranged pits are also present (24%). The pits are generally touching (88%) with some spaced (12%). Resin ducts are also present in radial section (Figure 2.11.d).

Rays seen in tangential section are generally uniseriate although some are biseriate. Some cells contain resinous material and walls are pitted. Horizontal resin canals with thick-walled epithelial cells are present (Figure 2.11.e). Rays are 1-21 cells high with a mean of 7. Preservation is poor however it appears there are 1-9 pits per cross-field either arranged side-by-side, vertically or randomly. The pits appear to be piceoid, taxodioid and possibly with some pinoid (Figure 2.11.f). It cannot be determined whether ray tracheids are present or not. The horizontal walls of ray cells are well pitted (Figure 2.11.g). Spiral thickenings and septa are absent.

2.5.2.5.2. Identification

Comparison with Kraüsel's (1949) scheme shows that BL125 has an affinity with *Palaepiceoxylon* due to the presence of the following characteristics: pits on radial walls of tracheids at least in part circular; if arranged in several rows opposite, mainly separated by bars of Sanio, pits on radial walls of tracheids mainly of mixed type with all possible gradations of structure, horizontal and tangential walls of medullary ray cells very densely pitted (Abietinaceous), resin canals in normal wood and horizontal and vertical resin canals present. *Palaepiceoxylon* appears to be representative of the Pinaceae however it still retains characters of pitting that indicate its affinities with Araucariaceae and Cordaitales, making it an intermediate form. It is suggested that *Palaepiceoxylon* could be included within the *Protopinaceae,* the generic name covering all wood types with affinities to Pinaceae but also retaining characteristics of more ancestral forms (Shilkina, 1967).

The only other record of *Palaepiceoxylon* reported is that of Shilkina (1967). This was a sample of fossil wood from the Early Cretaceous of Franz-Josef Land, although his spelling differs from that presented by Kraüsel (*Palaeopiceoxylon*). This indicates that *Palaepiceoxylon* was present at that time but was probably only a minor component of the forests.

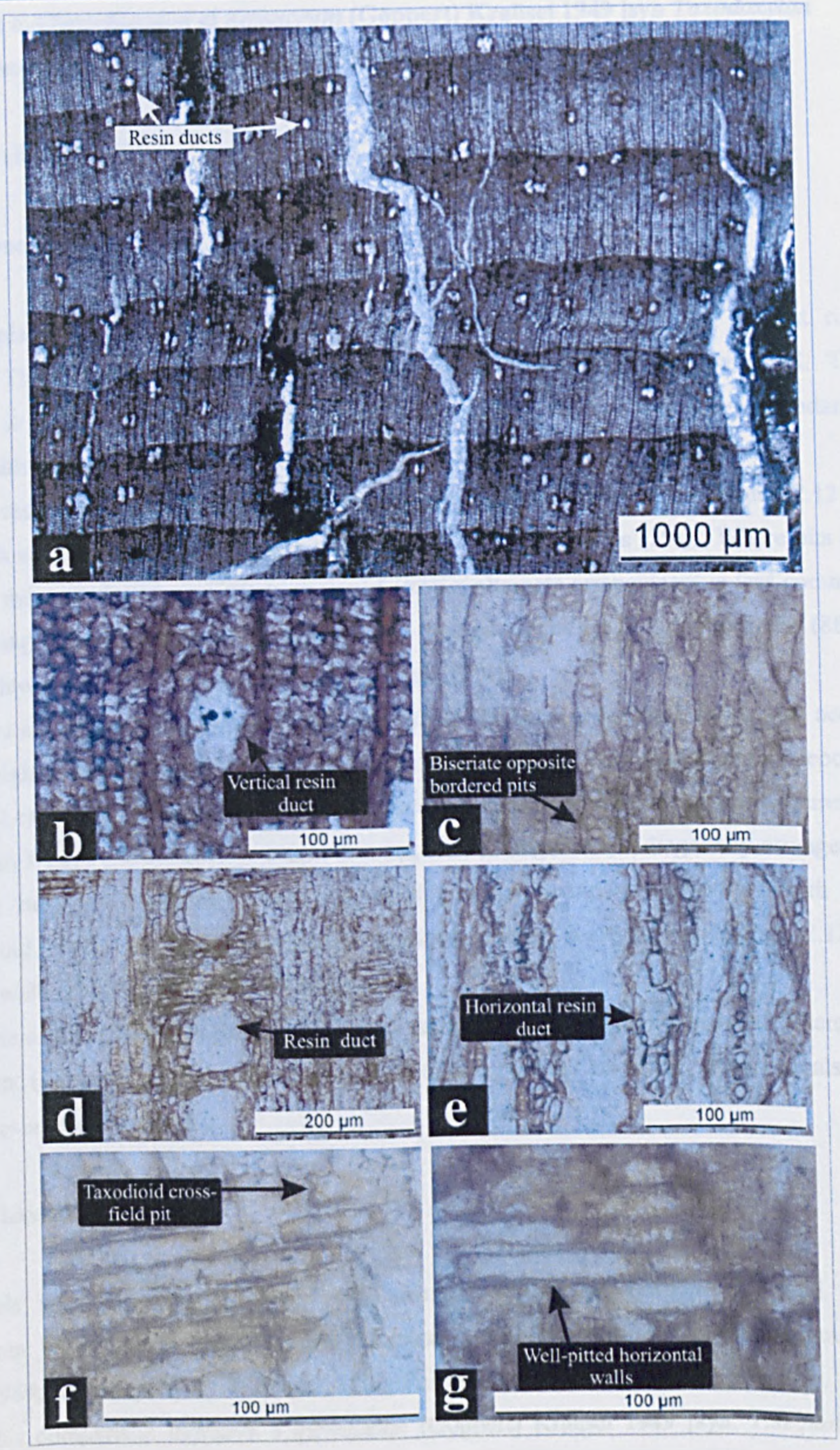


Figure 2.11. Type E (*Palaepiceoxylon*) BL125. a) Transverse section showing straight ring boundaries and numerous resin ducts. b) Transverse section showing vertical resin duct. c) Radial section showing uni- and biseriate alternate and oppositely arranged bordered pits. d) Radial section showing resin ducts. e) Tangential section showing poorly preserved resin duct. f) Radial section showing taxodioid cross-field pits. g) Radial section showing well pitted horizontal ray cells.

2.5.2.6. Type F_1 (*Taxodioxylon* cf *gypsaceum* (Göppert) Kraüsel 1949 [syn *Taxodoxylon sequoianum* (Mercklin) Gothan, 1905])

Specimen: Svalbard LD131

2.5.2.6.1. Description

Sample LD131 is probably derived from a mature stem due to the straight ring boundaries. There is no compression wood present, indicating that this is trunk material. The preservation is poor. The sample has 21 growth rings that are distinct with wavy boundaries and the transition from early to latewood is conspicuous (Figure 2.12.a).

The radial walls of tracheids bear mainly uniseriate (66%) bordered pits (Figure 2.12.b). Biseriate pits also occur (31%) and there are occasional triseriate forms (3%). Where pits are multiseriate the majority are oppositely arranged (62%); alternate arrangement is less common (38%). Pitting is both spaced and contiguous but contiguous pitting is more common (88%) with only a few spaced more than 1 pit diameter apart (12%).

Rays in tangential section are commonly uniseriate but rare biseriate forms also occur, 1-11 cells high, mean of 4 cells. Many of the ray cells are filled with dark resinous deposits (Figure 2.12.c). In radial section cross-fields contain 1-6 pits showing various arrangements; some contain 1 large pit whilst others have 2 in opposite arrangement, 3 diagonally arranged or up to 6 in random orientation. The cross-field pits are dominantly taxodioid with rare glyptostroboid forms having very narrow borders, almost windowlike (Figure 2.12.d). Horizontal walls of ray cells are thin and smooth.

Xylem parenchyma is present but spiral thickenings/checkings are absent. There are septa present (although not abundant, Figure 2.12.e) and rare ray tracheids. Resin canals and traumatic resin ducts are absent.

2.5.2.6.2. Identification

This specimen was compared with various species of *Taxodioxylon* and other taxodiaceous fossil woods (Phillips, 1941; Kraüsel, 1949; Greguss, 1955; Ramanujam and Stewart, 1969; Ramanujam, 1971; Meijer, 2000; Fairon-Demaret *et al.*, 2003) (Table 2.6).

This comparison indicates *T.gypsaceum* (Göppert) Kraüsel 1949 [syn. *T.sequoianum* (Mercklin) Gothan, 1905] is most similar to LD131, due to there being in excess of 3 pits per cross-field (taxodioid and glyptostroboid types), transverse walls of resin parenchyma mainly smooth and traumatic resin ducts absent. Meijer (2000) also mentions that ray heights can be low (1-8), similar to this sample. Because of the poor preservation of the cross-field pits this

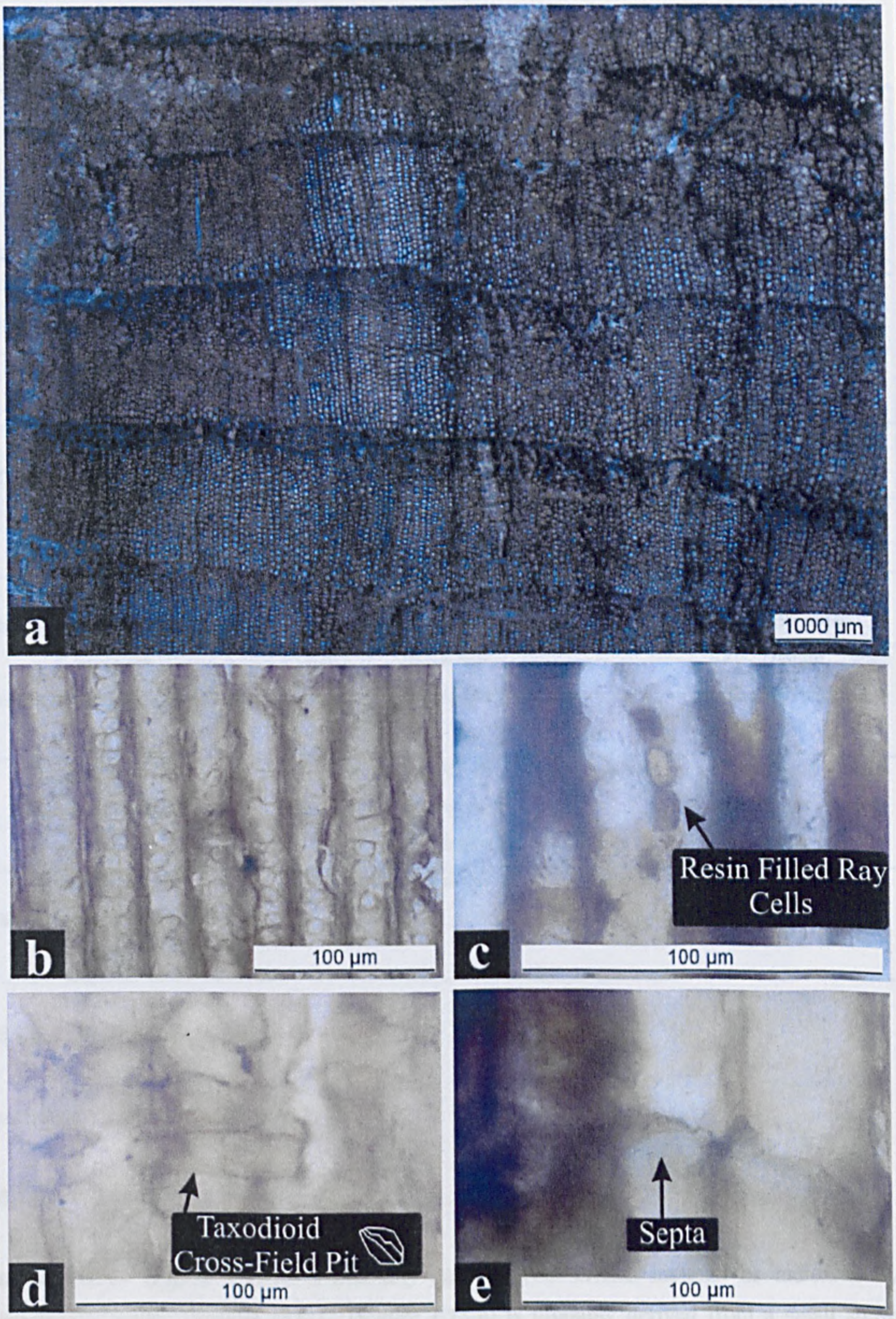


Figure 2.12. Type F_1 (*Taxodioxylon*) LD131. a) Transverse section showing poorly preserved ring boundaries. b) Radial section showing uni- and biseriate opposite bordered pits. c) Ray cells filled with dark resinous material. d) Radial section showing taxodioid cross-field pit (label shows sketch of the pit highlighted). e) Radial section showing septa.

material is therefore referred to as *Taxodioxylon* c.f. *gypsaceum*.

Table 2.6. Salient features of different Cretaceous species of *Taxodioxylon* (after Meijer, 2000).

Species	Number of cross field pits	Nature of cross field pits	Traumatic resin ducts	Miscellaneous features
T.albertense (Penhallow) Shimakura 1937	1-3	Taxodioid/ Cupressoid	Absent	Ray height 1 – 70 cells
T.burgessii (Penhallow) Kraüsel 1949	1-3	Taxodioid (always)	Possible (vertical/radial)	
T.taxodii Gothan 1905	>3	Taxodioid	Absent	Parenchyma cross walls pitted
T.gypsaceum (Göppert) Kraüsel 1949	>3	Taxodioid/ Glyptostroboid	Radial ducts absent	Parenchyma cross walls smooth
T.montanense (Torrey) Kraüsel 1949	>3	Taxodioid	Radial ducts present	Parenchyma cross walls smooth
T.drummhellerense Ramanujam and Stewart 1969	2-4	Taxodioid/ Glyptostroboid		Parenchyma cross walls well pitted
T.antiquum Ramanujam and Stewart 1969	2-5	Taxodioid (single row)		Ray height >80 cells, ray width 1-4 cells
T.cryptomerioides (Hartig) Gothan 1905	1-4	Taxodioid/ Cupressioid/ Podocarpoid	Absent	Parenchyma walls smooth or widely spaced pits
T.multiseriatum Ramanujam and Stewart 1969b	1-4	Taxodioid	Absent	Rays 2-70 cells high

2.5.2.6.3. Type F_2 (*Taxodioxylon*)

Specimens: Svalbard LD129 and LD133

2.5.2.6.3.1. Description

Sample LD129 (Figure 2.13.a) is probably derived from branch material as indicated by compression wood. Sample LD133 (Figure 2.13.b) is probably derived from a small stem. Although the central rings show pronounced curvature, the outer rings are reasonably straight with no compression wood. Growth rings are distinct in both samples (Table 2.7, Figures 2.13.a and b). The transition from early to latewood is either abrupt (LD129) or gradual (LD133).

The radial walls of tracheids bear mainly uniseriate, occasionally biseriate or rarely triseriate bordered pits (Table 2.7, Figures 2.13.c and d). Where pits are multiseriate most are alternately arranged (Figure 2.13.d), although opposite pitting can be quite common, crassulae were observed in both samples (Table 2.7). Pitting is touching or spaced (Table 2.7).

Rays observed in tangential section are generally uniseriate with only rare biseriate forms, 1-18 cells high with means of 4 and 7 cells (Table 2.7 and Figure 2.13.e). Some cells contain dark resinous material. In radial section horizontal walls are thin and unpitted, with ray tracheids, if present, being rare. The number of pits per cross-field seems to vary from 1-2 in LD129 (Figure 2.13.f) to 1-6 in LD133 (Figure 2.13.g). In both samples the majority of cross-field pits seem to contain 1 large narrow bordered taxodioid pit. Occasional slit-like apertures were observed in LD133. Xylem parenchyma is present, being abundant in the latewood in sample LD129, but spiral thickenings, septa, resin canals and traumatic resin ducts are absent.

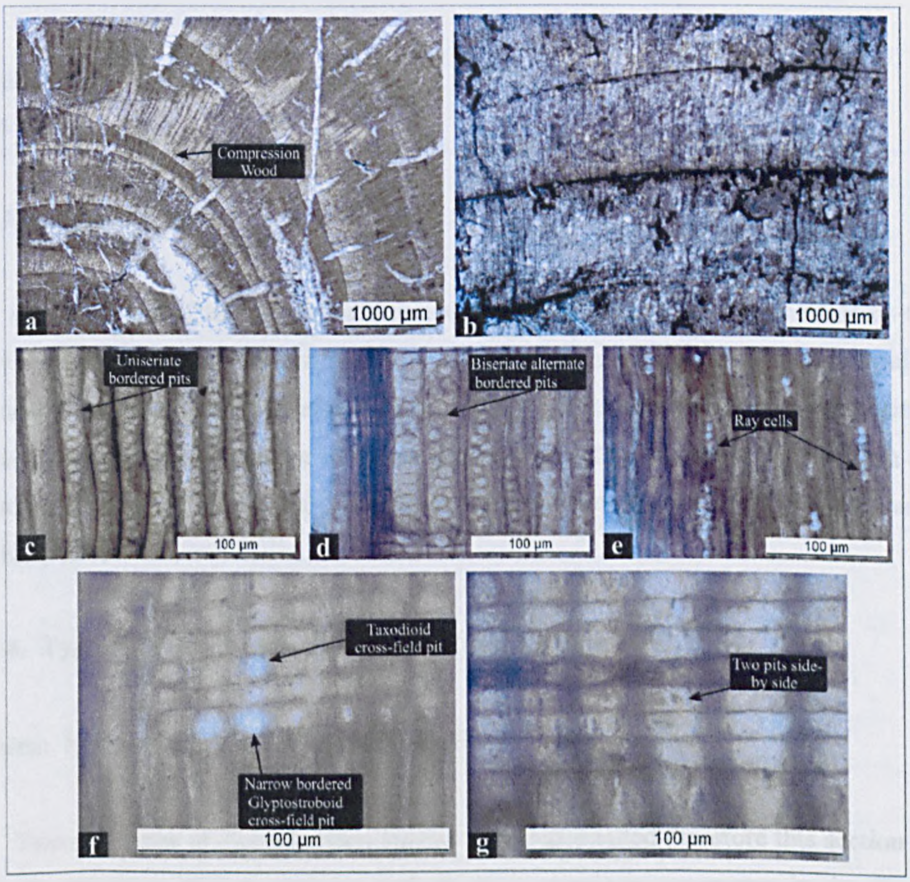


Figure 2.13. Type F_2 (*Taxodioxylon*). a) Transverse section of branch material showing compression wood (LD129). b) Transverse section showing relatively straight, evenly spaced ring boundaries (LD133). c) Radial section showing uniseriate bordered pits (LD133). d) Radial section showing biseriate alternate bordered pits (LD129). e) Tangential section showing ray cells (LD129). f) Radial section showing singly arranged glyptostroboid and taxodioid cross-field pits (LD129). g) Radial section showing multiple cross-field pits (two side-by-side in centre of image) (LD133).

Table 2.7.Table showing data collected for identification of samples LD129 and LD133.

	LD129	LD133
N° of rings present	16	12
Bordered pit type (%)		
Uniseriate	80	92
Biseriate	13	8
Triseriate	7	0
Bordered pit arrangement (%)		
Opposite	49	25
Alternate	51	75
Touching	100	31
Spaced	0	69
Ray height	1-13	1-18
Mean ray height	4	7

2.5.2.6.3.2. Identification

Identification of taxodioid fossil wood puts emphasis on the types of cross-field pits present (Kraüsel, 1949; Fairon-Demaret *et al.*, 2003) and on the form of the horizontal walls of the parenchyma cells (Fairon-Demaret *et al.*, 2003). However, the poor preservation of the cross-field areas in these samples makes it difficult to determine these factors with certainty therefore these samples have been placed in the general form-genus *Taxodioxylon* Hartig 1848 em Gothan, 1905.

2.5.2.6.4. Type F_3 (*Taxodioxylon* Hartig 1848 em. Gothan 1905)

Specimens: Svalbard LD129, LD131 and LD133

Two sub-types of *Taxodioxylon* appear to be represented therefore this section gives the general identification of *Taxodioxylon* and discusses previous occurances in the fossil record before comparing these samples with extant wood of *Taxodium*.

2.5.2.6.4.1. Identification

Taxodioxylon is identified by the presence of the following features: distinct growth rings, smooth to sparsely pitted horizontal walls of ray cells; 1-30 cells high rays with generally uniseriate but occasionally 1-2 biseriate in the body, 1-6 taxodioid to glyptostroboid pits in the cross-fields and the absence of resin ducts and spiral thickenings (Greguss, 1955; Fairon-Demaret *et al.*, 2003). In the absence of any other evidence these woods are notoriously difficult to assess because of overlapping characteristics (Fairon-Demaret *et al.*, 2003).

Included within the Taxodiaceae are *Athrotaxis, Crytomeria, Cunninghamia, Glyptostrobus, Sequoia* (inc. *Sequoiadendron*), *Taiwania, Taxodium* and *Sciadopitys* (Phillips, 1941; Greguss, 1955). Recently, this classification has been changed using a combined morphological and molecular approach (Gadek *et al.*, 2000; Kusumi *et al.*, 2000) which has placed *Sciadopitys* Siebold *et.al.* 2000 in the monotypic family of the Sciadopityaceae Luerss (Fairon-Demaret *et al.*, 2003). *Sciadopitys* is distinguished from all other Taxodioideae by its lack of wood parenchyma and the presence of large, solitary, simple pits (Phillips, 1941; Meijer, 2000). These features are different to those found in the fossil samples presented therefore this genus is excluded from further consideration. Likewise *Taiwania* can be discounted as this genus displays only cupressoid cross-field pits and not the taxodioid type seen in all other members of this family (Phillips, 1941) and the fossils under consideration.

Northern Hemisphere *Taxodioxylon* wood has been reported from the Upper Cretaceous (Campanian) Oldham and (Maastrichtian) Edmonton Formations (Ramanujam and Stewart, 1969; Ramanujam, 1971), both of Alberta, Canada. The Edmonton Formation has also yielded cones and leaf impressions and compressions (Horrell, 1991). Taxodiaceae pollen of Aptian age has been recovered from the Pechora Depression in Siberia (Vakhrameev, 1991). Twigs of *Sequoia* and rare *Glyptostrobus* have also been recorded from the upper Albian and Cenomanian strata in the Southern Urals (Vakhrameev, 1991). Cones of Taxodiaceae are recorded from Cenomanian Pâtût in Western Greenland (Seward, 1926) and complete shoots from the Albian-Cenomanian Nanushuk Group from the North Slope of Alaska (Spicer and Parrish, 1986). In Eastern Siberia leaf impressions, shoots and cones of *Sequoia* and *Glyptostrobus* have been found of late Albian-early Cenomanian age and various Taxodiaceae remains in the Turonian-Santonian, Vilyui Basin (Nizhny Chyrimin Floral Complex and Sym suite) and Khatanga Basin (Vakhrameev, 1991). Seeds belonging to *Glyptostrobus*, *Sequoia* and *Taxodium* have been recorded in European strata of Cenomanian age (Fairon-Demaret *et al.*, 2003). *Sequoia* cones have also been reported from late Albian-Campanian strata in the Chandler-Colville Region of Alaska (Smiley, 1969; Spicer and Parrish, 1986; Vakhrameev, 1991). Twigs and shoots of *Taxodium, Athrotaxis* and *Glyptostrobus* are recorded from the Fort Union Formation of the USA (second half of the Late Cretaceous) and the Potomac Group of Puddledock, Virginia, USA (~early Albian) (Vakhrameev, 1991; Srinivasan, 1995). This evidence indicates that Taxodiaceous trees were widespread across the Northern Hemisphere throughout the Cretaceous.

2.5.2.6.4.2. Comparison with extant wood

LD131 resembles extant *Sequoia* in its thin and smooth horizontal walls of wood and ray parenchyma, uni-, bi- or triseriate radial tracheid pitting and rare occurrences of thin-walled marginal ray tracheids. Notched bordered pits are common in *Sequoia* but absent in this sample therefore it is discounted (Meijer, 2000). In the remaining specimens notched bordered pits were not observed and rays are low therefore *Sequoia sempervirens* can be discounted (Barefoot and Hankins, 1982). *Sequoiadendron* is discounted for all specimens because in this genus bordered pits are always in a single vertical row even in wide tracheids (Meijer, 2000) which does not compare with these fossil samples.

Taxodium is mainly confined to the Northern Hemisphere, in humid, temperate to sub-tropical regions of East Asia and North America (Meijer, 2000). The typical habitat of this genus is in wetlands sites with swampy terrain and on river banks up to 520m elevation. It forms pure stands that can tolerate temperatures as low as -30°C (Vidakovic, 1991). *T. mucronatum* can grow up to 2300m elevation in temperate regions.

2.5.2.7. Type G (*Juniperoxylon* Houlbert 1910 em. Kraüsel 1949)

Specimens: Svalbard LD101

2.5.2.7.1. Description

Sample LD101 is probably derived from branch material as indicated by the uneven widths present within individual growth rings (compression wood), its small size and the pronounced curvature of the ring boundaries. Six distinct growth rings are present (Figure 2.14.a). The transition from early to latewood is conspicuous. The tracheids are generally rounded so that intercellular spaces frequently occur (Figure 2.14.b).

The radial walls of tracheids bear mainly uniseriate (94%) bordered pits, although occasional biseriate (6%) pits also occur (Figure 2.14.c). Where pits are biseriate they are always oppositely arranged. Pits are mainly touching (80%) however pits spaced more than 1 pit diameter apart do also occur (20%).

Rays seen in tangential section are generally uniseriate but a few multiseriate forms were observed, 1-14 cells high, mean of 4 cells. Many of the cells are filled with dark resinous deposits and tangential walls often show sieve-like thickenings (Figure 2.14.d).

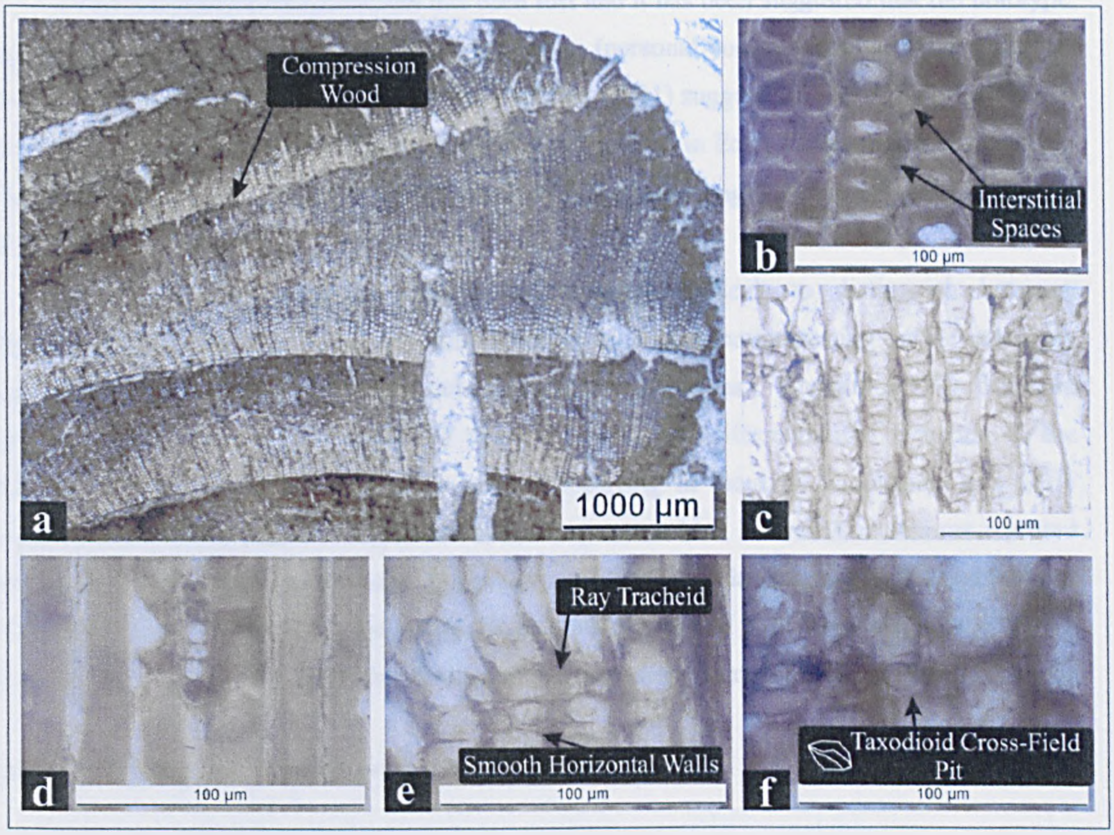


Figure 2.14. Type G (*Juniperoxylon*) LD101. a) Transverse section showing compression wood. b) Transverse section showing interstitial spaces. c) Radial section showing uni- and biseriate alternate pits. d) Tangential section showing resin filled cells. e) Radial section showing ray tracheid and smooth horizontal walls. f) Radial section showing taxodioid cross-field pit (sketch on label shows outline of the pit).

In radial section horizontal walls of ray cells are thin or thickened and smooth to well pitted ray tracheids are present and dentate (Figure 2.14.e). Tangential walls contain bead-like thickenings. Cross-fields appear to contain 1-4 pits arranged singly or with 1 pit in each corner of the cross-field. The cross-field pits appear to be mainly cupressioid with some taxodioid types also present (Figure 2.14.f).

Xylem parenchyma is frequent, commonly with resin content but spiral thickenings/checkings are absent. Septa are present although scattered, with poor preservation making them difficult to recognize. Resin canals and traumatic resin ducts are absent.

2.5.2.7.2. Identification

Comparison to Kraüsel's (1949) scheme indicates that LD101 should be included within *Juniperoxylon* due to the bordered pits being generally circular and opposite, the lack of resin ducts and spiral thickenings and abundant parenchyma.

The holotype of *Juniperoxylon* has been lost and it has been suggested that the holotype may display differences to the published description (personal communication, Marc Philippe, Bamford and Philippe, 2001). Bamford and Philippe (2001) suggest the name has been validly published. They also report that *Juniperoxylon* is not present in Early Cretaceous rocks because it has not been previously reported from strata of this age although, as can be seen below, the foliage has been observed.

Stewart (1983) indicates that it is extremely difficult to distinguish between Cupressaceae and Taxodiaceae from macrofossils, with determination resting on the decussate (Cupressaceae) or helical (Taxodiaceae) arrangement of leaves. Stewart (1983) therefore suggests a possible common origin for these families with differentiation occurring in the Jurassic and the emergence of modern genera occurring in the Late Cretaceous and Early Tertiary, therefore making all Cretaceous samples questionable. However, shoots are reported for two species of *Juniperus* from the Upper Cretaceous of Canada (Stewart, 1983) and remains of middle Albian to Coniacian age of the Chandler-Colville and Kuk River regions of Alaska (Smiley, 1966; 1969). No other descriptions of *Juniperoxylon* were found from the Cretaceous.

2.5.2.7.3. Comparison with extant wood

Type G wood is most similar to *Juniperus* grouped within the Taxodiaceae, traditionally included within the Cupressaceae with Thujoideae and Cupressoideae (Greguss, 1955). Greguss (1955) identifies an anatomically more or less independent group of Taxodioideae including *Arceuthos*, *Cupressus*, *Diselma*, *Fitzroya*, *Juniperus*, *Libocedrus* and *Pilerodendron*. Sample LD101 appears to be part of this group due to the presence of the following features: wood parenchyma is present, horizontal walls never perfectly smooth, but varicose, slightly nodular or thickened beadlike, ray cells likewise uneven, nodular, or pitted, while tangential walls are commonly with beadlike thickenings. Within the conifers transverse tracheids fit closely together without intercellular spaces with only a few exceptions (Wilson and White, 1986). Of the Northern Hemisphere species *Juniperus* spp. can be distinguished from others by this feature, having somewhat rounded tracheids, so that intercellular spaces are produced between them at the cell corners (Phillips, 1941; Wilson and White, 1986). Sample LD101 displays this feature indicating a strong affinity with the Juniperoideae.

Juniperus is widely distributed in the Northern Hemisphere, mostly confined to temperate regions of Europe and northern regions of Asia, China, America and Africa (Vidakovic, 1991). The habitat of this genus ranges from moist sheltered to semiarid regions on thin soils and exposed to strong winds ranging in elevation from 600 to 4500m in open woodland to mountainous areas (Vidakovic, 1991; Lanner, 2002).

2.5.2.8. Type H (*Protocedroxylon* Gothan)

Specimens: Svalbard LD120

2.5.2.8.1. Description

Sample LD120 is probably derived from branch material as indicated by the presence of uneven width growth rings (compression wood) and pronounced curvature of the ring boundaries. Thirty five distinct growth rings are present (Figure 2.15.a). The transition from early to latewood is conspicuous. Tracheid cells, particularly in the latewood, contain resinous material (Figure 2.15.b).

The radial walls of tracheids bear uniseriate (49%) and biseriate (46%) bordered pits, with rare triseriate (5%) forms also observed (Figure 2.15.c). Where pits are multiseriate they are arranged alternately (52%) or oppositely (48%) sometimes with crassulae present. The majority of pits are touching (98%) although a few are spaced more than 1 pit diameter apart (2%). Rays seen in tangential section are mainly uniseriate although a few are biseriate within the body. The rays are 1-25 cells high, mean 7 cells (Figure 2.15.d).

In radial section cross-fields appear to contain 1-6 possibly 7 pits per field. The pits are arranged in various orientations including 1 single large pit per field, 6 organised in 2 horizontal rows and 4 arranged side-by-side. Most are taxodioid but there are also some cupressoid forms (Figures 2.15.e). Horizontal ray walls are thick and very smooth to well pitted (Abietinaceous). Ray tracheids may be present although the preservation is poor. Xylem parenchyma is present. Spiral thickenings, septa, normal and traumatic resin canals are absent.

2.5.2.8.2. Identification

Comparison to Kraüsel's (1949) scheme indicates that LD120 should be included within the form-genus *Planoxylon* due to its alternately arranged bordered pits, numerous small cross-field pits and pitted horizontal walls (Abietinaceous pitting). However *Planoxylon* has since been separated from *Protocedroxylon* based on the difference in tracheal pitting (Medlyn and Tidwell, 1986). *Planoxylon* has been retained for wood having typical Araucarian pitting and vertical pairs of pits in cross-fields, which does not match LD120. Sample LD120 combines features of both Araucarian and Abietinaceous conifers, placing it within the form-genus *Protocedroxylon* (Medlyn and Tidwell, 1986).

Protocedroxylon has a narrow range covering only the Middle Jurassic to the upper Lower Cretaceous (Medlyn and Tidwell, 1986). *P. transiens* has been identified from the

Lower Cretaceous of King Charles Land and the Upper Jurassic or Lower Cretaceous of Spitsbergen (Medlyn and Tidwell, 1986) but no other occurrences have been found.

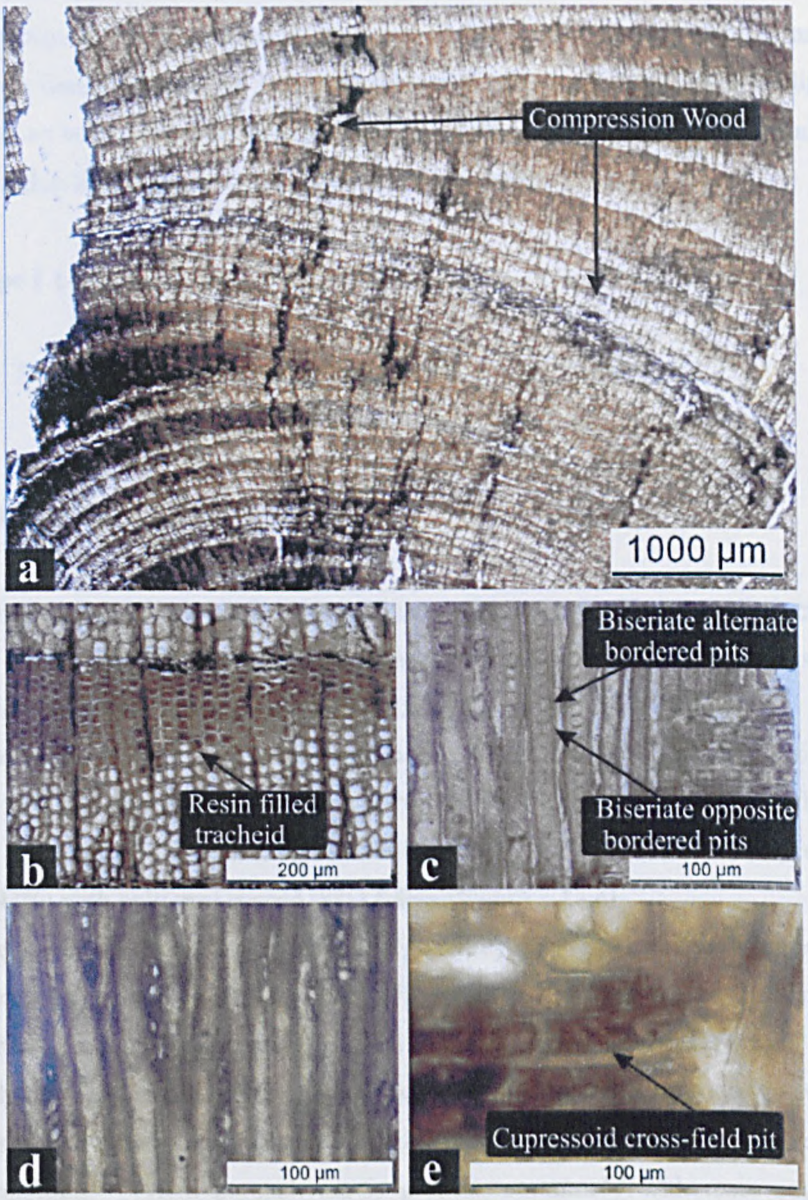


Figure 2.15. Type H (*Protocedroxylon*) LD120. a) Transverse section showing copious compression wood. b) Transverse section showing resin filled tracheids. c) Radial section showing uni- and biseriate opposite and alternate bordered pits. d) Tangential section showing resin filled ray cells. e) Cross-fields showing cupressoid pits.

Protocedroxylon and *Araucariopitys* have been considered as taxonomical synonyms (personal communication, Marc Philippe, University of Lyon, France). Eckhold (1923) suggested that these genera were synonyms however he kept the younger name

Protocedroxylon. Bamford and Philippe (2001) have questioned the validity of *Araucariopitys* because it was only used as a provisional name by Jeffrey (1907). This situation remains unclear and both names are still in use (Jeffrey, 1907; Medlyn and Tidwell, 1986; Falcon-Lang and Cantrill, 2000; Poole and Cantrill, 2001). This situation is worsened because the type fossil of *Araucariopitys* is missing therefore it is argued that, until both sets of type material can be compared, no final decision can be made (personal communication, Marc Philippe). It was decided that, as both names are still widely used, both could be used in this study by placing specimens within the form-genus that was most comparable.

2.5.2.9. Type I (*Araucariopitys* Jeffrey 1907)

Specimens: Svalbard LD108

2.5.2.9.1. Description

Sample LD108 is probably derived from a mature stem. Thirty six distinct growth rings are present in this sample (Figure 2.16.a). The transition from early to latewood is conspicuous. The tracheids frequently contain resinous material (Figure 2.16.a).

The radial walls of tracheids bear mainly uniseriate (85%) bordered pits with a few biseriate (15%) pits also present (Figure 2.16.b). Where the pits are multiseriate they are mostly oppositely arranged (95%) with only rare alternate (5%) forms. The majority of the pits are touching (92%) with only rare spaced (8%) forms (Figure 2.17.c).

Rays seen in tangential section are generally uniseriate although some are partially biseriate with 1-2 paired cells in the body (Figure 2.16.d). Rays are 1-10 cells high, mean 4 cells which are frequently filled with resinous material. Cross-field areas appear to contain 1-3 pits, usually arranged side-by-side although when 3 they are often arranged in two rows. The pits appear to be cupressioid with some possibly pinoid (Figure 2.16.e). Horizontal walls are thin and unpitted. Xylem parenchyma is present, commonly with resin contents. Spiral thickenings are also present. Septa, normal and traumatic resin canals are absent.

2.5.2.9.2. Identification

Several modern species of *Araucaria* and *Agathis* have uniseriate radial tracheid pitting with some biseriate, alternately arranged pitting also present, and spiral thickenings often absent in some species. Spiral thickenings are present but hardly discernable (Greguss, 1955), supporting an araucarian affinity for LD108.

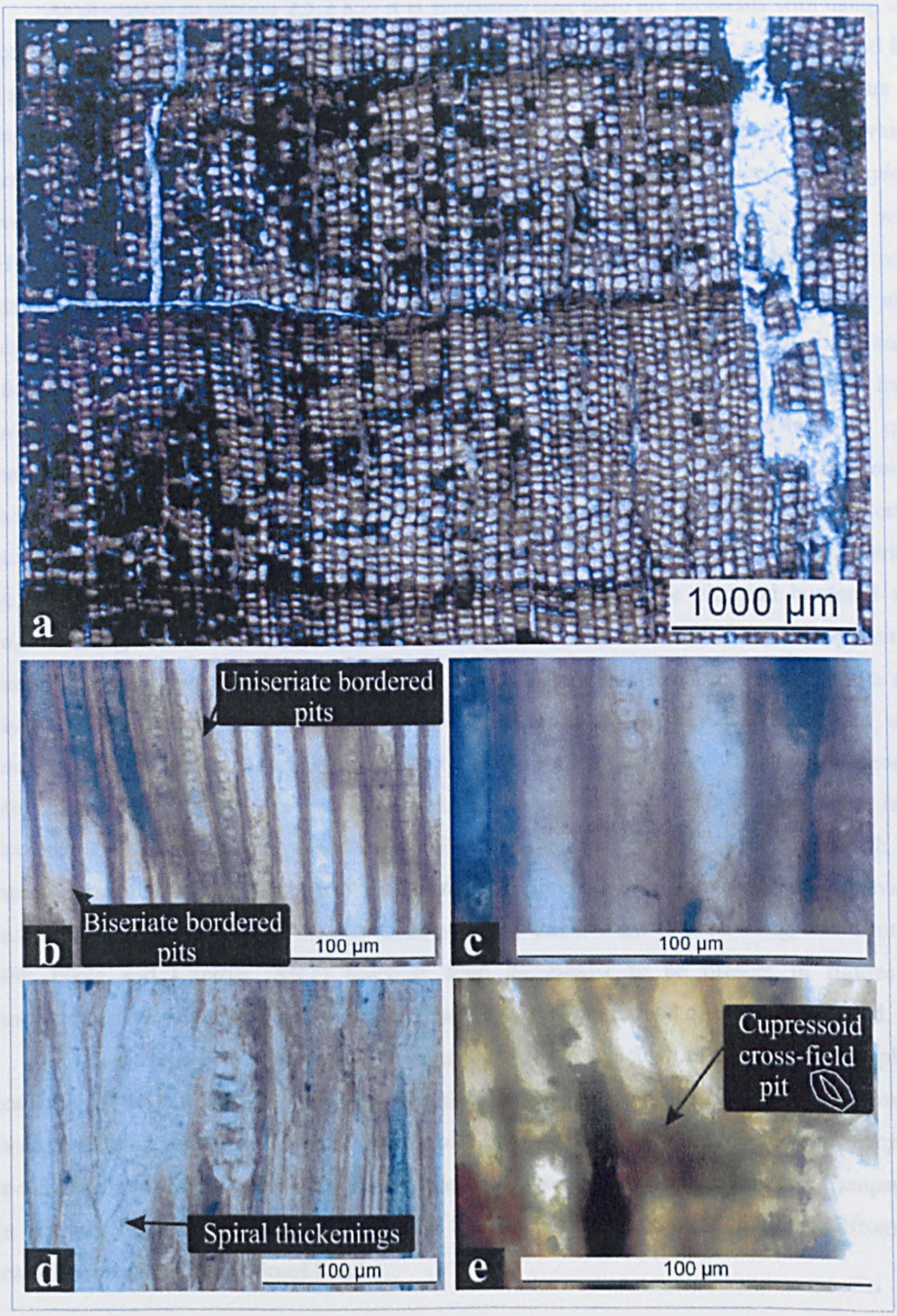


Figure 2.16. Type I (*Araucariopitys*) LD108. a) Transverse section showing straight ring boundaries and copious resin filled cells. b) Radial section showing uni- and biseriate oppositely arranged bordered pits. c) Radial section showing spaced and touching bordered pits. d) Tangential section showing a uni- and biseriate ray and spiral thickenings. e) Radial section showing a cupressoid cross-field pit (sketch of pit shown in label).

As discussed in section 2.5.2.8.2. it is suggested that there are problems with using the name *Araucariopitys*. As this name is still widely used it was decided that it could be used for this sample as the specimen was most comparable to previous descriptions of this form-genus. Using Kraüsel's (1949) scheme for this specimen proved difficult, depending on which characteristics were followed. LD108 seems to have affinities with *Protocupressinoxylon*, *Protophyllocladoxylon* or *Araucariopitys*. *Protocupressinoxylon* shares characteristics with LD108 such as the absence of resin canals and the presence of only a few cross-field pits. It also contains cupressoid cross-field pits as seen in LD108 (Kraüsel, 1949). However it also contains taxodioid and glyptostroboid type cross-field pits and very dense Abietinaceous pitting in the horizontal walls, not observed in LD108 (Kraüsel, 1949). LD108 also differs from *Protocupressinoxylon* in having some alternately arranged bordered pits and biseriate rays (Francis, 1983). Therefore *Protocupressinoxylon* is discounted. *Protophyllocladoxylon* is discounted because, although LD108 contains the araucarian aspects of this genus, other features do not match. *Protophyllocladoxylon* is characterized by the presence of araucarian-type cross-field pitting, the presence of podocarpoid or dacrydioid type pits and bordered pits rarely touching which exclude LD108 even though it shares the features of 1-3 oppositely arranged bordered pits and smooth horizontal walls of ray cells (Kraüsel, 1949; Medlyn and Tidwell, 1975). According to Kraüsel's (1949) scheme, LD108 has closest affinity with *Araucariopitys* in having mixed type bordered pits (transitional forms) and smooth horizontal walls of ray cells. LD108 is very similar to the *Araucariopitys* of late Albian age from Alexander Island, Antarctica, described by Falcon-Lang and Cantrill (2000), although the tangential rays are shorter and strictly uniseriate in their sample, unlike LD108. Previous descriptions of *Araucariopitys* do not mention spiral thickenings (Falcon-Lang and Cantrill, 2000; Poole and Cantrill, 2001) however they do appear to be present in figures of *Araucariopitys* presented in Shilkina's (1967) paper on the fossil wood of Franz-Josef Land.

Cretaceous age *Araucariopitys* has mainly been described from Southern Hemisphere sites such as the late Albian specimen of Falcon-Lang and Cantrill (2000) from Alexander Island, Antarctica discussed above. Poole and Cantrill (2001) also described *Araucariopitys* from the Williams Point beds of Livingston Island, Antarctica of Cenomanian-early Campanian age. However, Northern Hemisphere samples have been reported by Shilkina (1967) from the Lower Cretaceous of Franz-Josef Land.

2.5.2.10. Type J (*Xenoxylon* Gothan 1905)

Specimens: Svalbard LD130

2.5.2.10.1. Description

Sample LD130 is probably derived from a mature stem. There are 11 growth rings present in this sample (Figure 2.17.a). Growth rings are sometimes indistinct and the transition from early to latewood is gradual (Figure 2.17.a).

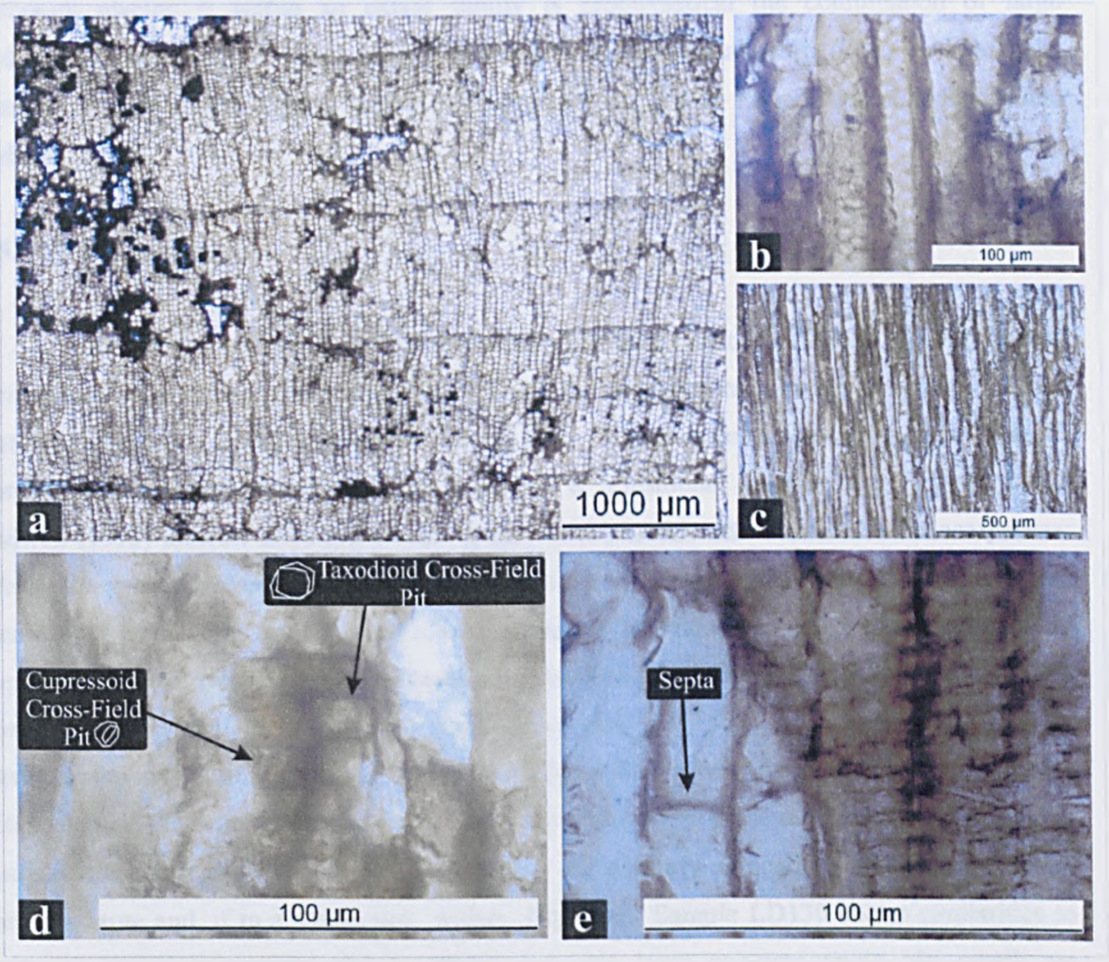


Figure 2.17. Type J (*Xenoxylon*) LD130. a) Transverse section showing straight ring boundaries. b) Radial section showing biseriate alternate pits. c) Tangential section showing long rays. d) Radial section showing cupressoid and taxodioid cross-field pits (sketch on labels show outlines of pits. e) Radial section showing septa.

The radial walls of tracheids bear mainly biseriate (55%) bordered pits with some uniseriate (32%) and a few triseriate (13%) forms also being observed (Figure 2.17.b). Where the bordered pits are multiseriate they are mainly arranged alternately (87%) with a minority being oppositely arranged (13%). The bordered pits are always touching (100%).

Rays seen in tangential section are uniseriate, 1-41 cells high, mean of 19 cells (Figure 2.17.c). In radial section cross-fields appear to contain mainly 2 pits arranged side-by-side or superimposed although upto 4 pits may be present in some areas. Cross-field pits seem to be mainly taxodioid with some cupressoid or podocarpoid, occasional slit-like apertures were also observed (Figure 2.17.d). The horizontal walls are thin and unpitted. Ray tracheids, spiral thickenings and horizontal and vertical resin canals are absent. Xylem parenchyma and septa are present (Figure 2.17.e).

As this sample represents an extinct genus, no comparison can be made to extant wood. Although placing it within an extant family is problematical the combination of large podocarpoid pits in cross fields, smooth horizontal and tangential walls of ray cells and the absence of resin canals suggest possible affinity with the family Podocarpaceae (Medlyn and Tidwell, 1975).

2.5.2.10.2. Identification

Comparison with Kraüsel's (1949) scheme indicates that LD130 has an affinity with *Xenoxylon* due to the presence of the following features: pits on radial walls of tracheids large, arranged alternately and cross-fields with large pits. The presence of some Araucarian features combined with modern ones indicates that this is a transitional conifer form. Medlyn and Tidwell (1975) indicate there are 3 fossil genera with possible affinities to the Podocarpaceae: *Mesembrioxylon*, *Protophyllocladoxylon* and *Xenoxylon*. *Mesembrioxylon* is an artificial genus established to include extinct genera with affinities to Podocarpaceae, replacing Gothan's genera *Podocarpoxylon* and *Phyllocladoxylon* (Medlyn and Tidwell, 1975). Sample LD130 contains cupressoid and taxodioid cross-field pits not seen in *Phyllocladoxylon* or *Podocarpoxylon* (Kraüsel, 1949). *Protophyllocladoxylon* is very similar to *Xenoxylon* with Kraüsel (1949) indicating that the only feature separating them is the nature of the pits in radial walls of tracheids: in *Protophyllocladoxylon* they are typically araucarioid whilst in *Xenoxylon* they are large and, if in a single row, widely dispersed. Sample LD130 shows similarities to both, having some araucarioid type pitting but also large non-araucarioid pits which are however touching, not dispersed. However Medlyn and Tidwell (1975) indicate that araucarioid type cross-field pitting occurs in all species of *Protophyllocladoxylon* which excludes LD130 from this genus and indicates a closer affinity with *Xenoxylon*.

Xenoxylon spans a rather narrow geological range of Middle Triassic to Lower Cretaceous (Medlyn and Tidwell, 1975), with the vast majority of examples occurring in pre-Cretaceous strata. Philippe and Thevenard (1996) indicate, from a review of *Xenoxylon* occurances, that during the Cretaceous *Xenoxylon* was limited to cool, wet areas of the high northern latitudes. Early Cretaceous species *X. latiporosus* and the Lower Cretaceous *X. barbery* are both reported from Franz-Josef Land by Shilkina (1967). Foliage of *Xenoxylon* is unknown although it has been suggested that there may be a relationship with *Elatides*, *Podozamites* or *Baiera* (Medlyn and Tidwell, 1975), none of which have been confirmed.

2.5.2.11. Type K (*Taxoxylon* Houlbert 1910)

Specimens: Svalbard SN25 4

2.5.2.11.1. Description

This sample is probably derived from branch material as there is a large proportion of compression wood present (Figure 2.18.a). There are 20 distinct growth rings present in this sample. The transition from early to latewood is gradual.

The radial walls of longitudinal tracheids bear mainly uniseriate (64%) bordered pits although biseriate (34%) and rare triseriate (2%) forms also occur (Figure 2.18.b). Where the bordered pits are multiseriate most are oppositely arranged (81%) with a minor alternate component (19%; Figure 2.18.c). The bordered pits are mainly touching (82%) with some being spaced >1 pit diameter apart (18%).

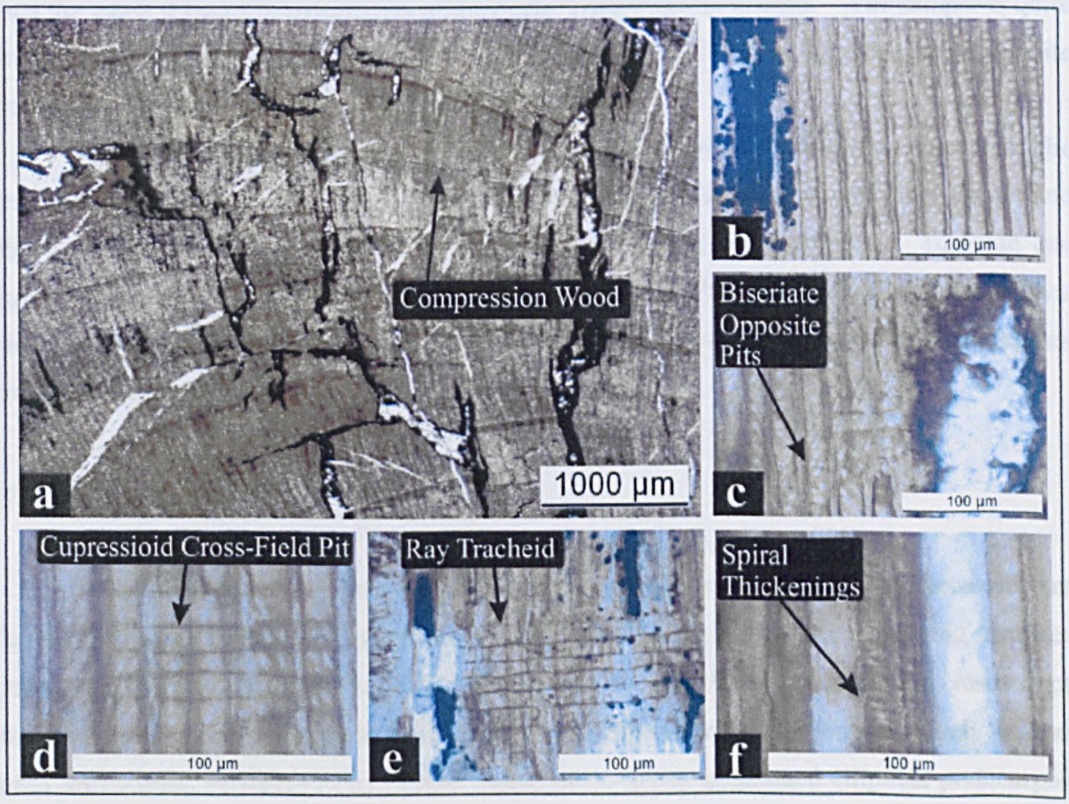


Figure 2.18. Type K (*Taxoxylon*) SN25 4. a) Transverse section showing compression wood. b) Radial section showing uni- and biseriate bordered pits. c) Radial section showing biseriate bordered pits. d) Radial section showing 1, 2, 3 and 4 pits per cross-field mainly cupressoid. e) Radial section showing ray tracheid. f) Radial section showing spiral thickenings.

Rays seen in tangential section are uniseriate. Some dark resinous material was seen within cells and some were also pitted. The rays are 1-11 cells high with mean of 5. The cross-field areas appear to contain 1-4 pits of piceoid, cupressoid or possibly taxodioid type (Figure 2.18.d). The pits are either arranged singly, vertically or horizontally side-by-side in two rows. The horizontal walls of ray cells are unpitted. Ray tracheids are present (Figure 2.18.e). Abundant spiral thickenings and some septa are present (Figure 2.18.f).

2.5.2.11.2. Identification

Using Kraüsel's (1949) scheme the closest match to the sample described here is *Taxoxylon*: pits on radial walls being at least in part circular, if arranged in several rows mainly separated by bars of Sanio, pits on radial walls of tracheids never typically araucarioid, generally or predominantly circular and opposite, normal wood without resin canals, spiral thickenings present. Fossil woods of Taxaceae have variously been described as *Taxoxylon*, *Taxaceoxylon* and *Torreyoxylon* (Roy, 1972). *Taxoxylon* is used in a more general sense whilst when the wood shows definite affinity to Taxaceae *Taxaceoxylon* is used. The sample is quite similar to *Taxaceoxylon mcmurrayensis* described by Roy (1972) but as the preservation is quite poor in this sample it has been included in *Taxoxylon*.

Taxaceoxylon wood has been described from the Early Cretaceous sediments of the Lower Athabasca River region of Alberta Canada. Although it is unclear whether shoots and other unspecified remains described by Vakhrameev (1991) from Neocomian, Turonian and Senomanian sediments in the Privelkhoyanje area of Lena Province and Vilyui Basin area, Siberia, are *Taxoxylon* or *Taxaceoxylon* it is clear that Taxaceae were present in those regions during those time periods.

2.5.2.11.3. Comparison with extant wood

When compared to extant wood this sample is most similar to Taxaceae and Cephalotaxaceae (Taxales) described by Greguss (1955) as having the following features: growth rings distinct or indistinct, tracheids rounded or angular in cross section, resin ducts absent in some genera only, occasionally wood parenchyma, in all tracheids relatively delicate spiral thickenings, in cross-field 1-3 (4-6) round or obliquely positioned elliptical podocarpoid or cupressoid pits, tangential walls of ray parenchyma always smooth, horizontal walls sporadically thickened, rays 1-28 cells high, biseriate in places. Although this is not a perfect fit to the sample described here Greguss (1955) notes that the description itself is not perfect and is unclear so cannot be regarded as final and absolute in all cases.

Taxus is largely distributed in the Northern Hemisphere particularly Europe, North Africa, Asia and North America (Vidakovic, 1991). The typical habitat of this genus is up to 2300m elevation within the temperature range of 1-10°C, above or below those temperatures for more than a few days will cause sterility (Vidakovic, 1991). It can however withstand shade and open positions and will grow equally well on poor, shallow and deep, rich soils.

2.5.2.12. Type L (*Cupressinoxylon* Goeppert 1850)

Specimens: Svalbard LD132
Canadian Arctic E137

2.5.2.12.1. Description

Sample E137 contains a lot of deformation in transverse section making it difficult to determine whether it is derived from branch or trunk material, however it has tentatively been classified as branch (Figure 2.19.a). Sample LD132 is probably derived from a small stem (Figure 2.19.b). Both samples have distinct growth rings (Table 2.8). The transition from early to latewood is conspicuous. There appears to be a high proportion of dark resinous cell contents present (Figure 2.19.b).

The radial walls of tracheids bear predominantly uniseriate bordered pits, however a few biseriate and rare triseriate forms also occur (Table 2.8 and Figure 2.19.c). Where the pits are multiseriate they are oppositely arranged although alternate forms also occur (Table 2.8 and Figure 2.19.d). The bordered pits are predominantly touching but a few are spaced (Table 2.8). There are resin spools present the in radial tracheids of E137 (Figure 2.19.e).

Rays seen in tangential section are predominantly uniserate with rare examples with biseriate cells in the body, again there is a lot of dark resinous material filling cells (Figure 2.19.f). Sample LD132 has bead-like thickenings on the tracheid walls in tangential section (Figure 2.19.f). Rays are between 1 and 12 cells high with mean values of 4 and 5 (Table 2.8). The cross-fields are poorly preserved in both samples but E137 appears to contain 1-2 pits in the main body and 4-5 pits in marginal cells, LD132 seems to contain 1-6 pits. In LD132 most pits are arranged singly although some have 2-3 pits arranged side-by-side and several were observed with 6 in tiers irregularly arranged. Horizontal walls are thin and smooth. Ray tracheids are present in sample E137. Cross-field pits appear to be piceoid, cupressoid or taxodioid (Figures 2.19.g and h). A few scattered septa are present in sample LD132. Spiral thickenings and resin ducts are absent.

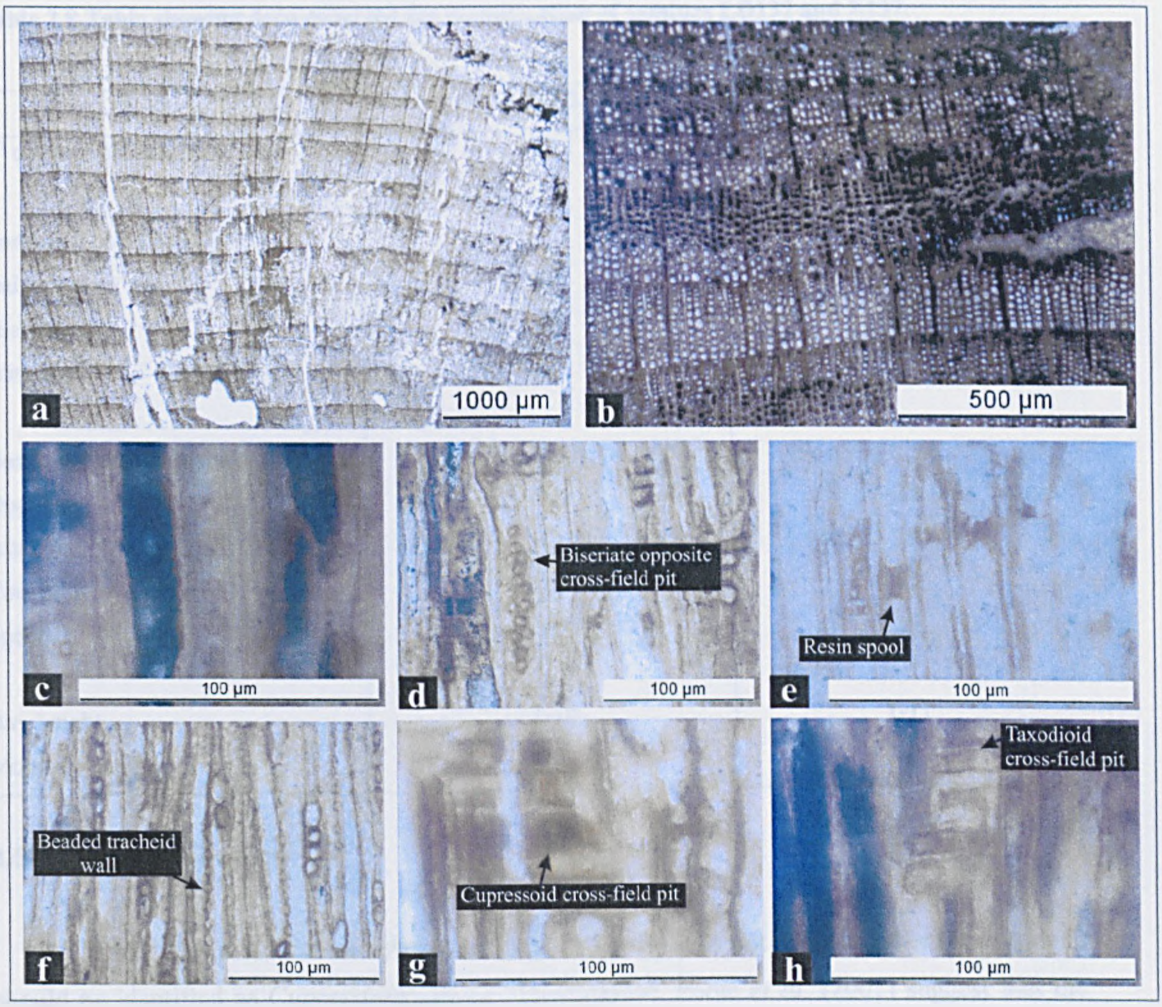


Figure 2.19. Type L (*Cupressinoxylon*). a) Transverse section showing poor preservation (E137). b) Transverse section showing reasonably straight ring boundaries (LD132). c) Radial section showing uniseriate bordered pits (LD132). d) Radial section showing biseriate oppositely arranged bordered pits (LD132). e) Radial section showing resin spools (E137). f) Tangential section showing beaded tracheid walls and resin filled ray cells (LD132). g) Radial section showing cupressoid cross-field pit (E137). h) Radial section showing taxodioid and narrow bordered (taxodioid/glyptostroboid) cross-field pits (LD132).

Table 2.8.Table showing data collected for identification of samples LD132 and E137.

	LD132	E137
N° of rings present	27	77
Bordered pit type (%)		
Uniseriate	79	90
Biseriate	19	8
Triseriate	2	2
Bordered pit arrangement (%)		
Opposite	57	71
Alternate	43	29
Touching	72	81
Spaced	28	19
Ray height	1-12	1-11
Mean ray height	5	4

2.5.2.12.2. Identification

Under the classification scheme of Kraüsel (1949) it is not clear whether these sample should be identified as *Cupressinoxylon* or *Taxodioxylon.* Poole *et al.* (2001) suggest that the presence of predominantly smooth tangential walls and cross-field regions characterized by cupressoid pits define the form-genus *Cupressinoxylon* but the samples here contain mixed types of pits and the tangential walls in LD132 are beadlike. However Falcon-Lang (2003) had difficulty distinguishing the two genera as his samples also contained both cupressoid and taxodioid cross-field pits therefore he classified his samples as *Cupressinoxylon/Taxodioxylon* type. Sample E137 described here has many similarities to the *Cupressinoxylon* describe by Poole *et al.* (2003) from King George Island, Antarctica although there are differences including the lack of taxodioid cross-field pits in their sample. Sample LD132 appeared to have many similarities to *Glyptostroboxylon* (Kraüsel, 1949). It was however felt that the samples described here had more similarity with *Cupressinoxylon* and they were therefore included in this form-genus. *Cupressinoxylon* has been described as an illegitimate renaming of *Retinodendron.* Bamford *et al.* (2002) proposed that *Cupressinoxylon* be conserved. *Cupressinoxylon* has been widely used in a broad sense for a genus comprising all woods of Cupressaceae type (Francis, 1983; Poole *et al.*, 2001; Bamford *et al.*, 2002; Falcon-Lang, 2003) whilst *Retinodendron* has not been used for over a century. Therefore conservation of *Cupressinoxylon* would avoid further confusion.

Cupressaceae remains are present across the Northern Hemisphere within Cretaceous sediments. Wood has been reported from Early Cretaceous sediments of Franz-Josef Land by Shilkina (1967). Although Seward (1926) reports twigs and leaves that may be attributable to *Cupressus* (although they may also be of *Libocedrus* or *Thuja*) from Skansen, Western Greenland it is suggested that the Cretaceous age may be questionable as the remains were recovered from loose blocks on a scree slope where both Cretaceous and Tertiary sediments are now known to occur. Further south Gröck *et al.* (1999) found Aptian age wood fragments on the Isle of Wight, UK and unspecified remains of Cupressaceae have been found in mid Albian age sediments of Lena Province, Siberia and Coniacian to Maastrichtian age of the Chandler-Coleville Region of Alaska (Smiley, 1969; Vakhrameev, 1991).

2.5.2.12.3. Comparison with extant wood

According to Barefoot and Hankins (1982), resin plugs only occur in *Araucaria, Callitris, Cupressus* spp., *Dacrydium, Fitzroya, Juniperus, Libocedrus, Podocarpus, Saxegotheae, Thuja* and *Widdringtonia* spp. Sample E137 seems to fit best with Greguss' (1955) description of *Cupressus*: growth rings distinct, tracheids in cross section angular and rounded, resin ducts absent, wood parenchyma frequent, commonly with resin content, in some species all walls of ray parenchyma smooth and thin, in others horizontal walls pitted and tangential walls smooth, but in most of them the horizontal walls are pitted while the tangential walls are thickened, unevenly punctate or beadlike, or quite exceptionally dentate, horizontal walls of longitudinal parenchyma smooth or from slightly to markedly thickened, nodular, in cross-fields 1-3 (4-5) cupressoid, taxodioid or podocarpoid pits, spiral thickenings absent, transverse tracheids in some species rarely present, rays 1-30 cells high, tangential walls of ray cells smooth or with scalariform or sievelike thickenings. LD132 fits this description particularly as from Greguss' (1955) descriptions the Cupressaceae appear to be the only family which can have bead-like tangential walls.

Cupressus occurs in warm moderate and subtropical regions of the Northern Hemisphere including the eastern Mediterranean, the Himalaya, China and in America from Oregon to Mexico. *Cupressus* is able to grow in diverse habitats, and it can withstand poor soil with virtually no nutrients in isolated sites on mountains. It can tolerate drought, frost, sleet, fog and shade between 1000 and 3000m elevation.

2.5.3. Climatic inferences based on Nearest Living Relative (NLR) analysis for Northern Hemisphere

In previous studies Nearest Living Relative analysis has often been used to determine the environmental and climatic conditions under which trees grew during past greenhouse periods (Horrell, 1991; Mosbrugger, 1999; Greenwood *et al.*, 2005; Moss *et al.*, 2005). These studies have produced some interesting findings from the material available but there are problems with this type of analysis because trees growing during the Cretaceous may have functioned differently with different physical limitations. It was shown by Royer *et al.* (2002) that the ability of plants to survive in different climate zones was different in a world with higher CO_2 concentrations than present. For example leaves from modern genera froze at warmer temperatures when grown in elevated CO_2 (800ppmv) and this effect occurred across all plant groups (e.g. palms, taxodiaceous conifers). It was therefore suggested that cold month mean temperatures produced by this method for fossil plants should be increased by at least 1.5 to 3°C because freezing of leaves occurs at warmer temperatures under elevated CO_2. Although these problems are recognized it was decided to use NLR here in order to compare the findings of this study with previous studies (Mosbrugger, 1999; see also Chapters 1, Section 1.4.1).

In the Northern Hemisphere the modern counterparts of the fossil conifers (Table 2.9) suggest that the habitat in Svalbard would have been moist in cool upland, mountainous areas and warm temperate in areas with rivers and/or swamps present in the lowlands. The dominance of *Taxodioxylon* suggests that the forests were similar to the warm temperate forests found near the coast of Louisiana, Florida and Georgia to North Carolina in the USA which are currently dominated by *Taxodium distichum* (swamp cypress) forests in wet, swampy areas (Moore, 1982). The presence of *Taxodium* type conifers also suggests that this may represent a microenvironment with mean annual temperatures that were around 24°C, making the conditions mesothermal to megathermal (Moss *et al.*, 2005). However, modern *Taxodium* is a relictual genus, occurring naturally only in small areas of the USA, although it is known to have had a wider distribution in the past and has been reintroduced to cooler areas such as the UK. Therefore climate inferences from nearest living relative analysis for *Taxodium* are uncertain. There also appears to have been upland areas close-by, which would have been the source of the more exposed species such as *Cupressus* and *Juniperus*. The presence of *Taxus* may suggest that the climate was cool rather than warm temperate, between 1-10°C, only falling below or above these temperatures for a few days per year (Vakhrameev, 1991; Vidakovic, 1991). This estimate is closer to that of Philippe and Thevenard (1996) who, from the associated floral assemblages, geographical distribution and sedimentology, suggest that the presence of *Xenoxylon* indicates wet and/or cool climate condtions with mean annual temperatures of between 5 and 15°C.

In the Canadian Arctic the fossil tree types present are similar to those in Svalbard. The dominance of *Pinuxylon* with relatively narrow growth rings suggesting moderate warmth.

Table 2.9. Habitat requirements of modern conifer genera represented in the high latitude forests of the Northern Hemisphere (Vidakovic, 1991; Lanner, 2002).

Genus	Elevation	Soil Type	Notes
Picea	sl to 480m	light, acid, porous	prefers shaded areas
Larix	200-2400m	moderately rich	most prefer moist boggy sites
Cedrus	1000-3000m	well drained	wet coastal sites or river terraces but also in dryer upland sites, prone to frost
Taxodium	sl to 520m (*T.mucronatum* upto 2300m)		grows on wetlands, swampy terrain or river banks can tolerate temperature of -30°C
Juniperus	600-4500m	thin soils	prefers moist, sheltered semiarid sites. Can survive exposure to strong winds.
Cupressus	1000-3000m	poor	survives diverse habitats, tolerates drought, frost, sleet, fog and shade
Taxus	upto 2300m	poor shallow to deep rich	can withstand shade and open positions. Temperatures above or below 1-10°C can cause sterility
Pinus	sl to 3650m	thin or poor sandy	grows in rocky terrains

2.6. Southern Hemisphere fossil woods

This section describes the mid-Cretaceous wood samples from the Southern Hemisphere.

2.6.1. Geological setting

Figures 2.20a and b provide details of the geological setting for the Southern Hemisphere fossil wood specimens examined.

2.6.2. Descriptions of fossil woods

Forty five samples were examined in total from Southern Hemisphere sites, eight from Australia and thirty seven from Antarctica. A full list of the samples used and their identification is given in Appendix B, Table B1.1.

2.6.2.1. Type M (*Podocarpoxylon* Gothan 1905)

Specimens: Australia 872/W17, 872/W166 and 872/W167
Antarctica KG1703.23, DJ141.13, DJ144.2 and DJ141.14

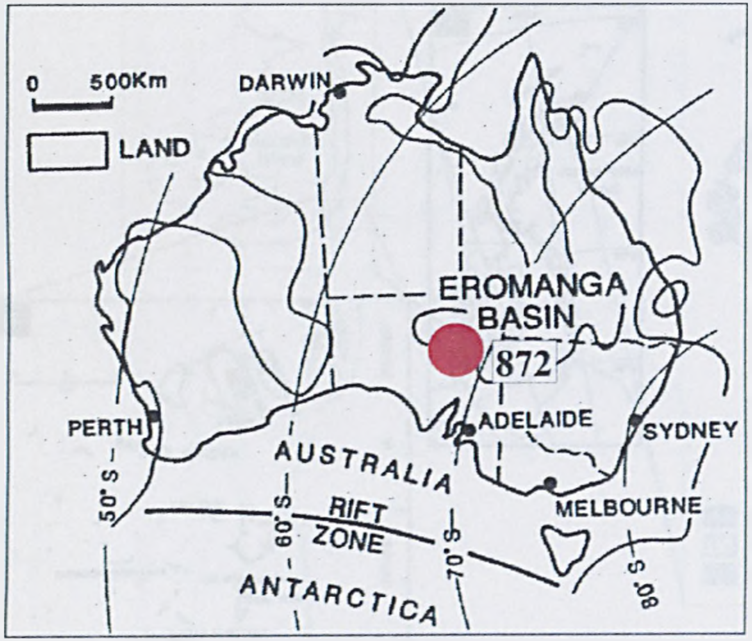
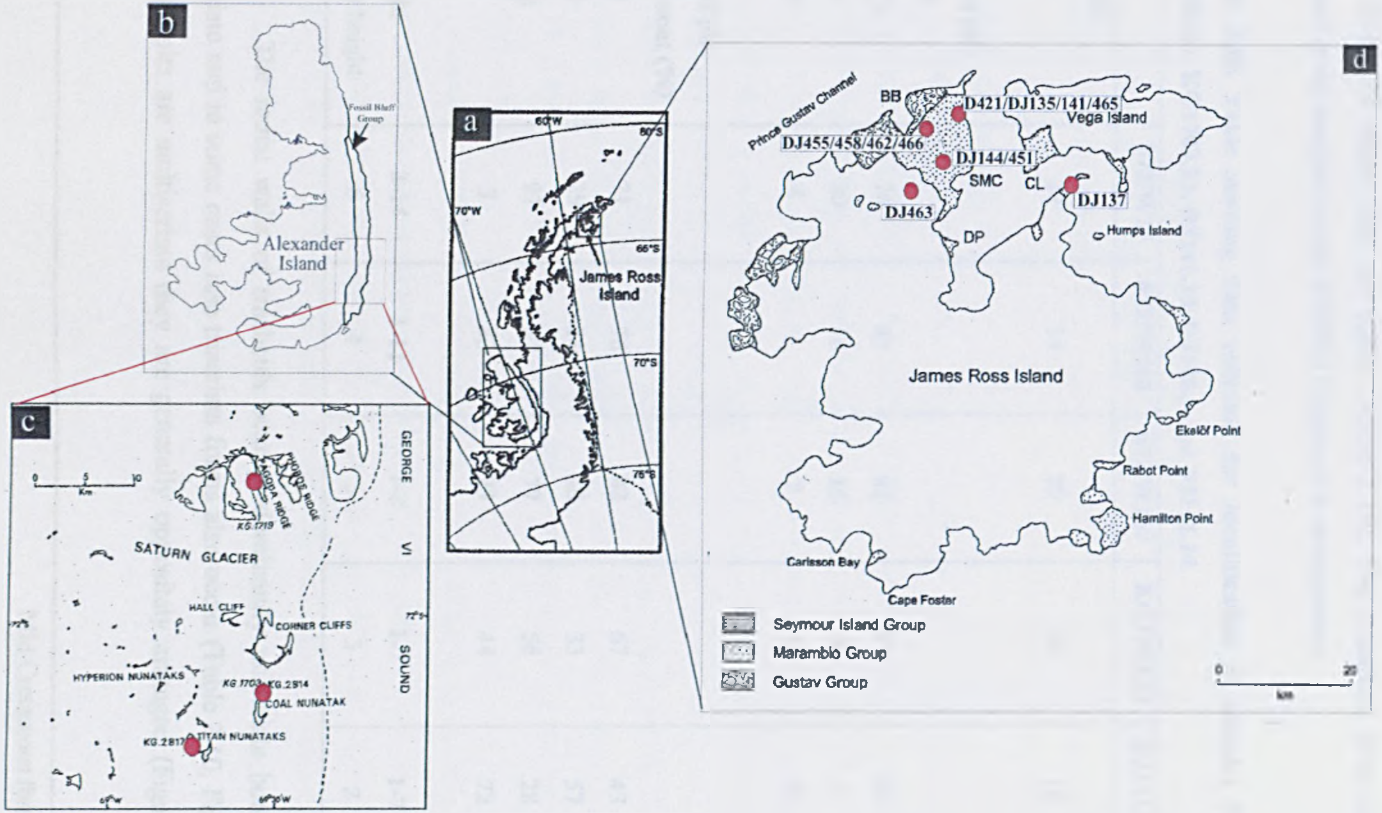


Figure 2.20.a. Geological setting of Australia (Frakes and Francis, 1990).

Location of wood specimens from Australia

- 872 = Uplands adjacent to Eromanga Basin
- Palaeolatitude in Cretaceous ~70-85°S
- Stratigraphic Unit: Bulldog Shale
- Age: Aptian-Albian
- Palaeoenviroment: Fossil wood represents trees that drifted from land into a marine basin and is preserved in fine grained mudstone. The wood is probably derived from two sources, a cool highland area and a warmer lower altitude area near the basin shoreline.



Location of wood specimens from Antarctica

- D = James Ross Island
  DJ = James Ross Island
  KG = Alexander Island
- Palaeolatitude in Cretaceous
  ~64°S for D and DJ woods
  ~70°S for KG woods
- Stratigraphic Unit: D and DJ - Marambio Group
  KG - Fossil Bluff Group
- Age: D and DJ - Turonian-Coniacian
  KG - Barremian-Albian
- Palaeoenviroment: Back-arc basin for D and DJ woods (James Ross Island). The trees grew on an emergent volcanic arc but the wood was transported out to the east into the sea where it became waterlogged and sank into basin sediments.
  Fore-arc basin for KG (Alexander Island). The woods represent braided and meandering fluvial environments. Some wood from *in situ* stumps but some from within the fluvial sediments.

Figure 2.20.b. Geological setting of Antarctica. a) Map of the Antarctic Peninsula (Francis, 1986). b) Enlarged view of Alexander Island (Howe, 2003) c) Detail of Fossil Bluff Group showing locations of some of the samples used in this thesis (Cantrill and Nichols, 1996; Falcon-Lang and Cantrill, 2001a). d) Detail map of James Ross Island showing location of specimens used in this thesis (Elliot, 1988; Crame *et al.*, 2004).

2.6.2.1.1. Description

Two samples appear to be derived from mature stem material (872/W17 and DJ141.14, Figure 2.21.a). Sample DJ144.2 may also be derived from stem material although this is difficult to confirm due to poor preservation. One sample (KG1703.23) is probably derived from branch material due to the presence of compression wood (Figure 2.21.b). Sample 872/W166 may also be derived from branch material although this is difficult to confirm due to poor preservation. In two samples (872/W167 and DJ141.13) it was not possible to identify if they originate from branch or trunk material due to the presence of feint ring boundaries and a high proportion of rot being present. Growth rings are distinct in all samples except 872/W166 and DJ141.13 where they are subtle (Table 2.10). The transition from early to latewood is gradual in all samples except 872/W17 where it is conspicuous.

Table 2.10. Table showing data collected for identification of samples 872/W17, 872/W166, 872/W167, KG1703.23, DJ141.13, DJ144.2 and DJ141.14.

	872/W17	872/W166	872/W167	KG1703.23	DJ141.13	DJ144.2	DJ141.14
N° of rings present	27	14	29	40	16	22	27
Bordered pit type (%)							
Uniseriate	76	83	82	92	93	88	98
Biseriate	20	16	16	8	7	12	2
Triseriate	4	1	2	0	0	0	0
Bordered pit arrangement (%)							
Opposite	71	76	82	67	43	67	50
Alternate	29	24	18	33	57	33	50
Touching	97	57	77	56	28	81	71
Spaced	3	43	23	44	72	19	29
Ray height	2-14	1-11	1-8	1-7	1-7	1-11	1-10
Mean ray height	6	4	3	3	2	4	3

The radial walls of tracheids bear predominantly uniseriate bordered pits although biseriate and in some cases rare triseriate forms also occur (Table 2.10, Figures 2.21.c and d). Where pits are multiseriate they are generally oppositely arranged (Figure 2.21.e) although alternate forms also occur (Table 2.10 and Figure 2.21.d). In general the pits are predominantly touching although some are spaced or >1 pit diameter apart (Table 2.10).

Rays seen in tangential section are predominantly uniseriate although rare biseriate cells are observed in the body of rays. The rays are low having 1-14 cells in height with mean values from 2 to 6 (Table 2.10 and Figure 2.21.f). All samples appear to have predominantly one pit per cross-field or occasionally 2. Where 2 pits are present these are arranged side-by-side or vertically (Figure 2.21.g). The pits appear to be predominantly podocarpoid in form however there may also be occasional taxodioid or piceoid (possibly slit-like) pits present (Figure 2.21.h). Horizontal walls of ray cells are thin and unpitted (Figure 2.21.c). Spiral thickenings are present (Figure 2.21.g). Septa and resin ducts are all absent.

2.6.2.1.2. Identification

When compared to Kraüsel's (1949) scheme five of the samples here (872/W167, DJ144.2, 872/W166, DJ141.13; KG1703.23) matched the description of *Podocarpoxylon* in having: pits on radial walls of tracheids at least in part circular, if arranged in several rows opposite, pits never typically araucarian, generally circular and opposite, normal wood without resin canals, spiral thickenings present, walls of medullary ray cells predominantly smooth and cross-field pits araucarian.

Sample DJ141.13 is similar to the Poole *et al.* (2001) description of *Podocarpus fildesense* in having subtle ring boundaries with narrow latewood zone 2-3 cells thick, radial pits typically podocarpoid as are cross-field pits, rays uniseriate 1-5 cells high. Samples 872/W167, KG1703.23, 872/W166 and DJ144.2 all have similarities to previously published form-genera, being particularly comparable to Falcon-Lang and Cantrill's (2000) *Podocarpoxylon* sp1, Ramanujam's (1971) *Podocarpoxylon ajkeanse* and Falcon-Lang and Cantrill's (2001b) *Podocarpoxylon* sp2. However there are minor differences, for example 872/W167 has a lower percentage uniseriate pitting and shorter rays than *Podocarpoxylon* sp1 (Falcon-Lang and Cantrill, 2000). However it was felt that these samples could be assigned with confidence to *Podocarpoxylon*.

Samples 872/W17 and DJ141.14 were more difficult to identify mainly due to their poor preservation. Comparison to Kraüsel's (1949) scheme lead to a variety of possible identities depending on which characteristics are followed including *Araucariopitys*, *Podocarpoxylon*, *Araucarioxylon* and *Protophyllocladoxylon*. However Falcon-Lang and Cantrill (2000) indicate that all *Araucarioxylon* species only contain alternately arranged pitting, not the mixed forms seen in these samples, therefore *Araucarioxylon* can be discounted. Sample 872/W17 also falls within Falcon-Lang and Cantrill's (2000) *Podocarpoxylon* sp1 area when plotted onto the comparison plots within their paper, having similar values of mean ray height, percentage touching pits and percentage uniseriate pitting.

Sample DJ141.14 contains large oval pits in cross-fields which is very distinctive of some living podocarps (Francis, 2000). All of these samples were therefore placed in the form-genus *Podocarpoxylon*. Although several species are probably represented no attempt was made to separate them.

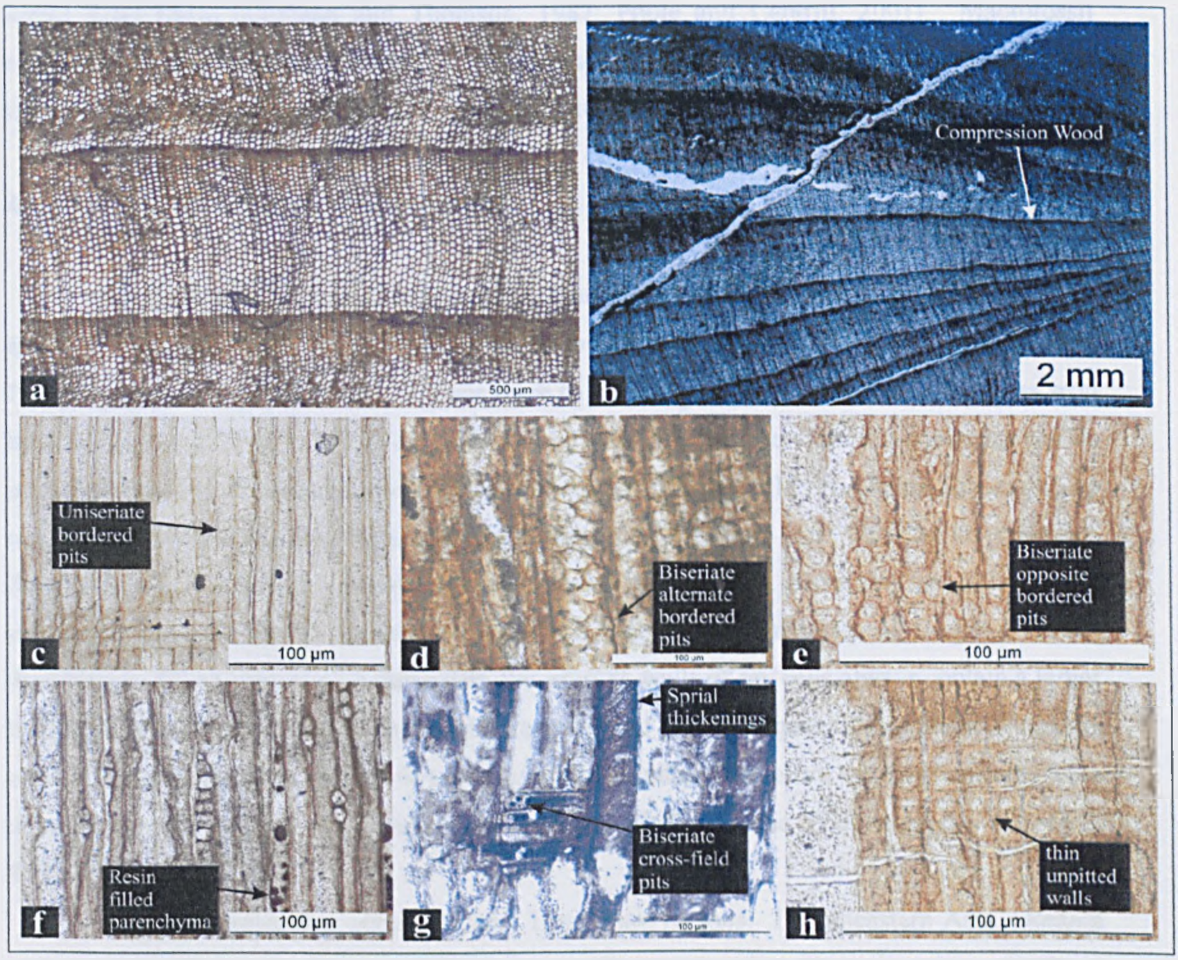


Figure 2.21. Type M (*Podocarpoxylon*). a) Transverse section showing straight ring boundaries (872/W17). b) Transverse section showing abundant compression wood (KG1703.23). c) Radial section showing uniseriate bordered pits (DJ141.14). d) Radial section showing biseriate alternate bordered pits (872/W17). e) Radial section showing biseriate opposite bordered pits (DJ141.14). f) Tangential section showing uni- and biseriate rays and resin filled parenchyma (DJ144.2). g) Radial section showing biseriate cross-field pits (KG1703.23). h) Radial section showing singly arranged taxodioid cross-field pits and unpitted thick horizontal ray walls (DJ141.14).

Evidence for the presence of Podocarpaceae during the Cretaceous is abundant for the Southern Hemisphere. *Podocarpoxylon* wood has been identified within the Aptian Cerro Negro Formation of the Byers Peninsula, Antarctica (Falcon-Lang and Cantrill, 2001b). Albian age wood, including from *in situ* trees, have also been found on Alexander Island, Antarctica with their identification being supported by the presence of leaves, shoots, cones and ovules (Francis, 1999; Falcon-Lang and Cantrill, 2000, 2001a and b). Leaves of podocarps dating from the Albian to the Cenomanian have also been reported by Parrish *et al.* (1998) from the Clarence Valley, New Zealand. Wood has been found within Cenomanian to Campanian sediments of Williams Point, Antarctica and this is supported by the presence of Podocarpaceae pollen (*Microcachrys* and *Dacrydium*) from the Coniacian to Campanian sediments of the James Ross Basin (Dettman and Thomson, 1987; Poole and Cantrill, 2001). Macrofossil evidence of Podocarpaceae wood (Cape Lamb, Antarctica) within the Maastrichtian is supported by pollen (Horrell, 1991; Cesari *et al.*, 2001).

2.6.2.1.3. Comparison with extant wood

Barefoot and Hankins (1982) suggest that thin horizontal walls of ray cells are only found in Araucariaceae, Podocarpaceae or a few Cupressaceae. They also indicate that Podocarpaceae is the only family of these three to include taxodioid cross-field pitting, as seen here in samples 872/W17, 872/W166, DJ144.14 and 872/W167, therefore these samples can be included within the Podocarpaceae. When compared to Greguss' (1955) scheme Araucariaceae can be discounted for the remaining three samples described here because he describes Araucariaceae as having 2-5 seriate bordered pits always arranged alternately and 2-16 minute pits in the cross-fields, all features not observed here. On examination of Greguss' (1955) description of the Cupressaceae those with thin smooth walls of ray cells always contain a larger number of cross-field pits than observed here and those pits were generally cupressoid such as seen in *Acuminatus* Parl. and *Widdringtonia whitei* Rendle. Therefore the Cupressaceae were also discounted and the remaining three samples placed in the Podocarpaceae (DJ144.2, DJ141.13 and KG1703.23).

Modern *Podocarpus* occurs in three large plant regions: I southeastern Asia, Oceania and Australia, II tropical Africa and Madagascar, III central and southern America, mostly in mountainous areas of tropical to sub-tropical regions of the Southern Hemisphere although it is also found in warm and cool temperate areas (Vidakovic, 1991). The typical habitat of this genus is in mountainous regions between 1500 and 3000m elevation. It grows in strongly seasonal areas with high rainfall and high summer temperatures (University of Hamburg website, http://biologie.uni-hamburg.de, accessed 4 July 2005).

2.6.2.2. Type F (*Taxodioxylon* Hartig 1848 em. Gothan)

Specimens: Antarctica KG4626.1, DJ451.4, DJ455.1, DJ458.1 and DJ462.5

2.6.2.2.1. Description

All of these samples appear to be derived from mature stem material (Figure 2.22.a). All specimens contain distinct growth rings (Table 2.11). The transition from early to latewood is either conspicuous, (DJ458.1, DJ462.5, DJ455.1 and KG4626.1) or gradual (DJ451.4). Only the transverse thin section was available for specimen KG4626.1 however it had previously been identified at the British Antarctic Survey (BAS).

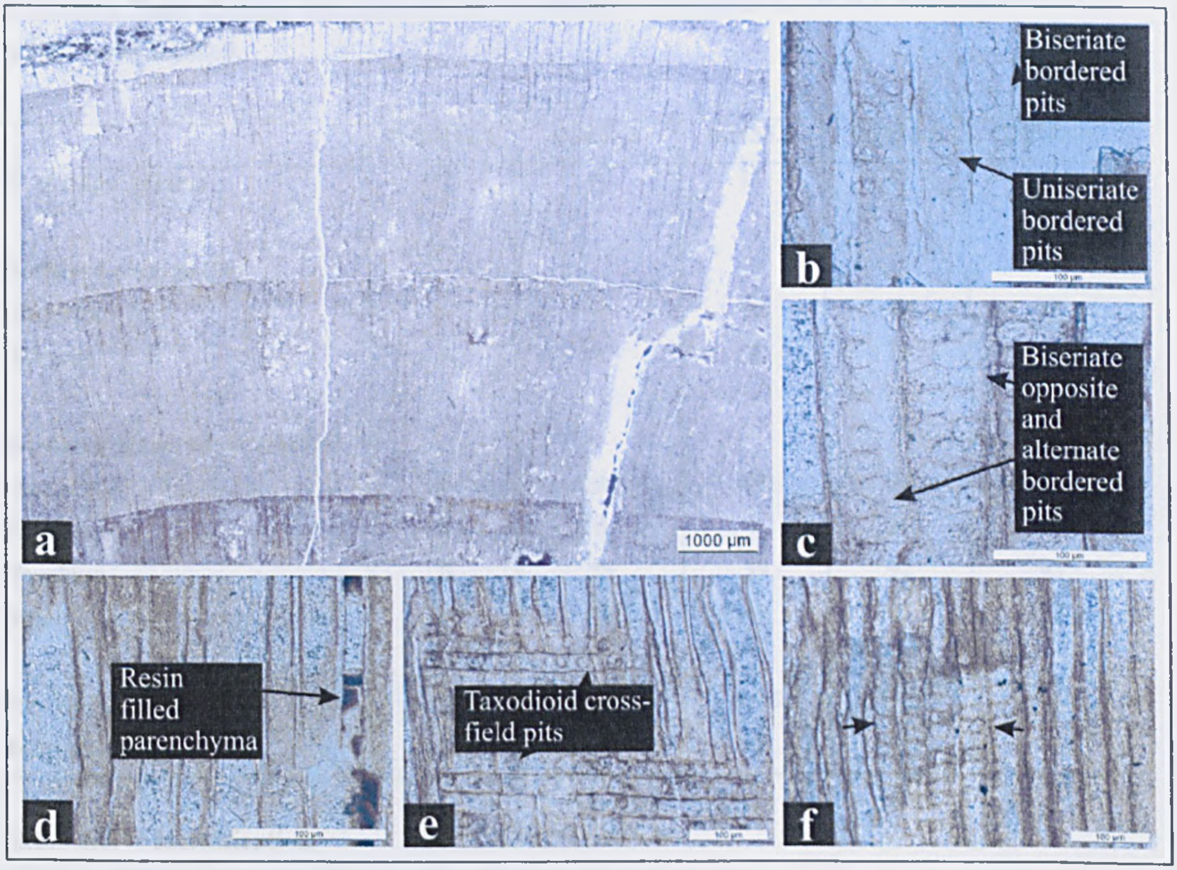


Figure 2.22. Type F (*Taxodioxylon*). a) Transverse section showing straight ring boundaries (DJ455.1). b) Radial section showing uni- and biseriate opposite bordered pits (DJ451.4). c) Radial section showing biseriate opposite and alternate bordered pits (DJ455.1). d) Radial section showing resin filled parenchyma (DJ462.5). e) Radial section showing taxodioid cross-field pits (DJ455.1). f) Radial section showing cross-field pits arranged singly or side-by-side (DJ458.1).

The radial walls of tracheids bear uniseriate bordered pits although rare biseriate forms also occur (Table 2.11 and Figure 2.22.b). Where bordered pits are multiseriate they are predominantly oppositely arranged although some alternately arranged pits are also present (Table 2.11 and Figure 2.22.c). The pits are either touching or spaced (Table 2.11). Xylem parenchyma is present in some of the samples with resin content (Figure 2.22.d).

Rays seen in tangential section are predominantly uniseriate although rare biseriate cells were observed in the body of rays (DJ451.4, DJ462.5, DJ458.1). Rays are 1-21 cells high with mean values between 5 and 8 (Table 2.11). The cross-field areas appear to contain 1-4 possibly 5 pits which are exclusively taxodioid (Figure 2.22.e). Where more than 1 pit is present they are side-by-side or in vertical pairs (Figure 2.22.f). The horizontal walls of ray cells are thin to thickened and are unpitted. Occasional spiral thickenings are present in DJ458.1. Septa and resin ducts are absent.

Table 2.11. Table showing data collected for identification of samples KG4626.1, DJ451.4, DJ455.1, DJ458.1 and DJ462.5.

	KG4626.1	DJ451.4	DJ455.1	DJ458.1	DJ462.5
N° of rings present	12	8	11	23	9
Bordered pit type (%)					
Uniseriate	0	96	98	88	97
Biseriate	0	4	2	12	3
Bordered pit arrangement (%)					
Opposite	0	100	100	70	50
Alternate	0	0	0	30	50
Touching	0	39	59	92	43
Spaced	0	61	41	8	57
Ray height	0	1-20	1-15	1-21	1-14
Mean ray height	0	5	5	8	5

2.6.2.2.2. Identification

These fossils were compared with various species of *Taxodioxylon* and other Taxodiaceous fossil wood (Kraüsel, 1949; Ramanujam and Stewart, 1969; Ramanujam, 1971; Falcon-Lang and Cantrill, 2000; Meijer, 2000; Fairon-Demaret *et al.*, 2003). All samples examined came out as being *Taxodioxylon* when compared to Kraüsel's (1949) scheme. Sample DJ451.4 is very similar to that described by Meijer (2000) however xylem parenchyma is present in their sample but appears rare to absent in the sample described here. The remaining samples appear to have strong affinities to *Taxodioxylon drumhellerense* (Ramanujam and Stewart, 1969).

In the Southern Hemisphere the Taxodiaceae are represented by wood, cones, shoots and leaves in Albian age sediments on Alexander Island, Antarctica (Falcon-Lang and Cantrill, 2000; Cantrill and Falcon-Lang, 2001).

2.6.2.2.3. Comparison with extant wood

These samples were identified as having affinities to modern Taxodiaceae on the basis of displaying the following characteristics when compared to Greguss' (1955) scheme: distinct growth rings, smooth to sparsely pitted horizontal walls of ray cells, 1-30 cells high rays with generally uniseriate but occasionally 1-2 biseriate in the body, 1-6 taxodioid to glyptostroboid pits in the cross-fields and the absence of resin ducts and spiral thickenings. Included within the Taxodiaceae family are *Athrotaxis*, *Cryptomeria*, *Cunninghamia*, *Glyptostrobus*, *Sequoia* (including *Sequoiadendron*), *Taiwania*, *Taxodium* and *Sciadopitys* (Phillips, 1941; Greguss, 1955). Horizontal walls in *Athrotaxis*, *Crytomeria*, *Sciadopitys* and *Taiwania* are described as being very rarely smooth unlike the samples here therefore these genera are discounted. *Sequoiadendron* can be discounted because this genus always has bordered pits in a single vertical row even in wide tracheids (Meijer, 2000) which is contrary to all samples here. The cross-fields pits in *Glyptostrobus* are glyptostroboid with narrow borders and do not include the taxodioid type seen here. The pit apertures in *Cunninghamia* are oriented vertically, not at an angle as seen here, therefore these two genera are discounted (Greguss, 1955). The samples described here show similarities to *Sequoia* in having thin and smooth horizontal walls however *Sequoia* has 1-3 seriate bordered pits and common notched pits not seen here therefore this genus is also discounted. Therefore the samples described here seem to be most similar to *Taxodium*.

Although mainly confined to the Northern Hemisphere the exception is *Athrotaxis* which occurs in the mountains of Tasmania (Vidakovic, 1991; Meijer, 2000). For typical habitat see section 2.5.2.6.4.2.

2.6.2.3. Type I (*Araucariopitys* Jeffrey 1907)

Specimens: Antarctica 5215 and DJ144.7

2.6.2.3.1. Description

Both samples may be derived from mature stems however preservation is poor and it is difficult to determine (Figure 2.23.a). Both samples contain distinct growth rings (Table 2.12). The transition from early to latewood is gradual in both cases.

Radial walls of tracheids bear predominantly uniseriate bordered pits, rare biseriate forms and also very rare triseriate forms (Table 2.12 and Figure 2.23.b). Where bordered pits are multiseriate they are either oppositely or alternately arranged (Table 2.12). The pits are either touching or spaced (Table 2.12).

Rays seen in tangential section are predominantly uniseriate although there are biseriate cells within the body of some. Rays are 1-17 cells high with mean values of 4 and 6 (Table 2.12). Cross-field areas appear to contain 1-4 pits although sample DJ144.7 may contain up to 6. The pits are in a variety of arrangements, single, side-by-side, in two rows or two vertically arranged (Figure 2.23.c). The type of pits appear to vary including taxodioid, podocarpoid, cupressoid and slit-like forms (Figure 2.23.d). The horizontal walls of ray cells are thin to thickened and are unpitted. Ray parenchyma, spiral thickenings, septa and resin ducts are all absent.

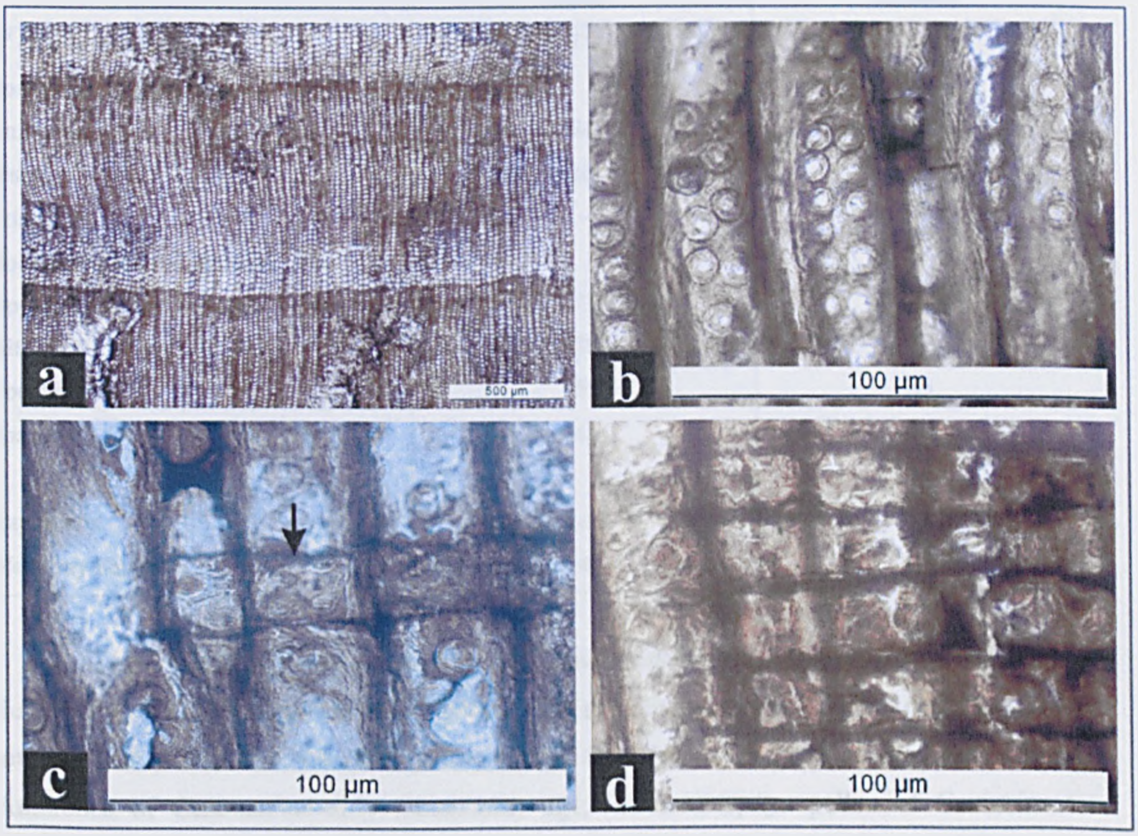


Figure 2.23. Type I (*Araucariopitys*). a) Transverse section showing straight ring boundaries (DJ144.7). b) Radial section showing uni- and biseriate alternate and opposite bordered pits (5215). c) Radial section showing 4 cross-field pits arranged in each corner (5215). d) Radial section showing slit-like and podocarpoid cross-field pits (5215).

2.6.2.3.2. Identification

When compared to Kraüsel's (1949) scheme both of these samples were assigned to *Araucariopitys* due to the presence of pits on radial walls of tracheids at least in part circular, if arranged in several rows opposite, mainly separated by bars of Sanio, pits on radial walls of tracheids mainly of mixed type with all possible gradations of structure, walls of medullary ray cells smooth, pits in 1-2 rows on tracheid walls, not particularly araucarioid (transitional forms). These samples have similarities to *Araucariopitys* described by both Falcon-Lang and Cantrill (2000) and Poole and Cantrill (2001) although there are minor differences.

As discussed in section 2.5.2.8.2 it is suggested that there are problems with using the name *Araucariopitys*. As this name is still widely used it was decided that it could be used for these samples as they were most comparable to previous descriptions of this form-genus.

Table 2.12. Table showing data collected for identification of samples 5215 and DJ144.7.

	5215	**DJ144.7**
N° of rings present	15	26
Bordered pit type (%)		
Uniseriate	84	95
Biseriate	16	4
Triseriate	-	1
Bordered pit arrangement (%)		
Opposite	71	43
Alternate	29	57
Touching	59	83
Spaced	41	17
Ray height	1-15	1-17
Mean ray height	4	6

Late Albian age *Araucariopitys* and leaves assigned to *Araucariopitys* have been described by Falcon-Lang and Cantrill (2000, 2001a) from Alexander Island, Antarctica. Poole and Cantrill (2001) also describe *Araucariopitys* from Williams Point of Livingston Island, Antarctica of Cenomanian-early Campanian age. *Araucariopitys* pollen of Coniacian to Campanian age has also been reported from the James Ross Basin (Dettman and Thomson, 1987).

2.6.2.4. Type L (*Cupressinoxylon* Goeppert 1850)

Specimens: Antarctica DJ137.6

2.6.2.4.1. Description

This sample contains a lot of split, bent rings with a high proportion of rot therefore it was not possible to determine whether it is derived from branch or trunk (Figure 2.24.a). This sample has 21 distinct growth rings. The transition from early to latewood is conspicuous.

The radial walls of tracheids bear predominantly uniseriate (93%) bordered pits although rare biseriate pits also occur (7%) (Figure 2.24.b). Where pits are multiseriate they are predominantly oppositely arranged (81%) although some are alternately arranged (19%). The pits are either touching (44%) or spaced (56%). Xylem parenchyma is present with resin content.

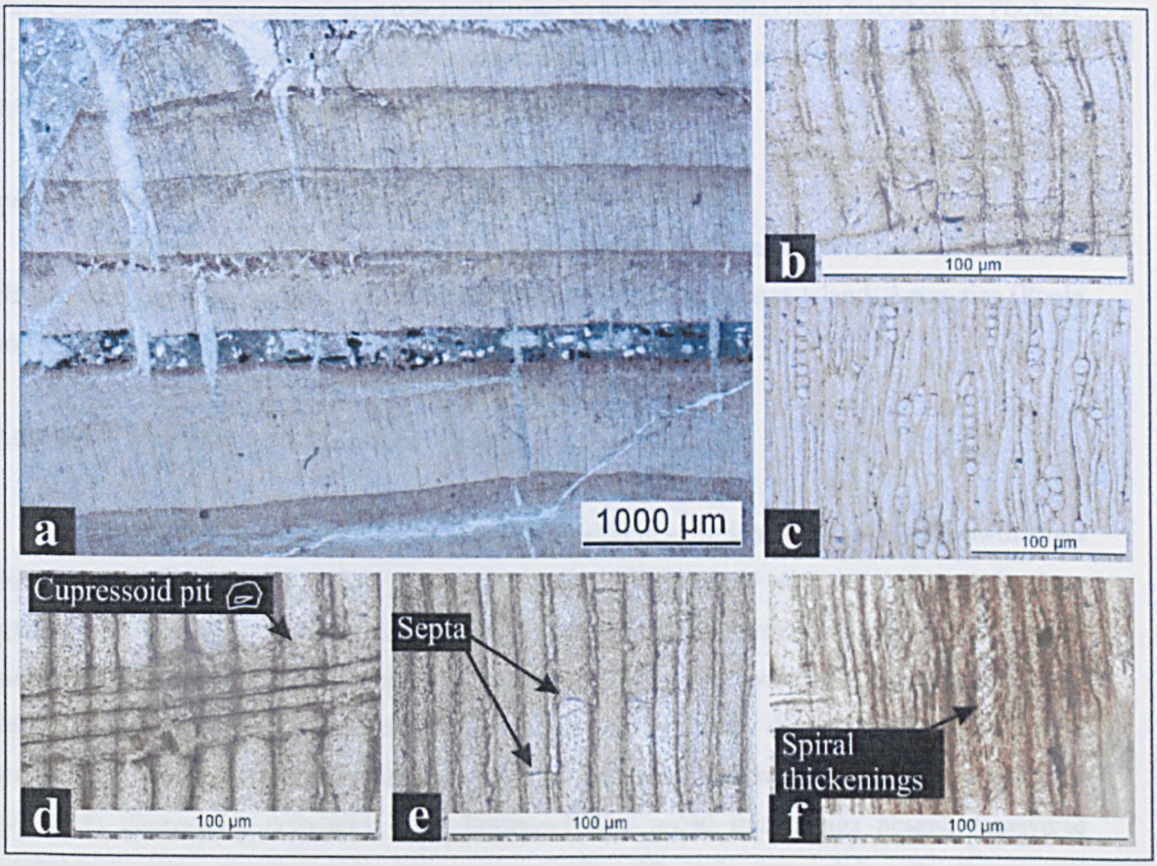


Figure 2.24. Type L (*Cupressinoxylon*) DJ137.6. a) Transverse section with straight ring boundaries. b) Radial section showing uni- and biseriate opposite and alternate bordered pits. c) Tangential section showing rare biseriate rays and beadlike tangential walls. d) Radial section showing cupressoid cross-field pits. e) Radial section showing septa. f) Radial section showing spiral thickenings.

Rays seen in tangential section are usually uniseriate although rare biseriate forms are also present (Figure 2.24.c). Some cells are also resin filled. Rays are 1-12 cells high (mean 4). The cross-field areas appear to contain mostly 1 pit although some may contain up to 4. The pits appear to be mostly cupressoid however some are also taxodioid (Figure 2.24.d).

Horizontal walls of ray cells are unpitted. Some bead-like thickening occurs in walls of tangential tracheids. Septa and spiral thickenings are present (Figures 2.24.e and f). Resin ducts are absent.

2.6.2.4.2. Identification

Under the classification scheme of Kraüsel (1949) it is not clear whether this sample is *Cupressinoxylon* or *Taxodioxylon*. This sample does however appear to be very similar to the sample of Falcon-Lang (2003) which he was unable to separated between *Taxodioxylon* and *Cupressinoxylon*. The sample also has similarities to the *Cupressinoxylon* described by Poole *et al.* (2001) and together with the presence of bead-like thickenings on tangential tracheid walls it was felt that this sample was most similar to *Cupressinoxylon*.

As discussed in section 2.5.2.12.2. above the use of *Cupressinoxylon* has been questioned, however it was decided to keep the name in this study.

Although several Northern Hemisphere examples have been reported the only Southern Hemisphere sample found was wood from the Eocene of King George Island, Antarctica (Poole and Cantrill, 2001).

2.6.2.4.3. Comparison with extant wood

This sample is most similar to Greguss' (1955) description of *Cupressus*: growth rings distinct, resin ducts absent, wood parenchyma frequent commonly with resin content, in some species all walls of ray parenchyma smooth and thin in others horizontal walls are pitted and tangential walls smooth but in most the horizontal walls are pitted while the tangential walls are thickened, unevenly punctate or bead-like, or quite exceptionally dentate, horizontal walls of longitudinal parenchyma smooth or from slightly to markedly thickened, nodular, in cross-field 1-3 (4-5) cupressoid, taxodioid or podocarpoid pits, spiral thickenings absent, transverse tracheids in some species rarely present, rays 1-30 cells high, tangential walls of ray cells smooth or with scalariform or sieve-like thickenings.

Currently *Cupressus* only occurs in warm cool-temperate and sub-tropical regions of the Northern Hemisphere (for typical habitat see section 2.5.2.12.3) (Vidakovic, 1991). However *Callitris* and *Fitzroya* of the Cupressaceae both occur in the Southern Hemisphere. *Callitris* is widespread in southeast Australia but also occurs in coastal regions from Newcastle to Queensland (Vidakovic, 1991). *Fitzroya* is native to southern Chile and northern Patagonia (Vidakovic, 1991).

2.6.2.5. Type N (*Agathoxylon* Greguss 1952: 160, 169 [non Hartig 1848])

Specimens: Antarctica DJ137.8 and DJ141.3

2.6.2.5.1. Description

Both samples are probably derived from mature stem material (Figure 2.25.a). Both samples contain distinct growth rings (Table 2.13). The transition from early to latewood is either subtle (DJ137.8) or conspicuous (DJ141.3).

Radial walls of tracheids bear mixed arrangements of pitting from uniseriate to 5-seriate (Table 2.13, Figures 2.25.b and c). Where pits are multiseriate they are mainly alternately but also oppositely arranged (Table 2.13). The pits are predominantly touching although a few are spaced (Table 2.13).

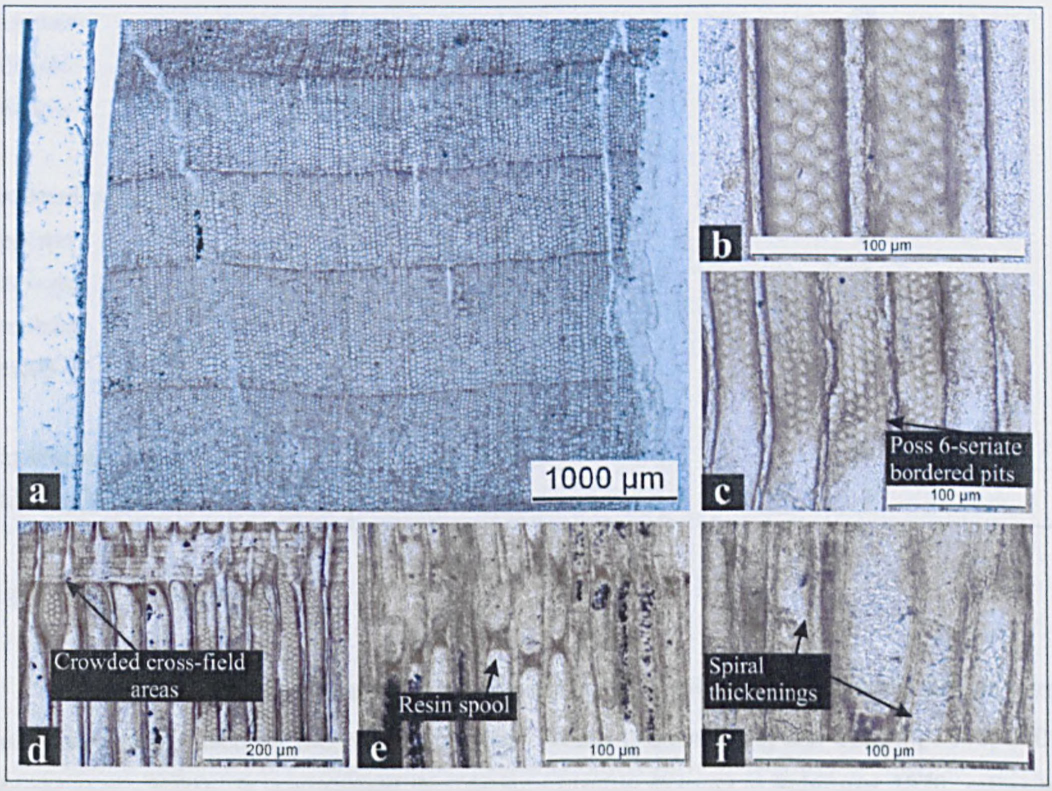


Figure 2.25. Type N (*Agathoxylon*). a) Transverse section showing straight growth rings (DJ141.3). b) Radial section showing triseriate alternately arranged bordered pits (DJ141.3). c) Radial section showing 5-6-seriate bordered pits? (DJ141.3). d) Radial section showing crowded cross-field areas (DJ141.3). e) Radial section showing resin spools (DJ137.8). f) Radial section showing spiral thickenings (DJ137.8).

Rays seen in tangential section are predominantly uniseriate with only rare biseriate forms seen in sample DJ137.8. Rays are 1-10 or 1-11 cells high but both have mean values of 5 (Table 2.13). Cross-field areas appear to contain 1-6 (DJ137.8) or 1-9 (DJ141.3) pits in some cases closely packed either side-by-side or in two rows (Figure 2.25.d). Cross-field pits appear to be araucarioid. Horizontal ray walls are unpitted and resin spools are present (Figure 2.25.e). Spiral thickenings appear to be present in sample DJ137.8 (Figure 2.25.f) but absent in DJ141.3. Septa, ray tracheids and resin ducts are absent.

Table 2.13. Table showing data collected for identification of samples DJ137.8 and DJ141.3.

	DJ137.8	**DJ141.3**
N° of rings present	27	22
Bordered pit type (%)		
Uniseriate	89	20
Biseriate	10	47
Triseriate	1	28
4-Seriate	0	4
5-Seriate	0	1
Bordered pit arrangement (%)		
Opposite	57	99
Alternate	43	1
Touching	90	100
Spaced	10	0
Ray height	1-11	1-10
Mean ray height	5	5

2.6.2.5.2. Identification

There is no consensus on the use of *Agathoxylon* or *Araucarioxylon* because both names have been widely used for Mesozoic araucarian woods (Falcon-Lang and Cantrill, 2000, 2001a; Barale *et al.*, 2002). It is suggested that *Araucarioxylon* (Kraus) in Schimper 1870 refers to a specific wood type and that all other araucarioid woods should be classified under the general name *Agathoxylon* (Philippe, 1993; Philippe *et al.*, 1999; Bamford and Philippe, 2001). However *Agathoxylon* is also suggested to be illegitimate as a later homonym of *Simplicioxylon* (Philippe *et al.*, 1999). To complicate this situation further Philippe (1993) indicates that *Simpicioxylon* is not synonomous with *Agathoxylon*. For the purposes of this thesis is it assumed that *Agathoxylon* should be used for all woods of Araucarian type but that it should be remembered that this type of wood may previously have been named *Araucarioxylon*.

Therefore in comparing this wood to other occurrences both *Agathoxylon* and *Araucarioxylon* were investigated.

Woods with araucarian cross-field pitting, occasionally having axial parenchyma, are classified as *Agathoxylon* therefore these samples can be placed in this category (Philippe, 1993). When compared to Ottone and Medina's (1998) table of diagnostic features of Cretaceous and Teritary araucarian wood, sample DJ141.3 appears most similar to *A. pluriresinosum* Torres and Biro-Bagoczky 1986 although there are some differences e.g. rays are uniseriate. Sample DJ137.8 is most similar to *A. chilense* Nishida 1970 although this species only contains uni-biseriate bordered pits.

Agathoxylon is described as ubiquitous across Gondwana by Philippe *et al.* (2004). It has been reported from the Early Cretaceous of James Ross Island, Antarctica (Ottone and Medina, 1998) which is supported by the presence of Araucariaceae pollen within Albian-Cenomanian sediments (Dettman and Thomson, 1987; Keating, 1992). *Araucarioxylon* is described from Aptian and late Albian sediments on Alexander and Livingston Islands, Antarctica, the presence of which is confirmed on Alexander Island by the occurrence of leaves, shoots and cone scales (Falcon-Lang and Cantrill, 2000, 2001a and 2001b). *Agathis* leaves have also been reported from Albian to Cenomanian sediments of the Middle Clarence Valley, New Zealand (Parrish *et al.*, 1998). Araucarian leaves are also present in Albian-Aptian sediments of Victoria, Australia (Douglas and Williams, 1982). Shoots of Araucariaceae are reported from Santonian-Maastrichtian sediments of King George Island, Antarctica (Birkenmajer and Zastawniak, 1989).

2.6.2.5.3. Comparison with extant wood

According to Barefoot and Hankins (1982) resin plugs only occur in *Araucaria, Callitris, Cupressus* spp, *Dacrydium, Fitzroya, Juniperus, Libocedrus, Podocarpoxylon, Saxegothea, Thuja* and *Widdringtonia* spp. The high number of rows of bordered and cross-field pits suggest greatest affinity with Greguss' (1955) description of Araucariaceae which he says has 1-5 seriate bordered pits and 2-16 cross-field pits.

Agathis is native to rainforests of Australia, New Zealand, New Caledonia, New Hebrides, Malaysia, Borneo, Celebes and the Moluccas. The typical habitat of *Agathis* is in moist forests where it is shade intolerant and can grow at low altitude or up to 1600m on ridge crests. It grows on acid or volcanic soil (Cedar Lodge Nurseries website, http://www.conifers.co.nz, accessed 4 July 2005). *Araucaria* occurs in south central Chile and adjacent parts of Argentina, New Guinea, New Caledonia, Norfolk Island, Brazil, Paraguay and eastern Australia (Veblen, 1982). It is mainly restricted to summits >1000m (1100-1300m). It will grow on poor, often wet, soil where it is shade intolerant but will regenerate in tree fall gaps and after stand-devastating disturbance e.g. fire (Veblen, 1982; Armesto *et al.*, 1995; Baxter *et al.*, 1998; Hildebrand-Vogel, 2002).

2.6.2.6. Type O (*Protophyllocladoxylon* Kraüsel 1939)

Specimens: Antarctica DJ141.6

2.6.2.6.1. Description

This sample contains crushed, bent and split rings making it difficult to determine whether it is derived from branch or trunk. It contains 40 distinct growth rings. The transition from early to latewood is gradual (Figure 2.26.a).

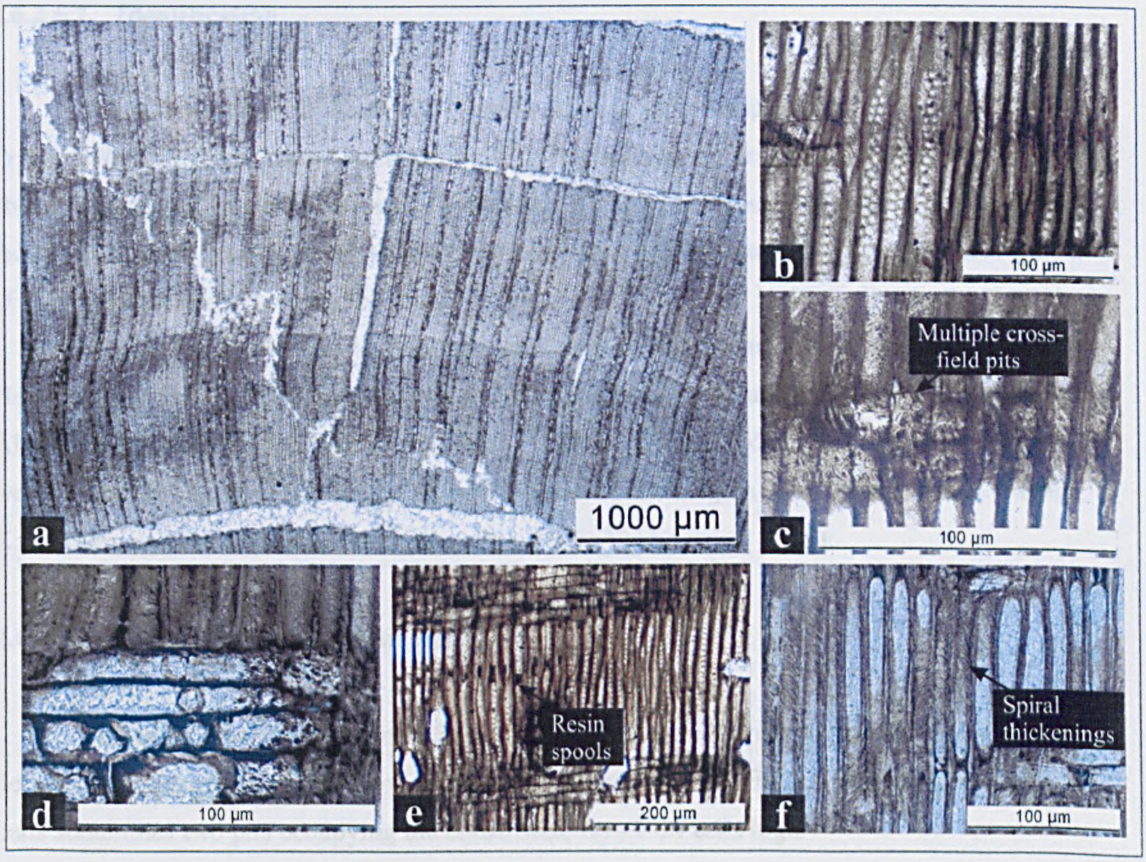


Figure 2.26. Type O (*Protophyllocladoxylon*) DJ141.6. a) Transverse section showing reasonably straight ring boundaries. b) Radial section showing uniseriate alternate and oppositely arranged multiseriate pits. c) Radial section showing multiple pits within cross-fields. d) Radial section showing large cupressoid pits. e) Radial section showing resin spools. f) Radial section showing spiral thickenings (also resin spools bottom middle).

Radial walls of tracheids bear predominantly uniseriate bordered pits (82%) although biseriate (17%) and rare triseriate (1%) forms also occur. There may also be 4- and 5-seriate types but preservation makes it difficult to confirm (Figure 2.26.b). Where pits are multiseriate they are predominantly alternately arranged (81%) with only a few opposite forms (19%). The pits are predominantly touching (92%) with only a minority spaced (8%). In places the pits are crowded and hexagonal in form.

Rays seen in tangential section are predominantly uniseriate although some cells were observed to be biseriate in the body. Rays are 1-14 cells high (mean of 4). Cross-field areas appear to contain 1-5 pits arranged singly, in pairs vertically or randomly (Figure 2.26.c). The pits appear to be cupressoid or araucarian although possibly also piceoid in form (Figure 2.26.d). The horizontal walls of ray cells are unpitted. Resin spools are present (Figure 2.26e). Spiral thickenings are present (Figure 2.26.f). Ray tracheids, septa and resin ducts are absent.

2.6.2.6.2. Identification

When compared to Kraüsel's (1949) scheme this sample most closely resembles *Protophyllocladoxylon*: pits on radial walls of tracheids never or very rarely circular, usually oblate, if arranged in several rows alternate often 5-6 angled, cross-field with a few large pits mostly oval pores, pits on radial walls of tracheids typically araucarioid. No other descriptions of *Protophyllocladoxylon* could be found.

All previous evidence of this type of wood of Cretaceous age is from the Northern Hemisphere. Various undefined remains and leaves have been found in the Yukon River area of Alaska (Krassilov, 1975; Vakhrameev, 1991). Other unspecified remains of the Cretaceous were found in Ainussian (eastern Russia), Kass River Region and Yilyui Basin Siberia, Kazakhstan and western Greenland (Krassilov, 1975; Vakhrameev, 1991).

2.6.2.6.3. Comparison with extant wood

Although this is an extinct form it has some similarities to modern *Phyllocladus* described by Greguss (1955): wood parenchyma absent, in cross-fields a single pit, in marginal cells sometimes two pits occupying the entire area, rays 1-14 cells high.

Phyllocladus occurs in south eastern Asia and the South Pacific. Three species are indigenous to New Zealand and one to western Tasmania. The typical habitat of this genus is in alpine/mountain to lowland forests between sea level and ~1500m in sheltered and shaded areas (Cedar Lodge Nurseries website, http://www.conifers.co.nz, accessed 4 July 2005).

2.6.2.7. Type P (*Sciadopityoxylon* Schamhausen 1877 em. Jurasky 1928)

Specimens: Antarctica DJ144.5 and DJ463.5

2.6.2.7.1. Description

Sample DJ144.5 is probably derived from branch material due to the presence of variable widths within individual rings (compression wood, Figure 2.27.a). It is not clear whether DJ463.5 is derived from branch or trunk due to poor preservation. Both samples have distinct growth rings (Table 2.14) The transition from early to latewood is gradual in both cases.

Table 2.14. Table showing data collected for identification of samples DJ144.5 and DJ463.5.

	DJ144.5	DJ463.5
N° of rings present	68	5
Bordered pit type (%)		
Uniseriate	91	95
Biseriate	9	5
Bordered pit arrangement (%)		
Opposite	69	80
Alternate	31	20
Touching	86	50
Spaced	14	50
Ray height	1-11	1-8
Mean ray height	4	3

Radial walls of tracheids bear predominantly uniseriate bordered pits although a few biseriate forms also occur (Table 2.14 and Figure 2.27.b). Where pits are multiseriate they are predominantly oppositely arranged with some alternately arranged (Table 2.14). Pits are either touching or spaced (Table 2.14).

Rays seen in tangential section are predominantly uniseriate with rare biseriate cells in the body in sample DJ144.5. A lot of ray cells in sample DJ463.5 are resin filled as is the xylem parenchyma observed (Figure 2.27.c). Rays are 1-11 cells high with mean values of 4 and 3 (Table 2.14). In cross-fields there appear to be 1-6 pits present in various orientations e.g. 2 side-by-side, 6 in two rows, 1 in each corner (Figure 2.27.d). The pits are of mixed type, cupressoid, taxodioid, pinoid, podocarpoid and possibly piceoid (Figure 2.27.e). Horizontal walls are thin and smooth. Ray tracheids, spiral thickenings, septa and resin ducts are absent.

2.6.2.7.2. Identification

When compared to Kräusel's (1949) scheme these samples are catagorised as *Sciadopityoxylon*: pits on radial walls of tracheids at least in part circular, if arranged in several rows opposite, mainly separated by bars of Sanio, pits on radial walls of tracheids never typically araucarian, generally or predominantly circular and opposite, normal wood without resin canals, spiral thickenings absent, walls of medullary ray cells predominantly smooth, pits in cross-fields oval pores various shapes and sizes. No other descriptions could be found for this genus.

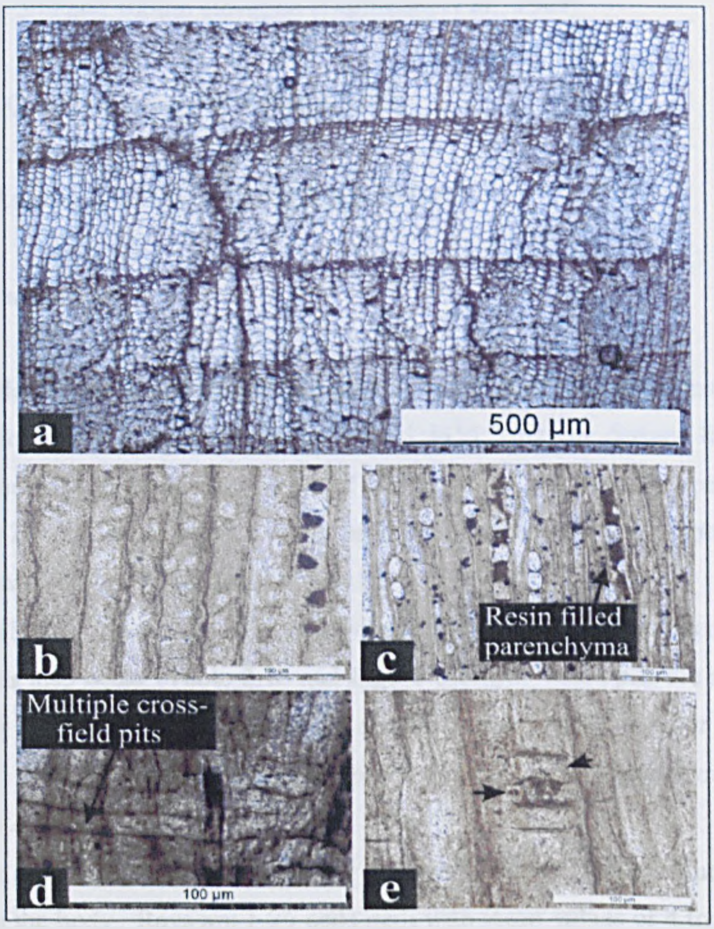


Figure 2.27. Type P (*Sciadopityoxylon*). a) Transverse section poorly preserved (DJ144.5). b) Radial section showing uni- and biseriate opposite bordered pits (DJ463.5). c) Tangential section showing resin filled xylem parenchyma (DJ463.5). d) Radial sction showing poorly preserved multiple cross-field pits (DJ144.5). e) Radial section showing piceoid and podocarpoid cross-field pits (DJ463.5).

This form-genus could only be found recorded from the Northern Hemisphere with leaves having been found in western Greenland (Seward, 1926).

2.6.2.7.3. Comparison with extant wood

This sample has some similarities to *Sciadopitys verticillata* Sieb and Zucc. having: distinct growth rings, large cross-field pits (often paired), resin ducts and parenchyma absent (Phillips, 1941).

Only one species of *Sciadopitys* has been reported from Japan. The typical habitat of this genus is in mountainous regions where it succeeds in sheltered positions on sandy loams with high nutrient content. It can tolerate low temperatures down to -25°C. This genus can withstand drought in rich, moist, acidic soils in full sun but dislikes wind (University of Conneticut website, http://www.host.uconn.edu/plants accessed on 4 July 2005). It is usually found between 500 and 1000m elevation (Dallimore *et al.*, 1967).

2.6.2.8. Type Q (*Circoporoxylon* Kraüsel 1949)

Specimens: Antarctica DJ455.3, DJ462.2 and DJ462.3

2.6.2.8.1. Description

Samples DJ462.3 and DJ462.2 appear to be derived from stem material although there is a lot of deformation present (Figure 2.28.a). DJ455.3 may be derived from branch material although again this sample contains a lot of deformation. All samples contain distinct growth rings (Table 2.15). The transition from early to latewood is either gradual (DJ462.3 and DJ462.2) or marginally conspicuous (DJ455.3).

Radial walls of tracheids bear predominantly uniseriate bordered pits although rare biseriate forms also occur (Table 2.15 and Figure 2.28.b). When pits are multiseriate they are either entirely or predominantly oppositely arranged with a small number alternately arranged (Table 2.15). Pits are either touching or spaced (Table 2.15). Parenchyma present and resin filled (Figure 2.28.c).

Rays seen in tangential section are predominantly uniseriate although a few biseriate cells occur in the body. Rays are 1-26 cells high with mean values of 4 to 6. Cross-field areas appear to contain 1-5 pits arranged in various orientations including one in each corner, singly or side-by-side (Figure 2.28.d). The pits seem to vary in type including podocarpoid, taxodioid and possibly piceoid (Figure 2.28.e). Ray tracheids, septa, spiral thickenings and resin ducts absent except in DJ462.3 which appears to contain spirals.

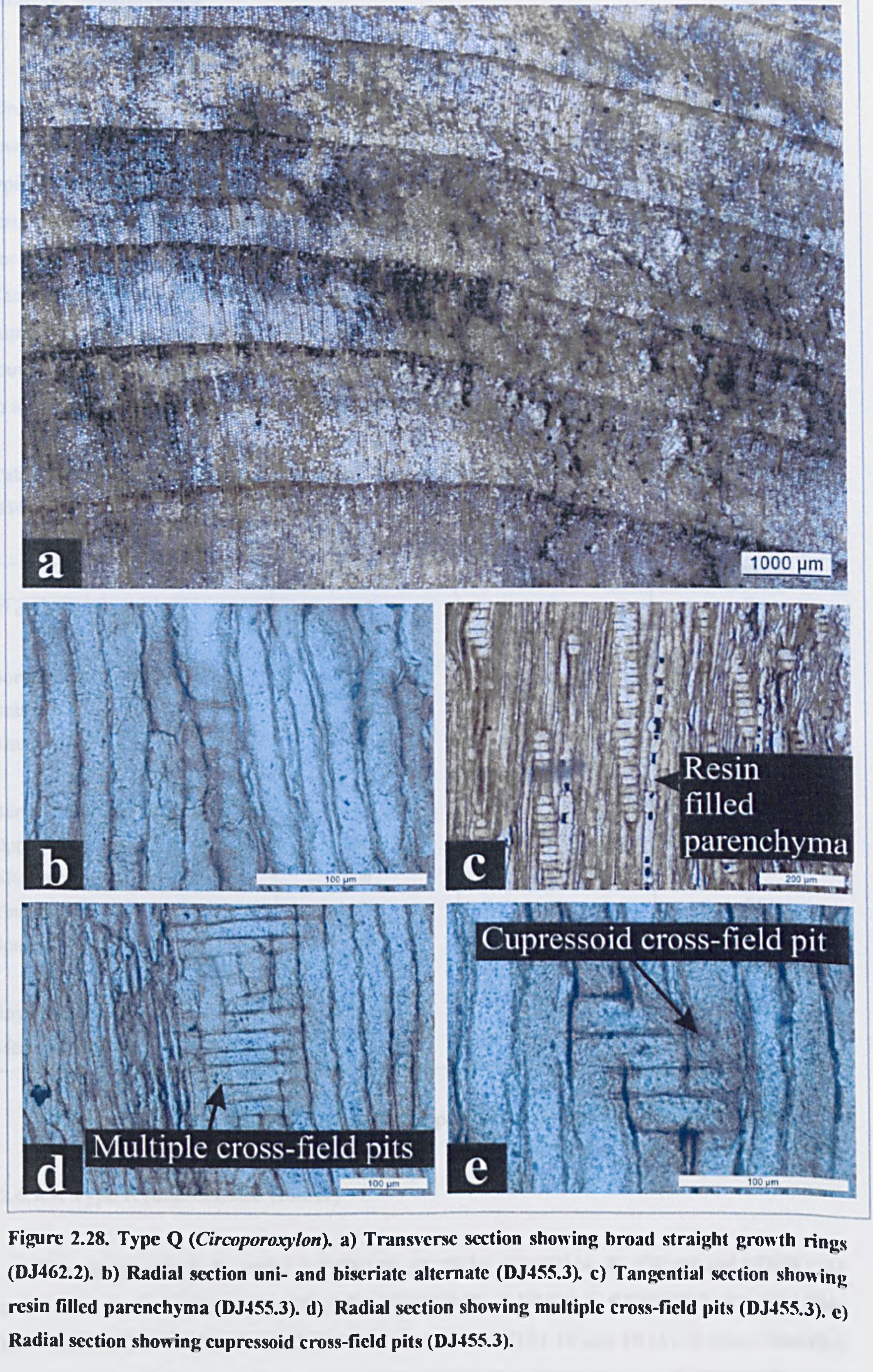


Figure 2.28. Type Q (*Circoporoxylon*). a) Transverse section showing broad straight growth rings (DJ462.2). b) Radial section uni- and biseriate alternate (DJ455.3). c) Tangential section showing resin filled parenchyma (DJ455.3). d) Radial section showing multiple cross-field pits (DJ455.3). e) Radial section showing cupressoid cross-field pits (DJ455.3).

2.6.2.8.2. Identification

When compared to Kraüsel's (1949) scheme these samples appear most similar to *Circoporoxylon*: pits on radial walls of tracheids at least in part circular, if arranged in several rows opposite, mainly separated by bars of Sanio, pits on radial walls of tracheids never typically araucarian, generally or predominantly circular and opposite, normal wood without resin canals, spiral thickenings absent, walls of medullary ray cells predominantly smooth, oval pores in cross-fields circular or rounded. *Circoporoxylon* is defined by Falcon-Lang and Cantrill (2000) as being the general label for anything that cannot be definitely placed into the cupressoid, taxodioid, glyptostroboid or podocarpoid generas. No other descriptions could be found with which to compare these samples. However as they could not be definitely referred to as another genus it was felt appropriate to leave them as *Circoporoxylon.*

Table 2.15. Table showing data collected for identification of samples DJ455.3, DJ462.2 and DJ462.3.

	DJ455.3	DJ462.2	DJ462.3
N° of rings present	15	9	7
Bordered pit type (%)			
Uniseriate	96	96	94
Biseriate	4	4	6
Bordered pit arrangement (%)			
Opposite	100	83	100
Alternate	0	17	0
Touching	77	40	51
Spaced	23	60	49
Ray height	1-15	1-11	1-26
Mean ray height	5	4	6

As this is an extinct transitional form it is not possible to compare it to modern genera.

2.6.2.9. Type R (unidentified conifer)

Five samples from Australia (872/W149, 872/W16, 872/W104, 872/W168 and 872/W128) and twelve from Antarctica (KG2817.20, KG1719.3b, KG4672.6, KG4717.43, KG2814.256, KG4710.1, KG2814.252, DJ466.2, DJ465.1, DJ144.3, DJ141.16 and DJ141.8) were classified as Type R, unidentified conifer. This was either because all three thin section orientations were not available or due to the preservation being too poor to allow observation of any fine detail. These samples were confirmed as being conifers due to the lack of vessels in transverse section which are always present in angiosperm wood. The preservation was good enough in transverse section to allow the samples to be used for the leaf life-span analysis.

2.6.2.10. Type S (unidentified araucarian)

Two samples from Antarctica (D421 and DJ366.7) were classified as Type S which were unidentified araucarian type. These samples were confirmed as being conifer wood by their lack of vessels in transverse section and enough detail could be seen to determine that in radial section the tacheids contained multiple rows of bordered pits that were sometimes crowded and hexagonal in shape indicating an araucarian affinity. These samples were also used in the leaf life-span analysis.

2.6.2.11. Type T (unidentified non araucarian)

Three samples from Antarctica (DJ135.3, DJ141.7 and DJ451.3) were classified as Type S which were unidentified non araucarian type. In radial section these samples appeared to contain only uni- or biseriate bordered pits in the tracheids and single large pits were occasionally observed in the cross-field areas suggesting a non araucarian affinity. Again these samples were well enough preserved in transverse section to use for the leaf life-span analysis.

2.6.3. Climatic inferences based on Nearest Living Relative analysis for Southern Hemisphere

In the Southern Hemisphere the presence of only *Podocarpoxylon* in Australia presents difficulties for identifying the Cretaceous climate as modern podocarps grow in a wide variety of environments (Table 2.16). However the wood displays distinct growth rings suggesting that the climate was seasonal. *Podocarpus* are also the dominant conifer genus in the modern warm-temperate forests of small areas of the Drakensburg mountains of Africa and a narrow strip along the south coast where there is sufficient moisture for them to survive (Moore, 1982). However *Podocarpus* also occurs in the northern Patagonian cool-temperate rain forests where they are tolerant of shade and can grow in thin poorly drained soils with frequent disturbance (Heusser, 1974; Veblen, 1982; Armesto *et al.*, 1995).

The Podocarpaceae and Araucariaceae dominated forests of Antarctica were similar in composition to living modern warm temperate rainforests of New Zealand and north-east

Australia, with mean monthly temperatures of 16-22°C in summer and 3-8°C in winter (Heusser, 1974; Veblen *et al.*, 1981; Moore, 1982; Howe, 2003). However the Araucarian forests could also have occupied the exposed higher mountainous areas >1000m with *Podocarpus* and Cupressaceae (*Fitzroya*) appearing on the lower slopes between 400-900m similar to the modern forests in the north Patagonian rain forests of Chile (Heusser, 1974; Veblen, 1982; Armesto *et al.*, 1995; Hildebrand-Vogel, 2002). This would suggest that these areas would have been more likely to have been cool temperate (average summer temperature 13-14°C) with high precipitation on thin nutrient poor soils. From her study of the palaeoflora and sedimentology Howe (2003) suggests that the forests of Alexander Island grew in a warm, temperate, semi-arid climate with annual rainfall and intermittent flooding. Therefore the wood in this study may represent a variety of microenvironments representing cooler higher altitude forests of *Podocarpus*, Araucarians (*Araucaria* or *Agathis*), *Phyllocladus* and Cupressaceae (*Fitzroya*) and warmer lower altitude forests of *Taxodium* and *Sciadopitys* from more sheltered, swampy, river bank settings within valleys.

Table 2.16. Habitat requirements of modern conifer genera of the Southern Hemisphere (Dallimore *et al.*, 1967; Vidakovic, 1991).

Genus	**Elevation**	**Soil Type**	**Notes**
Podocarpus	400-3000m	thin, poorly drained	grows in a variety of environments: in mountainous areas, rainforest tropical to sub-tropical regions, warm-temperate and cool-temperate. Some can resprout after fire and can grow on ridge crests. Tolerant of frequent disturbance and shade.
Taxodium	sl-520m	-	grows on wetlands, swampy terrain or river banks, can tolerate temperatures of -30°C
Cupressaceae (*Cupressus*, *Fitzroya* and *Callitris*)	600-3000m	directly over bare rock, volcanic substrate, waterlogged	enjoys frequent disturbance, is fire resistant and intolerant of shade. Grows in warm- to cool-temperate areas. Can be frost hardy.
Agathis and Araucaria	150-1600m	acid, volcanic, poor	grows in rainforests or on summits >1000m often near swamps or bogs, is shade intolerant and likes moisture
Phyllocladus	sl to ~1500m		grows in alpine mountain and lowland forests, most prefer to be in shaded areas
Sciadopitys	500-1000m	rich, moist, acid	can withstand drought but dislikes wind and requires full sun

2.7. Summary: the conifer trees within mid-Cretaceous polar forests

Table 2.17 gives details of the composition of the mid-Cretaceous polar conifer forests. This analysis indicated that the forests of the Cretaceous polar regions had high diversity of conifers with the exception of Australia. This may be due to preservation bias because few specimens from Australia were well enough preserved for identification. The forests of the Northern Hemisphere appear to have been slightly more diverse than in the Southern Hemisphere. *Araucariopitys*, *Taxodioxylon* and *Cupressionoxylon* were present in both hemispheres.

Table 2.17. Summary of mid-Cretaceous polar conifer forest composition.

Location	No of Samples	No of Genera Represented	Genera Present	Dominant Genus
Canadian Arctic	10	5	*Pinuxylon, Piceoxylon, Cedroxylon, Palaepiceoxylon, Cupressinoxylon*	*Pinuxylon* (33%)
Svalbard	13	10	*Piceoxylon, Laricioxylon, Cedroxylon, Taxodioxylon, Juniperoxylon, Protocedroxylon, Taxoxylon, Araucariopitys, Xenoxylon, Cupressinoxylon*	*Taxodioxylon* (25%)
Australia	8	1	*Podocarpoxylon*	*Podocarpoxylon* (100%)
Antarctica	37	8	*Podocarpoxylon, Taxodioxylon, Araucariopitys, Cupressinoxylon, Agathoxylon, Protophyllocladoxylon, Sciadopityoxylon, Circoporoxylon*	*Taxodioxylon* (14%)

In the Northern Hemisphere the forest composition seems to suggest cool temperatures in upland areas with the presence of conifers similar to modern *Taxus* suggesting temperatures may have been between 1 and 10°C for all but a few days per year. The dominance of *Pinus* with narrow growth rings in the Canadian Arctic indicates cool temperate climates. However the dominance of *Taxodium* in Svalbard suggests that the valleys would have been moist and at least seasonally warm (warm temperate). Overall the forest composition at both sites suggests microthermal (mean annual temperature <13°C) to mesothermal (mean annual temperature 13-24°C) conditions with cold month mean >2 °C and mean annual precipitation >100cm/year.

Forest composition in the Southern Hemisphere suggests that the samples represent two microenvironments with climates probably warm temperate in the low altitude valleys with mean monthly summer temperatures of 16-22°C and in winter 3-8°C or cool temperate at higher altitudes with average summer temperatures of 13-14°C and in winter ~8°C. It should be noted that the estimates of temperature given above are derived from NLR analysis and are therefore estimates only, given that there are known to be problems with the NLR method as shown in Section 2.5.3. However this analysis suggests that the Southern Hemisphere polar regions may have been slightly warmer than the Northern Hemisphere high latitude areas. This may be due to a combination of factors, including the Northern Hemisphere sites having been nearer to the palaeopole than the Southern Hemisphere sites, ocean circulation taking warmer water south to produce a milder maritime climate for the forests to grow in etc.

Chapter 3 Leaf life-span determination in extant wood

3.1. Introduction

In this project it was necessary to determine the leaf life-spans of mid-Cretaceous polar conifer trees in order to test the outputs of the new University of Sheffield Conifer Model (USCM). The testing with proxy data needed to be carried out before the USCM could be confidently coupled to global climate models to investigate the effects of this more accurate representation of high latitude vegetation on climate.

The leaf habit of fossil trees, that is whether they were evergreen or deciduous, is difficult to determine. Some authors have assumed a deciduous habit simply due to the abundance of fossil leaves in litter layers e.g. *Glossopteris* in the Permian (Retallack, 1980, 1999; Pigg and Taylor, 1993). Other methods rely on assuming leaf habit was the same as in living relatives (Nearest Living Relative analysis, Section 3.2.1) or on leaf trace analysis (Section 3.2.2) but both of these methods have problems associated with them (discussed in Chapter 2, Section 2.5.3 and in this Chapter Sections 3.2.1 and 3.2.2).

More recently Ring Markedness Index (RMI) and Percentage Skew, new techniques for determining leaf habit using structural features in conifer wood, have been devised (Falcon-Lang 2000a and b). The methods used to determine RMI and Percentage Skew are presented and problems associated with them are discussed (Section 3.3). RMI has been developed much further during this project (Section 3.3.4.1) because, unlike Percentage Skew, in addition to determining leaf habit it also provides a quantitative estimate of the leaf life-span (LLS) of the tree, that is, the length of time the conifer held on to its leaves. As discussed in Chapter 1 (Sections 1.2.2 and 1.4.2) the length of time the trees retained their leaves may be an important factor in assessing the magnitude of the forest's interaction with climate and it is an integral part of the USCM (see also Chapter 7).

Once Ring Markedness Index had been refined and developed in this project it was applied to a large collection of extant wood. This was undertaken in order to determine a relationship for use in the derivation of leaf life-spans in fossil wood (Section 3.4, 3.4.1 and 3.4.2, see also Chapter 4).

Since it is not always possible to determine if fossil wood is from branch or trunk, analysis was undertaken on both branches and trunks of living wood. Results were checked to see if intra-tree variability (Sections 3.4.3 to 3.4.3.3, Chapman, 1994; Falcon-Lang 2005a) affected the results. The effect of damage to wood structure on LLS in conifers was also investigated because it was not known if the wood growth and hence RMI would be substantially altered by damage to the tree (Section 3.4.4). Comparisons were also made between woods from species grown in natural stands and cultivated stands at various latitudes and altitudes (Section 3.4.5). The effects of the high-latitude light regime were also considered by examining a sample obtained from a modern high latitude forest (Section 3.4.6, see Appendix A, Section 1.1.6 for details of the collection site).

Investigations into the validity of the Percentage Skew calculation (as used by Falcon-Lang, 2000b and discussed in Section 3.5), using the large number of extant conifers in this study, are reviewed within Section 3.5. Finally Section 3.6 summarises the analysis carried out on extant conifer wood to determine the relationship between RMI and LLS, to be used to determine the LLS in fossil woods (Chapter 4).

3.2. Methods of determining deciduous or evergreenness (leaf life-span) in fossil plants

In this section methods used to determine fossil leaf habit are discussed and new developments in the determination of leaf habit and LLS from conifer wood are presented.

3.2.1. Nearest Living Relative analysis (NLR)

Leaf habit for fossil plants has often been determined by using Nearest Living Relative analysis (NLR) (Horrell, 1991; Mosbrugger, 1999). This uses the rationale that if a fossil plant has a close living relative then it can be assumed that the leaf habit and climatic requirements of the fossil plant were close to those of its modern counterpart (Mosbrugger, 1999). However there are several problems with this approach:

1 It assumes fossil taxa are correctly identified.
2 It assumes that the meteorological stations provide adequate and reliable data to describe the climatic tolerances of modern taxa.
3 It is impossible to determine the leaf habit of extinct genera that have no modern analogues (Krassilov, 1973).
4 In the context of leaf habit this method assumes that the conifers growing during the past had the same habit as their modern relatives.

For the purposes of this research project it was felt that this method was not appropriate for accurately determining leaf habit of the polar conifers. However some NLR analysis was carried out in order to estimate the environment of growth of the fossil forests for comparison with previous studies (see Chapters 2 and 5).

3.2.2. Leaf traces

Leaf traces are thin strands of xylem that connect the living leaf to the protoxylem at the centre of the stem (Schweingruber, 1996). After leaf fall the trace is filled with parenchyma cells and is eventually covered over as wood growth continues (Figure 3.1). Leaf life-span can therefore be determined by counting the number of annual growth rings through which the leaf trace passed before it was filled with parenchyma cells (Falcon-Lang, 2000b).

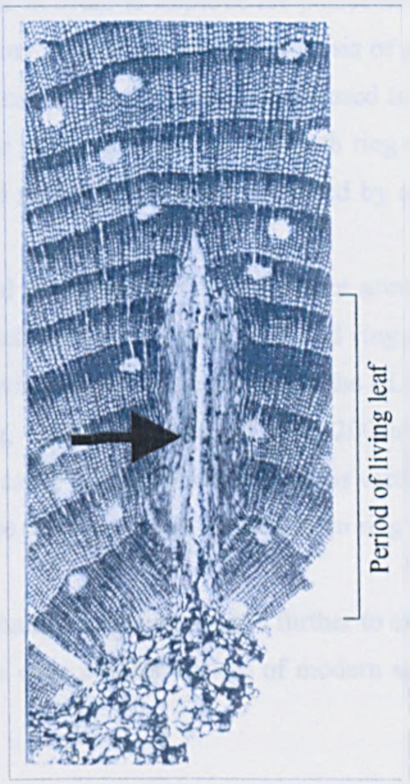


Figure 3.1. Microscopic cross section (transverse section) of a leaf trace in *Pinus mugo* (x40) (image from Schweingruber, 1996). The trace passes through six ring increments therefore the leaf lived for six years. Callusing began after it died in the autumn of the fifth year. The trace remains macroscopically visible for about one vegetative period after death (Schweingruber, 1996). Black arrow points to trace.

There are several problems with this method:-

- The main problem is that leaf traces are extremely difficult to find in a section of wood, relying on trial and error in the cutting of the wood specimen. Only very few examples have been reported in fossil wood (Falcon-Lang and Cantrill, 2000; 2001a).
- It is very difficult to cut a section where the entire leaf trace passes through the plane of section, although if part of the trace is seen it would provide a minimum LLS.
- There is a suggestion that the leaf traces in some species may continue to extend in length after leaf fall, although this has not been confirmed (Eames and McDaniels, 1947). If it is correct the estimates for LLS may be too high (Falcon-Lang and Cantrill, 2001a).

Having initially examined both the modern and fossil wood used in this study it was decided that this was not a suitable method as no samples displayed leaf traces and none were encountered on cutting fossil wood.

3.2.3. Determining leaf habit by analysis of fossil wood

Falcon-Lang (2000a) investigated the relationship between growth ring characteristics and LLS for modern conifers growing within a single climatic regime. His research aimed to clarify the factors that influence growth ring style in order to improve the palaeoenvironmental data extracted from fossil woods. This method involved a quantitative analysis of growth ring anatomy and, although only a small number of extant conifer samples were used in his trial, it appeared to show that there was an inverse linear relationship between growth ring markedness and leaf longevity, with more weakly developed growth rings being produced by species with greater leaf life-span (LLS).

Given the narrow range of environmental conditions in which the trees grew in Falcon-Lang's (2000a) work, it was unlikely that the relationship between LLS and ring markedness was entirely due to the variability of growing environments. This suggested the LLS is, at least in part, genetically determined (Falcon-Lang, 2000a). Falcon-Lang (2005a), however, suggested that caution should be applied when using this analysis because his method was not well tested on a large set of samples, and because there was large variability in ring markedness values in his dataset.

In this thesis Falcon-Lang's (2000a) technique was investigated further to establish how robust the method was and to see if it held true over a wider variety of modern species and a larger data set.

3.3. Methods

In this project it was necessary to determine the leaf habits and LLS's of mid-Cretaceous polar conifer trees in order to test the outputs of the University of Sheffield Conifer Model (USCM).

The LLS of the fossil trees was calculated using the Ring Markedness Index (RMI), a measure of the markedness of the growth ring boundaries, originally devised by Falcon-Lang (2000a) (Section 3.3.3). This method is based on the fact that the rhythmic activity of the vascular cambium, which gives rise to growth rings in wood, is controlled by an endogenous phytohormonal rhythm, with the phytohormones being produced by the cyclic growth and senescence of the leaves. The method uses the change in tracheid diameter (cell size) across the ring because in deciduous conifers the entire canopy is replaced each year, resulting in a phytohormonal rhythm with a high amplitude and marked growth rings in which tracheid diameter gradually declines across the ring increment (Falcon-Lang, 2000a). However in evergreen conifers the new flush of leaves in spring may only represent 15% of the entire canopy, resulting in a phytohormonal rhythm with low amplitude and subtle growth rings in which tracheid diameter remains large across the growth ring, declining only in the last few cells (Figure 3.2). Therefore the markedness of the ring boundaries can provide a quantitative measure from which LLS can be calculated.

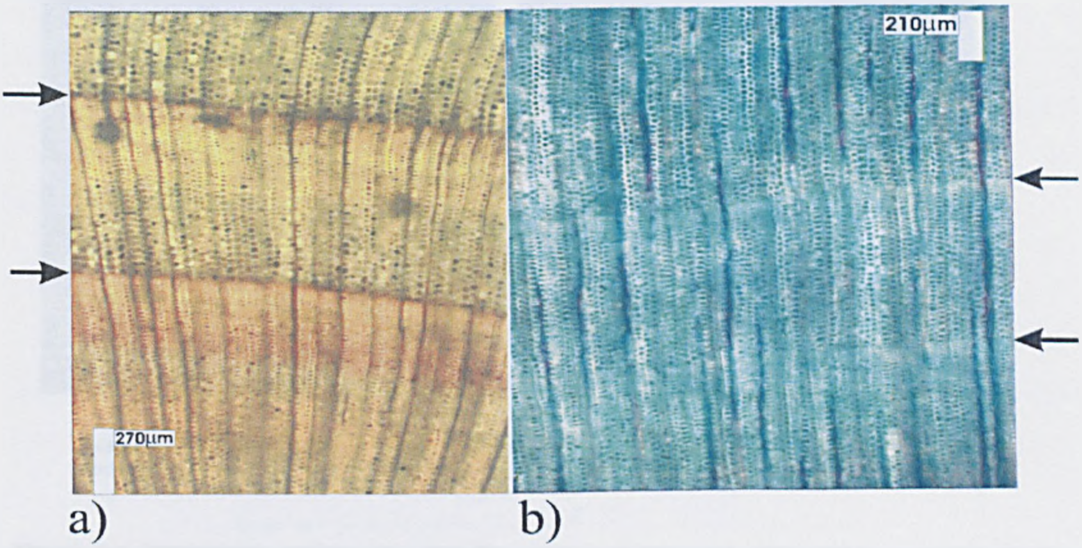


Figure 3.2. a) Modern deciduous *Larix decidua* (Larch, sample TAP-01-15) (transverse section) showing marked growth ring boundaries (shown by black arrows) with tracheid diameter gradually declining across the ring increment. b) Modern evergreen *Araucaria araucana* (Monkey Puzzle, sample LEEDS-02-1) (transverse section) showing subtle growth ring boundaries (shown by black arrows) with tracheid diameter remaining constant across the growth until the last few cells.

RMI is calculated in three stages:-

- Calculation of Percentage Latewood (the percentage of wood that grew late in the growing season, small thick-walled cells).
- Calculation of Percentage Diminution (the reduction in cell size across the tree ring expressed as a percentage).
- Calculation of Ring Markedness Index. Ring Markedness Index combines the two calculations above to determine the markedness of the ring boundary. The RMI can then be correlated with the known LLS of extant conifers and the resulting relationship used to calculate the LLS of fossil samples.

These three stages are explained in detail in sections 3.3.1 to 3.3.3 below.

3.3.1. Percentage Latewood

This approach was devised by Creber and Chaloner (1984b) and is defined as the percentage of wood that forms late in the growing season (the latewood cells have smaller radial diameters and thus smaller lumina than those formed earlier in the season) (Figure 3.3).

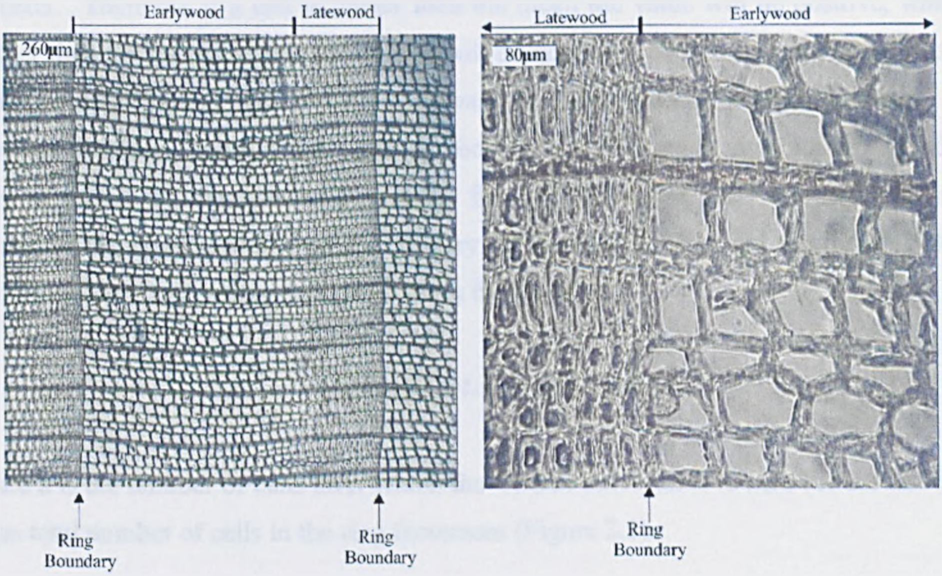


Figure 3.3. Transverse sections showing the early and latewood cells within a sample of *Tsuga Canadensis* (Sample A1-1) from Francis' collection at the University of Leeds.

Creber and Chaloner (1984b) carried out a review of the methods of distinguishing earlywood from latewood cells, as different methods have been adopted by researchers. Mork's (1928) definition has been used widely for visual identification of latewood. This states that a latewood cell is defined as having a lumen radial diameter equal to or less than twice the thickness of the combined cell walls separating the lumen from that in the previous cell (Figure 3.4).

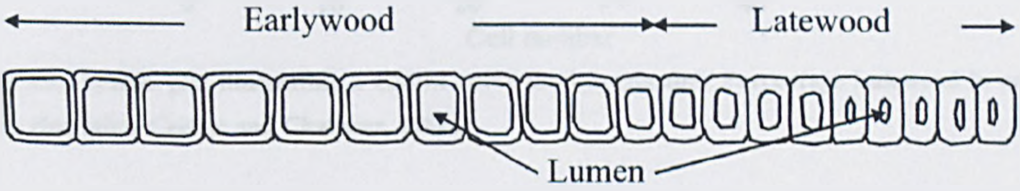


Figure 3.4. A diagrammatic representation of the positioning of the earlywood-latewood boundary in conifer wood, based on measurements of lumen diameter and wall thickness (diagram from Creber and Chaloner, 1984a).

Although Mork's method gives a good first impression of the percentage of latewood, Creber and Chaloner (1984b) expanded this method to determine Percentage Latewood quantitatively by measuring the radial diameter of the cells across each growth ring. The cumulative algebraic sum of each cell's deviation from the mean radial cell diameter is calculated and plotted on a graph (CSDM curve) (Figure 3.5). This is done by subtracting the mean cell radial diameter (for the file being considered) from each individual cells radial diameter. Therefore if a cell is bigger than the mean the value will be positive, whilst if it is smaller than the mean the value produced will be negative. When the cumulative sum of these results is calculated it will therefore increase in value (adding positive numbers) until the latewood boundary where it will begin to decrease as more negative values are included. The point at which the cumulative sum curve finally turns to zero for the last time is used to determine the earlywood/latewood boundary in the ring (Creber and Chaloner, 1984a). The percentage latewood is then calculated using the equation:

$$\text{Percentage Latewood} = (a/b)*100$$

where a is the number of cells after which the CSDM curve turns to zero for the last time and b is the total number of cells in the ring increment (Figure 3.5).

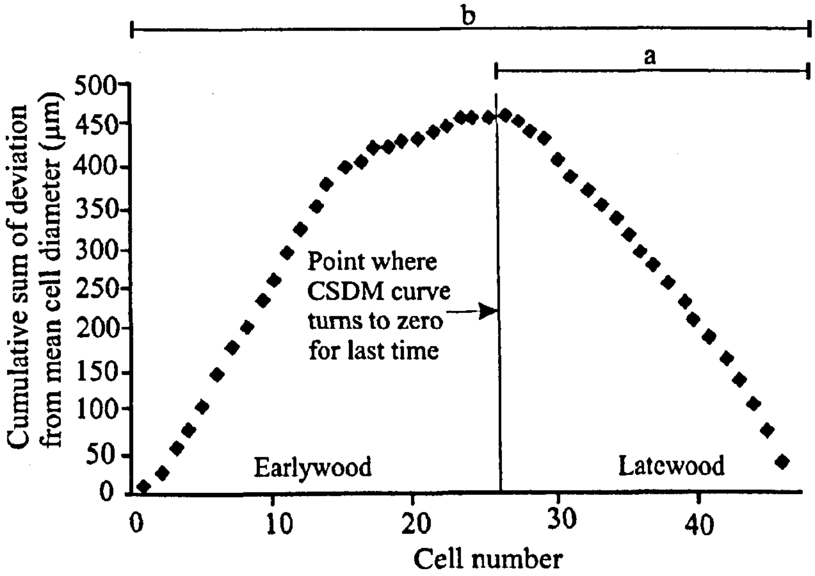


Figure 3.5. Scatter plot illustrating a CSDM curve used to calculate Percentage Latewood in one growth ring (after Creber and Chaloner, 1984a).

3.3.2. Percentage Diminution

The Percentage Diminution is defined as the percentage reduction in cell diameter across the growth increment (Falcon-Lang, 2000a). This calculation requires the collection of cell radial diameter data, therefore the same dataset used for the Percentage Latewood calculation can also be used here. These data are inserted into the equation below to determine Percentage Diminution:

$$\text{Percentage Diminution} = (c/d)*100$$

where d is the difference in cell radial diameter between the minimum and maximum cell radial diameter and c is the maximum cell radial diameter (Figure 3.6).

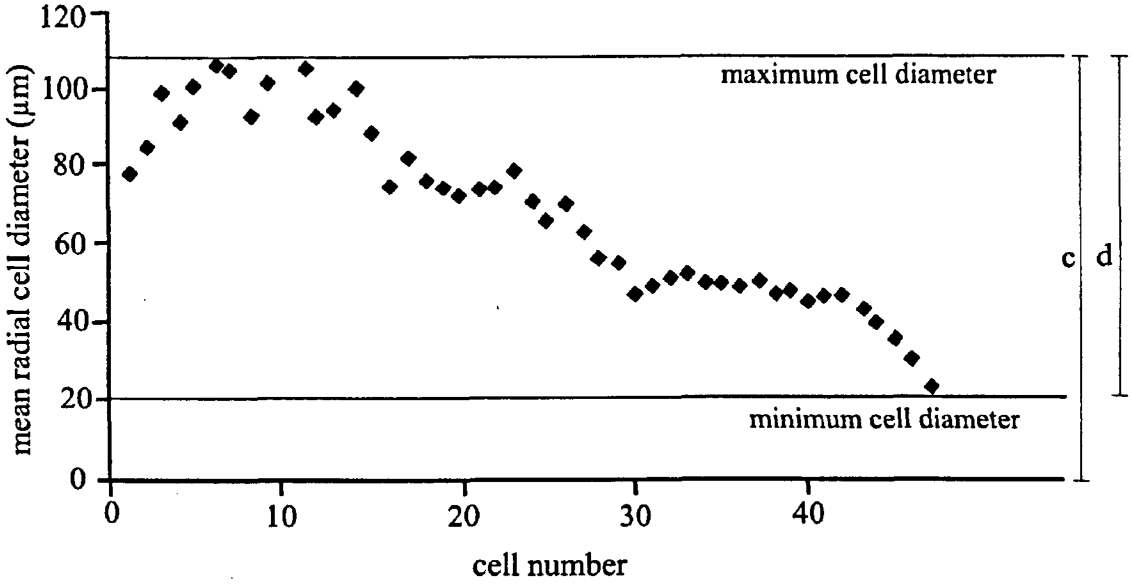


Figure 3.6. Scatter plot illustrating the reduction in cell diameter across a ring increment used to determine Percentage Diminution (Falcon-Lang, 2000a).

3.3.3. Ring Markedness Index

Ring Markedness Index is a quantitative measurement of the markedness of a growth ring boundary. This method combines Percentage Latewood and Percentage Diminution, as seen in the equation below.

$$\text{Ring Markedness Index (RMI)} = \frac{\text{Percentage Diminution}}{\text{Percentage Latewood}} \times 100$$

Falcon-Lang (2000a) showed that when values of RMI were plotted against the known LLSs of extant species, high values of RMI indicated a deciduous leaf habit whilst low values indicated an evergreen leaf habit (see Figure 3.7). It can be seen from Figure 3.7 that the deciduous species (*Larix decidua*) produces the highest values of RMI (between ~35 and 45) and the other species examined produced decreasing values of RMI with increasing known LLS. *Araucaria araucana* has an extremely long leaf LLS and produces the lowest value of RMI (between ~2 and 10).

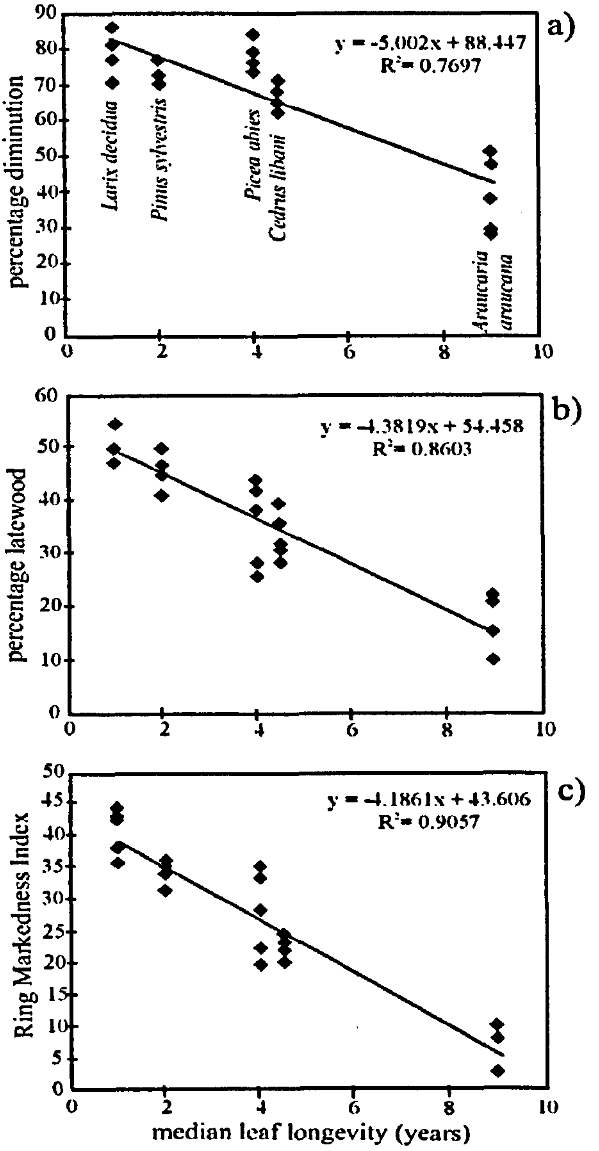


Figure 3.7. a) Percentage Diminution, b) Percentage Latewood and c) Ring Markedness Index scatter graphs showing the relationship between median leaf longevity and the Ring Markedness parameters for individual rings for a small sample set of modern conifer woods (Falcon-Lang, 2000a).

3.3.4. Development of the Ring Markedness Index method in this project

Falcon-Lang (2000a) was not confident in his use of RMI because his dataset was too small. Therefore he did not develop the method further. This project expands and develops his previous work by using a larger selection of extant conifer species to investigate whether the relationship between LLS and RMI holds true.

Some problems with Falcon-Lang's (2000a) work have been identified. For example, in his initial work on RMI he measured the radial diameter of five files (columns) of cells per growth ring. However in his samples the files were not the same length nor did they have the same number of cells in each file. To overcome this he correlated ring boundaries but chose arbitrary placement for the insertion of spaces between cells within rings, introducing considerable errors (Figure 3.8). He then averaged cell diameters for tangential rows of cells across the five files in the ring (e.g. cell a, Figure 3.8b) and Percentage Diminution, Percentage Latewood and RMI were then calculated using these average values. This method assumed that tangentially adjacent cells grew at the same time, which may not have been the case so, this method produced a wide variation in results, as noted by Falcon-Lang (2005a). This method makes the analysis unrepeatable as it relies on an individual's discretion as to where the additional cells or cell correlations are placed.

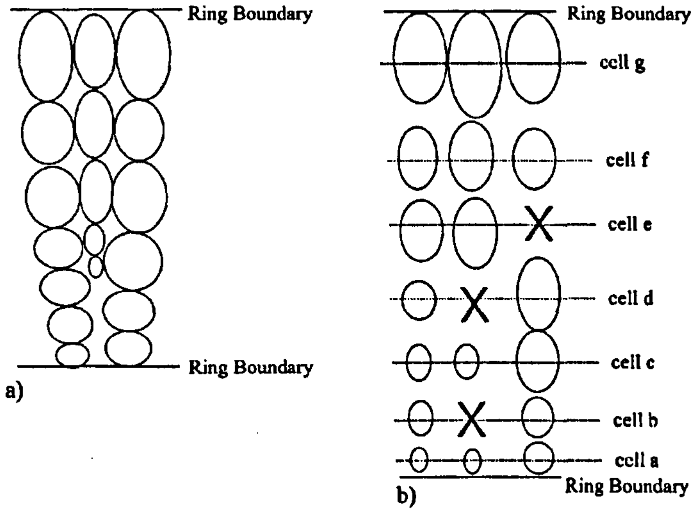


Figure 3.8. a) Diagrammatic representation of how the cells appear in files within the rings, showing different file lengths and number of cells present. b) Diagram showing how Falcon-Lang (2000a) spread out the cells to make the ring boundaries correlate within his spreadsheets. X = inserted space in his method.

However it was felt that the principle behind the basic method was sound and that it could be adapted to produce more reliable results. Therefore in this project methods were developed to prevent errors, such as described above, to ensure that the technique was more robust (see Section 3.3.4.1).

3.3.4.1. Measurement of cell diameters used in this study

Measurements of cells were made through individual files of cells and the results from the separate files then averaged to obtain a value of Percentage Diminution, Percentage Latewood and RMI for each ring (Figure 3.9). Only files that reached from one boundary to the next were included, as in Figure 3.9, any files that appeared incomplete as in Figure 3.8a (centre file) were not used. This method omitted the need to correlate across the cells. After trying various methods, it was found that this method produced much less variability and was therefore more reliable. The errors in this method were assumed to be incurred only from the precision of measurement. It was therefore decided to use this much more robust and reliable method for all extant and fossil samples within this study.

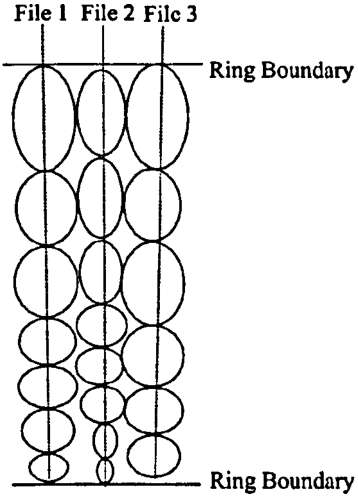


Figure 3.9. Diagrammatic representation of the method of measuring files of cells used within this study to prevent errors caused by inserting spaces (see figure 3.8.b).

A second set of trials was then carried out to investigate how many files and rings were required to produce the most reliable data set with maximum time efficiency. It was concluded that where possible 10 files of cells per ring and 10 rings per specimen should ideally be measured in modern woods, but only 5 files and rings in fossil samples. The smaller number in fossil samples is due the preservation often being poor which restricts the number of files and rings available for measurement. It should also be noted that it is not always possible to measure 10 rings in modern and 5 rings in fossil specimens if the rings were wide due to the limited size of thin section slides or if the wood was damaged and full files could not be obtained therefore as many rings as possible were measured up to a maximum of 10 in modern and 5 in fossil. The number of files measured was always 10 in modern and 5 in fossil specimens for consistency. If this number of intact files could not be found in a ring it was not included in the sample set.

Only files with greater than 30 cells width were used because narrow increments are found to produce anomalously high values of Percentage Latewood compared to wide rings of the same tree (Creber and Chaloner, 1984a).

3.3.5. Percentage Skew

Percentage Skew is a method devised by Falcon-Lang (2000b) to quantitatively distinguish the woods of deciduous and evergreen trees. This method uses a plot of the Cumulative Sum of Deviation from the Mean (CSDM).

The CSDM curve is plotted, then the Percentage Skew of the zenith of the CSDM curve with respect to the centre of the plot is calculated for each growth increment using the equation below.

$$\text{Percentage Skew} = y/x*100$$

where y is the number of cells from the centre point to the zenith and x is the number of cells to the mid point of the ring, as shown on Figure 3.10.

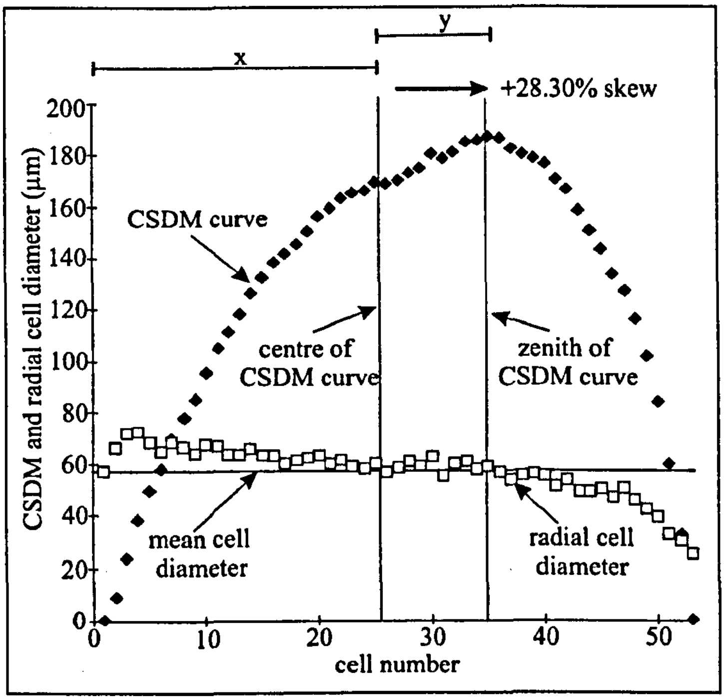


Figure 3.10. Scatter plot illustrating the CSDM curve used to calculate Percentage Skew taken from Falcon-Lang (2000b).

Perfectly symmetrical CSDM curves produce zero values of Percentage Skew whilst CSDM curves with the zenith occurring either to the left or right of the centre produce either negative or positive Percentage Skew respectively.

Falcon-Lang (2000b) reported that deciduous conifers dominantly possess symmetrical or left-skewed CSDM curves (negative values) whilst evergreen conifers produce dominantly right-skewed CSDM curves (positive values) (Figure 3.11). Values between -10% and +10%

are considered to be ambiguous as this range contains data points from both deciduous and evergreen species (Figure 3.11). Falcon-Lang (2000b) also included *Ginkgo biloba*, a gymnosperm of the subdivision Conipherophytina, within this sample set as it appears to have been a common element within some fossil floras.

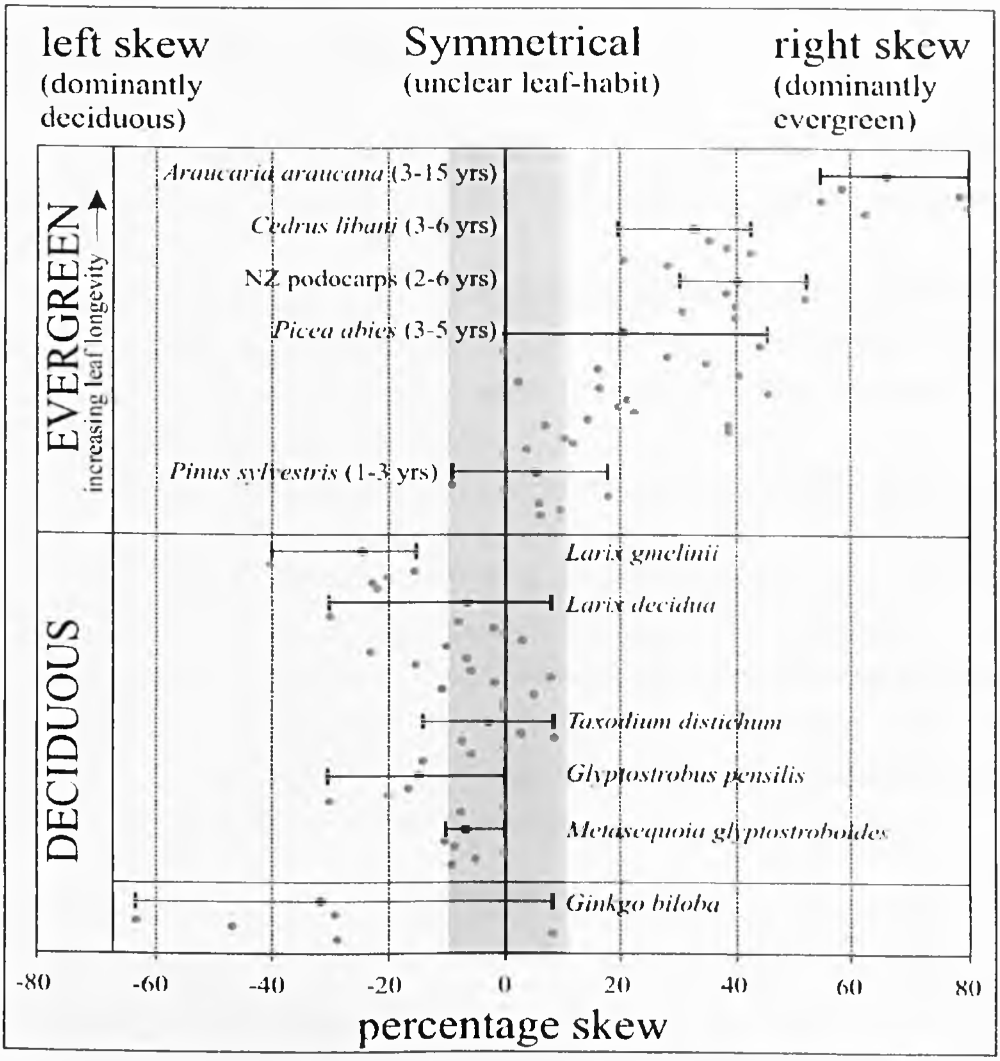


Figure 3.11. Skewness data set for deciduous and evergreen gymnosperm taxa used by Falcon-Lang, 2000b. Grey circles indicate individual rings. Bars with black circles indicate data range and mean for each taxonomic group (Falcon-Lang, 2000b).

However, although Falcon-Lang (2005b) suggests that this method may be used alone to determine LLS, when tested in this project it was found to produce unreliable results for a large data set of extant trees and was therefore not used for the fossils within this study (Section 3.5).

3.4. Leaf life-span analysis of extant conifer woods

This section presents the results of LLS analysis using extant woods. A much larger set of extant conifer wood samples were collected than used in Falcon-Lang's (2000a) trial and cell dimensions measured, as outlined in Section 3.3 (Table 3.1). The RMI of the extant conifers was then determined and the relationship between RMI and LLS derived. This relationship forms the basis for the derivation of leaf life-spans in fossil wood (Chapter 4).

3.4.1. Results of leaf life-span analysis in extant woods

In this section data from extant woods are used to produce one dataset of extant wood (36 specimens representing 28 species of conifers). Full details of the materials used are given in Table 3.1.

For each extant wood sample cells within growth rings were measured, as described in Section 3.3. From these data Percentage Latewood and Percentage Diminution were calculated (Sections 3.3.1 and 3.3.2) and then RMI calculated (Section 3.3.3). Results for each extant sample are presented in Appendix A, Table A1.1.

The LLS (in months) for each species of extant conifer was obtained from previous publications and via personal communication with other researchers who had determined modern conifer LLSs in the field (see Table 3.1). Average LLSs per species were used because the length of time a tree keeps its leaves can vary. The average LLSs were obtained in various ways by different authors. One method involved counting the number of annual leaf clusters (cohorts) with at least 50% of their leaves remaining on the branch (Figure 3.12). Other methods involve direct observation of leaf birth and death using tagging and drawing techniques (Reich *et al.*, 1999; Lusk, 2001; Lusk and Reich, 2003).

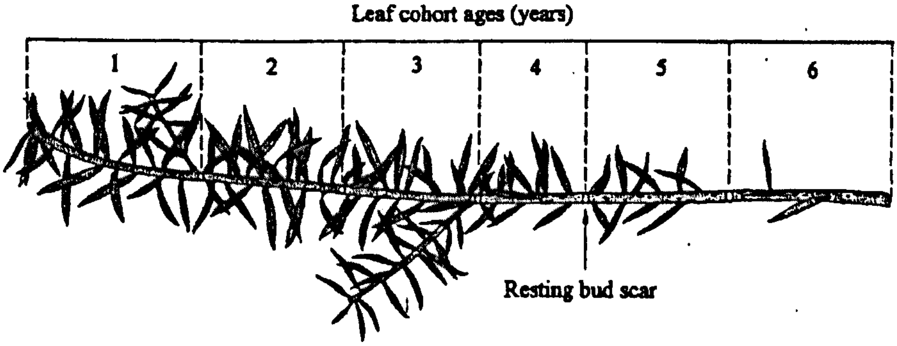


Figure 3.12. Branchlet of *Podocarpus nubigena*, showing resting bud scars delimiting successive leaf cohorts used to estimate the average leaf life-span of the tree. Leaf population on this branchlet suggests an average leaf life-span of *ca.* 5 years because about 50% of the leaves from the 5th most-recent cohort have died (Lusk, 2001).

Table 3.1. Table showing extant conifer wood samples examined. Sample numbers denote the location from which the sample was collected, the sample set it belongs to and the individual sample number.

Sample N°	Species	Common Name	Location	Altitude (m)	Material Type Branch (B) Trunk (T)	Natural Stand (N) Cultivated (C)	Known LLS (average in years)	N° of Growth Rings Measured	Source of LLS Data
A1-1	*Tsuga canadensis*	Eastern Hemlock	Australia	-	T	-	60 months (5 years)	3	Reich *et al.*, 1999
A1-2	*Pinus strobus*	Weymouth Pine	Australia	-	T	-	21 months (1.75 years)	2	Reich *et al.*, 1999
A1-3	*Larix occidentalis*	Western Larch	Australia	-	T	-	5-6 months (0.46 years)	6	Personal communication P.B.Reich
A1-4	*Pseudotsuga menziesii*	Douglas Fir	Australia	-	T	-	36 months (3 years)	4	Osborne and Beerling, 2002
A1-5	*Picea sitchensis*	Sitka Spruce	Australia	-	T	-	48 months (4 years)	4	Osborne and Beerling, 2002
A1-6	*Pinus contorta*	Beach or Shore Pine	Australia	-	T	-	47.5 months (3.96 years)_	7	Schoettle and Fahey, 1994
A1-7	*Juniperus virginiana*	Pencil Cedar	Australia	-	T	-	30-50 months (3.33 years)	3	Personal communication P.B.Reich
LEEDS-02-1	*Araucaria araucana*	Chile Pine or Monkey Puzzle Tree	Leeds, UK	208	T	C	108 months (9 years)	4	Falcon-Lang, 2000a
TAP-01-1	*Taxodium distichum*	Swamp Cypress	Tapton Experimental Gardens, Sheffield, UK	190	B	C	6.5 months (0.54 years)	2	Reich *et al.*, 1999
TAP-01-2	*Cedrus deodara*	Deodar	Tapton Experimental Gardens, Sheffield, UK	190	B	C	54 months (4.5 years)	2	Personal communication C.Osborne

Continued ....

Sample N°	Species	Common Name	Location	Altitude (m)	Material Type Branch (B) Trunk (T)	Natural Stand (N) Cultivated (C)	Known LLS (average in years)	N° of Growth Rings Measured	Source of LLS Data
TAP-01-3	*Pinus rigida*	Northern Pitch Pine	Tapton Experimental Gardens, Sheffield, UK	190	B	C	33 months (2.75 years)	1	Reich *et al.*, 1999
TAP-01-4	*Larix leptolepis*	Japanese Larch	Tapton Experimental Gardens, Sheffield, UK	190	B	C	5-6 months (0.46 years)	1	Personal communication P.B.Reich
TAP-01-5	*Cedrus libani*	Cedar of Lebanon	Tapton Experimental Gardens, Sheffield, UK	190	B	C	54 months (4.5 years)	1	Falcon-Lang, 2000a
TAP-01-6	*Araucaria araucana*	Chile Pine or Monkey Puzzle Tree	Tapton Experimental Gardens, Sheffield, UK	190	B	C	108 months (9 years)	-	Falcon-Lang, 2000a
TAP-01-7	*Sequoiadendron giganticum*	Redwood	Tapton Experimental Gardens, Sheffield, UK	190	B	C	40-60 months (4.2 years)	2	Personal communication P.B.Reich
TAP-01-8	*Abies veitchii*	Veitch's Silver Fir	Tapton Experimental Gardens, Sheffield, UK	190	B	C	30-60 months (3.75 years)	2	Personal communication Prof.P.B.Reich
TAP-01-9	*Pseudotsuga menziesii*	Douglas Fir	Tapton Experimental Gardens, Sheffield, UK	190	B	C	36 months (3 years)	2	Osborne and Beerling, 2002
TAP-01-10	*Pinus strobus*	Weymouth Pine	Tapton Experimental Gardens, Sheffield, UK	190	B	C	21 months (1.75 years)	3	Reich *et al.*, 1999
TAP-01-11	*Metasequoia glyptostroboides*	Dawn Redwood	Tapton Experimental Gardens, Sheffield, UK	190	B	C	6 months (0.5 years)	-	Personal communication C.Osborne

Continued ....

Sample N°	Species	Common Name	Location	Altitude (m)	Material Type Branch (B) Trunk (T)	Natural Stand (N) Cultivated (C)	Known LLS (average in years)	N° of Growth Rings Measured	Source of LLS Data
TAP-01-12	*Pinus banksiana*	Jack Pine	Tapton Experimental Gardens, Sheffield, UK	190	B	C	66-90 months (6.50 years)	2	Osborne and Beerling, 2002
TAP-01-13	*Saxegothaea conspicua*	Prince Alberts Yew	Tapton Experimental Gardens, Sheffield, UK	190	B	C	50 months (4.2 years)	3	Lusk, 2001
TAP-01-14	*Larix decidua*	European Larch	Tapton Experimental Gardens, Sheffield, UK	190	B	C	6 months (0.5 years)	2	Reich *et al.*, 1999
TAP-01-15	*Larix decidua*	European Larch	Tapton Experimental Gardens, Sheffield, UK	190	B	C	6 months (0.5 years)	4	Reich *et al.*, 1999
TAP-01-16	*Sequoia sempervirens*	Coast Redwood	Tapton Experimental Gardens, Sheffield, UK	190	B	C	40-60 months (4.2 years)	2	Personal communication P.B.Reich
TAP-01-17	*Sequoia sempervirens*	Coast Redwood	Tapton Experimental Gardens, Sheffield, UK	190	B	C	40-60 months (4.2 years)	3	Personal communication P.B.Reich
TAP-01-18	*Picea abies*	Norway Spruce	Tapton Experimental Gardens, Sheffield, UK	190	B	C	48 months (4 years)	4	Falcon-Lang, 2000a
TAP-01-19	*Taxus baccata*	Common Yew	Tapton Experimental Gardens, Sheffield, UK	190	T	C	96 months (8 years)	2	Personal communication C.Osborne
AME-05-01	*Taxodium distichum*	Swamp Cypress	Tapton Experimental Gardens, Sheffield, UK	-	T	N	6.5 months (0.54 years)	7	Reich *et al.*, 1999

Continued ....

Sample N°	Species	Common Name	Location	Altitude (m)	Material Type Branch (B) Trunk (T)	Natural Stand (N) Cultivated (C)	Known LLS (average in years)	N° of Growth Rings Measured	Source of LLS Data
NZ-03-01	*Dacrydium cupressinum*	Rimu	Whirinaki, central North Island, New Zealand.	460	T	N	48 months (4 years)	-	Personal communication M.McGlone
NZ-03-02	*Prumnopitys taxifolia*	Matai	Whirinaki, central North Island, New Zealand.	460	B	N	36 months (3 years)	2	Personal communication M.McGlone
NZ-03-03	*Podocarpus totara*	Totara	Whirinaki, central North Island, New Zealand.	460	T	N	38 months (3.16 years)	10	Personal communication C.Osborne
NZ-03-04	*Pinus radiata*	Monterey Pine	Whirinaki, central North Island New Zealand.	380	T	C	30 months (2.5 years)	2	Warren and Adams, 2000
NZ-03-05	*Dacrydium cupressinum*	Rimu	Tihoi, central North Island, New Zealand.	740	B	N	48 months (4 years)	-	Personal communication M.McGlone
NZ-03-06	*Prumnopitys taxifolia*	Matai	Tihoi, central North Island, New Zealand.	740	B	N	36 months (3 years)	1	Personal communication C.Osborne
NZ-03-07	*Prumnopitys ferrugina*	Miro	Tihoi, central North Island, New Zealand.	420	T	N	36 months (3 years)	2	Personal communication C.Osborne

Continued ....

Sample N°	Species	Common Name	Location	Altitude (m)	Material Type Branch (B) Trunk (T)	Natural Stand (N) Cultivated (C)	Known LLS (average in years)	N° of Growth Rings Measured	Source of LLS Data
NZ-03-08	*Phyllocladus trichomanoides*	Tanekaha	Tihoi, central North Island New Zealand.	420	T	N	24 months (2 years)	-	Personal communication M McGlone
NZ-03-09	*Pseudotsuga menziesii*	Douglas Fir	Tihoi, central North Island, New Zealand.	540	T	C	36 months (3 years)	5	Osborne and Beerling, 2002
NZ-03-10	*Pinus radiata*	Monterey Pine	Kaingaroa, central North Island New Zealand.	500	T	C	30 months (2.5 years)	4	Warren and Adams, 2000
NZ-03-11	*Cupressus macrocarpa*	Monterey Cypress	Rotoehu New Zealand.	220	T	C	-	-	-
NZ-03-12	*Podocarpus totara*	Totara	Northland, New Zealand.	120	T	N	38 months (3.16 years)	8	Personal communication C.Osborne
NZ-03-13	*Agathis australis*	Kauri	New Plymouth, New Zealand.	40	T	Native but ~120km south of natural southern limit.	36 months (3 years)	2	Personal communication M.McGlone
KEW-06-01 L2	*Metasequoia glyptostroboides*	Dawn Redwood (Water Spruce)	China	-	T	N	6 months (0.5 years)	2	Personal communication C.Osborne

Continued ....

Sample N°	**Species**	**Common Name**	**Location**	**Altitude (m)**	**Material Type Branch (B) Trunk (T)**	**Natural Stand (N) Cultivated (C)**	**Known LLS (average in years)**	**N° of Growth Rings Measured**	**Source of LLS Data**
KEW-06-02 19058	*Taxodium mucronatum*	Mexican Cypress, Montezuma Bald Cypress, Sabino	Mexico	-	T	N	-	1	-
KEW-06-03	*Taxodium distichum*	Swamp Cypress, Bald Cypress	Florida, USA	-	T	N	6.5 months (0.54 years)	3	Reich *et al.*, 1999
RUSS-07-1	*Picea obovata*	Siberian Spruce	Komi Republic Russia	-	T	N	72 months (6 years)	10	Nisbet, 1893; Vidakovic, 1991

Ring Markedness Index and LLS for each extant wood sample were then plotted on a scatter graph, shown in Figure 3.13. Values of LLS of less than 12 months (deciduous) are shown within the brown area and values of LLS greater than 12 months (evergreen) are shown in the green area of the graph. It can be seen that, as with Falcon-Lang's (2000) original trial, high values of RMI (>40) indicate a deciduous habit whilst low values of RMI (<40) indicate an evergreen habit, showing that the relationship holds true over this larger data set (Figure 3.13).

The relationship between RMI and LLS was determined as a regression line, using MATlab software. This is plotted on the graph in Figure 3.13 as a solid black line. The 95% confidence levels are plotted as a dark dashed line (assuming an infinite number of samples could be examined) and a dotted line (assuming only one sample could be examined). Therefore all samples should fall between the dashed and dotted lines.

The relationship between LLS and RMI was derived as the formula:

$$\mathrm{RMI} = -7.67 \ln(\mathrm{LLS}) + 51.81$$

or

$$\mathrm{LLS} = \mathrm{EXP}((\mathrm{RMI} - 51.81)/ -7.67)$$

This formula can therefore be used to calculate the LLSs of the fossil material.

Ring Markedness Index and LLS data obtained for all extant conifer samples are given in Appendix A, Table A1.1. These data were analysed using one-way analysis of variance (ANOVA) to test the significance of the relationship between samples (Figure 3.14). This analysis tests whether samples are statistically likely to be part of the same population or from different populations. Where samples are statistically determined to be part of the same population the error bars will overlap, however if a sample is determined to be from a different population the error bars will not overlap. The error bars can be set to the required confidence interval. The results show that there is a very strong relationship, to the 95% confidence level, between RMI and LLS. Note that deciduous species (*Larix decidua*, *L. occidentalis* and *Metasequoia glyptostroboides*) form a separate population from species with an evergreen habit.

3.4.2. The problem of *Taxodium distichum*

All *Taxodium distichum* samples (TAP-01-1, KEW-06-3 and AME-05-1, shown as red crosses on Figure 3.13) appear to be problematic because they produce an evergreen signal (of approximately 18-24 months) in their wood, even though this species is widely accepted to be deciduous. This evergreen signal is produced in both branch and trunk material. This appears to be due to *T. distichum* possessing two types of foliage. The majority of the leaves are shed annually but a small proportion are perennial, being held for approximately 24 months (personal

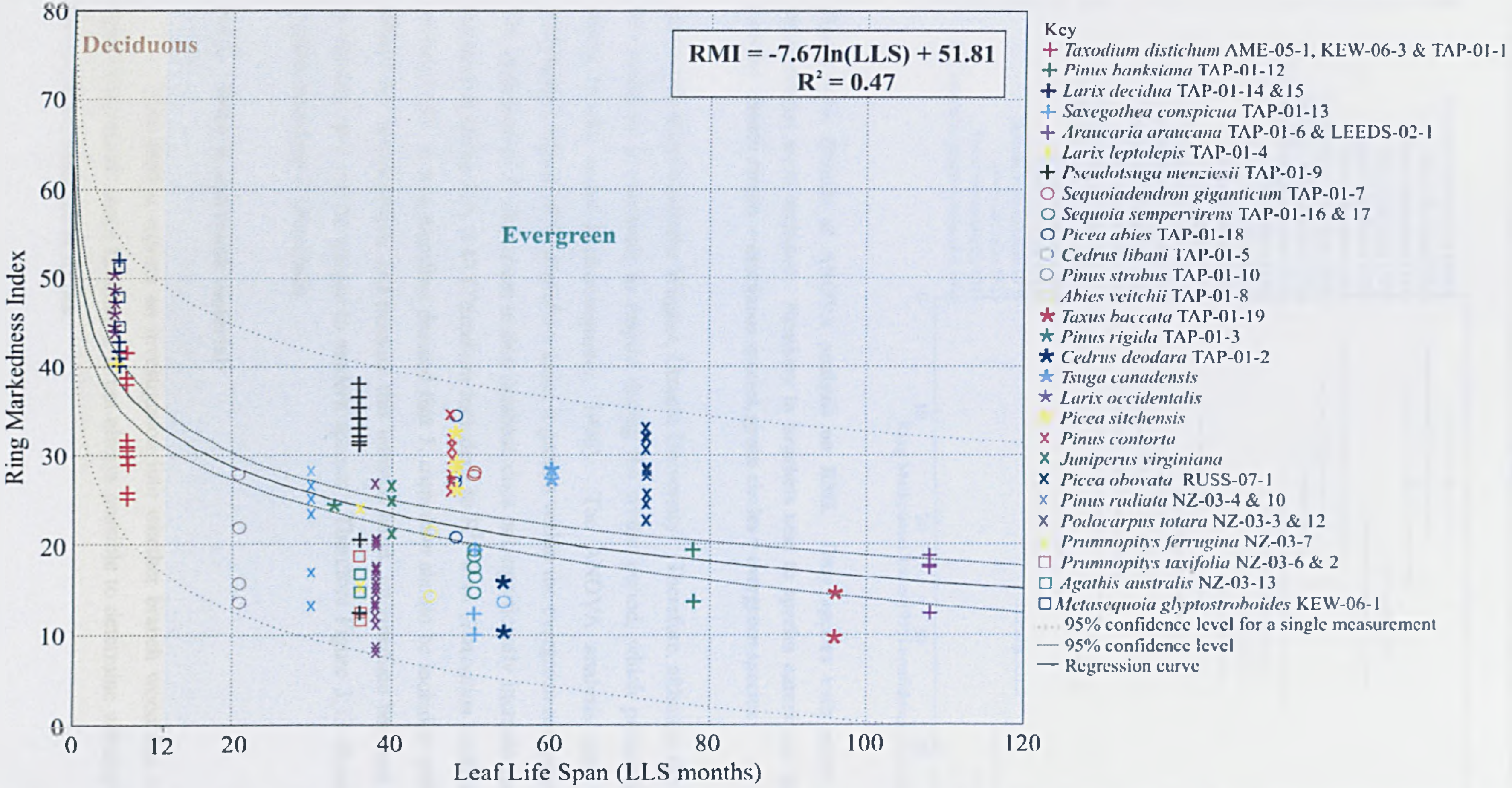


Figure 3.13. Scatter graph showing a plot of LLS against RMI for extant conifer woods. The symbols represent individual rings within conifer samples therefore there may be multiple points for a single sample (see Chapter 3, Section 3.4.1). The full dataset for these samples is shown in Table 3.1 and Appendix A, Table A1.1.

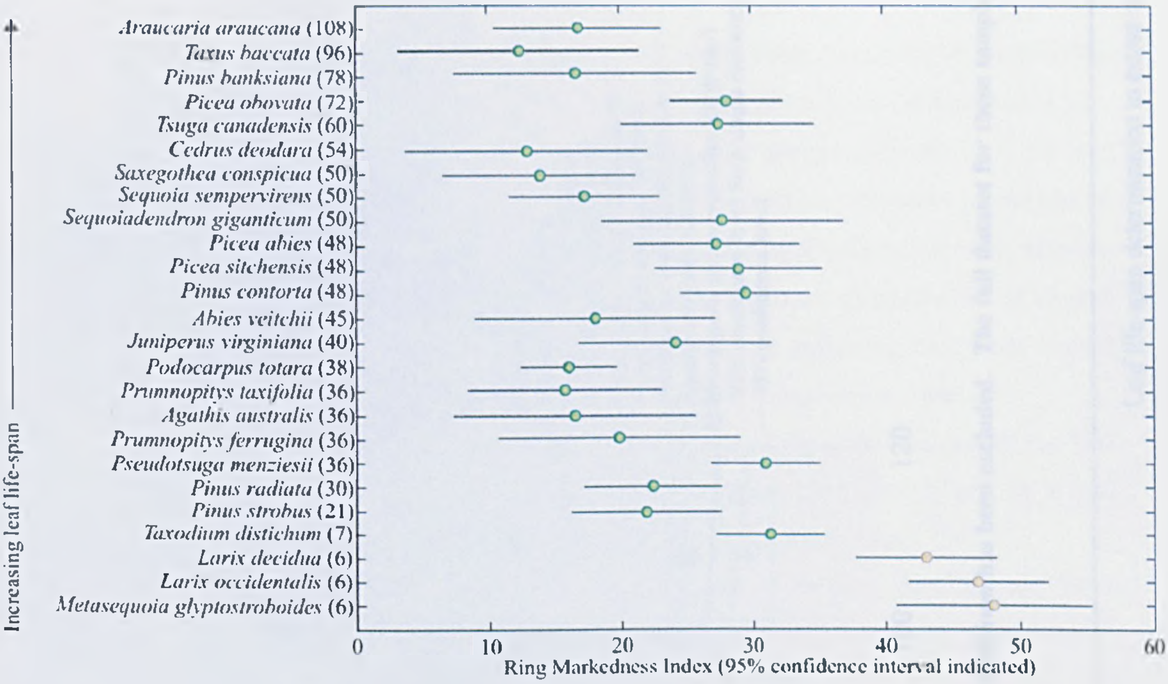


Figure 3.14. Results of ANOVA analysis on RMI. Only species with more than one ring measurement were included. Numbers in brackets next to species names are leaf life-spans in months. Brown circles = deciduous species, green circles = evergreen species.

communication Friederike Wagner, Utrecht University). Therefore, although the tree appears to be deciduous it continues to respire during the winter period, which produces an evergreen signal in the wood (Schweingruber, 1996). The ANOVA analysis also highlights the problematic nature of *T. distichum* since it groups within the evergreen category (Figure 3.14). The inclusion of *T. distichum* in this database does not significantly increase the variability of the dataset (from $R^2 = 0.47$ (*Taxodium* included) to $R^2 = 0.44$ (*Taxodium* omitted), Figure 3.13 versus 3.15). It was therefore decided that *T. distichum* should be included within the modern dataset for completeness and because this unusual habit, intermediate between deciduous and evergreen, may not be unique to modern species. Therefore Figure 3.13 shows the complete dataset including *T. distichum*.

3.4.3. Branch and trunk material

This section reports an investigation into whether branch wood has a different LLS signal from trunk wood because it is not always possible to determine whether fossil wood is derived from branches or trunks.

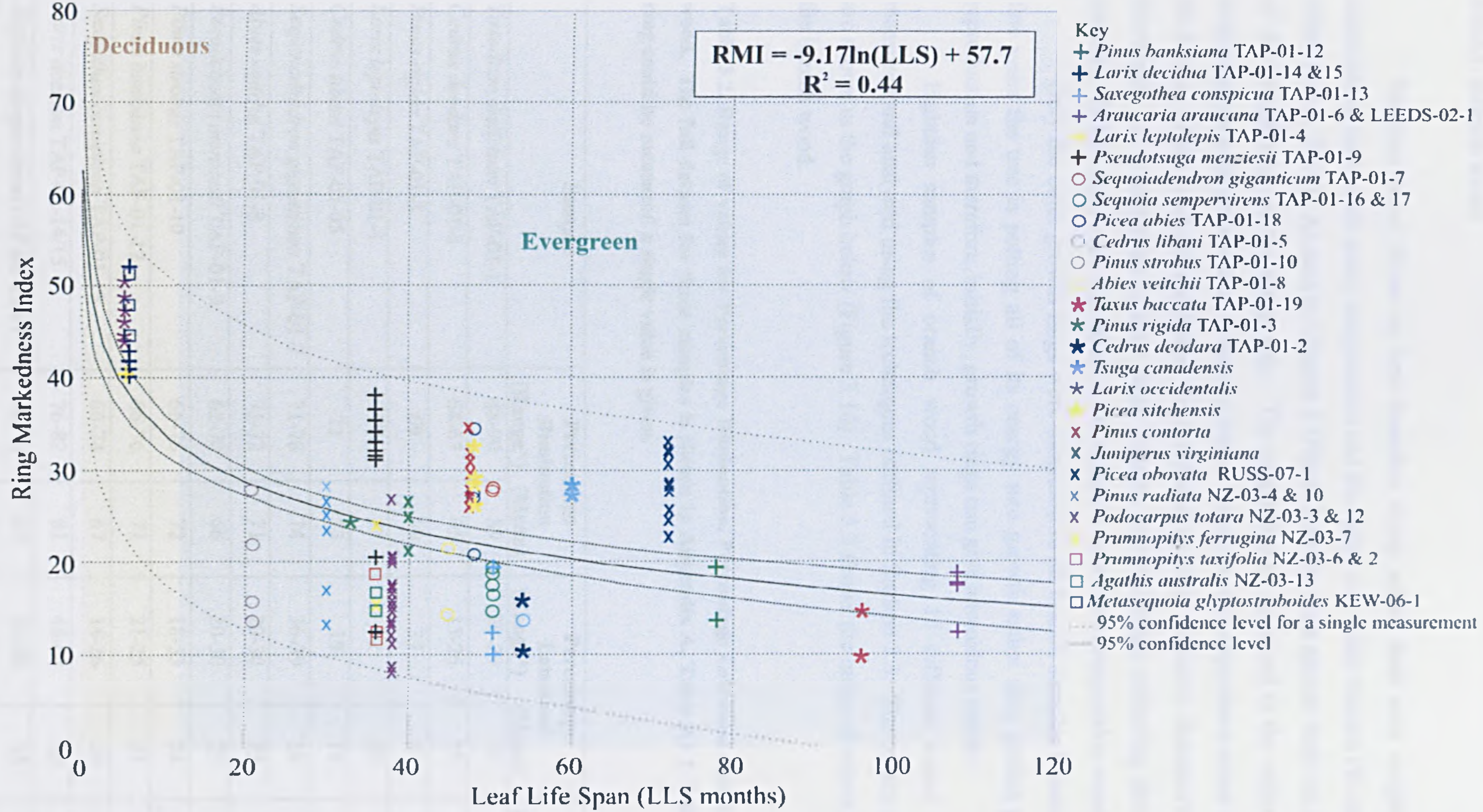


Figure 3.15. Scatter graph showing the results of extant wood analysis from which *Taxodium distichum* has been excluded. The full dataset for these samples is shown in Table 3.1. and Appendix A, Table A1.1.

3.4.3.1. Branch wood

Reaction wood forms as tree branches droop under their own weight, putting the underside of the branch under compression and the upper side under tension (Wilson and White, 1986; Ennos, 2001). As seen in Chapter 2 (Figure 2.5) the rings appear wider on the lower side of the branch than on the upper side. The proportion of latewood in the wider compression rings appears to be greater than in normal rings. However, this appearance arises more from the thickening of the tracheid walls than from reduced tracheid diameter characteristic of normal latewood. It is important to bear these features in mind when collecting data from branch material. In this study care was taken not to measure cells from compression wood.

Only the outer growth rings were measured in all branch samples because for the first few years the tree is putting all of its energy into growth rather than putting part of it into reproduction and therefore, initially, growth rings can give anomalous results.

Eighteen samples of branch wood representing 15 different extant species were measured and analysed using the techniques outlined in Section 3.3. The results of the analysis are shown in the graph below (Figure 3.16). Table 3.2 shows the range of values obtained from the branch wood.

Table 3.2. Range of values for Percentage Diminution, Percentage Latewood and RMI for branch wood. The full dataset for these samples is shown in Appendix A, Table A1.1. * Where only one ring could be measured a single value is given.

Sample	Percentage Diminution		Percentage Latewood		RMI	
	(Range*)	(Mean)	(Range*)	(Mean)	(Range*)	(Mean)
Taxodium distichum TAP-01-1	88-90	89	28-29	29	25-26	25
Cedrus deodara TAP-01-2	64-67	65	15-26	20	10-16	13
Pinus rigida TAP-01-3	69	69	37	37	24	24
Larix leptolepis TAP-01-4	77	77	52	52	40	40
Cedrus libani TAP-01-05	73	73	19	19	14	13
Sequoiadendron giganticum TAP-01-7	71-78	74	36-39	38	28	28
Abies veitchii TAP-01-8	71-72	71	20-30	25	15-22	18
Pseudotsuga menziesii TAP-01-9	62-70	66	20-30	25	12-21	16
Pinus strobus TAP-01-10	66-76	72	18-33	24	14-17	17
Pinus banksiana TAP-01-12	66-76	71	21-25	23	14-19	17
Saxgothea conspicua TAP-01-13	66-74	67	14-26	20	10-20	14
Larix decidua TAP-01-14/15	76-82	81	48-64	52	40-52	42
*Sequoia sempervirens*TAP-01-16/17	60-74	67	22-28	25	15-19	17
Picea abies TAP-01-18	71-78	75	29-47	37	21-35	27
Prumnopitys taxifolia NZ-03-2/6	86-90	88	14-21	17	12-19	15

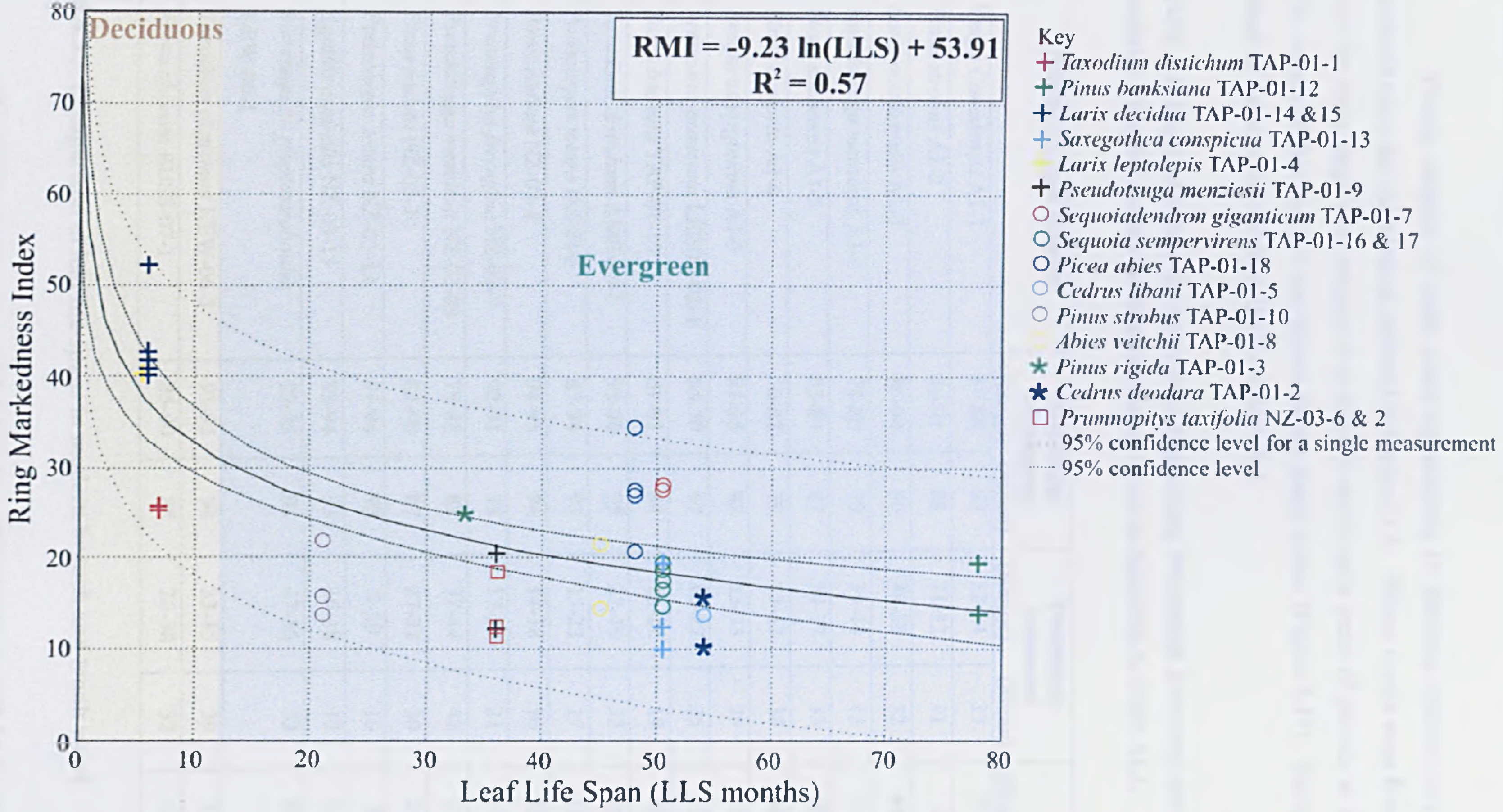


Figure 3.16. Scatter graph showing Ring Markedness Index versus Leaf Life-span (in months) for extant branch wood. Each data point represents an individual ring for each sample. The full data set for these plots is shown in Appendix A, Table A1.1.

3.4.3.2. Trunk wood

Twenty samples of trunk wood representing 16 different species were measured and analysed using the calculations outlined in Section 3.3. Where trunks were from juvenile trees only the outer rings were measured in order to avoid early years of growth as in the branches. The results of this analysis are shown on the graph below (Figure 3.17). Table 3.3 shows the range of values obtained from the trunk material.

Table 3.3. Range of values for Percentage Diminution, Percentage Latewood and RMI for trunk material. The full dataset for these samples is shown in Appendix A, Table A1.1.

Sample/Sample Number	Percentage Diminution		Percentage Latewood		RMI	
	(Range)	(Mean)	(Range)	(Mean)	(Range)	(Mean)
Tsuga Canadensis A1-1	81-88	83	32-34	33	27-28	28
Pinus strobus A1-2	86-91	88	31-32	31	28	28
Larix occidentalis A1-3	86-94	90	48-59	52	44-51	47
Pseudotsuga menziesii A1-4	78-80	79	39-44	42	31-35	33
Picea sitchensis A1-5	85-89	87	29-37	33	26-33	29
Pinus contorta A1-6	76-82	79	33-42	38	26-35	27
Juniperus virginiana A1-7	81-85	83	25-33	29	21-27	24
Araucaria araucana LEEDS-02-1	65-70	67	19-27	25	13-19	17
Taxus baccata TAP-01-19	61-67	64	16-22	19	10-15	12
Taxodium distichum AME-05-1	93-96	95	27-40	32	25-38	39
Podocarpus totara NZ-03-3	87-94	93	13-23	17	11-21	16
Pinus radiate NZ-03-4	94-95	94	14-18	16	13-17	15
Prumnopitys ferrugina NZ-03-7	92-93	93	17-27	21	15-24	20
Pseudotsuga menziesii NZ-03-09	78-88	82	37-44	42	31-38	34
Pinus radata NZ-03-10	82-90	87	27-31	30	24-28	26
Podocarpus totara NZ-03-12	91-94	93	9-29	16	8-27	15
Agathis australis NZ-03-13	93-94	93	16-18	17	15-17	16
Metasequoia glyptostroboides KEW-06-1	92-95	93	47-56	52	45-51	48
Taxodium distichum KEW-06-3	93-95	94	33-45	39	31-42	37
Picea obovata RUSS-07-1	85-90	88	26-38	32	23-33	29

3.4.3.3. Comparison of leaf life-spans in modern branch and trunk wood

The results for branch wood fall into two distinct groups, with LLS either less or greater than 18 months. Given that 16 of the 18 samples of branch wood grew under a very narrow range of environmental conditions (at Tapton Experimental Gardens, Sheffield, UK)

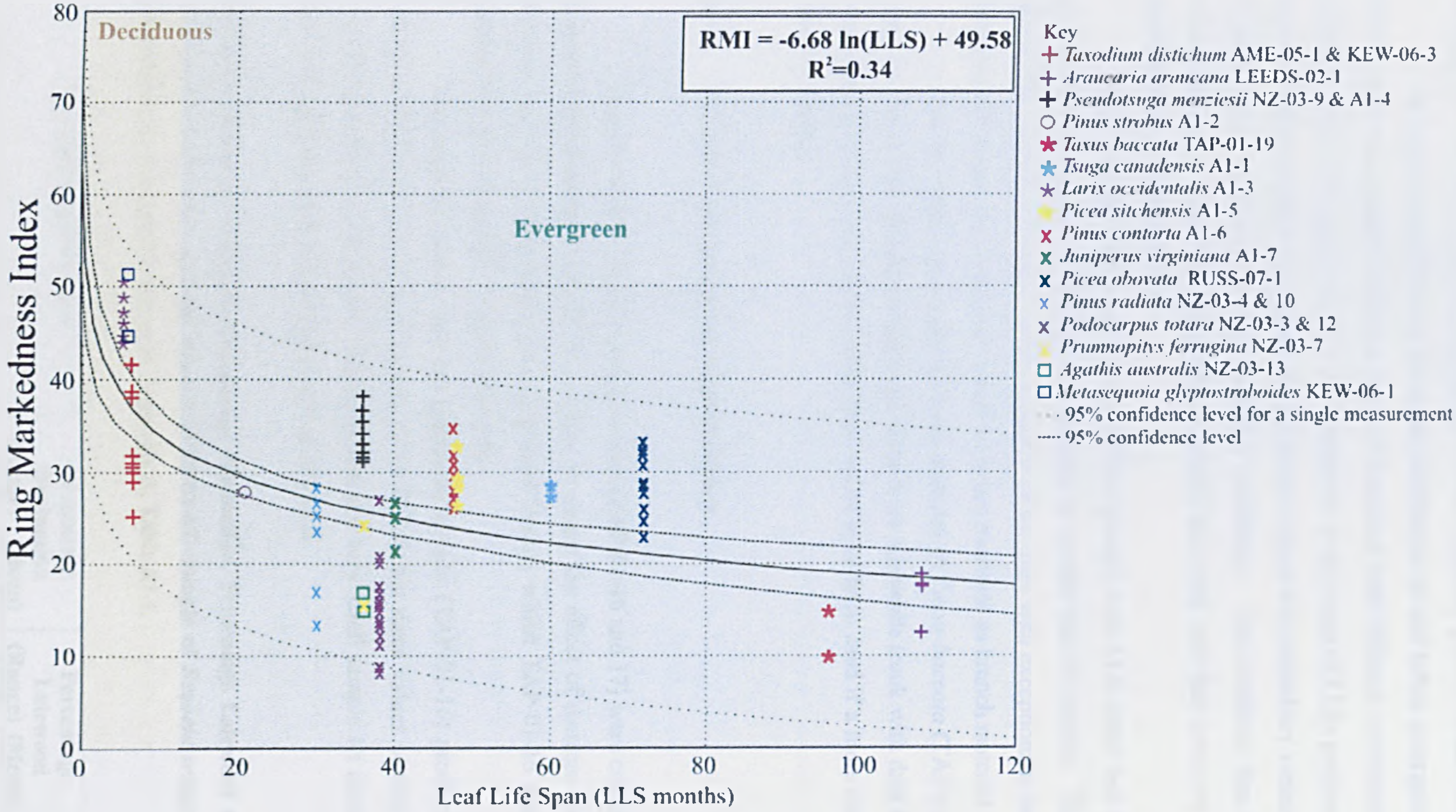


Figure 3.17. Scatter graph showing Ring Markedness Index versus Leaf Life-span (in months) of extant trunk wood. The full data set for these plots is shown in Appendix A, Table A1.1.

it is highly unlikely that the logarithmic relationship between RMI and LLS is an artifact of variable growing environments, suggesting at least a partially genetic control on leaf habit.

The trunk material shows the same distribution of leaf habits (evergreen or deciduous) even though this material is from a range of locations with different environmental conditions. However, there does appear to be wider variations in the range of LLSs produced by individual species. This suggests a strong underlying genetic signal with subsidiary variations in the range of LLS values produced by environmental conditions. This confirms that branch material carries the same signal as that produced within the trunk and that intra-tree wood structure variability does not affect LLS.

The trunk data fall within three distinct groups, with LLS either less than 18 months, greater than 18 months but less than 90 months, or greater than 90 months. The third grouping within this material is created by the presence of samples with exceptionally long LLSs (*Taxus baccata* and *Araucaria araucana*), which were not available as branch material.

The low values produced by trunk material of *Taxus baccata* (TAP-01-9, Figure 3.13) may be due to this sample having been taken from a juvenile trunk with data being taken from rings closer to the centre of the stem than would have been used if a more mature sample had been available.

3.4.4. The effect of damage on wood structure

Two samples of *Sequoia sempervirens* (TAP-01-16 and 17) were collected from Tapton Experimental Gardens in Sheffield in order to assess the effect of damage on the LLS signal. Sample TAP-01-17 was taken from a pruned branch whilst TAP-01-16 was taken from an unpruned branch (Figure 3.18 and Table 3.4).

This analysis shows that the unpruned sample (TAP-01-16) produces slightly lower values of RMI than the pruned sample (TAP-01-17) but these values overlap and there is no significant difference in results. Although this is a very small sample set there is no indication that damage to the tree affects cell structure and LLS.

Table 3.4. Range of values for Percentage Diminution, Percentage Latewood and RMI for one unpruned (TAP-01-16) and one pruned (TAP-01-17) sample of *Sequoia sempervirens*. The full dataset for these samples is shown in Appendix A, Table A1.1.

Sample/Sample Number	Percentage Diminution		Percentage Latewood		RMI	
	(Range)	(Mean)	(Range)	(Mean)	(Range)	(Mean)
Sequoia sempervirens TAP-01-16	60-67	63	22-28	25	15-16	16
Sequoia sempervirens TAP-01-17	66-74	71	24-26	25	17-19	19

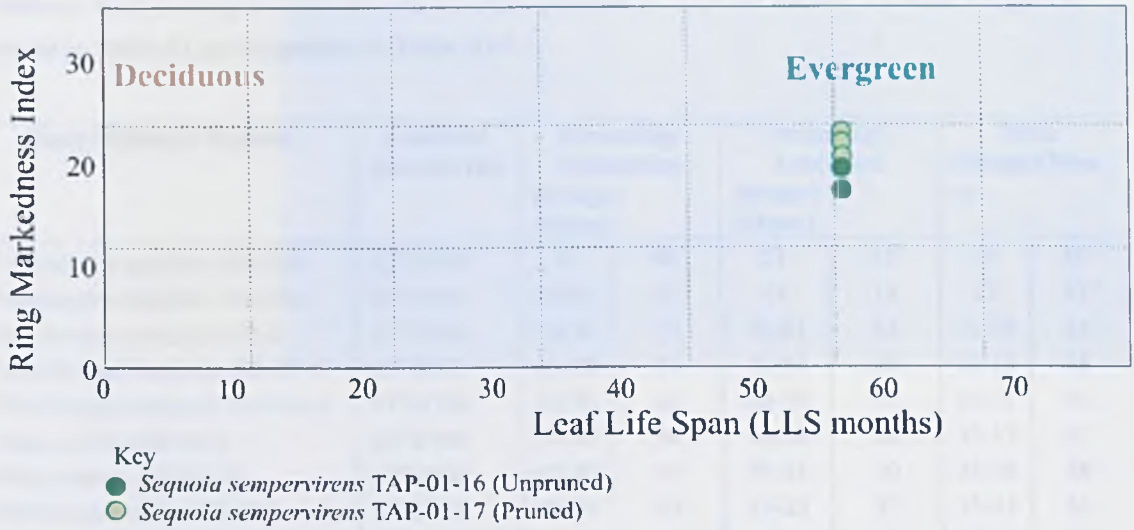


Figure 3.18. Scatter graph showing the results of the analysis of one unpruned and one pruned sample of *Sequoia sempervirens* in order to see if damage to the tree affects leaf life-span.

3.4.5. Comparison of leaf life-spans from natural stands and variable latitudes and altitudes

Observational studies of leaf habit carried out using methods such as the leaf tagging or counting of leaf clusters discussed in Section 3.4.1 have generally shown that LLS increases with increased latitude and altitude (Reich *et al.*, 1995; Schweingruber, 1996; Oleksyn *et al.*, 2003). Oleksyn *et al.* (2003) showed that this may be due to nutrient conservation being enhanced with the increased time that the leaves are held on the tree, therefore making it more productive for the tree to keep its leaves longer. Reich *et al.* (1995) suggested that several factors within the environment may be responsible for the increase in LLS, such as temperature, soil fertility and length of growing season (see also Schweingruber, 1996). In order to test if this trend is reflected in the wood structure 11 samples representing 5 individual species that grew at different latitudes and altitudes were measured and analysed (Figure 3.19a and Table 3.5).

These data do not appear to show any trend towards increasing altitude and latitude with increasing LLS or vice versa. However all values were plotted using the mean LLS (Figure 3.19a) and subtle variations cannot be seen between samples. Therefore in order to examine their relationship further the LLS were calculated for each sample using the regression formula shown in Figure 3.13 rather than using the same mean value for each sample of an individual species. These values were then plotted against altitude and latitude (Figures 3.19 b and c). Figures 3.19 b and c show again that there is no obvious trend in these values.

Table 3.5. Range of values for Percentage Diminution, Percentage Latewood and RMI for samples collected from a range of altitudes and latitudes (column 2). The full dataset for these samples is shown in Table 3.1 and Appendix A, Table A1.1.

Sample/Sample Number	**Latitude/ Altitude (m)**	**Percentage Diminution (Range) (Mean)**		**Percentage Latewood (Range) (Mean)**		**RMI (Range)(Mean)**	
Prumnopitys taxifolia NZ-03-6	62°S/740	90	90	21	21	19	19
Prumnopitys taxifolia NZ-03-2	62°S/460	86-87	87	14	14	12	12
Pseudotsuga menziesii A1-4	35°S/100	78-80	79	39-44	42	31-35	33
Pseudotsuga menziesii NZ-03-9	62°S/540	81-88	84	37-44	42	32-38	35
Pseudotsuga menziesii TAP-01-9	54°N/190	62-70	66	20-30	25	12-21	16
Pinus radiata NZ-03-4	62°S/380	94-95	94	14-18	16	13-17	15
Pinus radiata NZ-03-10	63°S/500	82-90	87	27-31	30	23-28	26
Podocarpus totara NZ-03-3	62°S/460	87-94	93	13-23	17	11-21	16
Podocarpus totara NZ-03-12	61°S/120	91-95	93	9-29	16	8-27	15
Pinus strobus A1-2	35°S/100	86-91	88	31-32	31	28	28
Pinus strobus TAP-01-10	54°N/190	67-76	72	18-33	24	14-22	17

Three of the five species examined appear to increase LLS with decreasing altitude (*Podocarpus totara*, *Pinus radiata* and *Prumnopitys taxifolia*) contrary to the expectation from observed trends (Reich *et al.*, 1995; Schweingruber, 1996; Oleksyn *et al.*, 2003) however one species shows increasing LLS with altitude as would be expected (*Pinus strobus*) (Figure 3.19.b). Additionally one species (*Pseudotsuga menziesii*) is represented by three specimens and shows a trend towards increasing LLS with altitude but then the LLS decreases again at higher altitudes (>200m).

When latitudes are plotted against LLS in the same way as for altitude they show the same trends as described for altitude above and are therefore also inconclusive (Figure 3.19.c).

These inconclusive values may be due to: a) the small number of samples used in this study, and b) the difference in altitude was not great enough to create a substantial difference in conditions, with the largest variation in elevation being only 340m.

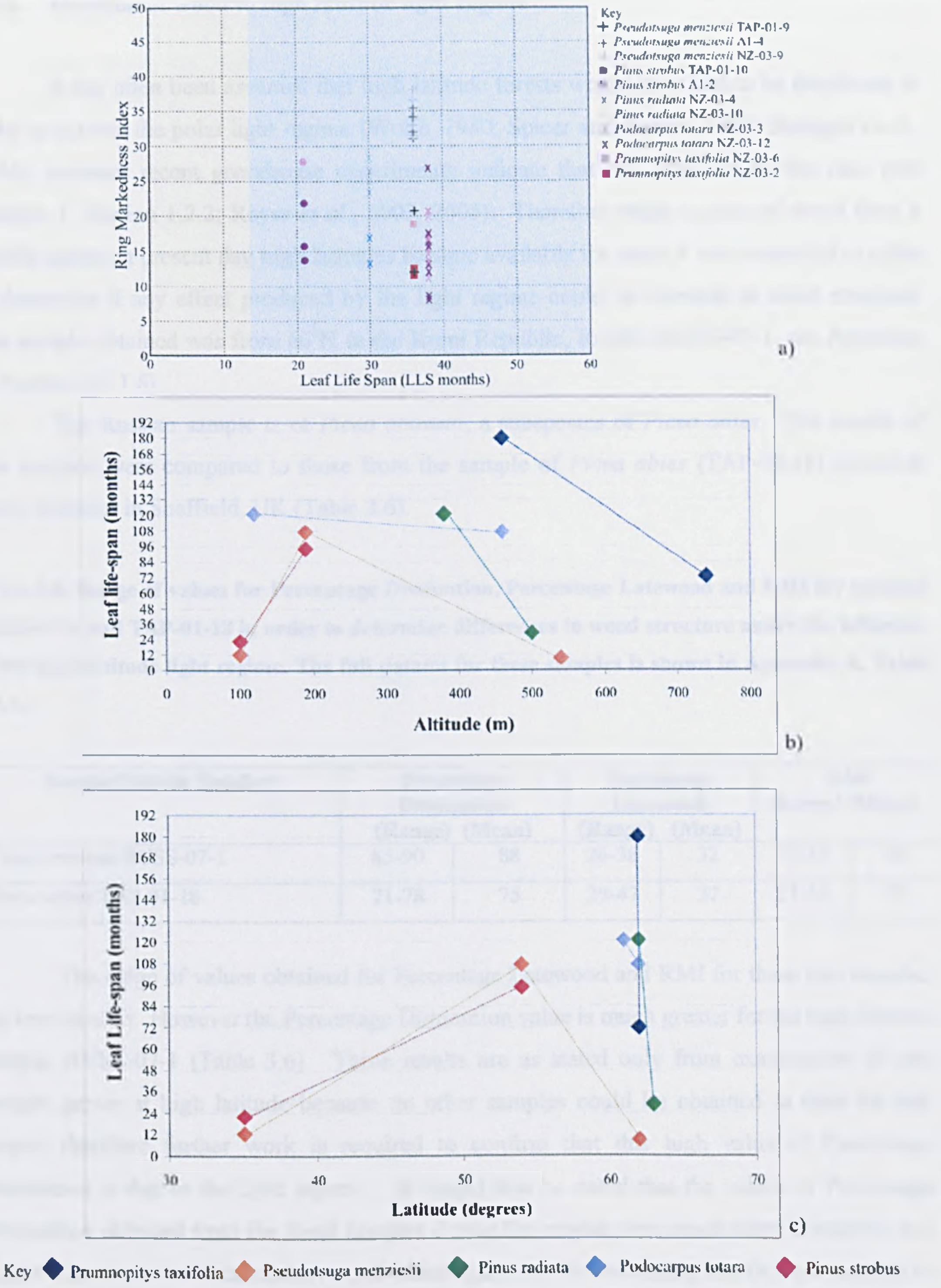


Figure 3.19. Scatter graphs of altitude and latitude data. a) Showing the spread of data from the analysis of trees grown at a variety of latitudes and altitudes in order to assess the effect of site of growth of the tree wood structure. b) Scatter graph showing the results of altitude plotted against leaf life-span c) Scatter graph showing the results of latitude plotted against leaf life-span. Each data point in b and c is the average for the each extant wood sample with leaf life-span calculated using the regression formula in Figure 3.13.

3.4.6. Reaction of wood to high latitude light regime

It has often been assumed that high latitude forests would have had to be deciduous in order to survive the polar light regime (Wolfe, 1980; Spicer and Parrish, 1986; Basinger *et al.*, 1994), however recent greenhouse experiments indicate that this may not be the case (see Chapter 1, Section 1.2.2; Royer *et al.*, 2003, 2005). Therefore when a piece of wood from a conifer grown at present day high latitudes became available for study it was examined in order to determine if any effect produced by the light regime could be detected in wood structure. The sample obtained was from 66°N in the Komi Republic, Russia (RUSS-07-1, see Appendix A, Section A1.1.6).

The Russian sample is of *Picea obovata*, a subspecies of *Picea abies*. The results of this analysis were compared to those from the sample of *Picea abies* (TAP-01-18) grown at lower latitudes in Sheffield, UK (Table 3.6).

Table 3.6. Range of values for Percentage Diminution, Percentage Latewood and RMI for samples RUSS-07-1 and TAP-01-18 in order to determine differences in wood structure under the influence of the high latitude light regime. The full dataset for these samples is shown in Appendix A, Table A1.1.

Sample/Sample Number	Percentage Diminution (Range)	(Mean)	Percentage Latewood (Range)	(Mean)	RMI (Range)	(Mean)
Picea obovata RUSS-07-1	85-90	88	26-38	32	23-33	29
Picea abies TAP-01-18	71-78	75	29-47	37	21-35	27

The range of values obtained for Percentage Latewood and RMI for these two samples are very similar. However the Percentage Diminution value is much greater for the high latitude sample, RUSS-07-1 (Table 3.6). These results are as stated only from examination of one sample grown at high latitude because no other samples could be obtained in time for this project therefore further work is required to confirm that this high value of Percentage Diminution is due to the light regime. It should also be noted that the values of Percentage Diminution obtained from the fossil samples during the project were much more consistent and higher than those found in modern wood which again may be indicating that this is a reaction to the unusual high latitude light suggesting that this warrants further investigation (see Appendix B, Table B1.3 for full fossil dataset).

3.5. New Percentage Skew results

Percentage Skew was calculated using the methods outlined in Section 3.3.5 for the same extant wood collection used to carry out the RMI calculations (Section 3.4, Table 3.1). Percentage Skew was calculated for branch (Figure 3.20) and trunk (Figure 3.21) wood separately in order to test if the two types of material produced different results.

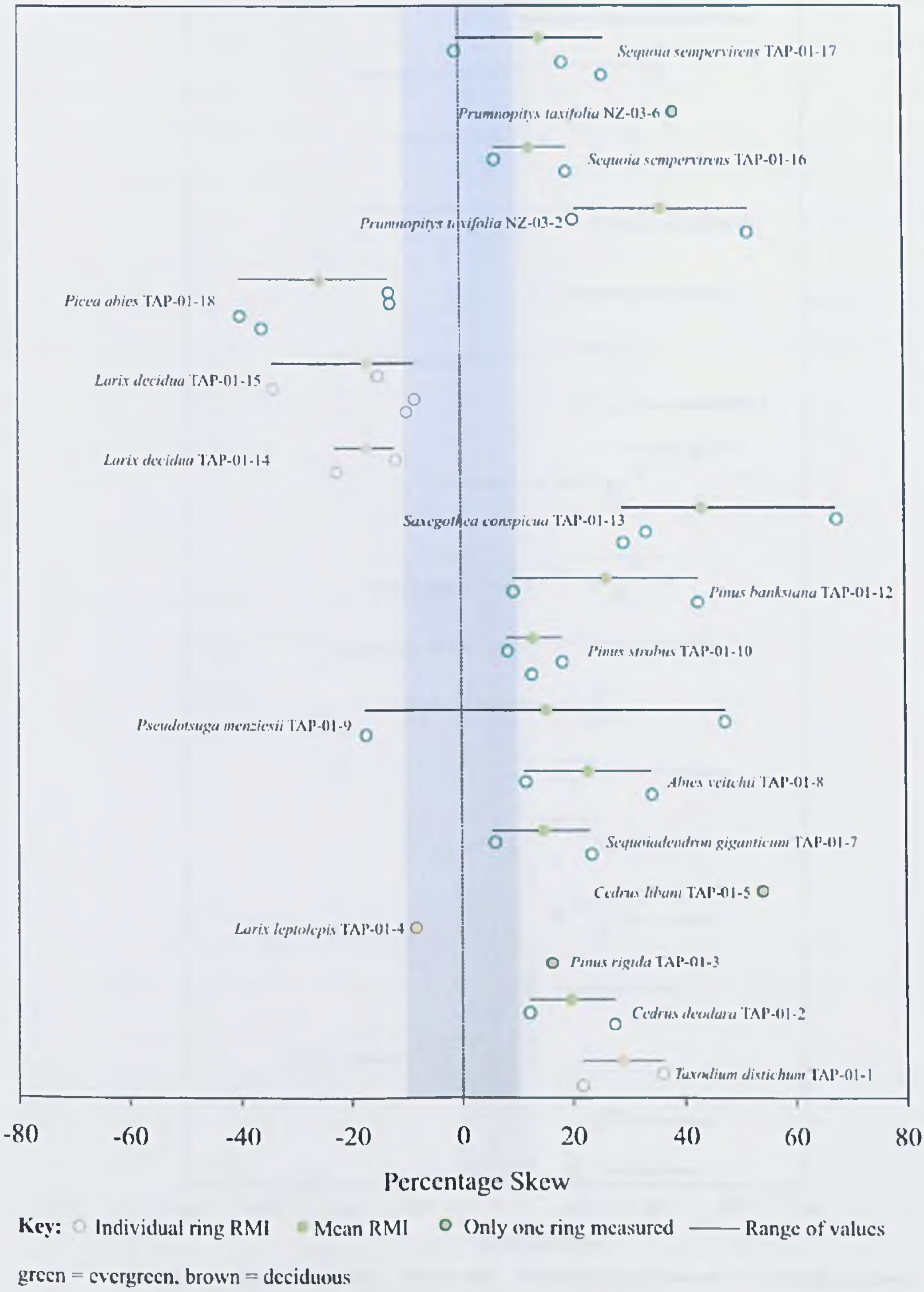
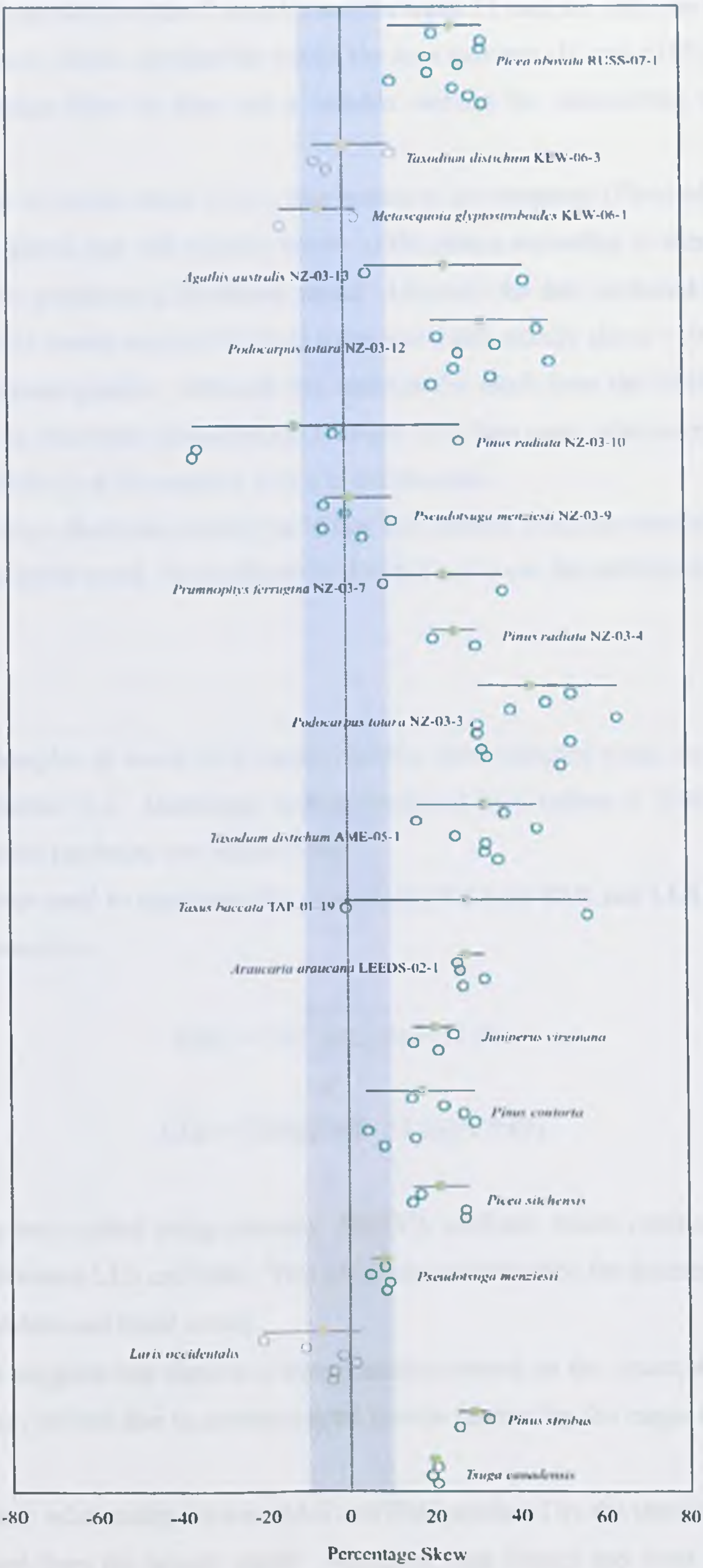


Figure 3.20. Percentage Skew plot for extant deciduous and evergreen branch wood. The grey zone highlights the area between -10 and +10 that Falcon-Lang (2000b) considered to be ambiguous.



Key: ○ Individual ring RMI ● Mean RMI ○ Only one ring measured —— Range of values

green = evergreen, brown = deciduous

Figure 3.21. Percentage Skew plot for deciduous and evergreen trunk wood. The grey zone highlights the area between -10 and +10 that Falcon-Lang (2000b) considered to be ambiguous.

For branch material there are 7 samples and for trunk 11 samples with one or more data point(s) (in some cases almost all) that fall within the area between -10 and +10%, the zone of ambiguity. Percentage Skew is thus not a reliable method for determining evergreen or deciduous habit.

One sample of branch wood from a tree known to be evergreen (*Picea abies* TAP-01-18) produced data points that fell entirely below -10%, hence according to this method this sample appears to be producing a deciduous signal. Likewise the data produced by *Taxodium distichum* (TAP-01-1) branch and (AME-05-1) trunk wood fall entirely above +10% suggesting that this is an evergreen species. Although this matches the result from the RMI calculations, this method seems to show that *Taxodium* has a longer LLS than some other evergreen species (e.g. *P. rigida* (TAP-01-3) at 33 months), which is not the case.

The Percentage Skew data clearly show that this method produces unreliable results for both the branch and trunk wood. It was therefore decided not to use this method in this project.

3.6. Summary

- Thirty eight samples of wood from extant conifers were analysed using the RMI method outlined in Section 3.3. Deciduous species produced high values of RMI (>40) whilst evergreen species produced low values (<40).
- This dataset was used to determine the relationship between RMI and LLS. The derived regression formula is:-

$$\mathrm{RMI} = -7.67\ \ln(\mathrm{LLS}) + 51.81$$

or

$$\mathrm{LLS} = \mathrm{EXP}((\mathrm{RMI} - 51.81)/ - 7.67)$$

These results were tested using one-way ANOVA analysis, which confirmed the strong relationship between LLS and RMI. This provides a new method for determination of LLS using both modern and fossil woods.

- This analysis suggests that there is a strong genetic control on the structure of wood with only subsidiary effects due to environmental factors (shown by the range of LLSs within species).
- The logarithmic relationship between LLS and RMI produced by the trunk wood is similar to that derived from the branch wood. Therefore both branch and trunk wood produce consistent results and can both be analysed using this method.
- *Taxodium distichum*, widely accepted to be a deciduous species, produced an evergreen signal using the RMI method. This is probably correct and due to a small proportion of the

leaves being perennial. Despite this, *T.distichum* is included within the modern dataset as this behaviour may not be restricted to extant forms.

- The lowest RMI values are produced by *Araucaria araucana*, a species which is endemic in the Southern Hemisphere and known to have exceptionally long LLSs (upto ~40 years in shaded or mountainous areas, see Chapter 1, Section 1.3).
- One damaged and one undamaged sample of *Sequoia sempervirens* were compared and it was shown that damage to the tree produced a statistically insignificant change in the ring signal.
- Eleven samples were analysed in order to determine if differences in altitude and latitude affect the ring signal. This analysis produced inconclusive results and requires further work on a larger sample set representing a wider range of altitudes and latitudes.
- One sample from a high latitude site produced high values of Percentage Diminution comparable to those produced by fossil wood from the polar regions suggesting that this may be a reaction to the unusual light regime. This finding requires further investigation.
- Analysis of the entire dataset using the percentage skew method proved to be unreliable therefore this method was not used to determine leaf life-spans of the fossil wood.

Chapter 4 Leaf life-span analysis of mid-Cretaceous fossil wood

4.1. Introduction

The previous chapter has established a robust method to determine leaf habit (evergreen or deciduous) and leaf life-span (LLS) based on analysis of cell and growth ring characteristics of modern woods. A relationship has been devised and tested that relates the nature of growth ring boundaries to LLS. In this chapter that relationship, expressed by Ring Markedness Index, is applied to fossil wood to determine the evergreen or deciduous habit and LLS of mid-Cretaceous wood (Section 4.2).

The leaf habit of many Cretaceous conifers has not been determined from fossil wood structure before so this study allowed leaf habit to be estimated in this way for the first time. It also allowed the leaf habits and LLSs to be related to specific fossil taxa, identified in Chapter 2 to see if LLSs of fossil form-genera are the same as or different to possible modern relatives. In this chapter the relationship between RMI and LLS is applied to mid-Cretaceous fossil wood from the northern (Svalbard and the Canadian Arctic; Section 4.3) and southern hemispheres (Antarctica and Australia; Section 4.4) (see Appendix B, Table B1.1 for full sample list). The leaf habit and LLSs of the mid-Cretaceous polar conifer forests are determined for the first time to widen our understanding of tree growth in these unusual environments (Sections 4.3 to 4.5). The data collected within this chapter allow comparisons to be made with the outputs of the new University of Sheffield Conifer Model (USCM; see Chapter 6).

4.2. Methods used for leaf life-span analysis of fossil wood

Ring Markedness Index for the fossil wood samples was calculated using the same methods applied to the extant wood, given in Chapter 3 (Section 3.3). Leaf life-spans for the fossil samples were then determined using the regression equation established for modern wood (Chapter 3, $LLS = EXP\ ((RMI - 51.81)/ - 7.67)$).

The results for the northern and southern hemisphere sites were plotted as scatter graphs, pie charts and histograms using Microsoft Excel^{TM}, to show the dominant LLS in each region. The quadrants on the pie charts were plotted as follows : percentage deciduous, evergreen <60 months and evergreen > 60 months. Sixty months was chosen as the cut-off between short and long lived evergreen foliage as it appeared from the extant LLS analysis that there was a natural dominant grouping below 60 months with the remainder of the evergreen species spread out after this point (see Chapter 3, Section 3.4). The dominant leaf-habit and dominant LLS are calculated as these variables are of interest because they are produced by the

University of Sheffield Conifer Model simulations and thus are required for model comparison (see Chapter 6, Section 6.3).

4.3. Leaf life-span of Northern Hemisphere fossil woods

This section presents results of LLS analysis for thirteen fossil wood samples from Svalbard and ten from the Canadian Arctic (see Chapter 2, Figures 2.6.a and b for sample location maps). The Percentage Latewood and Percentage Diminution were calculated from cell width measurements and the RMI was then calculated for each fossil wood sample. The LLS was then determined using the regression formula derived from extant wood analysis.

4.3.1. Svalbard

The wood from Svalbard was collected by J.Francis, University of Leeds from the mid-Cretaceous sediments of Lundstromdalen and Storknausen (Chapter 2, Figure 2.6.a). During the mid-Cretaceous Svalbard was at a palaeolatitude of ~71°N. Both sample sets are from the Carolinefjellet Formation of Aptian to Albian age (personal communication J.Francis, see also Harland, 1997). The wood was identified in Chapter 2, Section 2.5 as belonging to the form-genera *Piceoxylon, Laricioxylon, Cedroxylon, Taxodioxylon, Juniperoxylon, Protocedroxylon, Taxoxylon, Araucariopitys, Xenoxylon* and *Cupressinoxylon,* with *Taxodioxylon* being the dominant form-genus.

The results of this analysis are shown in Table 4.1. Figure 4.1 below is a scatter graph of the Svalbard data with the RMI plotted against mean LLS (months), calculated from the regression formula derived from extant wood (for RMI values of the Svalbard wood see Table 4.1, for full dataset see Appendix B, Table B1.3). Ring Markedness Index is plotted on the x axis because it is the measured variable and LLS is on the y axis because it is the derived variable. Figure 4.1 shows that the majority of the Svalbard samples were evergreen, with the RMI calculation highlighting that a wide range of evergreen LLSs are represented, falling in the green section of the graph. However, two samples produced LLSs <12 months and plot in the brown section of the graph. Figure 4.2 shows a pie chart of the same data as in the scatter graph in Figure 4.1.

Figures 4.2 shows that 85% of the Svalbard samples were evergreen. Six of these evergreen samples had LLS of >12 months but less than 60 months (47%) and 6 samples had LLS of >60 months (38%). Only 2 samples, 15%, produced deciduous LLSs <12 months.

The two samples from Svalbard with LLS <12 months (deciduous leaf habit), LD123 and LD126, have mean LLSs of 6 and 3 months respectively (Table 4.1, see Appendix B, Table B1.3 for full dataset). These samples were identified as *Laricioxylon.* The supposed nearest living relative of *Laricioxylon*, *Larix*, is also deciduous.

Table 4.1. Table showing mean values of Percentage Diminution, Percentage Latewood and Ring Markedness Index for fossil samples from Svalbard plus the mean leaf life-span and Standard Deviation (SD) for full dataset see Appendix B, Table B1.3.

Form Genus/ Sample Number	Mean Percentage Diminution	Mean Percentage Latewood	Mean Ring Markedness Index	Leaf Life-span (months) Mean	SD
SVALBARD					
Juniperoxylon					
LD101	72	34	24	35	0
Cedroxylon					
LD102	79	20	16	110	48
Piceoxylon					
LD105	81	32	26	30	23
Araucariopitys					
LD108	81	24	19	69	31
Protocedroxylon					
LD120	82	34	28	21	36
Laricioxylon					
LD123	88	45	39	6	3
LD126	78	56	44	3	2
Taxodioxylon					
LD129	89	32	28	21	20
LD131	92	29	27	25	15
LD133	93	15	14	137	0
Xenoxylon					
LD130	93	19	17	89	67
Cupressinoxylon					
LD132	91	27	25	35	31
Taxoxylon					
SN25 4	90	13	12	180	80

Two samples of *Taxodioxylon* (sp 1, LD129 and sp 2, LD131) produced RMI values of between 21 and 37 (see Appendix B, Table B1.3 for full dataset). These values lie within the range of modern *Taxodium distichum* (which was 25 to 42, Appendix A, Table A.1.1). The mean LLSs of these samples are over 12 months but less than 30 months, which is again similar to modern *T. distichum* (Table 4.1). However one sample of *Taxodioxylon* (sp 3, LD133) produced an RMI of 14 and a LLS of ~137 months (Table 4.1). This is much longer than any of the other *Taxodioxylon* samples or modern *T.distichum*. It is more similar to modern *T.*

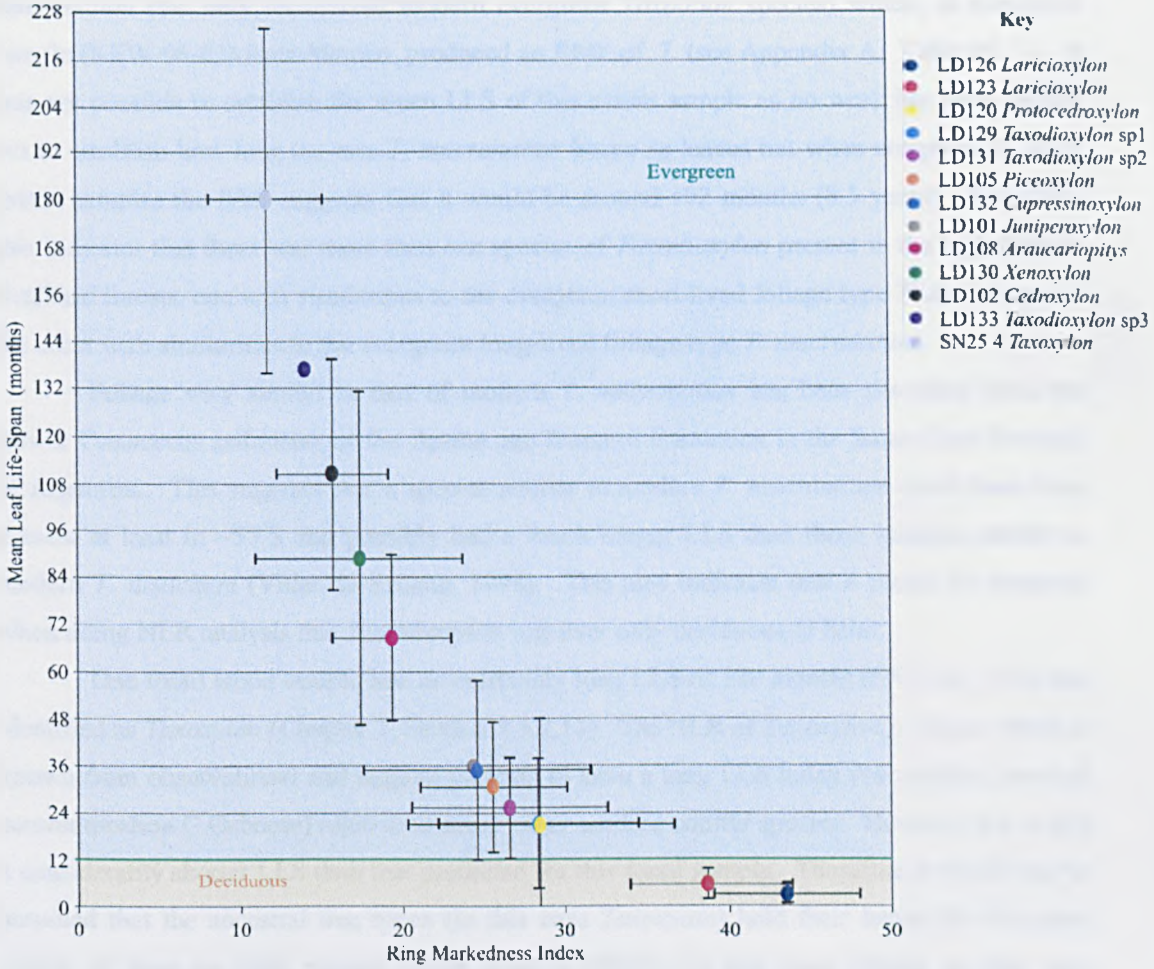


Figure 4.1. Scatter Graph showing Ring Markedness Index against mean leaf life-span (months) for the twelve Svalbard fossil wood samples. Error bars are the standard deviation from the mean.

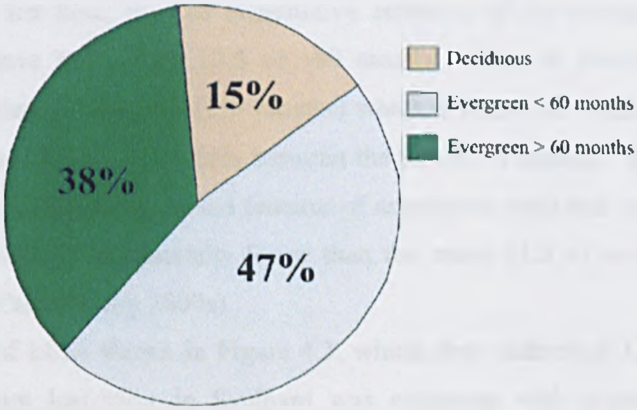


Figure 4.2. Pie chart showing the percentages of deciduous (brown), evergreen <60 months (light green) and evergreen >60 months (dark green) samples from Svalbard n=13.

mucronatum (the only recognized modern evergreen *Taxodium* species) which, in a modern sample (KEW-06-02) from Mexico, produced an RMI of 7 (see Appendix A, Table A1.1). It was not possible to establish the mean LLS of this extant sample as no work has been carried out to establish how long the rare *T. mucronatum* keeps its leaves but when compared to other extant samples the RMI suggests that it would be around 102 months (8.5 years). Therefore, this indicates that there was more than one species of *Taxodioxylon* present in the high latitude Svalbard forests, one with similarities to the evergreen short-lived foliage type *T. distichum* and the other with similarities to the evergreen long-lived foliage type *T. mucronatum*.

Foliage very similar to that of modern *T. mucronatum* has been described from the Lower Cretaceous sediments of the Aptian age Baquero Formation in the Santa Cruz Province of Argentina. This suggests that a species similar to modern *T. mucronatum* could have been present at least to ~55°S and possibly had a much longer LLS than those samples similar to modern *T. distichum* (Villar de Seoane, 1998). This also indicates that it cannot be assumed when doing NLR analysis that *Taxodioxylon* was ever only deciduous in habit.

One fossil wood sample had an extremely long LLS of 180 months (SN25 4). This was identified as *Taxoxylon* (Chapter 2, Section 2.5.2.11). The NLR of *Taxoxylon* is *Taxus*, which is known from observational and tagging projects to have a long LLS today (96 months, personal communication C.Osborne) relative to many other modern conifer species. However this is still a considerably shorter LLS than that predicted for this fossil sample. Therefore it should not be assumed that the ancestral tree types (in this case *Taxoxylon*) held their leaves for the same length of time as their nearest living relative (NLR) (in this case *Taxus*) as this may considerably over- or under- estimate the LLS, as appears to be the case here.

The LLSs of the genera that are extinct are of special interest. The evergreen or deciduous nature of extinct types have not been determined in the past because there are no NLRs for comparison, this includes *Xenoxylon*, *Protocedroxylon* and *Araucariopitys*. However this study can, for the first time, provide quantitative estimates of the extinct genera LLSs. *Xenoxylon* appears to have had a long LLS of ~89 months. That of *Protocedroxylon* (21 months) is much lower than *Cedroxylon* (110 months) which is nearer in wood structure to the modern form *Cedrus*, the LLS of which falls between the two at 54 months. One sample was classified as *Araucariopitys* (showing mixed features of araucarian type) and produced a mean LLS of ~68 months, which is substantially lower than the mean LLS of modern *Araucaria araucana* (108 months, Falcon-Lang 2000a).

The histogram of LLSs shown in Figure 4.3, which plots individual LLS per sample, indicates that the dominant leaf-habit in Svalbard was evergreen with a dominant LLS of ~33 months.

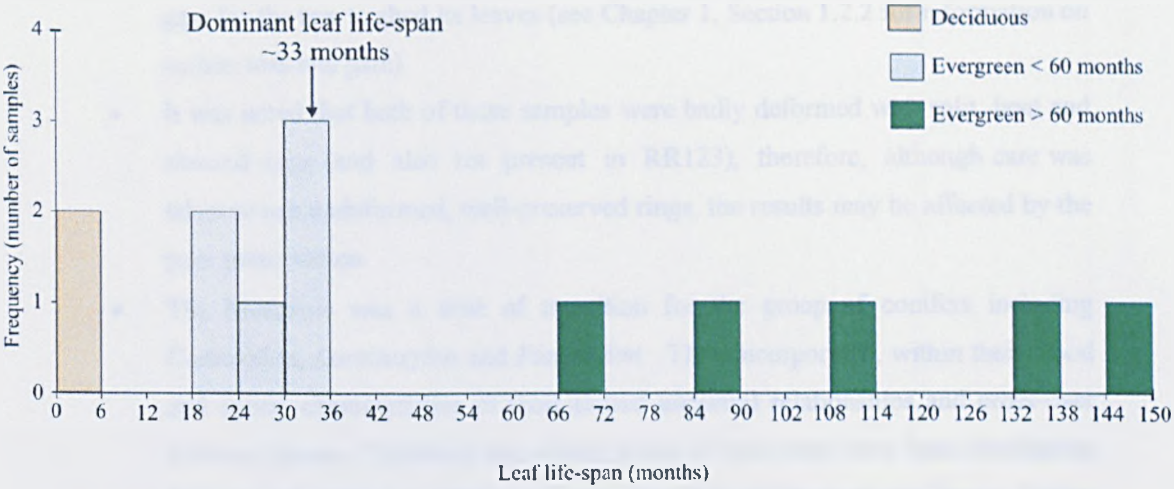


Figure 4.3. Histogram showing the leaf life-span (months) of the samples from Svalbard.

4.3.2. Canadian Arctic

The wood from the Canadian Arctic was collected on Ellesmere and Axel Heiberg islands from the Aptian-Albian Christopher Formation (see also Chapter 2, Figure 2.6.b). This wood is less diverse than Svalbard in terms of form-genera and includes only *Pinuxylon, Piceoxylon, Cedroxylon, Palaepiceoxylon* and *Cupressinoxylon* (see Chapter 2, Section 2.5.2 for descriptions). The dominant form-genus was *Pinuxylon,* which represented 33% of the sample set.

Table 4.2 displays the results of this analysis. Figure 4.4 below shows a scatter graph of the Canadian Arctic data with the RMI plotted against mean LLS (months). Figure 4.5 shows a pie chart for the same data showing the percentages of deciduous, evergreen <60 months and evergreen >60.

Figures 4.4 and 4.5 show that, like Svalbard, the Canadian Arctic forests were predominantly evergreen (90%). Only one sample had a deciduous LLS of <12 months (10%). Most samples had LLSs of >12 months but <60 months (n=8, 80%) and one sample had a value >60 months (10%) (Table 4.2, Figures 4.4 and 4.5).

The deciduous sample (RR123) was identified as *Cedroxylon* (Chapter 2, Section 2.5.2.4), possibly similar to modern *Cedrus*. However modern *Cedrus* produces a mean LLS of 54 months (Falcon-Lang, 2000a; personal communication C.Osborne), much greater than that derived here for the fossil. The fossil sample, RR123, had a mean LLS of 11 months, very similar to a second *Cedroxylon* sample in this dataset (RR121), which had a mean LLS of 13 months. There may be several reasons for this:

- This is a small sample set and further examples should be examined.
- It may be due to the environmental conditions at the site of growth having been unfavorable for this genus and thus making it more profitable in terms of carbon

gain for the tree to shed its leaves (see Chapter 1, Section 1.2.2 for information on carbon loss and gain).

- It was noted that both of these samples were badly deformed with split, bent and sheared rings (and also rot present in RR123), therefore, although care was taken to use undeformed, well-preserved rings, the results may be affected by the poor preservation.
- The Mesozoic was a time of transition for the group of conifers including *Cedroxylon*, *Laricioxylon* and *Piceoxylon*. They incorporated, within their wood and cones, characteristics of their shared ancestral relationships and cross-over between genera. Therefore this whole group of trees may have been developing their growth habit and, where as *Larix* retained its ability to be deciduous, *Cedrus* eventually found it more profitable to develop a longer LLS. This may have been because the trees used different methods to deal with the conditions of growth. Although it is suggested that leaf shedding can help to conserve carbon, the retention of leaves can help to conserve nutrients such as nitrogen. Therefore on nitrogen poor soils it would be beneficial for the trees to keep their leaves longer.

Table 4.2. Table showing mean values of Percentage Diminution, Percentage Latewood and Ring Markedness Index for fossil samples from the Canadian Arctic plus the mean leaf life-span and Standard Deviation (SD) for full dataset see Appendix B, Table B1.3.

Form Genus/ Sample Number	**Mean Percentage Diminution**	**Mean Percentage Latewood**	**Mean Ring Markedness Index**	**Leaf Life-span (months) Mean**	**SD**
CANADIAN ARCTIC					
Piceoxylon					
RR102	95	19	18	80	53
RR113	94	30	28	22	14
Pinuxylon					
RR111	93	26	24	36	39
RR122	96	27	26	30	0
E139	92	31	28	22	23
E140	95	23	22	52	27
Cedroxylon					
RR121	95	34	32	13	5
RR123	95	35	33	11	0
Palaepiceoxylon					
BL125	93	23	22	50	34
Cupressinoxylon					
E137	92	27	25	35	47

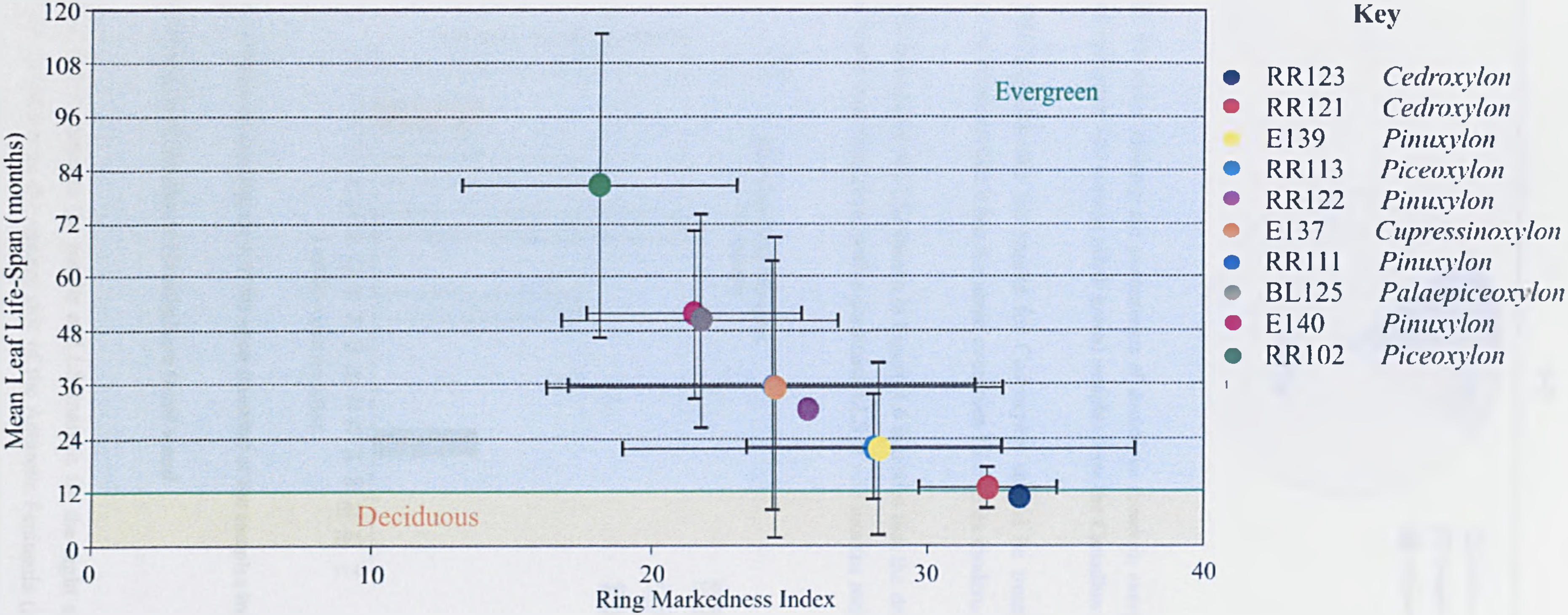


Figure 4.4. Scatter graph showing Ring Markedness Index against mean leaf life-span (months) for the twelve Canadian Arctic fossil wood samples. Error bars are standard deviation from the mean.

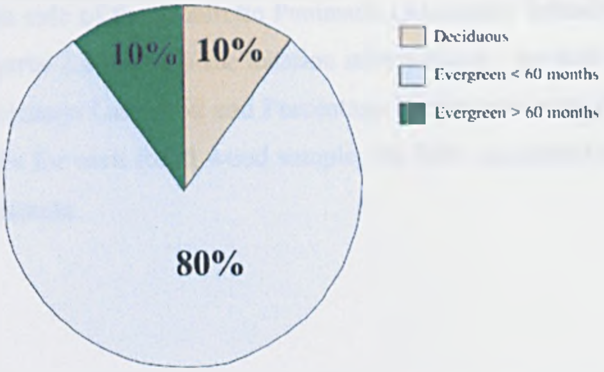


Figure 4.5. Pie chart showing the percentages of deciduous (brown), evergreen <60 months (light green) and evergreen >60 months (dark green) samples from the Canadian Arctic n=10.

This suggests that the results for *Cedroxylon* should be treated with caution and it should not be assumed that it has the same evergreen LLS as its modern counterpart *Cedrus* (54 months).

The histogram of LLSs shown in Figure 4.6 indicates that the dominant leaf habit in the Canadian Arctic was evergreen, with a dominant LLS of ~33 months matching that of Svalbard.

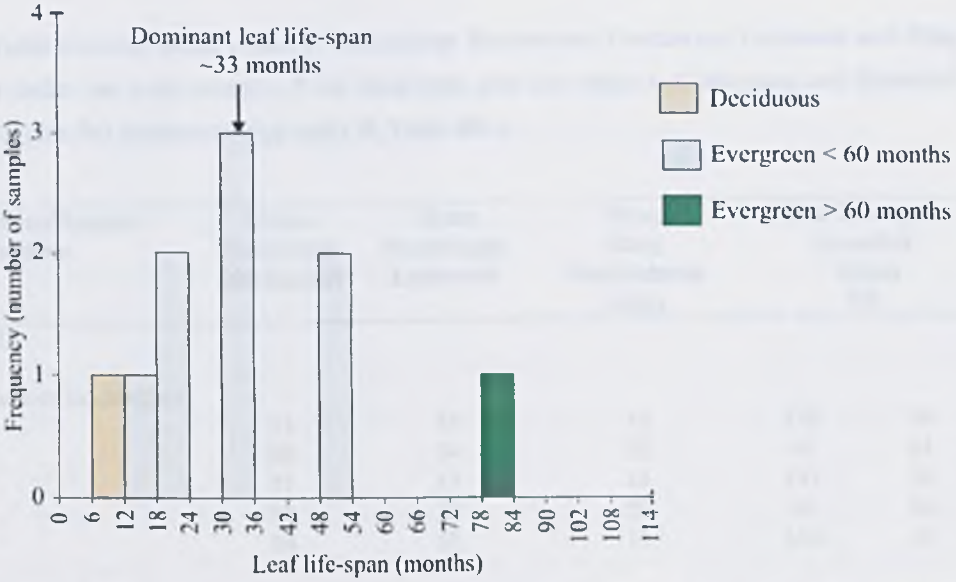


Figure 4.6. Histogram showing the leaf life-span (months) of the samples from the Canadian Arctic.

4.4. Leaf life-span of Southern Hemisphere fossil wood

This section presents the results of LLS analysis for the eight samples from Australia, twenty eight samples from the eastern side of the Antarctic Peninsula (James Ross Island) and nine samples from the western side of the Antarctic Peninsula (Alexander Island) identified in Chapter 2 (see Chapter 2, Figures 2.20a and b for location information). As with the Northern Hemisphere samples, the Percentage Latewood and Percentage Diminution were obtained from the measurement of cell widths for each fossil wood sample, the RMI calculated and then LLS derived from the regression formula.

4.4.1. Australia

This is the smallest sample set used in this study because the preservation was poor and a substantial number of samples had growth rings that were less than 30 cells wide, making them unsuitable to use as they would produce anomalous results (see Chapter 3, Section 3.3.4.1). These samples are from the Aptian-Albian Bulldog Shale in the Eromanga Basin (see also Chapter 2, Figure 2.20a). All of the Australian samples were identified as *Podocarpoxylon*.

Table 4.3 illustrates the results of the analysis. Figure 4.7 below shows a scatter graph of the Australian data with the RMI plotted against mean LLS (months). Figure 4.8 shows a pie chart for the same data showing the percentages of deciduous, evergreen <60 months and evergreen >60.

Table 4.3. Table showing mean values of Percentage Diminution, Percentage Latewood and Ring Markedness Index for fossil samples from Australia plus the mean leaf life-span and Standard Deviation (SD) for full dataset see Appendix B, Table B1.3.

Form Genus/ Sample Number	Mean Percentage Diminution	Mean Percentage Latewood	Mean Ring Markedness Index	Leaf Life-span (months) Mean	SD
AUSTRALIA					
Type R (Unidentified conifer)					
872/W16	91	14	14	136	70
872/W104	85	24	20	62	41
872/W128	91	15	14	147	32
872/W149	88	22	20	66	16
872/W168	94	13	13	165	0
Podocarpoxylon					
872/W17	91	26	24	38	14
872/W166	94	12	11	204	69
872/W167	95	23	22	48	18

Figures 4.7 and 4.8 show that the Australian forests were entirely evergreen. A quarter of the samples had LLSs of >12 months but <60 months (n=2, 25%) and 6 samples had values >60 months (75%) (Table 4.3, Figures 4.7 and 4.8). However these samples appear to fall into three natural groupings: >24 months but <96 months (n=4), >96 months but <168 months (n=3)

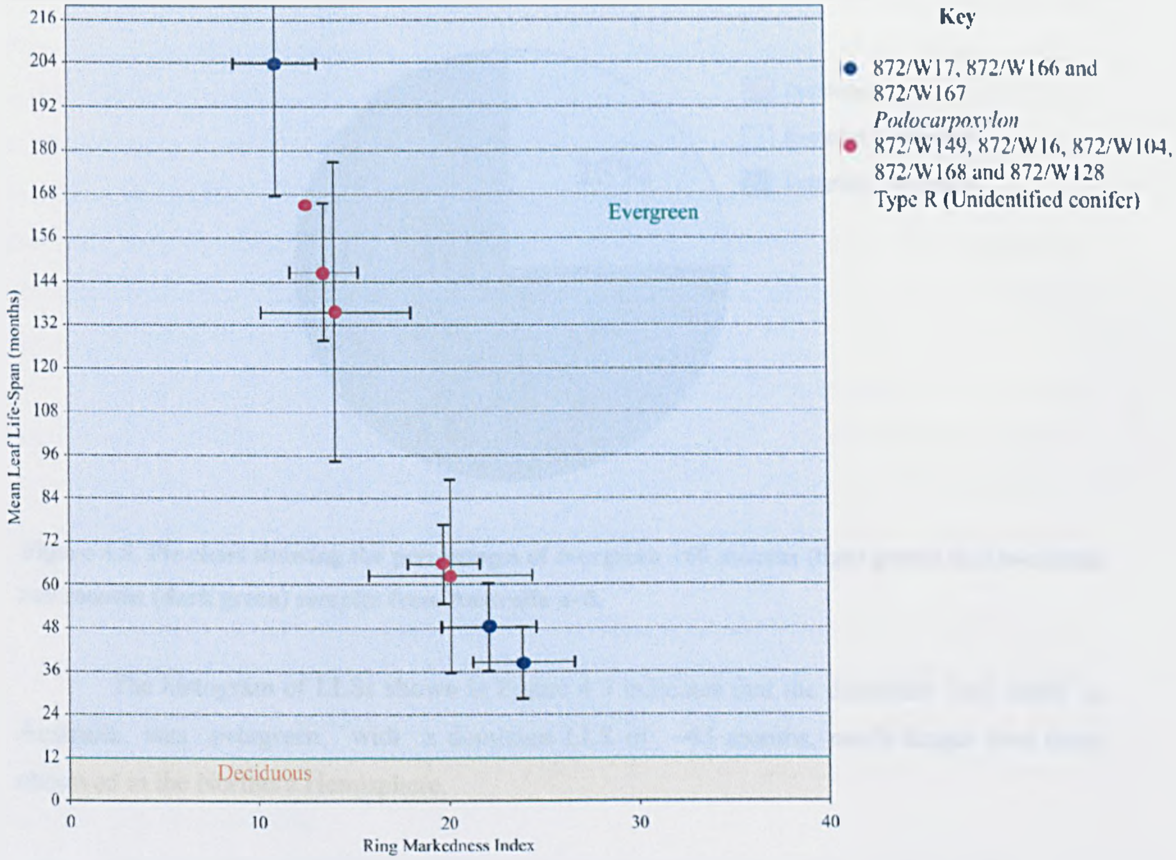


Figure 4.7. Scatter graph showing Ring Markedness Index against mean leaf life-span (months) for the eight Australian fossil wood samples. Error bars are standard deviation from the mean.

and >168 months (n=1) (Figure 4.7.). Five of these samples were unidentifiable to form-genus level but it appears that there are at least two species of *Podocarpoxylon* represented here, one with LLS of <96 months and one with LLS of >168 months. The grouping between 96 and 168 months may represent a third species of *Podocarpoxylon* but it was not possible to confirm this due to poor preservation. It is also possible that the samples may represent only one species with a wide range of LLSs.

The group with lowest LLS (>24 but <96 months) appears to be in line with various modern Podocarpaceae, because *Podocarpus totara* has a mean LLS of 38 months and *Dacrydium cupressinum* has a LLS of 48 months (personal communication M. McGlone and C.Osborne). The remaining samples (872/W16, 872/W128, 872/W166 and 872/W168) have much longer LLSs than the values obtained for modern Podocarpaceae, again emphasizing that it should not be assumed that LLSs of possible ancestral groups are the same as their modern counterparts.

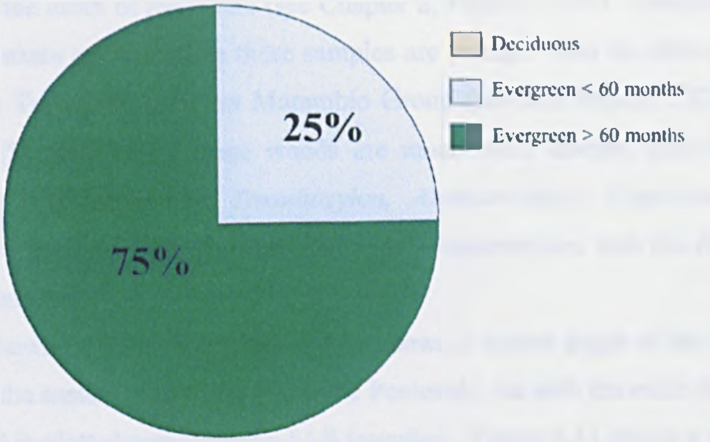


Figure 4.8. Pie chart showing the percentages of evergreen <60 months (light green) and evergreen >60 months (dark green) samples from Australia n=8.

The histogram of LLSs shown in Figure 4.9 indicates that the dominant leaf habit in Australia was evergreen, with a dominant LLS of ~63 months, much longer than those observed in the Northern Hemisphere.

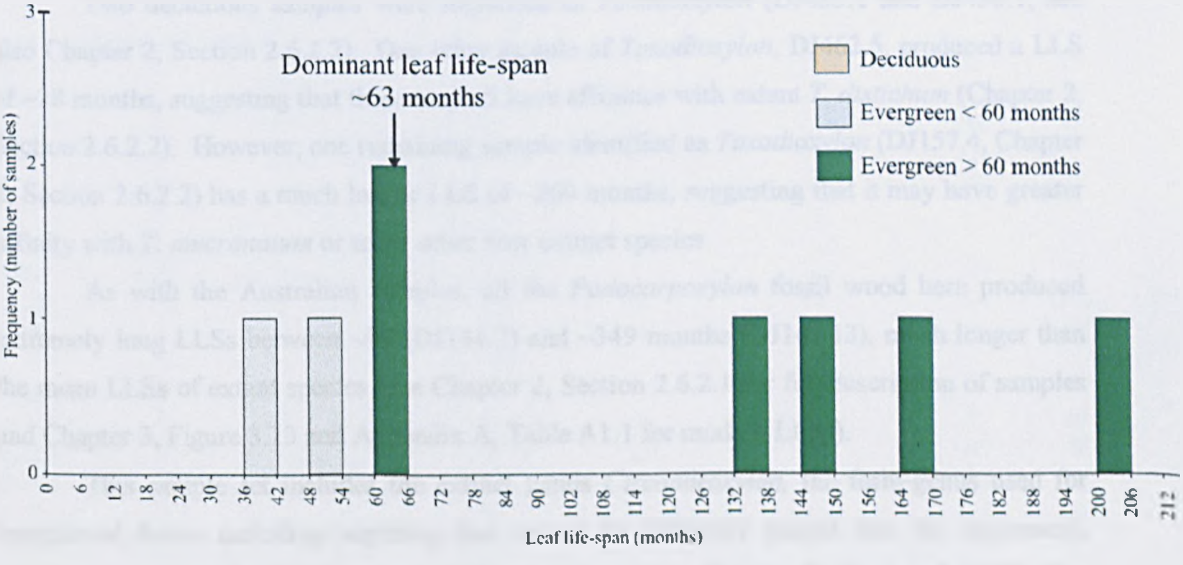


Figure 4.9. Histogram showing the leaf life-span (months) of the samples from Australia.

Preliminary findings of Falcon-Lang and Cantrill (2001a) suggest that the Albian conifers of southeastern Australia (primarily podocarps and *Agathis*, an araucarian conifer) were almost exclusively evergreen, supporting the findings here.

4.4.2. Antarctica (James Ross Island)

The samples from James Ross Island on the eastern side of the Antarctic Peninsula are from various locations in the north of the island (see Chapter 2, Figure 2.20.b). Because of the rarity of mid-Cretaceous strata on Antarctica these samples are younger than the others in this study, all being from the Turonian-Coniacian Marambio Group (see also Figure 2.20.b). As described in Chapter 2 (Section 2.6.2), these woods are much more diverse than those of Australia and represent *Podocarpoxylon, Taxodioxylon, Araucariopitys, Cupressinoxylon, Agathoxylon, Protophyllocladoxylon, Sciadopityoxylon* and *Circoporoxylon,* with the dominant form-genus being *Taxodioxylon.*

The results are shown in Table 4.4. Figure 4.10 shows a scatter graph of the samples from James Ross Island, the eastern side of the Antarctic Peninsula. As with the other locations, presented above, the RMI is plotted against mean LLS (months). Figure 4.11 shows a pie chart for the same data showing the percentages of deciduous, evergreen <60 months and evergreen >60.

Figures 4.10 and 4.11 show that the eastern Antarctic forests were predominantly evergreen (89%). The samples display a wide range of LLSs with three samples <12 months (11%), 10 samples >12 months but <60 months (36%) and 15 samples >60 months (53%) (Table 4.4, Figures 4.10 and 4.11). However most of the samples appear to have LLSs clustered between 12 and 96 months.

Two deciduous samples were identified as *Taxodioxylon* (DJ455.1 and DJ458.1, see also Chapter 2, Section 2.6.2.2). One other sample of *Taxodioxylon*, DJ462.5, produced a LLS of ~28 months, suggesting that these may all have affinities with extant *T. distichum* (Chapter 2, Section 2.6.2.2). However, one remaining sample identified as *Taxodioxylon* (DJ157.4, Chapter 2, Section 2.6.2.2) has a much longer LLS of ~260 months, suggesting that it may have greater affinity with *T. mucronatum* or some other now extinct species.

As with the Australian samples, all the *Podocarpoxylon* fossil wood here produced extremely long LLSs between ~95 (DJ144.2) and ~349 months (DJ141.13), much longer than the mean LLSs of extant species (see Chapter 2, Section 2.6.2.1 for full description of samples and Chapter 3, Figure 3.13 and Appendix A, Table A1.1 for modern LLSs).

This sample set includes the extinct genus *Circoporoxylon,* the form-genus used for transitional forms including anything that cannot be definitely placed into the cupressoid, taxodioid, glyptostroboid or podocarpoid genera (see also Chapter 2, Section 2.6.2.8). The extinct form-genus *Protophyllocladoxylon* is present, possibly representing a transitional form similar to extant *Phyllocladus,* as is *Araucariopitys* which cannot be placed within any one group but has mixed araucarian features. The three *Circoporoxylon* samples have a reasonably narrow range of LLS values from ~43 (DJ445.3) to ~93 months (DJ462.3). *Protophyllocladoxylon* has a long LLS of ~141 months, much higher than the 24 month mean LLS of modern *Phyllocladus trichomanoides* (personal communication M. McGlone). The two

Table 4.4. Table showing mean values of Percentage Diminution, Percentage Latewood and Ring Markedness Index for fossil samples from Antarctica, James Ross Island plus the mean leaf life-span and Standard Deviation (SD) for full dataset see Appendix B, Table B1.3.

Form Genus/ Sample Number	Mean Percentage Diminution	Mean Percentage Latewood	Mean Ring Markedness Index	Leaf Life-span (months)	
				Mean	SD
JAMES ROSS ISLAND ANTARCTICA					
Araucariopitys					
5215	88	10	9	282	206
DJ144.7	89	23	20	60	11
Type S (Unidentified Araucarioid)					
D421	87	13	11	196	122
DJ366.7	91	21	20	67	44
Type T (Unidentified Non Araucarioid)					
DJ135.3	91	33	30	16	7
DJ141.7	91	16	15	123	0
DJ451.3	95	18	17	88	40
Cupressinoxylon					
DJ137.6	92	32	29	19	17
Agathoxylon					
DJ137.8	90	24	22	50	56
DJ141.3	96	31	30	17	4
Protophyllocladoxylon					
DJ141.6	84	17	14	141	92
Type R (Unidentified conifer)					
DJ141.8	80	31	25	35	18
DJ141.16	89	14	13	164	32
DJ144.3	87	26	23	44	42
DJ465.1	91	53	48	2	1
DJ466.2	94	7	6	377	0
Podocarpoxylon					
DJ141.13	88	8	7	349	0
DJ141.14	85	16	14	142	126
DJ144.2	87	19	17	95	67
Sciadopityoxylon					
DJ144.5	93	21	19	71	40
DJ463.5	81	15	12	179	0
Taxodioxylon					
DJ451.4	89	10	9	260	10
DJ455.1	94	41	39	6	5
DJ458.1	90	39	36	8	0
DJ462.5	91	29	26	28	45
Circoporoxylon					
DJ455.3	92	25	23	43	48
DJ462.2	91	23	21	53	35
DJ462.3	89	19	17	93	29

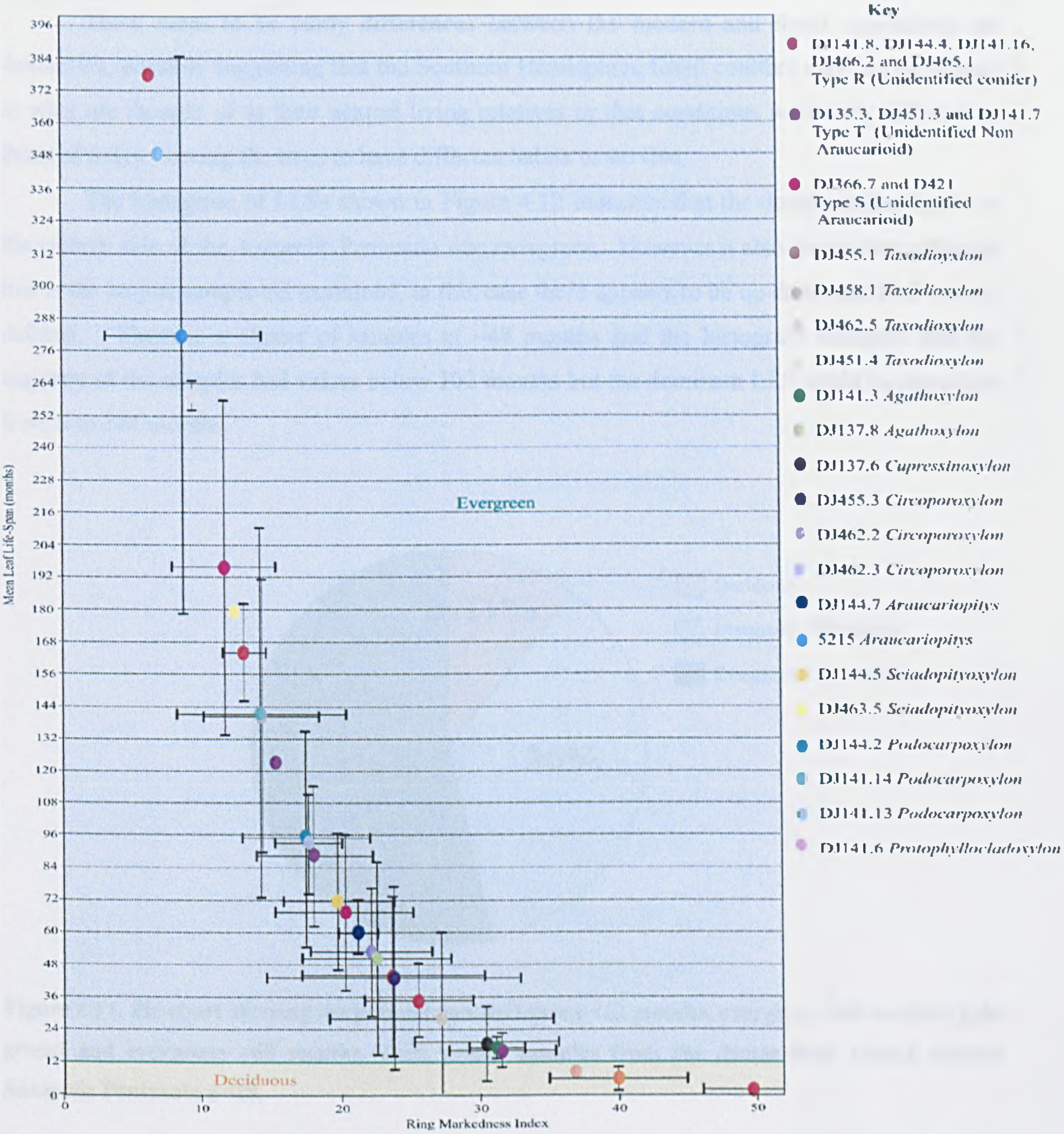


Figure 4.10. Scatter graph showing Ring Markedness Index against mean leaf life-span (months) for the twenty eight James Ross Island, eastern Antarctic Peninsula fossil wood samples. Error bars are standard deviation from the mean.

samples identified as *Araucariopitys* produced very different values of LLS: DJ144.7, ~60 months and 5215, ~282 months, both of which are unlike modern *Araucaria araucana*, which has a mean LLS of 108 months, or *Agathis australis* with a lower value of 36 months (personal communication M. McGlone).

The two samples identified as *Agathoxylon* fall both below and above the value of modern *Agathis australis* at 36 months, with DJ141.3 being ~17 months and DJ137.8 being ~50 months (personal communication M. McGlone).

There seem to be many differences between the modern and fossil equivalents on Antarctica, possibly suggesting that the Southern Hemisphere fossil conifers may not be related to what are thought of as their nearest living relatives or that conditions were very different to those of today, forcing the trees to have different habits to survive.

The histogram of LLSs shown in Figure 4.12 indicates that the dominant leaf habit on the eastern side of the Antarctic Peninsula was evergreen. However it also shows that although this is the largest sample set examined, in this case there appears to be no dominant LLS clearly defined. There is a cluster of samples at ~48 months and the histogram indicates that the majority of the samples had values below 102 months but the dominant LLS could be anywhere from 0 to 144 months.

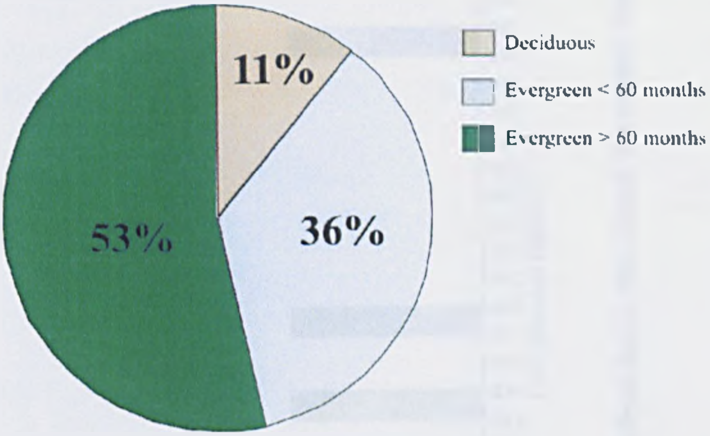


Figure 4.11. Pie chart showing the percentages deciduous <12 months, evergreen <60 months (light green) and evergreen >60 months (dark green) samples from the James Ross Island, eastern Antarctic Peninsula n=28.

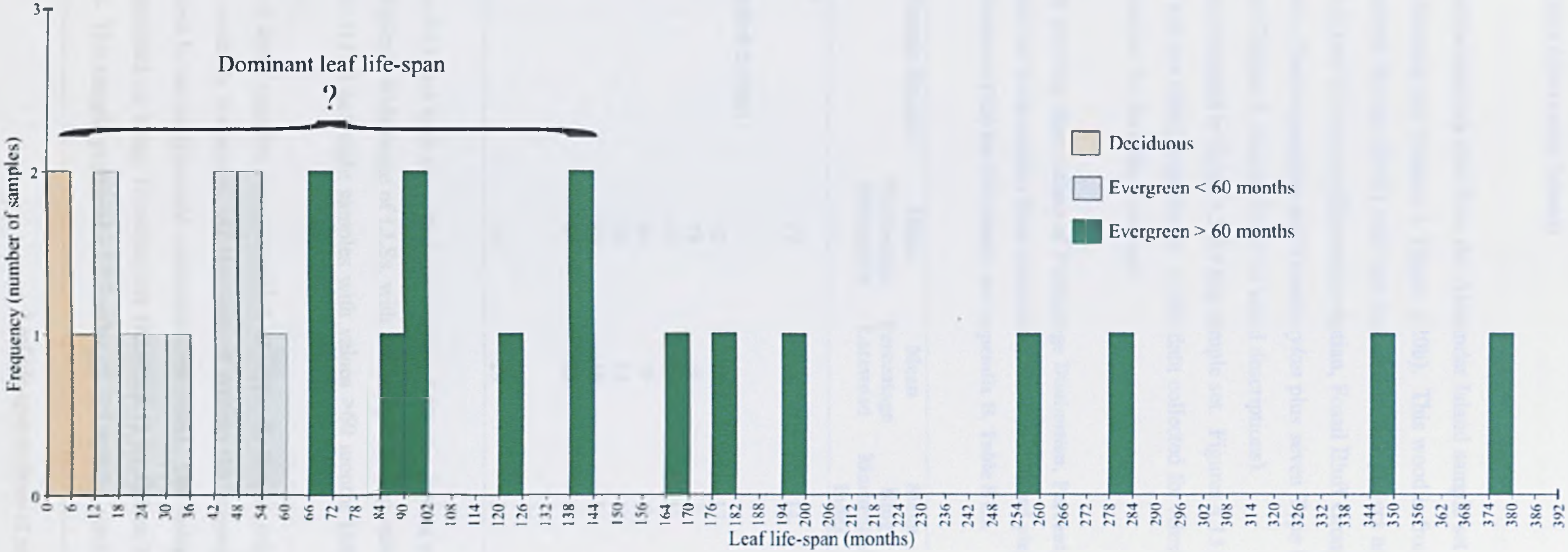


Figure 4.12. Histogram showing the leaf life-span (months) of the samples from James Ross Island, the eastern Antarctic Peninsula.

4.4.3. Antarctica (Alexander Island)

This section presents data from the Alexander Island sample set on the western side of the Antarctic Peninsula (see Chapter 2, Figure 2.20b). This wood is from the collection held at the British Antarctic Survey (BAS) and was included in this project as it represents the only available wood of mid-Cretaceous (Barremian-Aptian, Fossil Bluff Group) age from Antarctica. The samples were *Podocarpoxylon* and *Taxodioxylon* plus seven Type R unidentified conifers also present (see Chapter 2, Section 2.6.2 for wood descriptions).

Data are presented in Table 4.5 for this sample set. Figures 4.13 and 4.14 below present a scatter graph and pie chart, respectively, of the data collected for Alexander Island, presented in the same format as for the other locations.

Table 4.5. Table showing mean values of Percentage Diminution, Percentage Latewood and Ring Markedness Index for fossil samples from Antarctica, Alexander Island plus the mean leaf life-span and Standard Deviation (SD) for full dataset see Appendix B, Table B1.3.

Form Genus/ Sample Number	Mean Percentage Diminution	Mean Percentage Latewood	Mean Ring Markedness Index	Leaf Life-span (months) Mean	SD
Podocarpoxylon					
KG1703.23	87	16	14	145	134
Type R (Unidentified conifer)					
KG1719.3b	92	18	17	96	53
KG2814.252	78	9	7	348	73
KG2814.256	87	15	13	151	n=1
KG2817.20	84	9	8	312	267
KG4672.6	89	14	13	164	204
KG4710.1	84	16	13	152	38
KG4717.43	85	23	20	66	23
Taxodioxylon					
KG4626.1	91	29	27	27	9

Figures 4.13 and 4.14 show that the western Antarctic forests were entirely evergreen. The samples display a wide range of LLSs, with one sample having values >12 months but less than 60 months (11%) and eight samples with values >60 months (89%) (Table 4.5, Figures 4.13 and 4.14).

Most of these samples were identified as Type R, due to only one (transverse) thin section being available for study. At the time of writing the missing radial and tangential sections could not be traced (personal communication BAS). One sample had been previously studied and identified as being *Taxodioxylon* (KG4626.1) by Falcon-Lang (Falcon-Lang and Cantrill, 2000). This sample produced a LLS value of ~27 months, similar to modern *Taxodium* *distichum*. One sample (three thin section slides available) was identified as *Podocarpoxylon*, which produced a LLS value of ~145 months which, as with the *Podocarpoxylon* found at the other sites in this study, is longer than extant *Podocarpus* LLSs.

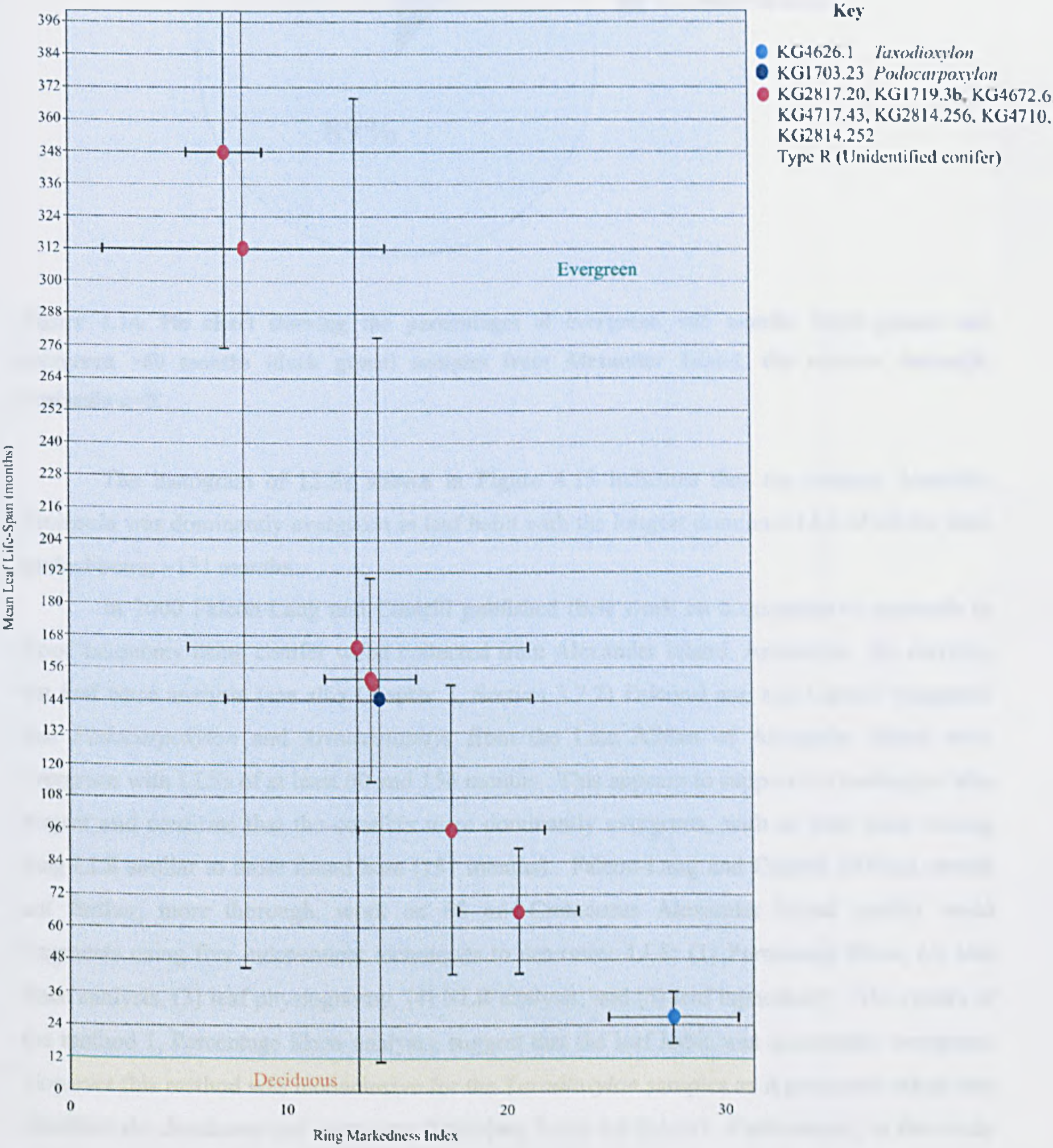


Figure 4.13. Scatter graph showing Ring Markedness Index against mean leaf life-span (months) for the nine samples from Alexander Island on the western Antarctic Peninsula fossil wood samples. Error bars are standard deviation from the mean.

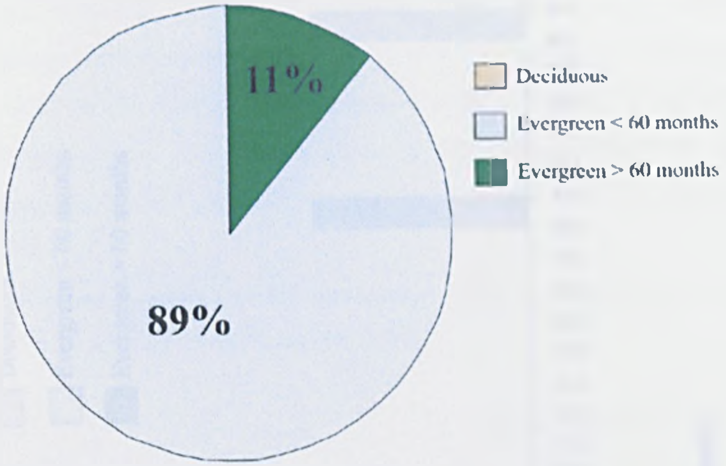


Figure 4.14. Pie chart showing the percentages of evergreen <60 months (light green) and evergreen >60 months (dark green) samples from Alexander Island, the western Antarctic Peninsula n=9.

The histogram of LLSs shown in Figure 4.15 indicates that the western Antarctic Peninsula was dominantly evergreen in leaf habit with the longest dominant LLS of all the sites studied being ~151 months.

In 2000 Falcon-Lang and Cantrill published their work on a quantitative approach to wood taxonomy using conifer wood collected from Alexander Island, Antarctica. By carrying out leaf trace analysis (see also Chapter 3, Section 3.2.2) Falcon-Lang and Cantrill suggested that *Podocarpoxylon* and *Araucariopitys* from the Late Albian of Alexander Island were evergreen with LLSs of at least 60 and 156 months. This appears to support the findings of this project and confirms that the conifers were dominantly evergreen, with at least some having long LLS similar to those found here (151 months). Falcon-Lang and Cantrill (2001a) carried out further, more thorough, work on 68 mid-Cretaceous Alexander Island conifer wood fragments using five independent techniques to determine LLS: (1) Percentage Skew, (2) leaf trace analysis, (3) leaf physiognomy, (4) NLR analysis, and (5) leaf taphonomy. The results of the method 1, Percentage Skew analysis, suggest that the leaf habit was dominantly evergreen. However this method was inconclusive for the *Taxodioxylon* samples as it produced values that straddled the deciduous and evergreen fields (see Table 4.6 below). Furthermore, in this study Percentage Skew is not considered reliable. The leaf trace analysis (method 2) in Falcon-Lang and Cantrill's (2001a) study again indicated *Podocarpoxylon* sp 1 was evergreen with LLSs of 6 to 156 months. Leaf physiognomy (method 3) and NLR analysis (method 4) suggest that, although the majority of the trees were evergreen, there were also some deciduous types present (taxodioid conifers, *Ginkgo* and taeniopterids). Leaf taphonomy (method 5) provided little data, suggesting only that *Ginkgo* and *Taeniopteris* (a cycadophyte) were deciduous due to the

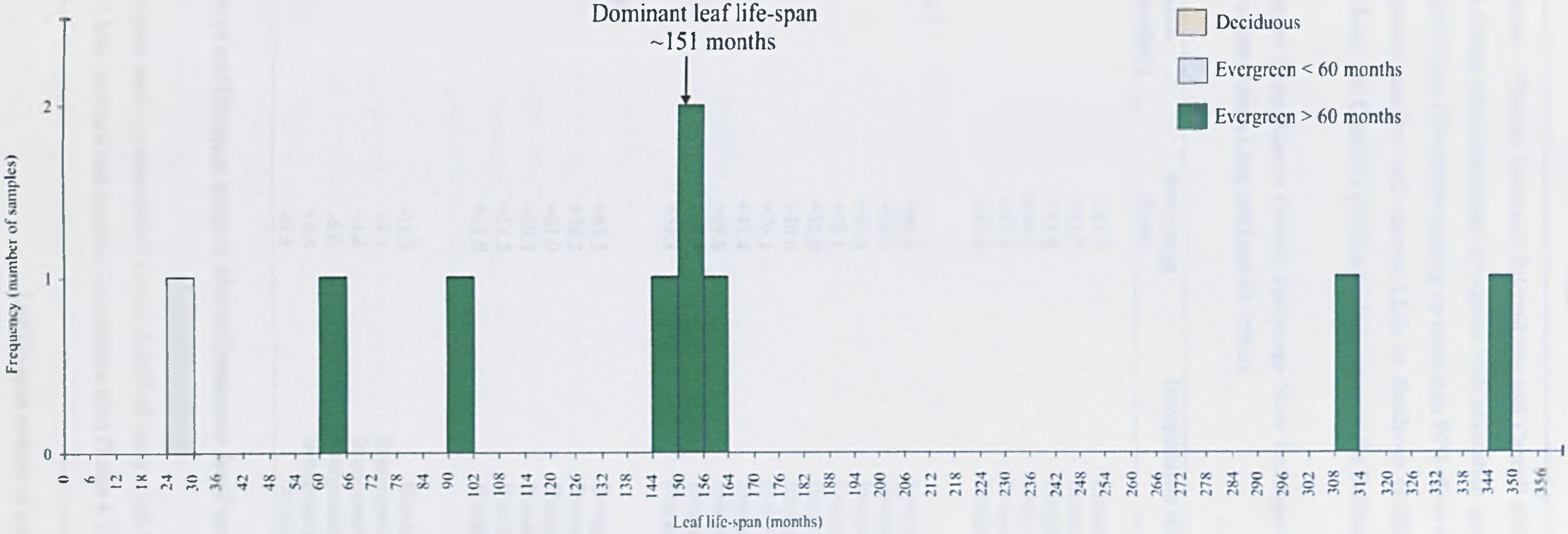


Figure 4.15. Histogram showing the leaf lie-span (months) of the samples from Alexander Island, the western Antarctic Peninsula.

presence of leaf mats. Overall, however, Falcon-Lang and Cantrill (2001a) showed that the Alexander Island forests were dominantly evergreen with araucarian and podocarp evergreen conifers with LLSs of 60 to 156 months making up more than 90% of the forest canopy and rare evergreen taxodiaceous conifers with shorter LLSs or deciduous *Ginkgo* and Taeniopterids. Therefore Falcon-Lang and Cantrill's (2001a) analysis supports the findings of this project.

Table 4.6. Results of Falcon-Lang's (2000b) Percentage Skew technique applied to Alexander Island coniferous woods (Falcon-Lang and Cantrill, 2001a).

Wood taxon (Specimen number)	Percentage Skew	Interpretation of leaf phenology
Araucariopitys		
KG4740.11	+51.1	Evergreen
KG4740.11	+34.6	Evergreen
KG4740.11	+61.8	Evergreen
KG4702.17	+40.0	Evergreen
KG4702.17	+52.2	Evergreen
Mean	+47.9	Evergreen
Podocarpoxylon sp 1		
KG4657.9	+66.7	Evergreen
KG4657.9	+58.3	Evergreen
KG4660.4	+43.6	Evergreen
KG4710.2	+38.1	Evergreen
KG4717.42	+52.9	Evergreen
KG4717.44	+40.0	Evergreen
KG4717.45	+76.1	Evergreen
KG4717.45	+41.4	Evergreen
KG4717.46	+69.8	Evergreen
KG4719.4	+64.4	Evergreen
Mean	+55.1	Evergreen
Podocarpoxylon sp 2		
KG2814.256	+83.1	Evergreen
KG2814.256	+54.2	Evergreen
KG4660.1	+61.0	Evergreen
KG4710.3	+59.1	Evergreen
KG4747.13	+51.5	Evergreen
Mean	+61.8	Evergreen
Taxodixoylon		
KG4626.1	-11.7	Deciduous
KG4626.1	+4.1	Evergreen/Deciduous
KG4626.1	+4.6	Evergreen/Deciduous
KG4626.1	-6.0	Evergreen/Deciduous
KG4626.1	+6.4	Evergreen/Deciduous
Mean	-0.5	Deciduous?

4.5. Summary of leaf life-span analysis of mid-Cretaceous fossil woods

Leaf life-span analysis was carried out on a total of sixty eight fossil samples of mid-Cretaceous age in both northern and southern hemisphere sites (Table 4.7).

Table 4.7 shows the results of the LLS analysis. The dominant leaf habit was evergreen at all locations. These data also clearly show that the dominant LLS is substantially longer for the Southern Hemisphere sites than for the Northern Hemisphere sites.

Table 4.7. Table showing the results of leaf life-span analysis for polar conifer forests.

Location	Dominant Leaf Habit	Percentage Deciduous	Percentage Evergreen <60 Months	Percentage Evergreen >60 Months	Dominant Leaf Life-span (months)
Svalbard	Evergreen (85%)	15%	47%	38%	~33
Canadian Arctic	Evergreen (90%)	10%	80%	10%	~33
Australia	Evergreen (100%)	0%	25%	75%	~63
Antarctica (James Ross Island)	Evergreen (89%)	11%	36%	53%	~48
Antarctica (Alexander Island)	Evergreen (100%)	0%	89%	11%	~151

This analysis has, for the first time, allowed the determination of LLSs of extinct conifers. All extinct genera were shown to have had evergreen leaf habits, with *Xenoxylon* having a mean LLS of ~89 months, *Protocedroxylon* ~21 months, *Araucariopitys* between ~60 and ~282 months, *Circoporoxylon* between ~43 and ~93 months and *Protophyllocladoxylon* ~141 months.

Taxodioxylon appears to have been represented by at least two fossil species, one with short LLS possibly similar to modern *T. distichum* and the other with a very long LLS possibly similar to modern *T. mucronatum*. *Podocarpoxylon* appears, in most cases, to have had a much longer LLS than extant *Podocarpus*. *Cedroxylon* may have been deciduous, producing much lower values of LLS than modern *Cedrus*. This analysis therefore shows that Nearest Living Relative analysis cannot be wholly relied upon to determine the leaf habit of fossil conifers and may produce values that are substantially over- or under-estimated.

These values for the leaf habit and LLSs of fossil mid-Cretaceous wood together with proxy data on the palaeoenvironment, discussed in Chapter 5, can then be compared with the outputs of the University of Sheffield Conifer Model (Chapter 6).

Chapter 5 Palaeoclimate analysis

5.1. Introduction

Although the cellular structure of growth rings in conifer wood in terms of Percentage Latewood, Percentage Diminution and RMI is strongly related to LLS and is predominantly a genetic signal (see Chapter 3), the width of growth rings show a strong, consistent relationship to climate, in particular mean annual temperature (MAT), mean annual temperature range (MATR) and cold month mean temperature (CMMT) (Falcon-Lang, 2005b). This approach therefore provides information on temperature that cannot be obtained directly from RMI studies. Variations in the growth rate achieved by co-occurring conifer species under a given climate can be attributed to genetics (Falcon-Lang 2005b) and therefore it should not be assumed that all species of conifers will produce the same ring width under the same climatic and environmental conditions e.g. a pine will not have the same ring widths as a swamp cypress in a warm humid climate. However, within an individual species the reaction will be the same in any given environment (assuming the conditions are the replicated e.g. water and nutrient supply, the trees are not diseased). For example a fifteen year old pine growing on a cool south facing hillside will produce similar ring widths to a pine of the same age growing on another cool south facing hillside. However the ring widths would be different to those produced by a sixty year old pine growing in a warm humid lowland setting. The collective ring widths from various climatic and environmental settings will therefore produce a distinctive signal and the mean ring width of the whole data set will reflect the climatic conditions rather than generic variability.

Variability in growth can be expressed in terms of mean and annual sensitivity. Palaeoclimate analysis using annual and mean sensitivity formulas have been extensively applied to both modern (Fritts and Schatz, 1975; Lamarche *et al.*, 1979) and fossil (Jefferson, 1982; Francis, 1986; Parrish and Spicer, 1988; Frakes and Francis, 1990; Spicer and Parrish, 1990; Falcon-Lang and Cantrill, 2002; Francis and Poole, 2002) conifer wood in past palaeoclimate studies. This chapter begins by presenting the annual and mean sensitivity formulas used in palaeoclimate analysis of fossil conifer wood growth rings (Section 5.2; Creber and Francis, 1999). These formulas are then used to gain an insight into the palaeclimate prevailing in the northern (Section 5.3) and southern hemisphere (Section 5.4) high latitude regions during the mid-Cretaceous. Comparisons are then made between climate analysis based on Nearest Living Relative analysis (results from Chapter 2) and the palaeoclimate analysis carried out here in order to establish if the climate analysis based on forest composition produces comparable results to the quantitative ring width palaeoclimate analysis (Section 5.5).

Finally, comparisons are made between the palaeclimate analysis results and previous computer model outputs for the mid-Cretaceous in order to establish how well the computer models have reproduced the climate in the past and where improvements are necessary (Section 5.6).

5.2. Growth ring analysis

Tree rings are an important source of information about the environment in which trees grew and their interaction with climate, providing detailed information about seasonality, annual growing conditions and water availability (Fritts *et al.*, 1965; Francis, 1986; Kumagai *et al.*, 1995; Cantrill and Nichols, 1996; Creber and Francis, 1999; Francis and Poole, 2002). In this section the annual and mean sensitivity formulas are introduced.

5.2.1. Annual sensitivity

Ring widths vary from year to year due to variation in factors affecting tree growth. If there is a distinct pattern of variation in ring widths this variation is known as a "signature" of the tree and is used in dendrochronology to correlate ring sequences for dating. With fossil wood it is not possible to use ring widths for absolute dating, because complete sequences for comparison and correlation purposes do not go back more than a few thousand years, but the variation in width between one ring and its neighbour can be used for palaeoclimate analysis. Wide rings indicate that the year's climate was moist and warm whilst narrow rings indicate it was dry or cold (Fritts, 1965). Growth rings that are evenly spaced and of regular appearance indicate growth under equable conditions but if irregularly spaced they indicate variation in growing conditions e.g. they may be reflecting an intermittent supply of water in a semi-arid environment. Annual sensitivity (AS) statistically represents this variation and is calculated using the following formula:

$$AS = \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|$$

where x is the ring width and t is the year number of the ring (Creber and Francis, 1999).

Creber and Francis (1999) concluded that, when plotted as histograms, the annual sensitivity frequency can provide an indication of the growth patterns within the tree. If the histograms show that the AS groupings have low values this indicates that the tree grew under equable conditions with a constant supply of all necessary requirements for growth (Figure 5.1 shaded columns). However if the AS groupings are at the higher end of AS values the tree probably grew under conditions that varied widely from year to year, particularly with respect to water supply (Figure 5.1 unshaded columns).

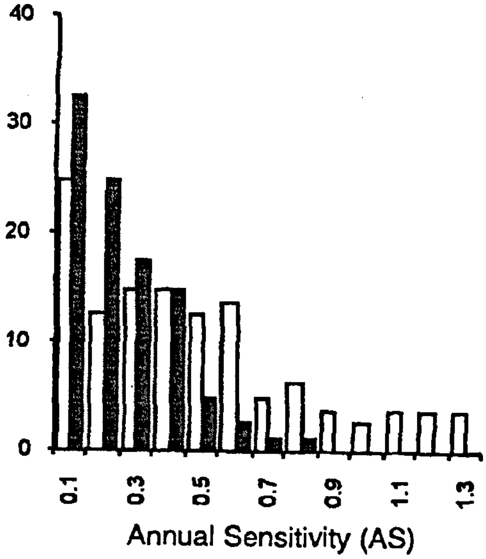


Figure 5.1. Histogram showing AS distribution in a Jurassic conifer grown under variable conditions with high values of AS (unshaded) and a recent larch grown under equable conditions with low values of AS (shaded) (diagram from Creber and Francis, 1999).

5.2.2. Mean sensitivity

Mean Sensitivity (MS) is the mean variability in ring width over a series of rings (or the average of the annual sensitivities) (Fritts, 1976; Creber and Francis, 1999). Most MS values fall between 0 and 2 and are calculated using the following formula (Creber and Francis, 1999):

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

where, in addition to x and $_t$ as above, n is the number of rings in the sequence.

Values of 0.3 to 2 indicate growth under variable climate with strongly limiting environmental factors, especially water. Values of 0.3 or less represent growth under equable conditions allowing production of rings with approximately constant width year to year (see Figure 5.1. and Creber and Francis, 1999). Figure 5.2, produced by Fritts *et al.* (1965) from a transect through a modern forest interior to the semi-arid forest border, shows this relationship and also shows that average ring width and arboreal dominance both decrease with increasing mean sensitivity. In addition MS values near to or over 0.4 are produced by conifers growing in semi-arid environments and low values (<0.2) of MS combined with narrow ring widths are produced from trees adapted to living close to the tree line (Fritts and Schatz, 1975).

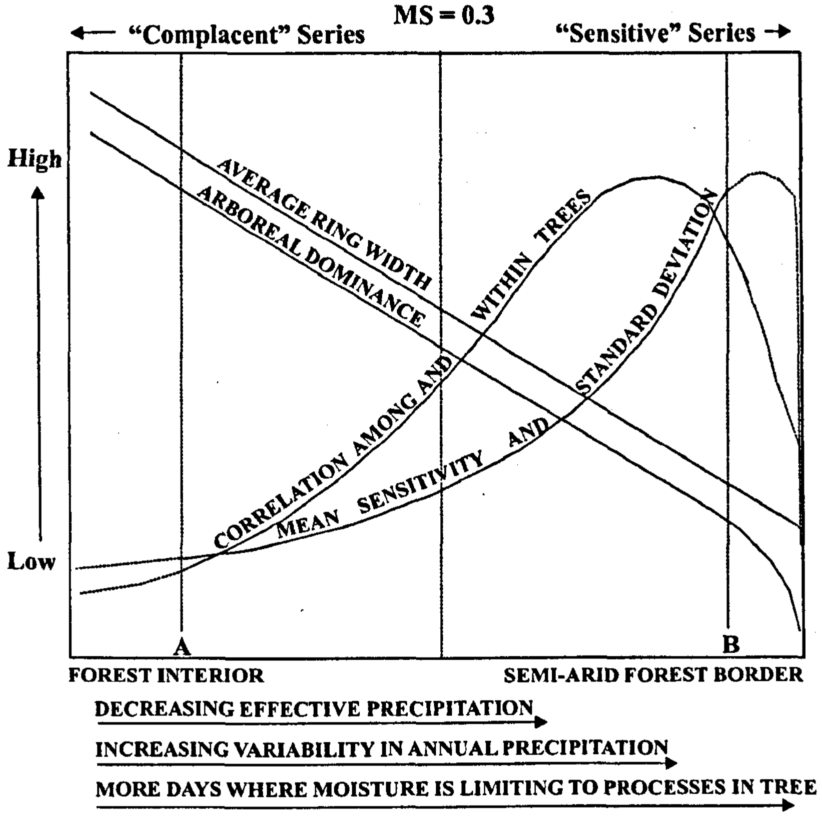


Figure 5.2. Diagram of changes in tree-ring characteristics taken along a transect from the forest interior to the semi-arid forest border (adapted from Fritts *et al.*, 1965). A = lower limit to usefulness of ring width variability, below this growth rings are not highly related to climatic variability. B – upper limit to usefulness of ring width variability, above this climate is too limiting to produce rings that can be used for diagnostic purposes.

Fritts (1965) indicates that tree-ring dating (and mean sensitivity analysis) can only be carried out between the area of A on the graph (Figure 5.2), where tree growth is not highly related to climatic variability and B, where climate is so limiting that a large number of diagnostic or narrow tree rings are absent from most series.

The findings of Fritts *et al.* (1965) appear to be supported by Falcon-Lang (2005b) in a study he carried out using 554 modern conifer wood ring sequences obtained from the International Tree-Ring Data Bank. In his study he plotted mean sensitivity against climate index, derived from equally weighted MAR (Mean Annual Rainfall) and MAT (Mean Annual Temperature) (Figure 5.3).

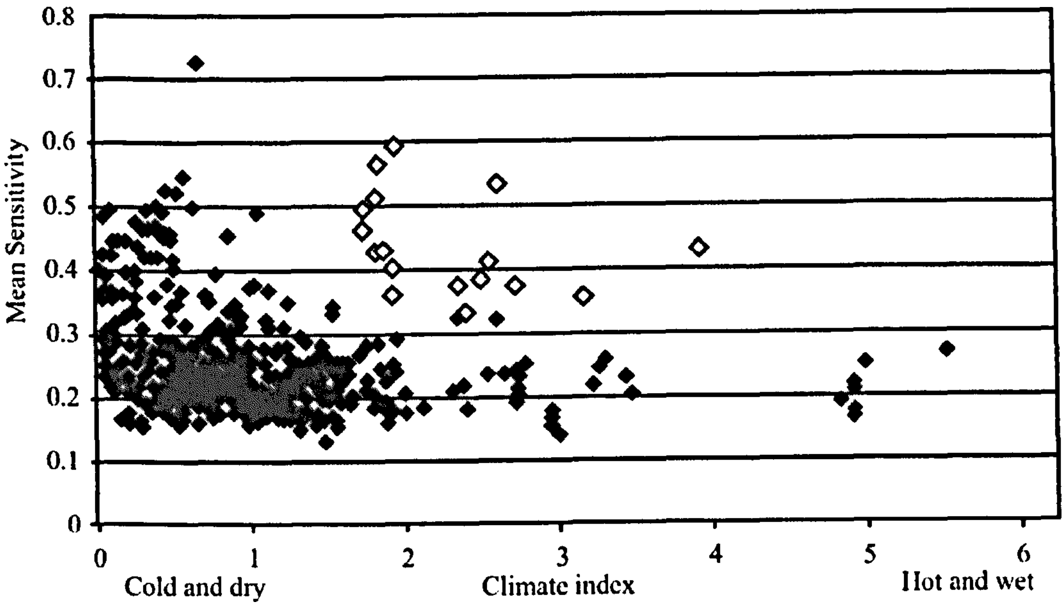


Figure 5.3. Relationship between Mean Sensitivity and MAR/MAT climate index for 554 conifer ring sequences. Open diamonds indicate stands of *Taxodium distichum*, *Taxodium mucronatum*, *Phyllocladus glaucus* and *Phyllocladus trichomanoides* that grew in flood-disturbed, streamside settings (n=17) (redrawn from Falcon-Lang, 2005b).

It can be seen from Figure 5.3 that the highest mean sensitivities (up to 0.7) occur in cool to cold and dry climatic conditions (these are mostly at modern high altitudes or latitudes close to the physiological threshold of the trees when small year to year variation in climate can cause significant variation in ring width) equivalent to Fritt *et al's*. (1965) semi-arid forest border. This study highlighted that complacent values of 0.3 or less occur across the entire climate range suggesting that the maximum mean sensitivity values are more significant in terms of climatic indicators as indicated by Fritts (1976). However the conifers at the hot and wet end of the scale produce a low range of MS values, all falling below 0.3 (0.16 to 0.27), suggesting that the range of values may also be diagnostic.

It should also be noted that *Taxodium*, which proved to be problematical in LLS analysis (see Chapter 3, Section 3.4.2), is also anomalous in this mean sensitivity study with *T. distichum*, and *T. mucronatum* being joined by *Phyllocladus glaucus* and *P. trichomanoides* in producing significantly sensitive values outside of the cold and dry zone, represented as open diamonds in Figure 5.3 (Falcon-Lang, 2005b). These conifer species prefer floodplain environments and it is suggested that the anomalously high values of mean sensitivity may be caused by local disturbance due to repeated flooding (Young *et al*, 1993). This stresses the importance of identifying the samples used in any palaeoclimate studies in order to avoid adding potentially anomalous values to datasets or to at least acknowledge that they may be problematical.

Ring widths may not only be characteristic of the macroclimate but also individual site factors such as topography, variations in soil types and site exposure to wind and radiation. However Fritts (1976) suggests that the underlying signal can be seen from a sample set as small as 10 trees, although where the site conditions are favourable for growth he suggests using a larger sample set to pick up minor fluctuations in climate.

5.3. Growth ring analysis data collection

Growth rings within the fossil wood from both the northern and southern hemisphere polar sites were analysed in transverse section and rings measured using the Leica IM1000 imaging system. The rings were measured along a radial line to obtain as long a ring series as the preservation allowed. The following data were collected from the wood in order to carry out palaeoclimate analysis:-

1 The presence or absence of growth rings in order to assess whether the palaeoclimate was seasonal or not (Francis, 1986; Creber and Francis, 1999; Ennos, 2001). Although the markedness of annual growth rings (the internal structure of rings e.g. Percentage Latewood) is strongly genetically related to LLS as discussed in Chapters 3 and 4, the presence or absence of rings and their width are related to the prevailing climate (Falcon-Lang, 2005b). For instance, annual growth rings tend not to occur in the tropics, although drought rings do (personal communication A.O'Dea, Smithsonian Tropical Research Institute, Panama; Creber and Francis, 1999). The presence of annual growth rings indicates that some factor in the environment occurred to induce cambial activity to slow or shut down completely. This may be the loss of leaves in winter as a carbon retention strategy halting wood growth, or the long periods of winter darkness at higher latitudes that slows the trees' metabolism etc.

2 The presence or absence of false rings. False rings are produced when the growing period is interrupted (Schweingruber, 1996) by freezing or drought (Fritts, 1976; Kumagai *et al.*, 1995). Frost rings may cause physical damage such as exploded cells formed by the expansion of ice within the lumen. False rings caused by drought tend to produce a few very small cells mimicking an end-of-season boundary (Fritts, 1976; Creber and Francis, 1999). False rings caused by insect attack are harder to confirm requiring physical evidence such as insect remains, burrowing or coprolites to have been preserved (Jefferson, 1982).

3 Mean sensitivity is determined in order to determine whether growth was constant or variable from year to year. Annual sensitivity shows annual variation in growth

from one year to the next and mean sensitivity is the average of this and indicates variability over the life of the tree (Fritts, 1976).

5.4. Growth ring analysis of Northern Hemisphere Cretaceous woods

All samples from Svalbard and the Canadian Arctic display growth rings that are easily discernable without the aid of a microscope, indicating that the climate in these areas was probably seasonal.

5.4.1. Svalbard

A total of 13 ring series were obtained from the Svalbard samples, varying in length from 4 to 48 rings (Table 5.1). The growth rings varied in width from 0.36 to 5.55mm with a mean for the sample set of 1.75mm, indicating that the trees had the potential for high growth rates but that in some cases the environment may not have been entirely favourable for rapid growth (Table 5.1).

The mean sensitivity values for these samples range from 0.11 to 0.56 with an average of 0.29 showing that growth was mainly complacent. Of the 13 samples 8 had values of 0.3 or less (62%) and 5 had values >0.3 (38%) although 80% of the values >0.3 were between 0.32 and 0.36 (low sensitive values). Three of these samples are *Taxodioxylon* similar to modern *Taxodium* and therefore may be producing anomalously high mean sensitivity values (LD129, LD131 and LD133, see Section 5.2.2). Only two of these *Taxodioxylon* samples produced mean sensitivities that were sensitive and both of these values were below 0.4 (LD129 = 0.34 and LD133 = 0.36) however in order to confirm that they were not having a detrimental effect on the average mean sensitivity they were removed from the dataset and it was found that exactly the same mean sensitivity value (0.29) was obtained from the remaining samples.

Most of the trees appear not to have been severely stressed but growing in areas with adequate water supply. Some appear to have suffered adverse affects from the climate for at least part of their lives, probably due to intermittent or restricted water supply. Of the seven samples that contained false rings only two were complacent (LD126 and SN25 4), the remainder being sensitive. Histograms of annual sensitivity values for each tree show that more values fall below 0.3 (61%) therefore it appears that these trees were growing under conditions that were constant and equable (Figure 5.4 and Table 5.1) and growth interruptions that formed false rings were rare.

Seven of the thirteen samples appear to contain false rings (Table 5.2). The majority of the false rings appear to occur in the summer to early autumn. No frost damaged cells were observed, indicating that they were probably caused by drought stress rather than frost. The form-genera that contain false rings are mostly types which may possibly have grown at higher altitudes therefore the false rings may be an artifact of growth on exposed sites with steep topography and thin soils making it difficult to retain moisture. One specimen was *Taxodioxylon* which may have grown on a swampy site that was susceptible to fluctuating water levels during dry summer spells.

Table 5.1. Table showing growth ring data for Svalbard (see Appendix B, Table B1.4 for full annual sensitivity data set).

Specimen N°	Wood Type	Mean Ring Width (mm)	Min-Max Ring Width (mm)		Mean Sensitivity	Complacent or Sensitive
LD101	*Juniperoxylon*	1.04	0.47	1.89	0.56	S
LD102	*Cedroxylon*	5.55	4.52	6.35	0.11	C
LD105	*Piceoxylon*	3.21	1.90	4.45	0.24	C
LD108	*Araucariopitys*	1.26	0.34	2.91	0.30	C
LD120	*Protocedroxylon*	0.36	0.12	0.93	0.32	S
LD123	*Laricioxylon*	1.12	0.40	1.84	0.32	S
LD126	*Laricioxylon*	0.65	0.17	1.38	0.28	C
LD129	*Taxodioxylon*	0.86	0.23	1.35	0.34	S
LD131	*Taxodixoylon*	1.46	0.91	2.40	0.23	C
LD130	*Xenoxylon*	2.77	1.67	4.13	0.22	C
LD132	*Cupressinoxylon*	0.93	0.34	2.44	0.23	C
LD133	*Taxodioxylon*	2.11	0.84	4.26	0.36	S
SN25 4	*Taxoxylon*	1.40	0.57	2.63	0.29	C

Table 5.2. Table showing the number of false rings present in the Svalbard samples and what season they appear to have formed in.

Sample N°	Form Genera	Number of False Rings	Total Number of Rings	Where False Rings Occur (EW = Earlywood LW= Latewood)	Season in which False Rings May Have Occurred
LD101	*Juniperoxlyon*	1	6	EW	Summer
LD108	*Araucariopitys*	1	36	EW to LW	Late Summer-Early Autumn
LD120	*Protocedroxylon*	9	35	EW	Summer
LD123	*Laricioxylon*	1	49	EW	Spring/Summer
LD126	*Laricioxylon*	4	49	EW to LW	Late Summer
LD129	*Taxodioxylon*	2	16	EW to LW	Late Summer-Early Autumn
SN25 4/a	*Taxoxylon*	3	20	EW and LW	Spring/Summer/Autumn

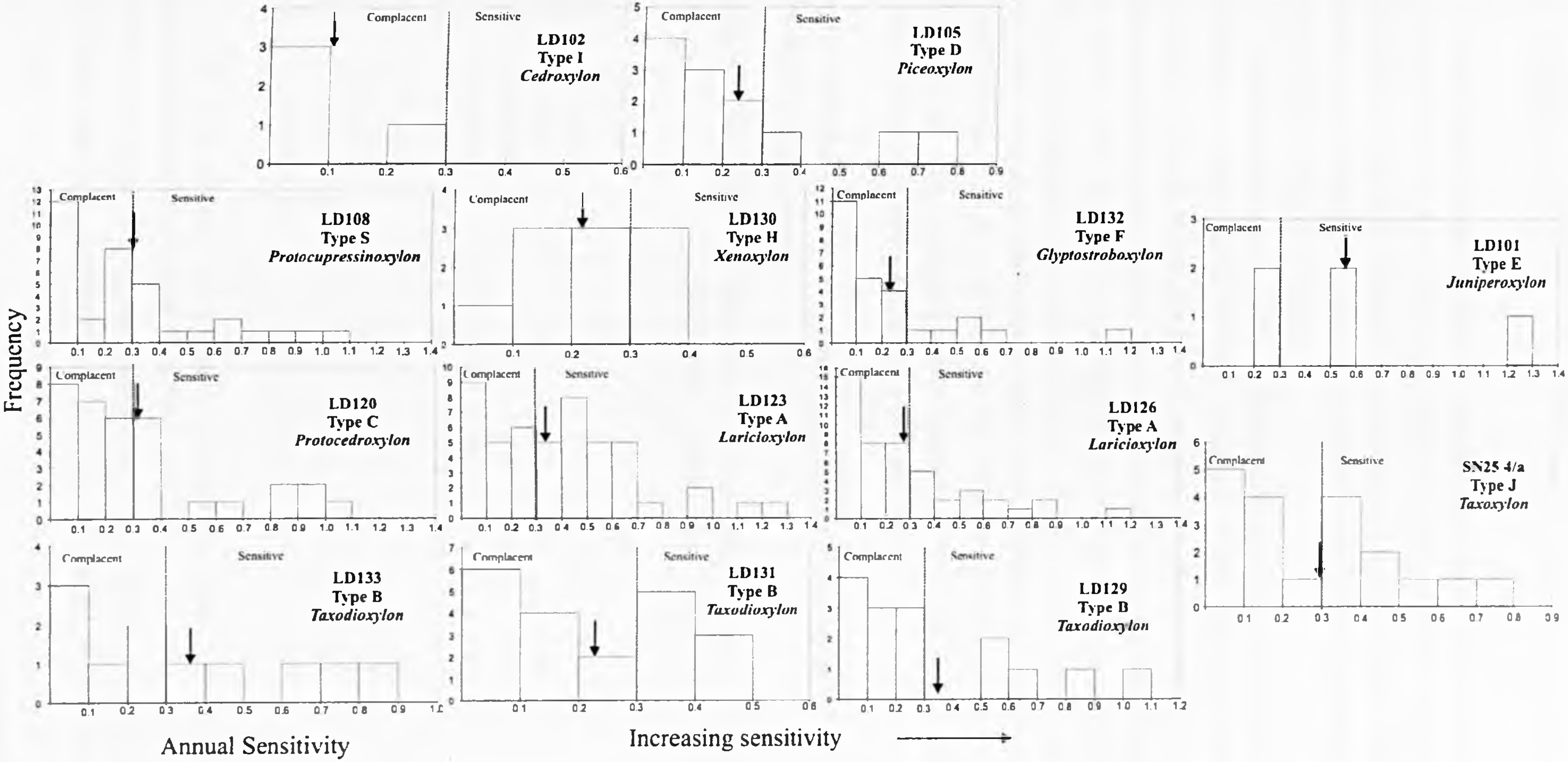


Figure 5.4. Histograms showing the amount of annual variation in growth patterns of Svalbard fossil trees. Arrows indicate the mean sensitivity.

5.4.2. Canadian Arctic

Ten ring series were obtained for the Canadian Arctic samples, from 6 to 77 rings long. Initial visual examination these samples appeared to suggest that the rings were narrower than those in Svalbard. This was confirmed when the rings were measured as they varied in mean width from 0.48 to 3.03mm, with a mean for the sample set of 1.27mm, indicating that growth was probably slow in this area (Table 5.3).

The mean sensitivity values of these samples range from 0.19 to 0.39 with an average of 0.27, slightly lower than that of the Svalbard samples (0.29) even though these trees had narrower rings indicating slower growth. This suggests that although growth was slow it was consistent from year to year. Of the 10 samples 7 had values of 0.3 or less (70%) and 3 had values of >0.3 (40%) indicating that the majority of the trees were complacent and probably grew in areas with adequate water supply (Table 5.3). Of the 5 samples that contained false rings 3 were complacent (60%) and 2 sensitive (40%) (Table 5.4). Histograms of annual sensitivity show that the majority of the values fall at the low end of the scale below 0.3 (68%) indicating that the trees were growing under equable conditions with a good supply of the necessary requirements for growth (Figure 5.5 and Table 5.3).

Table 5.3. Table showing growth ring data for the Canadian Arctic (see Appendix B, Table B1.4 for full annual sensitivity data set).

Specimen N°	Wood Type	Mean Ring Width (mm)	Min-Max Ring Width (mm)		Mean Sensitivity	Complacent or Sensitive
RR102	*Piceoxylon*	3.03	2.25	3.99	0.27	C
RR113	*Piceoxylon*	0.58	0.18	1.78	0.34	S
RR111	*Pinuxylon*	1.10	0.36	2.35	0.33	S
RR122	*Pinuxylon*	0.89	0.34	2.07	0.39	S
E139	*Pinuxylon*	0.48	0.14	0.99	0.23	C
E140	*Pinuxylon*	1.95	1.14	3.03	0.25	C
RR121	*Cedroxylon*	1.32	0.35	2.64	0.23	C
RR123	*Cedroxylon*	1.51	0.77	2.16	0.27	C
BL125	*Palaepiceoxylon*	1.09	0.46	1.68	0.23	C
E137	*Cupressinoxylon*	0.72	1.56	0.22	0.19	C

Half of the Canadian Arctic samples contained false rings (5 out of 10), a similar proportion to those found in Svalbard (Table 5.4). The majority of the false rings seem to occur in the spring and summer, although they were also observed in the early autumn part of the ring. However frost rings were not observed, therefore this may suggest that the false rings were caused by arid conditions. As with Svalbard the majority of the trees containing false rings may have grown at higher altitudes suggesting that they were growing on thin, rocky soils susceptible to drought.

Table 5.4. Table showing the number of false rings present in the Canadian Arctic samples and what season they may to have formed in.

Sample Number	Form Genera	Number of False Rings	Total Number of Rings	Where False Rings Occur (EW = Earlywood LW= Latewood)	Season in which False Rings May Have Formed
RR113	*Piceoxylon*	3	43	EW	Spring/Summer
RR111	*Pinuxylon*	15	63	EW and LW	Spring/Summer/Autumn
RR122	*Pinuxylon*	5	49	EW and LW	Spring/Summer/Autumn
E140	*Pinuxylon*	2	29	EW	Spring/Summer
BL125	*Palaepiceoxylon*	1	59	EW	Spring

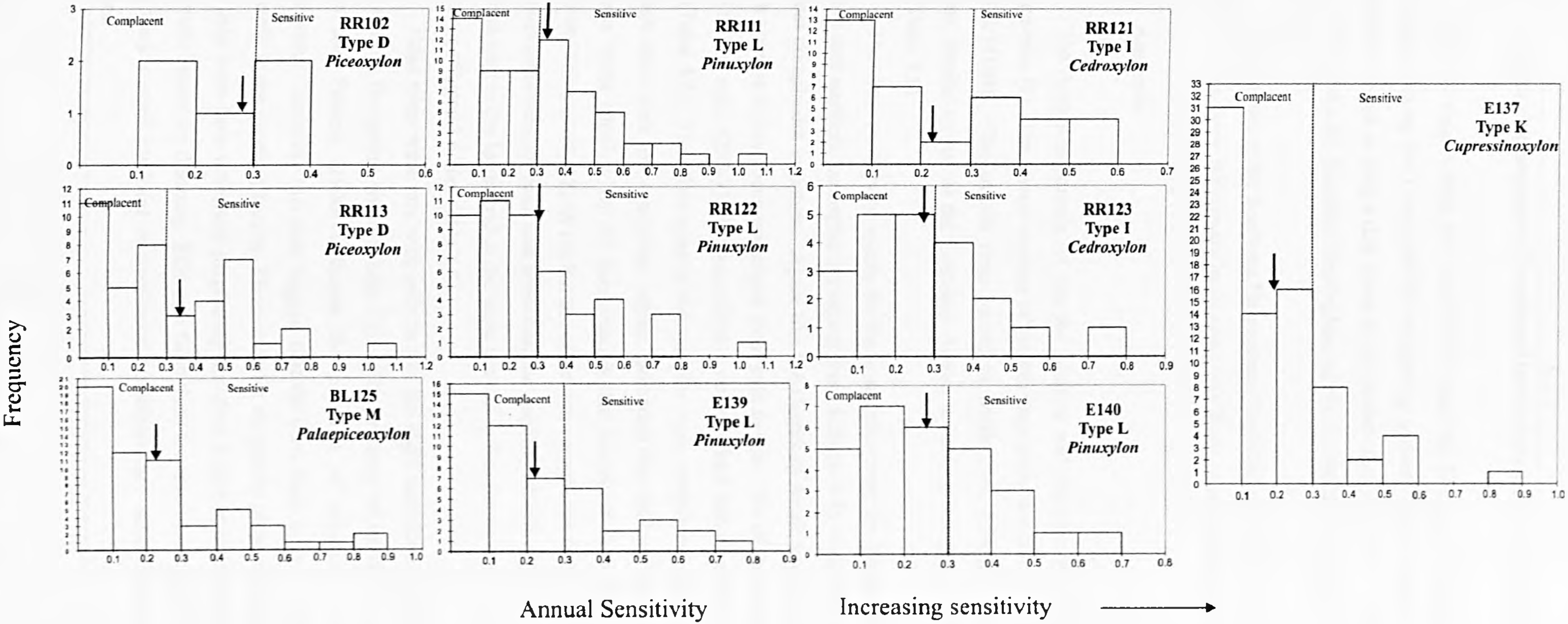


Figure 5.5. Histograms showing the amount of annual variation in growth patterns of the Canadian Arctic fossil trees. Arrows indicate the position of mean sensitivity.

5.5. Growth ring analysis of Southern Hemisphere Cretaceous woods

Growth rings within the fossil wood from the Southern Hemisphere polar sites were also analysed using the Leica IM1000 imagining system. The rings were measured along a radial line to obtain as long a ring series as the preservation allowed. The same kind of datasets were collected for the Southern Hemisphere as for the Northern Hemisphere sites (Section 5.3. points 1-3).

All samples in the Southern Hemisphere displayed growth rings indicating that, like the Northern Hemisphere, the climate in all areas was likely to have been seasonal.

5.5.1. Australia

The Australian sample set was the smallest and therefore produced the lowest number of ring series (8). The lowest number of growth rings present was 14 (872/W17) and the largest 75 (872/W104). The growth rings varied in width from 0.56 to 2.45mm with a mean of 1.25mm, similar to that of the Canadian Arctic, indicating that growth was again slow in this area (Table 5.5).

The mean sensitivity values for these samples were the lowest of all of the sites (both northern and southern hemisphere) ranging from 0.20 to 0.35 with an average of 0.25 making the trees complacent in nature. Again like the Canadian Arctic samples, although growth was slow it appears to have been consistent from year to year. Six of the samples (75%) had values of 0.3 or less and 2 (25%) had values of >0.3, one of which had an average of 0.32 and the other 0.35 (Table 5.5). Therefore most of the samples were complacent with only 2 being sensitive, although these were low sensitivity values, indicating that the trees were growing in areas with adequate water supply. Of the two samples that contained false rings one had the highest sensitivity value (0.35, 872/W16) but the other was complacent (0.29, 872/W168). Histograms of annual sensitivity for each tree show that the majority of values are 0.3 or less (71%) mostly clustered near to the lower end of the scale indicating that the trees were growing under equable conditions (Figure 5.6 and Table 5.5).

False rings were rare with only two of the eight samples appearing to contain just two rings each in the spring wood (Table 5.6). The presence of ice-rafted boulders suggested by Frakes and Francis (1990) indicates the presence of seasonal ice, hence cold winter temperatures. Therefore this may suggest that the false rings in these samples were caused by frost early in the growing season. These samples are poorly preserved making it difficult to see if the cells have been deformed (exploded) therefore it cannot be determined whether the false rings were caused by freezing. However false rings are rare which would suggest that the false rings were caused by local microclimate conditions not something as widespread as cold winters.

Table 5.5. Table showing growth ring data for Australia (see Appendix B, Table B1.4 for full annual sensitivity data set).

Specimen N°	Wood Type	Mean Ring Width (mm)	Min-Max Ring Width (mm)		Mean Sensitivity	Complacent or Sensitive
872/W17	*Podocarpoxylon*	1.10	0.55	1.95	0.20	C
872/W166	*Podocarpoxylon*	2.39	1.43	3.67	0.23	C
872/W167	*Podocarpoxylon*	0.83	0.47	1.47	0.20	C
872/W16	Type R (Unidentified conifer)	0.56	0.19	1.60	0.35	S
872/W104	Type R (Unidentified conifer)	0.78	0.33	2.45	0.21	C
872/W128	Type R (Unidentified conifer)	2.45	1.17	3.50	0.20	C
872/W149	Type R (Unidentified conifer)	0.74	0.32	2.60	0.32	S
872/W168	Type R (Unidentified conifer)	1.17	0.38	2.67	0.29	C

Table 5.6. Table showing the number of false rings present in the Australian samples and the season in which they appear to have formed.

Sample Number	Form Genera	Number of False Rings	Total Number of Rings	Where False Rings Occur (EW = Earlywood LW= Latewood)	Season in which False Rings Appear to Occur
872/W16	Type R (Unidentified conifer)	2	67	EW/LW	Spring/late Summer
872/W168	Type R (Unidentified conifer)	2	46	EW	Spring

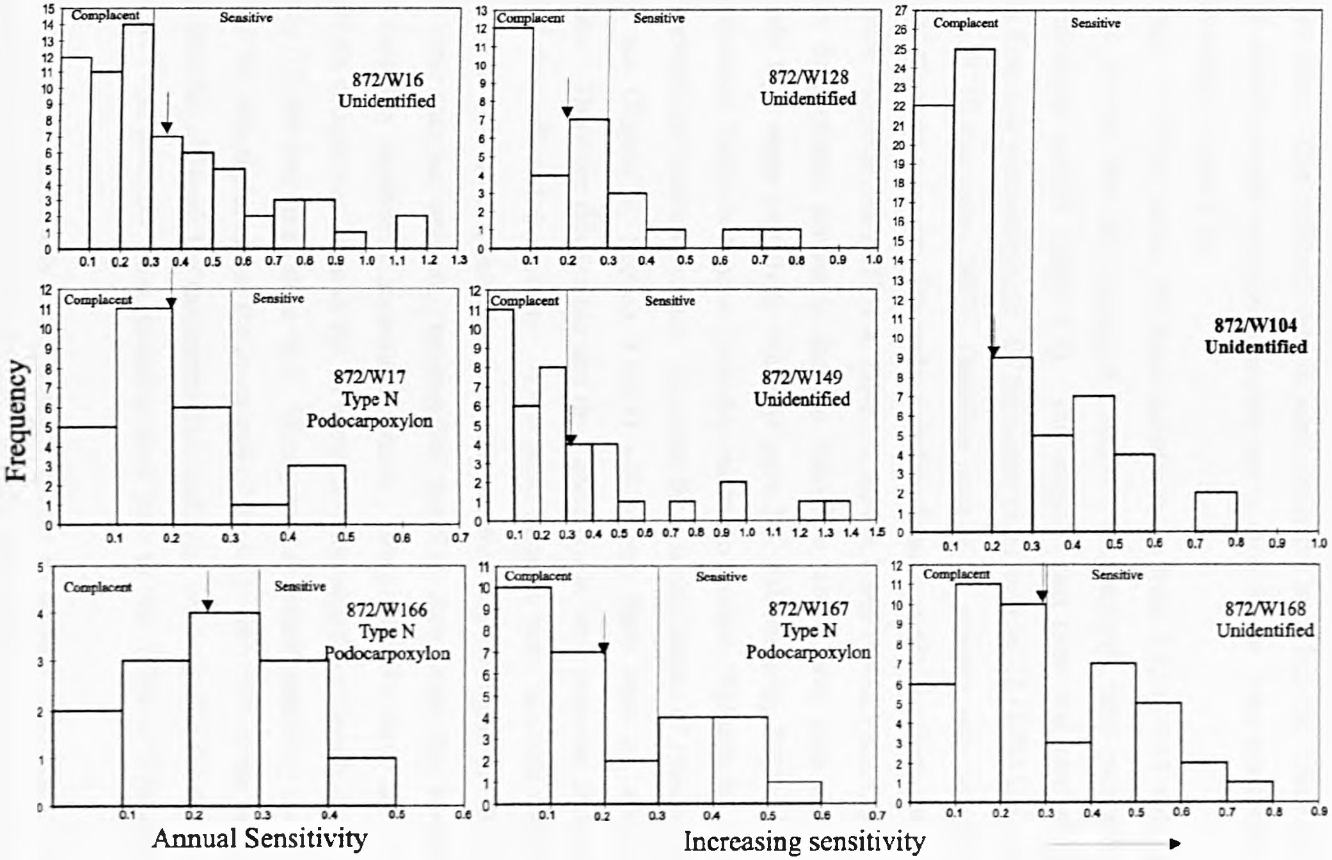


Figure 5.6. Histograms showing the amount of annual variation in growth patterns of the Australian fossil trees. Arrows indicate the mean sensitivity.

5.5.2. Antarctica (James Ross Island)

The James Ross Island collection provided the largest sample set with a total of twenty eight ring series obtained ranging from 5 to 68 rings in length and from 0.73 to 4.16mm in width with a mean for the sample set of 1.76mm which was the widest of all of the Southern Hemisphere sites. This indicates that in some areas the trees had the potential of moderate growth but overall growth was slow therefore one or more factor in the environment may have been unfavourable (Table 5.7).

Mean sensitivity values for these samples range from 0.12 to 0.58 with an average of 0.32 making this the first site to produce a sensitive ring analysis value even though the trees achieved moderate growth (Table 5.7). This suggests that there was moderate variation in conditions from one year to the next. Of the twenty eight samples 12 (43%) had values of 0.3 or less and 16 (57%) had values >0.3. Therefore most of the samples were sensitive, indicating that most of the trees were growing under variable climatic conditions from year to year. Four samples were *Taxodioxylon* (DJ451.4, DJ455.1, DJ458.1 and DJ462.5 see Chapter 2, Section 2.6.2.2 for descriptions) similar to modern *Taxodium* which have been shown to produce anomalously high mean sensitivity values (Figure 5.3, Falcon-Lang, 2005b) but none of the samples represent *Phyllocladoxylon,* probably related to modern *Phyllocladus* which may also produce anomalously sensitive values. However there is one sample of *Protophyllocladoxylon* (DJ141.6, see Chapter 2, Section 2.6.2.6) which may have been an ancestral form of *Phyllocladus*. Therefore this sample and the *Taxodioxylon* were removed from the dataset to establish if they affected the results. When these samples were removed the average mean sensitivity value still remains sensitive, indeed it becomes slightly higher at 0.33. It was noted that 5 of these samples were also unidentified therefore these were also removed from the dataset in case they represented anomalous species. This produced a value of 0.30 just making the sample set complacent. Nine of the 14 samples containing false rings had values >0.3, one was exactly 0.3 and four had values <0.3. Histograms of annual sensitivity for each tree show that most of the values plot nearer the lower end of the scale with 59% of the values 0.3 or less. This indicates that although the environmental conditions were equable for the majority of the samples there was probably some variation from year to year (Figures 5.7a and b and Table 5.7).

Fourteen of the twenty eight samples appear to contain false rings, a very similar proportion of the sample set to those found in the Northern Hemisphere, however there are very few false rings in those samples that do contain them (Table 5.8). The highest number of false rings were found in sample D421 which has 6 false rings in the total of 45 (Table 5.8). The majority of the false rings appear to have formed in the spring and summer therefore were probably produced by aridity in a warm environment rather than freezing.

Table 5.7. Table showing growth ring data for James Ross Island, Antarctica (see Appendix B, Table B1.4 for full annual sensitivity data set).

Specimen N°	Wood Type	Mean Ring Width (mm)	Min-Max Ring Width (mm)		Mean Sensitivity	Complacent or Sensitive
5215	*Araucariopitys*	2.23	1.21	5.03	0.41	S
DJ144.7	*Araucariopitys*	1.62	0.76	3.54	0.32	S
DJ137.6	*Cupressinoxylon*	1.07	0.36	3.05	0.30	C
DJ137.8	*Agathoxylon*	0.73	0.17	1.45	0.36	S
DJ141.3	*Agathoxylon*	1.31	1.31	2.04	0.25	C
DJ141.6	*Protophyllocladoxylon*	1.23	0.39	3.01	0.32	S
DJ141.13	*Podocarpoxylon*	1.02	0.32	1.90	0.39	S
DJ141.14	*Podocarpoxylon*	1.23	0.53	3.49	0.27	C
DJ144.2	*Podocarpoxylon*	1.25	0.65	2.08	0.31	S
DJ451.4	*Taxodioxylon*	2.74	1.45	3.67	0.34	S
DJ455.1	*Taxodioxylon*	2.66	1.60	4.30	0.21	C
DJ458.1	*Taxodioxylon*	2.08	1.20	3.15	0.15	C
DJ462.5	*Taxodioxylon*	1.99	1.53	2.61	0.30	C
DJ463.5	*Sciadopityoxylon*	1.42	0.86	2.28	0.24	C
DJ144.5	*Sciadopityoxylon*	0.79	0.12	2.72	0.27	C
DJ455.3	*Circoporoxylon*	1.64	0.69	3.20	0.25	C
DJ462.2	*Circoporoxylon*	2.04	0.98	3.24	0.21	C
DJ462.3	*Circoporoxylon*	2.36	1.38	4.16	0.44	S
D421	Type S (Unidentified Araucarioid)	0.85	0.14	3.03	0.36	S
DJ366.7	Type S (Unidentified Araucarioid)	1.19	0.39	2.99	0.33	S
DJ135.3	Type S (Unidentified Araucarioid)	2.25	1.03	3.16	0.37	S
DJ141.7	Type T (Unidentified Non Araucarioid)	4.16	3.34	4.73	0.12	C
DJ451.3	Type T (Unidentified Non Araucarioid)	3.55	0.53	6.27	0.52	S
DJ141.16	Type R (Unidentified conifer)	1.52	0.55	2.35	0.34	S
DJ141.8	Type R (Unidentified conifer)	0.82	0.14	1.88	0.41	S
DJ144.3	Type R (Unidentified conifer)	1.09	0.36	1.75	0.21	C

Continued .....

Table 5.7. continued

Specimen N°	Wood Type	Mean Ring Width (mm)	Min-Max Ring Width (mm)		Mean Sensitivity	Complacent or Sensitive
DJ465.1	Type R (Unidentified conifer)	1.51	0.25	3.08	0.58	S
DJ466.2	Type R (Unidentified conifer)	2.88	1.16	3.89	0.37	S

Table 5.8. Table showing the number of false rings present in the James Ross Island samples and what season they appear to have formed in.

Sample Number	Form Genera	Number of False Rings	Total Number of Rings	Where False Rings Occur (EW = Earlywood LW= Latewood)	Season in which False Rings Appear to Occur
5215	*Araucariopitys*	3	15	EW	Summer
DJ137.6	*Cupressinoxylon*	1	21	EW	Spring
DJ137.8	*Agathoxylon*	2	27	LW	Late Summer-Early Autumn
DJ141.3	*Podocarpoxylon*	2	22	EW	Summer
DJ141.6	*Protophyllocladoxylon*	4	40	EW/LW	Summer-Early Autumn
DJ144.5	*Sciadopityoxylon*	2	68	EW	Spring
D421	Araucarioid Type	6	45	EW/LW	Summer-Early Autumn
DJ366.7	Araucarioid Type	3	11	EW/LW	Summer-Early Autumn
DJ141.7	Type T Unidentified Non Araucarioid	1	8	EW	Summer
DJ451.3	Type T Unidentified Non Araucarioid	3	16	EW	Spring-Summer
DJ141.16	Type R Unidentified conifer	1	16	LW	Early Autumn

Continued .....

Table 5.8. continued

Sample Number	Form Genera	Number of False Rings	Total Number of Rings	Where False Rings Occur (EW = Earlywood LW= Latewood)	Season in which False Rings Appear to Occur
DJ141.8	Type R Unidentified conifer	1	62	EW	Spring-Summer
DJ144.3	Type R Unidentified conifer	2	32	EW and LW	Spring-Summer-Early Autumn
DJ466.2	Type R Unidentified conifer	2	7	EW	Spring

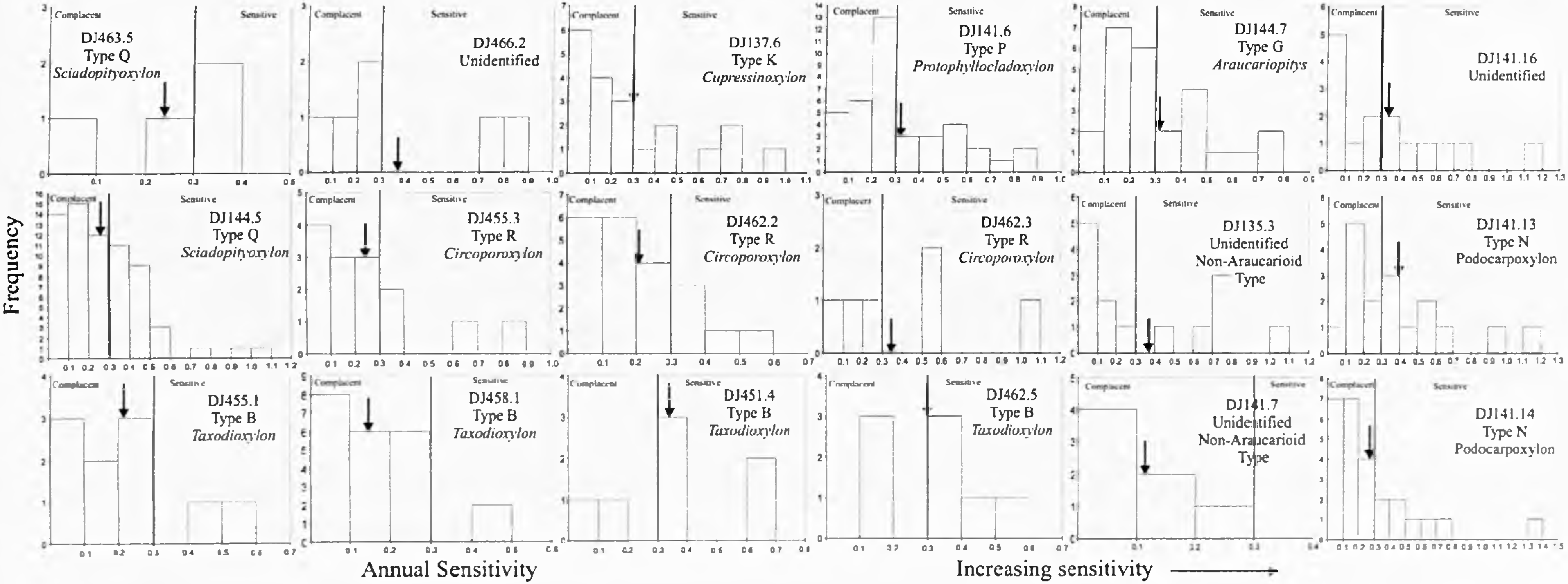


Figure 5.7a. Histograms showing the amount of annual variation in growth patterns of the James Ross Island fossil trees. Arrows indicate the position of mean sensitivity.

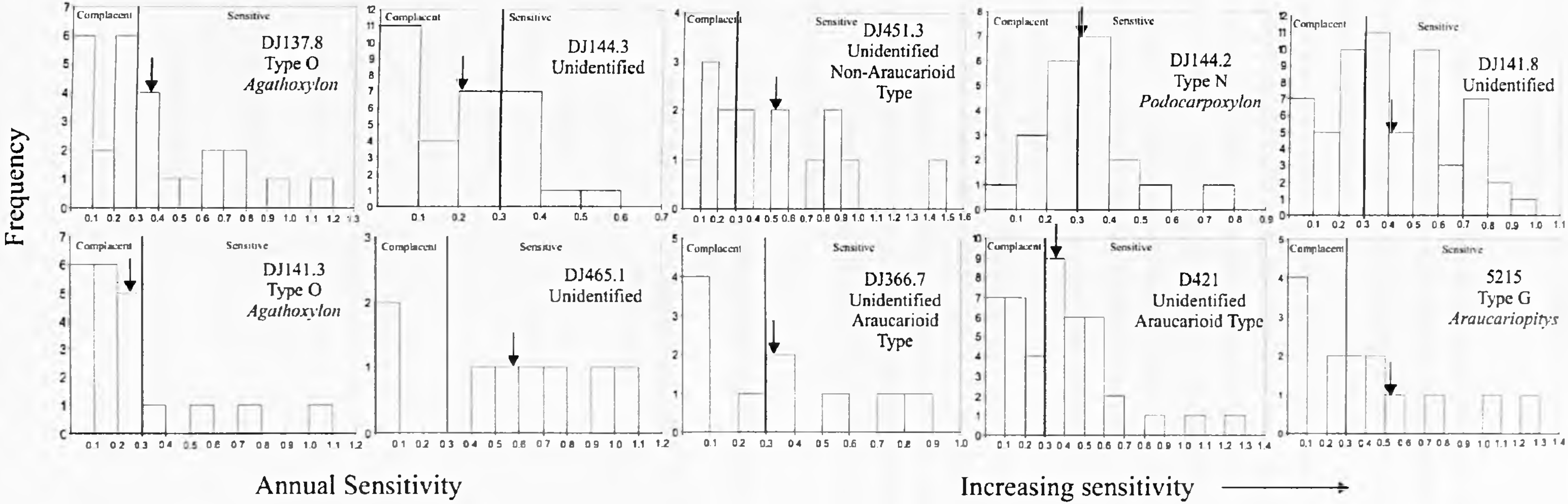


Figure 5.7b. Histograms showing the amount of annual variation in growth patterns of the James Ross Island fossil trees. Arrows indicate the mean sensitivity.

5.5.3. Antarctica (Alexander Island)

Only nine ring series were obtained from the Alexander Island samples, varying in length from 12 to 51 rings. The growth rings varied in width from 0.58 to 3.74mm with a mean value for the sample set of 1.42mm, indicating growth was quite slow therefore one or more factors in the environment may have been unfavourable (Table 5.9).

The mean sensitivity values for these samples range from 0.29 to 0.46 with an average of 0.36 making them sensitive with the highest sensitivity value of all of the sites examined. Of the 9 samples only 1 (11%) had a value of <0.3 (KG2817.20, 0.29). Although 5 samples had values <0.35 the samples were almost exclusively sensitive indicating that the trees were growing in an area of variable water availability (Table 5.9). One sample was *Taxodioxylon* (KG4626.1) similar to modern *Taxodium*. However, when this potentially problematic species was removed from the dataset it made no significant difference to the value of mean sensitivity obtained (without *Taxodioxylon* 0.37).

Seven of the nine samples were Type R, unidentified conifers (see Chapter 2, Section 2.6.2) and therefore may or may not represent species that produce anomalous results, however the removal of anomalous or unidentified species from other sites has made little or no difference to the results and it is therefore assumed that the unidentified samples here represent the area as a whole. The relatively high values of mean sensitivity may suggest however that the area had a seasonally dry climate.

Table 5.9. Table showing growth ring data for Alexander Island, Antarctica (see Appendix B, Table B1.4 for full annual sensitivity data set).

Specimen N°	Wood Type	Mean Ring Width (mm)	Min-Max Ring Width (mm)		Mean Sensitivity	Complacent or Sensitive
KG1703.23	*Podocarpoxylon*	0.79	0.19	2.45	0.46	S
KG1719.3b	Type R (Unidentified conifer)	1.16	0.53	3.83	0.43	S
KG2814.256	Type R (Unidentified conifer)	1.53	0.55	3.82	0.39	S
KG2817.20	Type R (Unidentified conifer)	1.33	0.34	3.05	0.29	C
KG4626.1	*Taxodioxylon*	3.74	1.87	5.76	0.32	S
KG4672.6	Type R (Unidentified conifer)	0.79	0.16	3.66	0.38	S
KG4710.1	Type R (Unidentiried conifer)	2.12	0.85	4.39	0.33	S

Continued ......

Table 5.9. continued

Specimen N°	Wood Type	Mean Ring Width (mm)	Min-Max Ring Width (mm)		Mean Sensitivity	Complacent or Sensitive
KG2814.252	Type R (Unidentified conifer)	0.78	0.08	2.39	0.34	S
KG4717.43	Type R (Unidentified conifer)	0.58	0.13	1.22	0.33	S

Seven of the nine samples appear to contain false rings, a higher proportion of samples than found in the wood from other sites examined (Table 5.10). The majority of the false rings appear to have formed in the spring and summer therefore were probably produced by aridity.

Table 5.10. Table showing the number of false rings present in the Alexander Island samples and what season they appear to have formed in.

Sample Number	Form Genera	Number of False Rings	Total Number of Rings	Where False Rings Occur (EW = Earlywood LW= Latewood)	Season in which False Rings Appear to Occur
KG1703.23	*Podocarpoxylon*	3	40	EW	Spring
KG2814.256	Type R (Unidentified conifer)	4	32	EW	Summer
KG4626.1	*Taxodioxylon*	1	12	EW	Spring
KG4672.6	Type R (Unidentified conifer)	2	38	EW	Summer
KG4710.1	Type R (Unidentified conifer)	5	26	EW and LW	Late Summer-Early Autumn
KG2814.252	Type R (Unidentified conifer)	11	51	EW	Summer
KG4717.43	Type R (Unidentified conifer)	10	44	EW and LW	Spring-Summer-Early Autumn

In addition to false rings some of these samples also contain rings that pinch out completely (Figure 5.8). In modern conifers if a tree is sufficiently crowded and the crown small the xylem may be discontinuous in this fashion particularly near to the stem base (Fritts, 1976). This indicates that the fossil trees from Alexander Island may have been growing in dense stands which would also explain the presence of false rings, as the trees would have been competing with each other for water during the summer. This phenomenon was also observed in Lower Cretaceous fossil wood samples from Alexander Island by Jefferson (1982). Jefferson (1982) suggested that this may be extreme reaction wood caused by rapid influx of sediment during flood events, that bent the tree trunks.

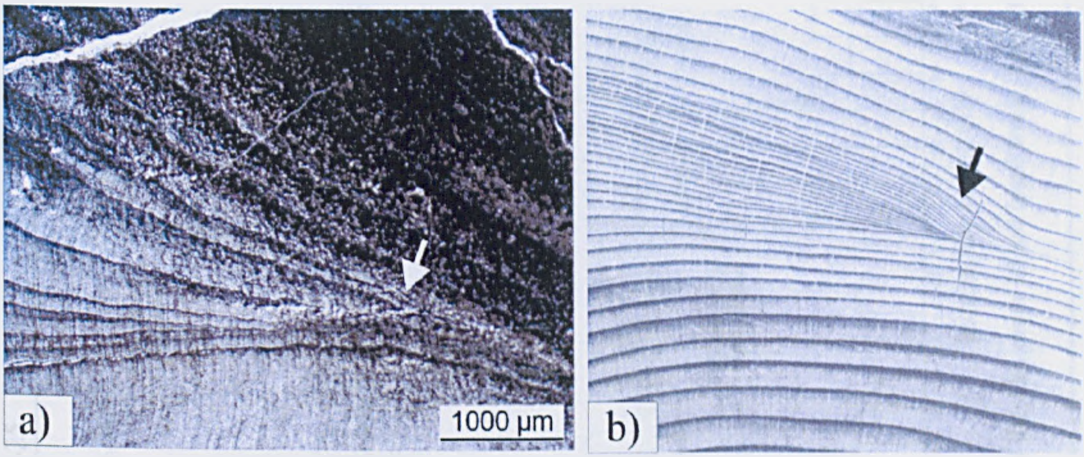


Figure 5.8. a) Fossil wood sample KG1703.23 from Alexander Island, white arrow pointing to pinched out rings. b) Modern wood sample (unidentified), black arrow indicating 18 growth rings absent (pinched out) (photograph of modern wood from Fritts, 1976).

Histograms of annual sensitivity show that although the data are spread across the scale most plot towards the lower end of scale with 54% having values <0.3 and 46% >0.3. This indicates that although the environmental conditions were probably equable there was some variation from year to year (Figure 5.9 and Table 5.9).

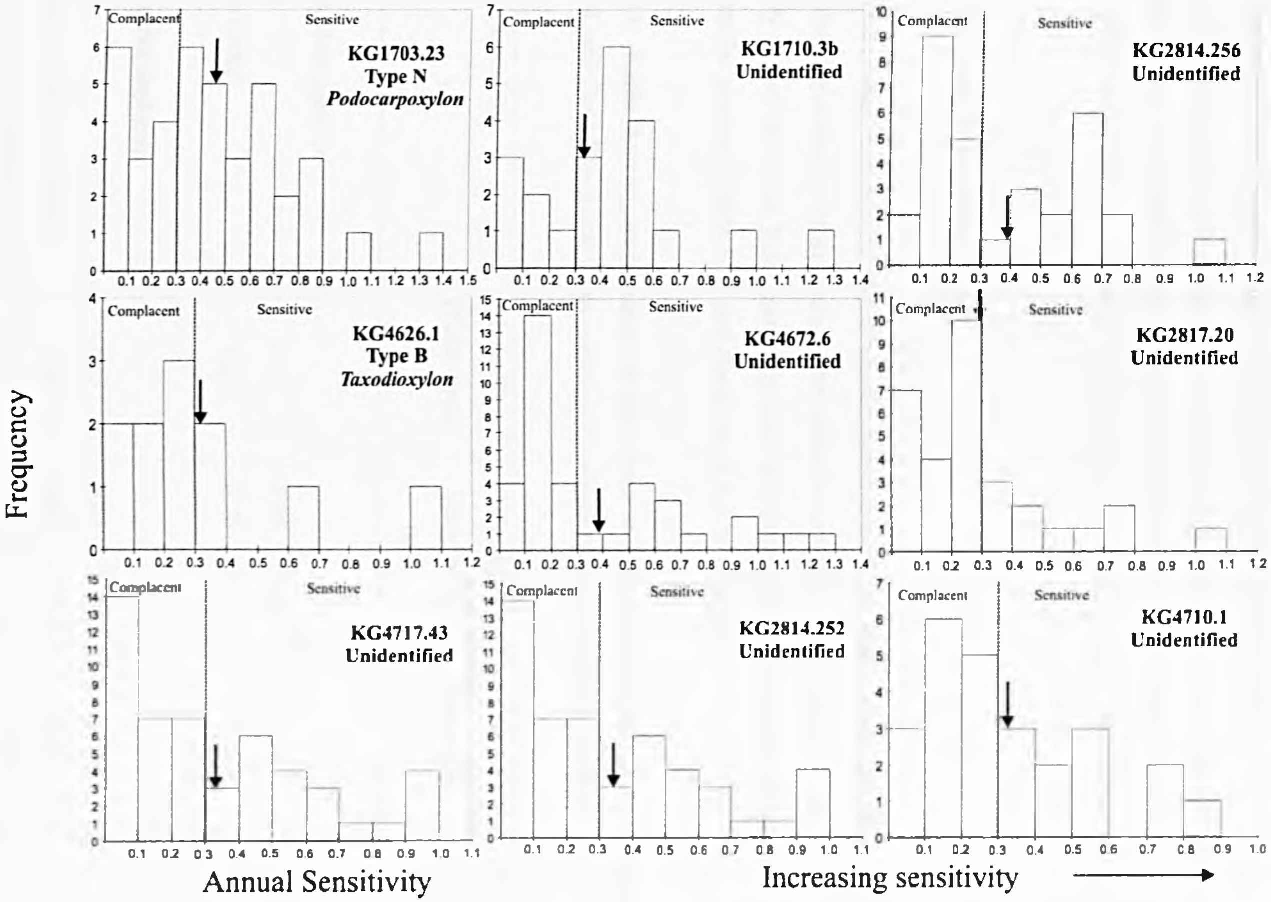


Figure 5.9. Histograms showing the amount of annual variation in growth patterns of the Alexander Island fossil trees. Arrows indicate the mean sensitivity.

5.6. Comparison of palaeoclimate analysis from tree rings with climatic interpretation of vegetation types

In this section comparison is made between the palaeoclimatic conditions suggested by the results of the growth ring analysis (see Table 5.11 for summary) and the inferences made from comparing the forest composition to modern equivalents.

As stated in Chapter 2 there are problems with making any analogy between modern forests and those of the mid-Cretaceous as there are no modern equivalents to the Cretaceous high latitude floras. However, assuming that the fossil conifer functions were equivalent to those of modern conifers a general idea of the prevailing environment and climate may be gained.

5.6.1. Northern Hemisphere

Tree ring analysis of fossil wood specimens from both Northern Hemisphere sites suggest the prevailing climate during the mid-Cretaceous was seasonal. However the mean sensitivity values for these fossil samples were all complacent, suggesting adequate year round conditions for growth (Table 5.11 and Sections 5.4.1 and 5.4.2).

Table 5.11. Table showing mean values of data from tree ring analysis for all sites in the northern (Svalbard and Canadian Arctic) and southern hemisphere (Australia and Antarctica).

Location	Mean Ring Width (mm)	Min-Max Ring Width (mm)		Mean Sensitivity	Complacent or Sensitive
Northern Hemisphere					
Svalbard	1.75	0.96	2.84	0.29	C
Canadian Arctic	1.27	0.76	2.09	0.27	C
Southern Hemisphere					
Australia	1.25	0.61	2.49	0.25	C
James Ross Island (Antarctica)	1.76	0.84	3.14	0.32	S
Alexander Island (Antarctica)-	1.42	0.52	3.40	0.36	S

Taken in its entirety the evidence from growth ring analysis in the fossil wood from Svalbard seems to suggest that the trees achieved moderate growth under equable conditions with a constant supply of all necessary requirements for growth, although some areas appear to have been susceptible to short periods of drought in the spring and late summer (Section 5.4.1).

If Falcon Lang's (2005b) analysis of modern conifer growth rings is applied to the fossils (Section 5.2.2, Figure 5.3) the range of mean sensitivity values in the Svalbard samples (Table 5.1) suggests that the forests were growing in cool to cold dry conditions. This seems to be supported by the evidence from the presence of ice-rafted deposits reported by Frakes and Francis (1988) and Harland (1997) indicating that sea ice was present at least seasonally. However, isotope analysis of bivalves gives MATs of 8.3°C for oceans and Herman and Spicer (1996) suggest that the Arctic Ocean was warm (>0°C). The range of MS values, however, is reflected well in the inferences made from the modern counterparts (Chapter 2, section 2.5.3) that suggest a range of habitats that would have been generally moist with cool upland areas with the potential to dry out quickly and warm temperate areas containing rivers and/or swamps in the lowlands that may have been susceptible to minor fluctuations in the water table. Therefore the cool to cold dry inference made from Falcon-Lang's (2005b) data may be misleading if taken as representing the general environmental conditions rather than a range of microenvironments.

The evidence from growth rings in the fossil wood from the Canadian Arctic appears to suggest that the trees grew in a relatively constant and favourable environment with adequate water, although some areas appear to have been susceptible to a more marked climatic influence (Section 5.4.2). The reasonably wide range of mean sensitivity values suggests a cool dry climate. This seems to be supported by the inferences made from modern counterparts (Chapter 2, section 2.5.3) that suggest this area would have had similar conditions to Svalbard but the dominance of *Pinuxylon* with narrow growth rings suggests that the area may have been cool temperate like modern northern Canada where current sensitivities and ring widths are low (Jefferson, 1982).

5.6.2. Southern Hemisphere

As in the Northern Hemisphere, all Southern Hemisphere fossil specimens contained growth rings suggesting that the prevailing climate was strongly seasonal in all areas. However unlike the Northern Hemisphere sites or Australia both of the Antarctic locations (James Ross and Alexander islands) produced wood with sensitive values (Table 5.11). This would suggest that the Southern Hemisphere trees were growing under more variable conditions than the Northern Hemisphere samples or those at slightly lower latitudes in Australia. Alexander Island was the most southerly location and produced the most sensitive values of all sites examined (mean for sample set 0.36) although the growth rings were wider than in both Australia or the Canadian Arctic. This suggests that although there may have been a lot of variation in conditions from year to year the trees could still achieve quite high growth rates (Table 5.11, see also palaeogeographic map Chapter 1, Figure 1.2 for locations).

Although the Australian sample set was small the evidence from growth rings in the fossil wood suggests that the trees grew under conditions with little variation from year to year (see Section 5.5.1). This site produced the lowest MS values of all sites examined (mean for location 0.25, Section 5.5.1 and Table 5.11). A study of a larger sample set from the Eromanga Basin in Australia for the Early Cretaceous carried out by Frakes and Francis (1990) produced similar results to those found here. They identified two populations of trees which they suggested represent two geographical locations, with Population A having grown in a cool climate, probably in highland areas, and Population B having grown under a warmer climate, possibly at lower altitudes near the basin shoreline. The samples herein appear to fall between the two. Comparison to the modern equivalents show that the presence of only *Podocarpus* type conifers also presents problems because modern *Podocarpus* can grow in a variety of environments. These environments include warm-temperate forests in small mountainous areas similar to those of the Drakensburg mountains of Africa (Chapter 2, section 2.6.3) but they also grow in the northern Patagonian cool temperate rain forests where they are tolerant of shade and can grow in thin poorly drained soils with frequent disturbance (Heusser, 1974; Veblen, 1982; Armesto *et al.*, 1995). However, the presence of ice-rafted boulders suggested by Frakes and Francis (1988, 1990) indicates the presence of seasonal ice formed on rivers draining into the Eromanga Basin. Therefore this suggests that the mid-Cretaceous forests probably grew under a cool temperate climate. This is supported by the reinterpretations of fossil and sedimentary evidence discussed by Frakes and Francis (1988) which suggests that the climate was a humid, cool temperate type with marked seasons, including short periods of winter freezing.

Taken as a whole the growth rings in the fossil wood from James Ross Island appear to suggest that the trees were growing under relatively uniform seasons (Section 5.5.2). However several genera may have suffered from a small amount of water stress during the summer period. When compared to Falcon-Lang's (2005b) modern data (Figure 5.3) the mean sensitivity data collected here shows a wide range of values (Table 5.7) suggesting that the climate of James Ross Island may have been cold to cool dry. However the forest composition dominated by *Podocarpus* and araucarian trees similar in composition to the warm temperate rainforests of New Zealand, Chile and north-east Australia which would not indicate a cold or cool dry interpretation but compares well to the findings from growth rings of relatively uniform width (Moore, 1982; Howe, 2003). The araucarian forests could also have occupied the exposed higher mountainous areas >1000m with *Podocarpus* and Cupressaceae (*Fitzroya*) appearing on the lower slopes between 400-900m, similar to the modern frequently disturbed forests in the northern rain forests of Chile that suggest cool temperate conditions rather than warm temperate (Heusser, 1974; Veblen, 1982; Armesto *et al.*, 1995; Hildebrand-Vogel, 2002).

This seems to match the growth ring data quite well as it also indicates there may have been a variety of microenvironments represented and it is only possible to say that the Cretaceous forests probably grew under temperate conditions. The large ranges of mean sensitivity values (0.12 to 0.58) appear to be a true reflection of values as there is no significant change in value when potentially anomalous species are removed and this may suggest that these forests had a greater similarity to the northern Chilean rainforests.

The evidence from growth rings on Alexander Island shows that the trees were probably growing in an equable environment with some water stress exerted in the summer (Section 5.5.3). This is also supported by the previous findings of Howe (2003) and Jefferson (1982) who suggest that there were well-drained mollisols that were rich and fertile in a climate that was warm temperate to semi-arid with seasonal precipitation, intermittent wet phases and long growing seasons that allowed rapid growth on Alexander Island during the mid-Cretaceous. Relatively high values of mean sensitivity may support this suggesting that the area may have been semi-arid. Very few of the samples from Alexander Island were identified due to poor preservation. However *Podocarpoxylon* and *Taxodioxylon* were present, suggesting from comparison to their modern counterparts, that the climate was probably warm temperate, supporting all of the previous fossil interpretations.

5.7. Palaeoclimate model outputs

In Chapter 1 (Section 1.4) it was suggest that the mid-Cretaceous may have been the warmest period of the Mesozoic and therefore an important example of a warm greenhouse period (Stanley, 1993; Herman, 1994; Dingle and Lavelle, 1998; Francis and Poole, 2002). It is therefore important for us to produce the most accurate models of this period if we wish to use it as a comparative or predictive tool in assessing the impact of future global warming. A great deal of work has been carried out on computer climate simulations for the Cretaceous, including assessment of the impacts of: continental configuration (Barron and Washington, 1982, 1984; Gerard and Dols, 1990; Hay *et al.*, 1990; Barron *et al.*, 1992), elevated CO_2 (Gerard and Dols, 1990; Barron *et al.*, 1992; Crowley, 1993) and ocean heat transport (Barron *et al.*, 1992, 1993; Crowley, 1993) (see also Chapter 1, Section 1.4.2). However these models did not produce high enough temperatures at the high-latitudes to match the proxy data (Barron and Washington, 1982, 1984; Barron *et al.*,1992, 1993; Valdes *et al.*, 1996).

In this section the environmental and climatic data collected during this research are compared to simulations of Cretaceous climate from computer model studies in order to assess whether the latest models can produce conditions comparable to the proxy data.

The MATs (Mean Annual Temperatures) for the mid-Cretaceous high latitude regions were estimated from NLR analysis of fossil conifers (this study) and from previous estimates from other proxy data including animal remains, leaf margin analysis and sedimentology (Table 5.12, Chapter 1, Section 1.4.1).

Table 5.12. Table showing the estimated MATs for the high latitude mid-Cretaceous locations summarized from data in Chapter 1, Tables 1.4 and 1.5.

Location	Estimated MAT (°C)
Svalbard	10
Canadian Arctic	11.5
Australia	16
Antarctica	19.5

Recent Cretaceous model simulations of Price *et al.* (1998) which were highly prescribed, inputting data such as values for sea surface temperature rather than allowing the model to be interactive, were used as a comparison to the proxy data. They ran two simulations representing "greenhouse" and "icehouse" palaeoclimates in the mid-Cretaceous, in order to compare differences in the processes linked to climate. These simulations were carried out using the UGAMP (UK Universities Global Atmospheric Modelling Project) General Circulation Model at a horizontal resolution of approximately 4° x 4° (Valdes *et al.*, 1996). In both simulations CO_2 was set at x4 present levels and the model used Late Albian/Early Cenomanian boundary conditions, incorporating mountains, surface roughness, albedo and the coastlines of Smith *et al.* (1994). In the "greenhouse" simulation the sea surface temperatures were fixed to range from 28°C in the tropics to 0°C at the poles and in the "icehouse" simulation equatorial temperatures of 24°C and polar temperatures -6°C were used (Sellwood *et al.*, 1994; Price *et al.*, 1998). No vegetation was included in these models. Figure 5.10 below shows the outputs of these models with the proxy data estimates from Table 5.12 added to them.

It can be seen from Figure 5.10 that in the Price *et al.* (1998) models both "greenhouse" and "icehouse" simulations produce temperatures at high latitudes that are between 4 and 13.5°C lower than the proxy data estimates (Table 5.13). Both simulations produce temperatures below freezing in North America, Alaska, Siberia, continental Antarctica and Greenland. It is suggested that differences between the "icehouse" and "greenhouse" results may be due to the lower sea surface temperatures in the "icehouse" simulation, that produced less atmospheric water vapour (a greenhouse gas) which leads to further cooling, which in turn results in more snow cover and increased albedo leading to further cooling (Price *et al.*, 1998).

Table 5.13. Table comparing the MAT estimated from proxy data with the estimates produced by the Price *et al.* (1998) "greenhouse" and "icehouse" simulations.

Location	Estimated MAT (°C) from proxy data	Estimated MAT (°C) from "greenhouse" simulation	Estimated MAT (°C) from "icehouse" simulation
Svalbard	10	8	0
Canadian Arctic	11.5	4	-2
Australia	16	12	8
Antarctica	19.5	14	10

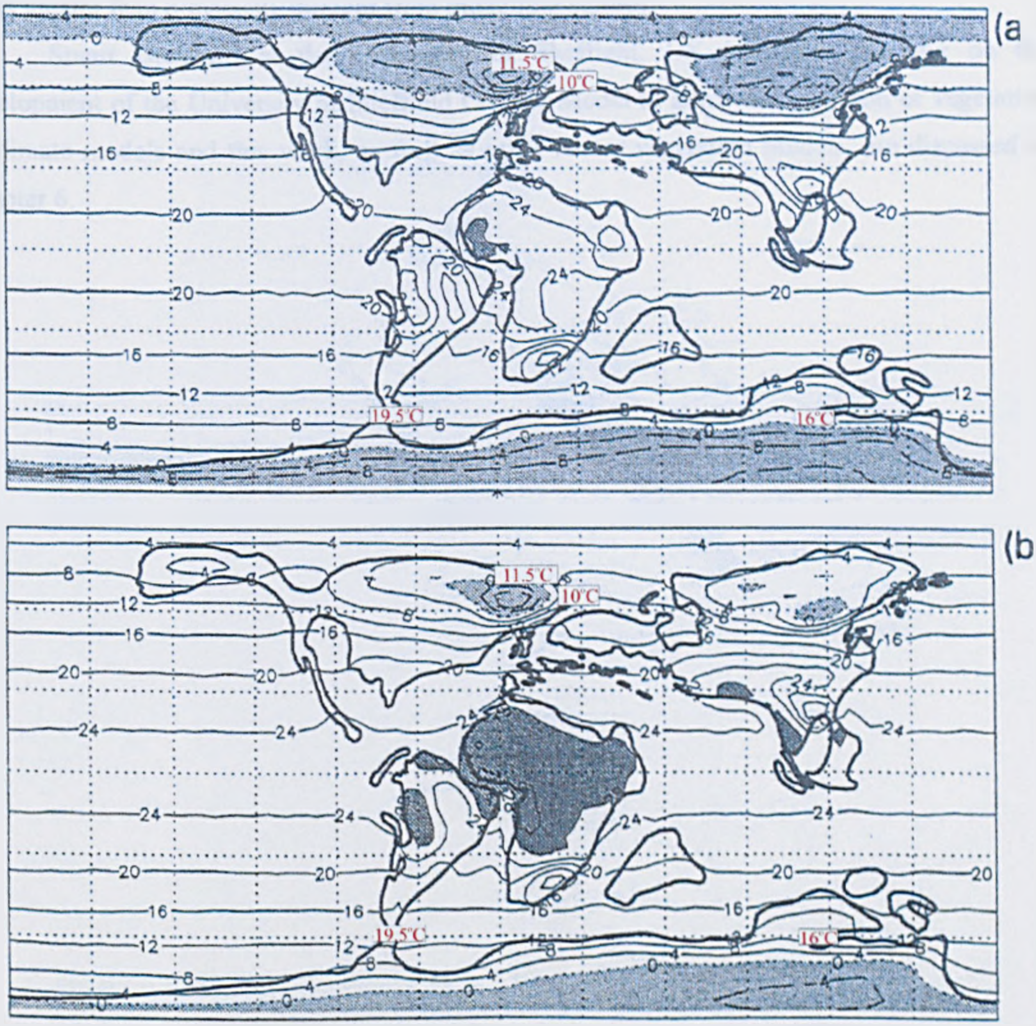


Figure 5.10. Simulated mean annual surface air temperatures. a) "Icehouse" simulation. b) "Greenhouse" simulation. Contours are in 4°C intervals, the zero contour is dotted and negative values are dashed. Light shading indicates temperatures below zero, and dark shading shows temperatures exceeding 28°C (Price *et al.*, 1998). The temperatures in red are from the proxy data in Table 5.12.

Chapter 6 Comparison of fossil wood analysis to the USCM simulations

6.1. Introduction

It was noted in the previous chapter (Section 5.7) that climate models have produced temperatures for the polar regions that are too low when compared to the fossil data. These early models did not include vegetation even though it has been shown by several authors from both computer modelling and observational studies of modern forests that vegetation could have had a huge impact on the climate through their interaction on both physical and functional levels (Price *et al.*, 1998; Upchurch *et al.*, 1998; Beringer *et al.*, 2005; see also Chapter 5, Section 5.7 and Chapter 1, Section 1.4.2).

More recent work on expanding computer climate models to include vegetation has produced some encouraging results and suggests that vegetation may have had a larger impact on climate than was previously thought (as reviewed in Chapter 1, Section 1.4.2). These new models indicate that vegetation may be key to producing climate models that more accurately reflect the proxy data in the high latitude regions whilst not overly inflating temperatures in the equatorial regions (Chapter 1, Section 1.4.2). The resolution and accuracy of the vegetation included within these models varies (Section 6.2) so it is of prime importance that vegetation models are developed to better reflect the terrestrial environment present in the past. This is not only because the presence or absence of vegetation is important in climatic interactions but also the types of vegetation are important (e.g. tundra has much higher albedo than dense forests).

Fossil evidence tells us that polar forests were an important part of past vegetation with conifers being a major component during the mid-Cretaceous (Chapter 1, Section 1.2). Therefore the aim of the main project has been to develop a new vegetation model, the University of Sheffield Conifer Model (USCM), which has been designed to provide more realistic representations of high latitude vegetation than have previously been available (Section 6.2). The model was designed at the Department of Animal and Plant Sciences at the University of Sheffield, UK by a team led by David Beerling with specialist input and development of a new soil module carried out by Stuart Brentnall (Brentnall *et al.*, 2005). The research described within this thesis was carried out as part of this main project in order to provide proxy data to test the model and verify the results it produced (Section 6.3).

The USCM will ultimately be coupled to global climate models to determine the effect of polar vegetation on regional and global climates.

6.2. University of Sheffield Conifer Model (USCM)

Early vegetation models had one fixed vegetation type as a global default (Barron *et al.*, 1992) or a best-guess distribution based on reference points from proxy data that did not provide a realistic representation of the terrestrial ecosystems (see Chapter 5, Otto-Bliesner and Upchurch, 1997; Upchurch *et al.*, 1998). Later, more complex vegetation models, such as the dynamic predictive models EVE (Equilibrium Vegetation Ecology) and TRIFFID (Top-down Representation of Interactive Foliage and Flora Including Dynamics), are more realistic and describe the physical characteristics of vegetation as a function of climate and ecological principles based on competition for light and succession after disturbance (Deconto *et al.*, 2000a; 2000b; Bergengren *et al.*, 2001). Although EVE's sub model LEAF has the capability to simulate leaf phenology and provides three basic leaf habit categories (evergreen, drought deciduous, winter deciduous) these are not realistic because this model is unable to simulate the range of LLSs produced by evergreen species. Therefore EVE overestimates the contribution of the evergreens to other canopy properties e.g. leaf area index. The LEAF model also does not include physiological processes such as photosynthesis and respiration, explicit water cycles or effects of soil heterogeneity, which are particularly important factors in high latitude areas.

Unlike EVE, TRIFFID includes photosynthesis, respiration, water fluxes and soil state (Cox, 2001). Leaf death varies in TRIFFID with temperature (with leaf turnover increasing when the temperature drops) but is not able to produce realistic phenology. TRIFFID is more appropriate for present and future modelling as it includes C_4 grasses which it is believed did not evolve until the Oligocene (personal communication C. Osborne; Pagani *et al.*, 2005). Although these dynamic models considerably improve the representation of vegetation within climate models they still have limitations, in particular, for the prediction of realistic LLSs. It is hoped that the University of Sheffield Conifer Model (USCM) will rectify these problems.

The USCM was therefore developed in order to produce a realistic vegetation model of these high latitude forests to investigate the controls on the distribution of evergreen and deciduous conifer forests in both hemispheres and their feedback on polar and global climates. The USCM uses a process-based approach to simulating conifer forest carbon, nitrogen and water fluxes by scaling up widely applicable relationships between LLS and function (Beerling and Osborne, 2002; Brentnall *et al.*, 2005). Leaf life-span is emphasized in the model because it can be determined from the anatomical characteristics of fossil conifer wood, providing a proxy for model outputs and also because it influences a range of ecosystem processes (see Chapter 1, Section 1.2.2 and 1.4.2, Chapters 3, 4 and Chapter 5, Section 5.7).

The USCM includes conifer growth, soil biogeochemistry and forest dynamics, including the contribution of conifer leaves to soils that affects soil nutrient status (the quantity of leaves available to contribute to the soils each year are affected by the deciduous or evergreen habit of the trees). Using climatic and soil parameters the model predicts the structural and functional characteristics of polar coniferous forests, in effect growing the forest itself (Beerling and Osborne, 2002; Brentnall *et al.*, 2005). The version of the model used here has been expanded and developed from Osborne and Beerling's (2000) vegetation module, which is a process-based model for conifer forest productivity (Figure 6.1.). The model now also includes a new soil nutrient cycling module based on Parton *et al.*'s (1993) Century soil biogeochemistry model of carbon and nitrogen dynamics (Brentnall *et al.*, 2005). This module is fed carbon and nitrogen in ratios calculated within the vegetation module (derived from the production of surface and root litter) and it feeds back soil nitrogen and water into the vegetation module (Parton *et al.*, 1993) (Figure 6.1).

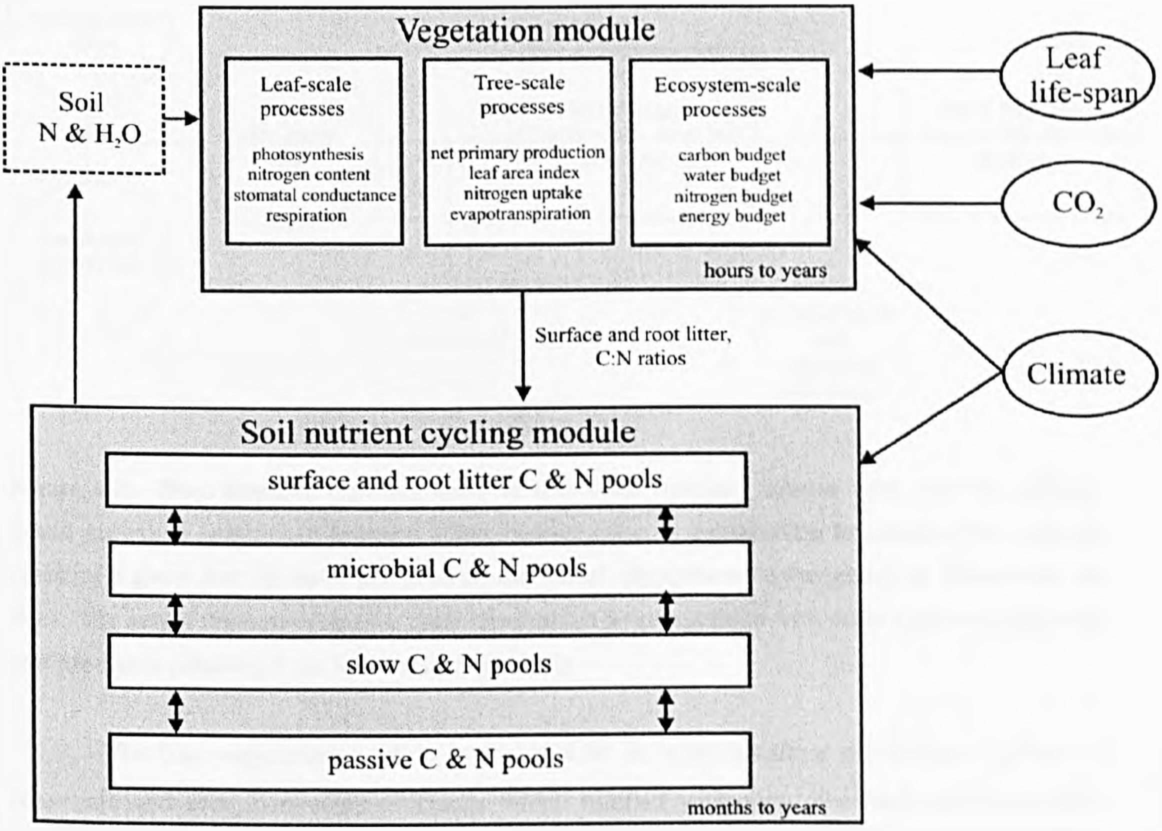


Figure 6.1. Schematic diagram showing key forest processes from leaf to regional scale simulated in the USCM (Brentnall *et al.*, 2005).

The CO_2 level is a prescribed boundary condition within the vegetation module (Figure 6.1). Monthly temperature, relative humidity and precipitation required by the model were produced by the Hadley Centre general circulation model (GCM) which is coupled to both vegetation and soil nutrient cycling modules (Figure 6.1). The USCM was run several times for 9 different prescribed LLSs separately (4, 6, 9, 12, 18, 24, 48, 72 and 96 months; see also Figure 6.1). This was carried out in order to determine the potential vegetated fraction of a grid-cell for a given leaf life-span under the conditions calculated within that grid-cell (Figure 6.2). The

LLSs were then combined within a forest dynamics scheme which allows the LLSs to compete and produce estimates of the actual percentages of trees with each LLS in any land surface grid-square (Figure 6.2). These simulations were carried out using both modern and Aptian climatologies. The modern climatology simulations were carried out in order to test the accuracy of the annual leaf area index and net primary productivity within the model (Brentnall *et al.*, 2005). These tests produced reasonable values in agreement with observations (Brentnall *et al.*, 2005).

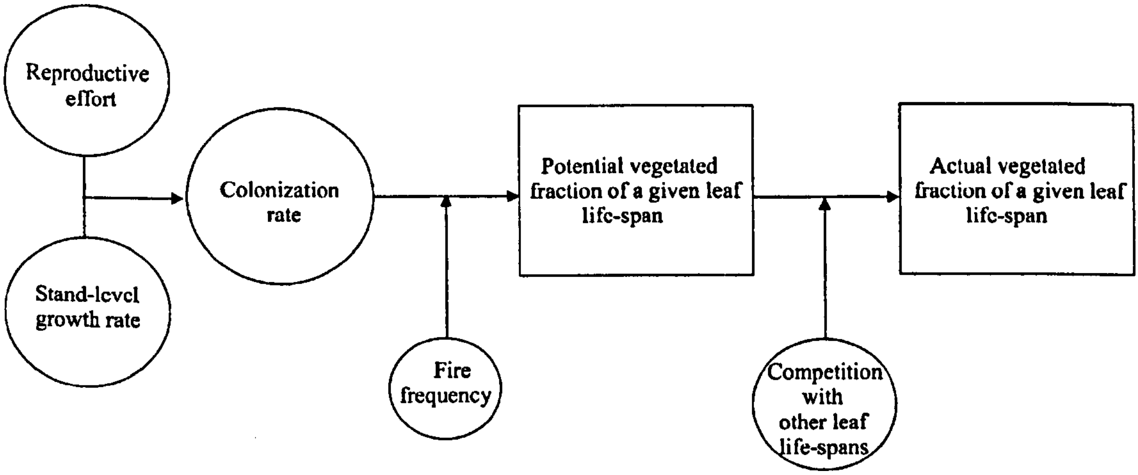


Figure 6.2. Diagrammatic representation of the forest dynamic scheme used with the USCM. Stand growth is partitioned between either reproduction or colonization to produce the potential cover of a given leaf life-span per pixel in the model (dependent on frequency of disturbance by fire). The actual vegetation cover is then determined by competition with other trees with different leaf life-spans (adapted from Brentnall *et al.*, 2005).

The base vegetation module in the USCM incorporates three sub-models: leaf-scale, tree-scale and ecosystem-scale processes which interact with each other and with prescribed mid-Cretaceous continental configuration, CO_2 levels, climate and LLSs to produce unique conditions within each land-surface grid-square in the model. This allows the growth of the conifer forest with the most suitable LLS to survive under those conditions. The interactions between the different components of the vegetation model are extremely complex therefore only a brief outline of the processes involved are described here for clarity.

Forest carbon, nitrogen and water fluxes are mathematically described and are sensitive to LLSs e.g. evergreen trees have greater annual net carbon gain and store more nitrogen in their leaves than deciduous trees (Gower and Richards, 1990; Warren and Adams, 2004). The model includes environmental effects on photosynthesis, respiration and stomatal activity within the leaf-scale sub-model for the calculated forest energy budget within the ecosystem-scale processes sub-model. Evapotranspiration (the process by which water is transferred from the land to the atmosphere by evaporation from the soil and other surfaces and by transpiration from plants) and photosynthesis are interdependent, linked between the leaf- and tree-scale process sub-models. Evapotranspiration is included to account for stomatal responses to soil water, atmospheric humidity and CO_2 (Brentnall *et al.*, 2005). The LLS directly influences the nitrogen content of the leaf tissues (leaf-scale processes sub-model) and the leaf mass:area ratios because trees with longer LLSs tend to have a larger amount of leaves (tree-scale processes sub-model). These factors in turn determine the tree's capacity for photosynthesis, respiration and stomatal conductance (Brentnall *et al.*, 2005). Nitrogen uptake (tree-scale processes) is dependent on the root mass, temperature and soil nitrogen content, linking the prescribed climate, to the soil nutrient cycling and the vegetation modules (Woodward *et al.*, 1995). Soil carbon content is also accounted for because this affects the ability of the trees to extract organic nitrogen from the soil (Woodward and Smith, 1994). Leaf Area Index (LAI) is a key to determining energy, water and carbon fluxes in this model and is calculated after the limitations of growth by water availability, nitrogen content and light have been accounted for.

Beerling and Osborne (2002) carried out experiments on extant species of conifers grown in environmentally controlled chambers in order to add further information on key aspects of physiology effects from light and CO_2 to the base model described above. Conifers believed to be related to those found in the mid-Cretaceous were used, including *Metasequoia glyptostroboides*, *Araucaria araucana*, *Taxodium distichum* and *Sequoia sempervirens*. This provided new insights about photosynthesis, photoinhibition and respiration effects of conifers growing in high latitude situations under greenhouse climates. The data collected allowed these key processes to be mathematically reproduced and included within the model.

The soil nutrient cycling module incorporated in the USCM has been developed by Brentnall *et al.* (2005) and contains eight soil, carbon and nitrogen pools representing different decomposition rates (two surface litter, two sub-surface litter (especially from roots), surface and soil microbial (active) pools and slow and passive soil organic matter pools). Decomposition rates and carbon fluxes between pools are a function of soil moisture, temperature and nitrogen fluxes. C:N ratios are controlled by the size of other pools and available mineral nitrogen. Soil carbon and nitrogen dynamics are produced by non-linear differential equations with parameters dependent on soil texture, temperature, precipitation, humidity, soil moisture, water flow, potential evaporation, litter quality and quantity and are solved on a monthly time-step (Brentnall *et al.*, 2005).

The USCM was forced with a mid-Cretaceous (Aptian) climate simulation produced by the Hadley Centre Atmospheric GCM (HadAM3). This model has a spatial resolution of 3.75°longitude x 2.5°latitude, 19 vertical levels and includes prescribed zonally symmetric sea-surface temperatures of 30cos(lat)°C. Atmospheric CO_2 levels were set at 1300ppm. The integration was run for 14 model years and the Aptian climate taken as an average of the last 10 years.

To obtain global biome maps suitable for comparison with the fossil dataset, the outputs of competition between the LLSs produced in the forest dynamics scheme (Figure 6.2) were used to produce dominant leaf habit (biome) maps to show "deciduous" (LLSs <12 months), "evergreen" (LLSs>12 months) or mixed (evergreen and deciduous) forests (Figures 6.3 and 6.4). Dominant leaf life-span maps were also produced that present estimates of the percentages of each LLS (between 4 and 96 months) present in any land surface grid-square (Figures 6.3 and 6.4).

Simulated structural and functional characteristics of the trees drive the forest dynamics scheme. The simulated characteristics include:-

- Tree height. Height is inversely proportional to the square root of evaporative demand. Stomatal conductance, and thus evaporative demand, decreases with increasing LLS, hence trees with longer-lived leaves tend to be taller.
- Wood production. The model allows trees to grow to their full height if undisturbed by fire or competition.
- Time since last disturbance. The rate of colonization by trees of each LLS is limited by intra and interspecific competition, including a term representing mortality due to fire, based on temperature and precipitation. Deciduous trees tend to act as pioneer species therefore terms are also included in which some of the production in deciduous trees with low Leaf Area Index (LAI) is diverted towards colonization and the larger the LAI (for a given LLS) the larger fraction of production goes towards colonization.
- Interspecific competition. Parallel simulations for trees with a range of LLSs are performed in order to produce a monoculture forest with a given LLS growing within each gridbox. Terms are also included for competition for light.
- Trees unable to grow (or reproduce) at a site due to the climate are excluded.

6.3. Comparison of the fossil data with outputs from the University of Sheffield Conifer Model

This section compares leaf habit of the fossil conifers, as derived in Chapter 4 of this thesis, with the outputs of the University of Sheffield Conifer Model to establish whether the model can replicate the results from fossil wood. This will give some indication of the accuracy and applicability of the model for northern and southern hemispheres during the mid-Cretaceous.

Figures 6.3 and 6.4 show the USCM outputs for predicted leaf habit and leaf life-span.

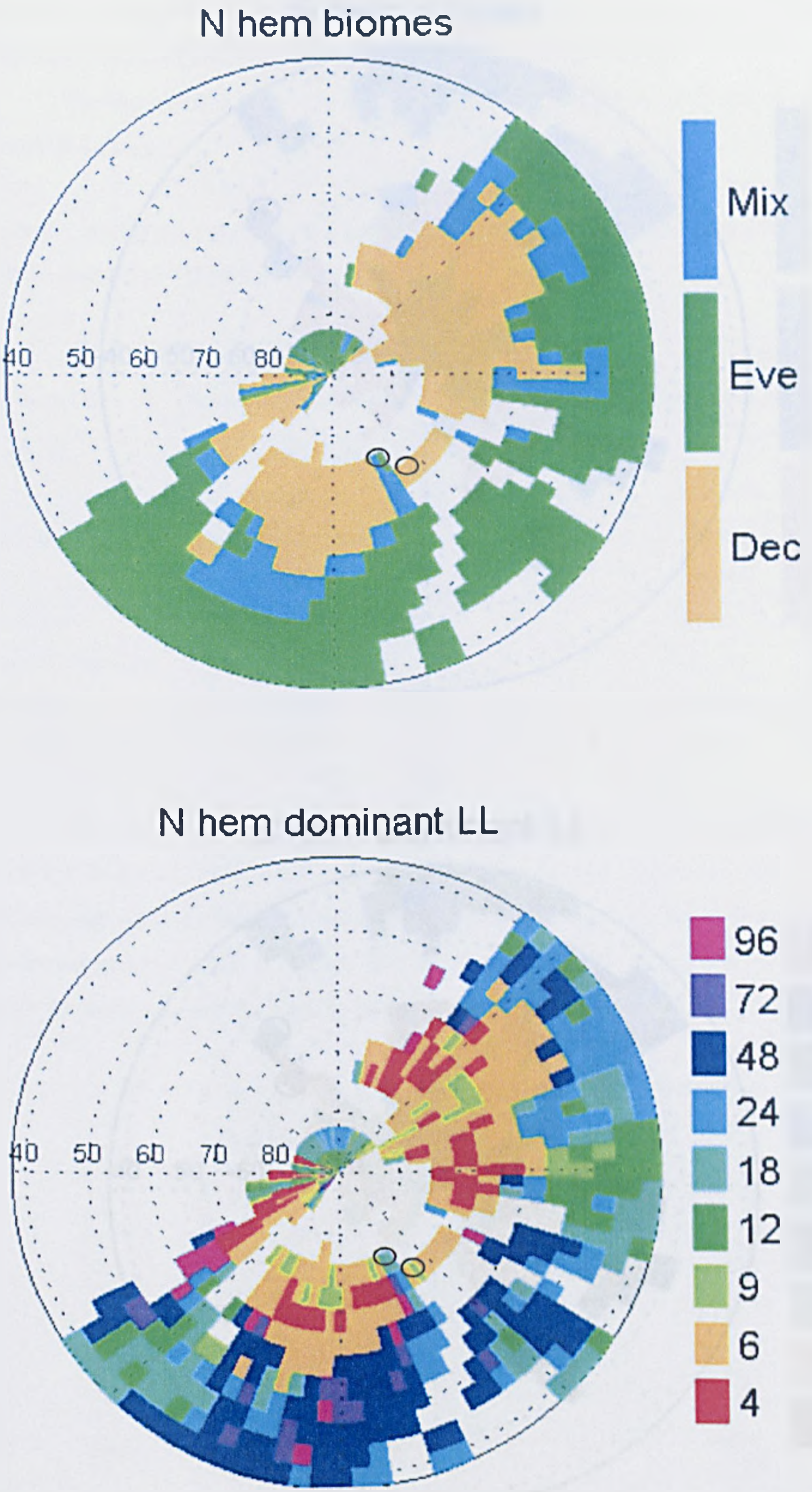


Figure 6.3. Northern Hemisphere Cretaceous outputs from USCM. Top diagram shows predicted biome types. Bottom diagram shows predicted leaf life-spans (in months). Locations from which fossil wood was derived are circled.

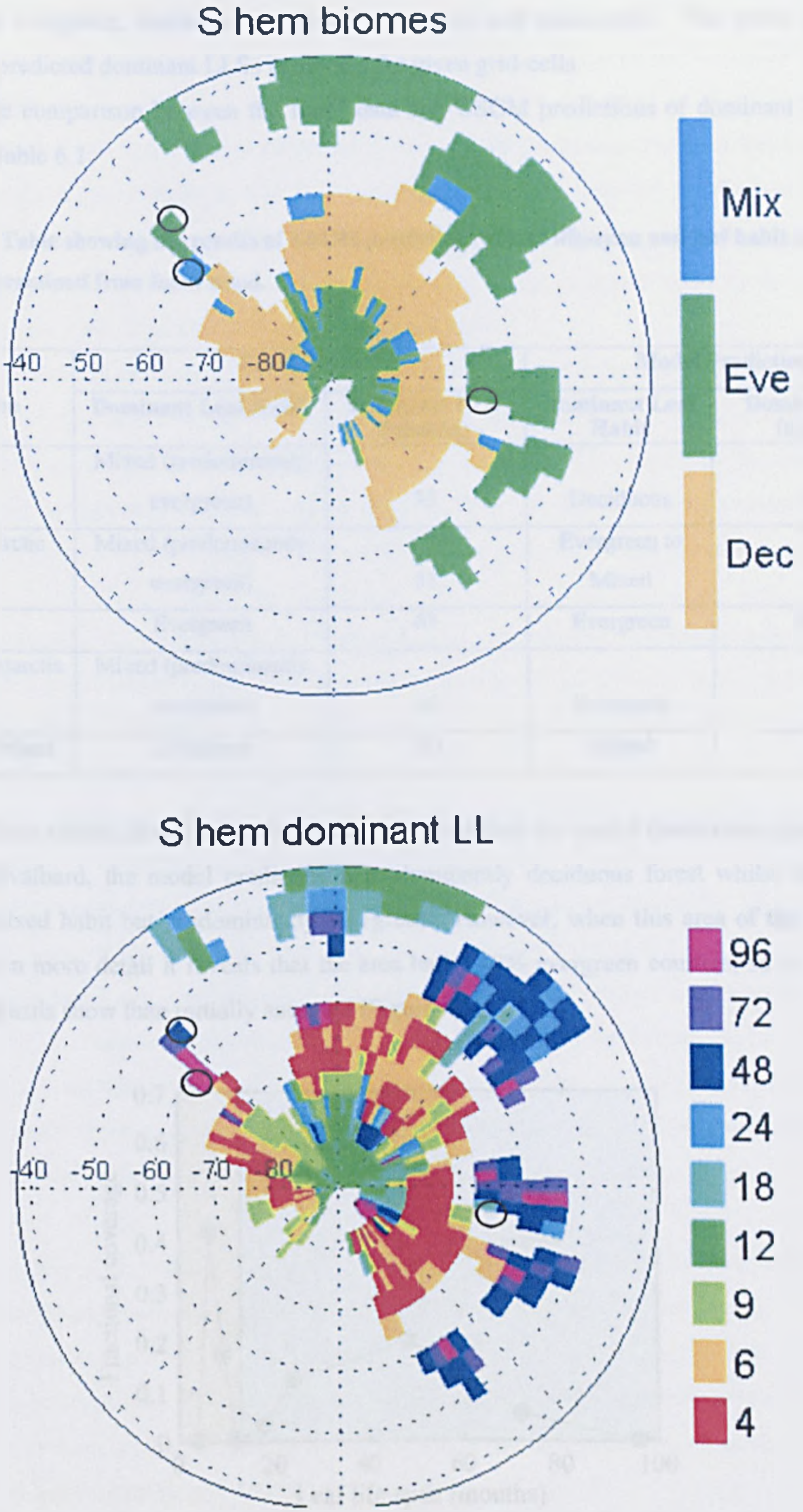


Figure 6.4. Southern Hemisphere Cretaceous outputs from USCM. Top diagram shows predicted biome types. Bottom diagram shows predicted leaf life-spans (in months). Locations from which fossil wood was derived are circled.

In both figures the upper diagram shows the predicted dominant leaf habit as dominantly evergreen, deciduous or mixed (evergreen and deciduous). The lower diagram shows the predicted dominant LLSs in months for given grid-cells.

The comparison between the fossil data and USCM predictions of dominant LLS are shown in Table 6.1.

Table 6.1. Table showing the results of USCM predictions of leaf life-span and leaf habit compared to those determined from fossil wood.

Location	Fossil Wood		Model Predictions	
	Dominant Leaf Habit	**Dominant LLS (months)**	**Dominant Leaf Habit**	**Dominant LLS (months)**
Svalbard	Mixed (predominantly evergreen)	33	Deciduous	6-9
Canadian Arctic	Mixed (predominantly evergreen)	33	Evergreen to Mixed	18
Australia	Evergreen	63	Evergreen	24-48
East of Antarctic Peninsula	Mixed (predominantly evergreen)	48	Evergreen	48
Alexander Island	Evergreen	151	Mixed	96

These results show that in the Northern Hemisphere the model predictions appear to be poor for Svalbard, the model predicting a predominantly deciduous forest whilst the fossils indicate mixed habit but predominantly evergreen. However, when this area of the model is examined in more detail it reveals that the area has ~ 40% evergreen conifers, so is nearer to what the fossils show than initially assumed (Figure 6.5).

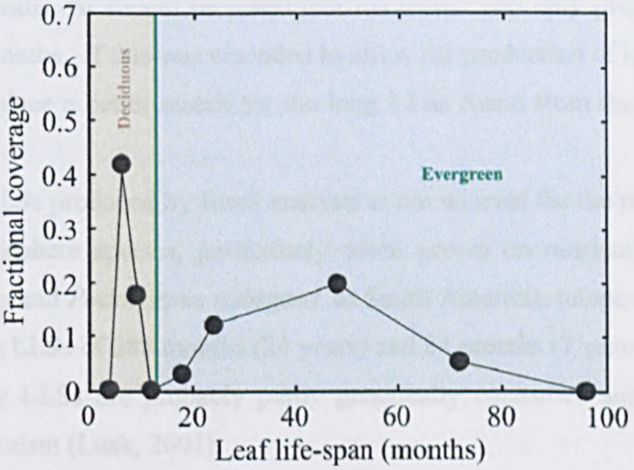


Figure 6.5. Graph showing modelled dominance of trees with different leaf life-spans in the Cretaceous polar conifer forests of Svalbard (redrawn from Brentnall *et al.*, 2005).

The higher proportion of deciduousness in the model for Svalbard may be due to the predicted fire return interval of 80 years not being long enough to allow the slower growing evergreen trees to become established. The dominant LLSs predicted by the model for this area of 6-9 months appear too short because the fossils give a dominant LLS of 33 months. However, again when examined in more detail the USCM produces a bimodal distribution of LLSs for Svalbard, with peaks at 6 and 48 months (Figure 6.5). For the fossil wood the LLS estimates fell into two distinct groups, with either less than (n = 2) or greater than (n = 10) 18 months LLS, producing mean LLSs of 5 and 56 months, which compares more favourably with the model results (see Appendix B for full fossil data set).

The model predictions are slightly better for the Canadian Arctic regarding dominant leaf habit as it predicts that there would have been some areas that were predominantly deciduous and some predominantly evergreen (Figure 6.3). This matches the mixed, but predominantly evergreen, habit shown by the fossils. However the modelled dominant leaf life-span of 18 months is short compared to the proxy data because the fossils indicate that it was 33 months.

In Australia the model predicts predominantly evergreen conifers, in agreement with the fossils (Figure 6.4). However the USCM predicted dominant leaf life-span is too short at 24 to 48 months compared with the proxy of 63 months.

On James Ross Island to the east of the Antarctic Peninsula the model predicts a predominantly evergreen forest. Although the fossils show that these areas had mixed evergreen and deciduous types, evergreens were dominant. Therefore this is a reasonable match. Both the model and the fossils produced a dominant LLS of 48 months. On Alexander Island to the west of the Antarctic Peninsula the model predicts a mixed leaf habit whilst the fossils suggest that it was predominantly evergreen. The model predicts a dominant leaf habit of 96 months for this area whilst the fossil woods produced the longest dominant LLS of all of the sites at 151 months. It should be noted that the model was only programmed to produce LLSs of up to 96 months. If this was extended to allow the production of longer LLS the model may be able to produce a better match for the long LLSs found from the wood on Alexander Island.

The long LLSs produced by fossil analysis is not unusual for the modern equivalents of the Southern Hemisphere species, particularly when grown on nutrient-poor soil. Modern *Araucaria araucana* and *Podocarpus nubigena* in South American temperate forests have been found to have mean LLSs of 288 months (24 years) and 84 months (7 years) respectively (Lusk, 2001). These long LLSs are probably partly genetically controlled and partially a nutrient conservation mechanism (Lusk, 2001).

The USCM predicts that in both hemispheres there are distinct zones of dominant leaf habit (Figures 6.3 and 6.4). At the highest latitudes (above ~80°) the forests during the mid-Cretaceous would have been entirely evergreen although with short LLSs (~12-18 months). A band of deciduousness is predicted for the region between ~80 and 60°. Evergreenness is once again dominant below 60°. In the Northern Hemisphere there appears to be a transmission zone of mixed evergreen and deciduous forest at approximately 60° but this is not present in the Southern Hemisphere (Figures 6.3 and 6.4).

It was initially thought that distributions of evergreen and deciduousness may have been caused by the climatology used in the model being too cool for the polar regions, therefore sensitivity studies were carried out using various climatologies that were either physics- or palaeontology-based.

In all sensitivity studies it seemed that deciduous trees just could not grow at very high latitudes because they were restricted by the conditions of growth whereas evergreens could. This may be for several reasons such as there not being enough nutrients to make it economical for the trees to replace their canopy every year therefore favouring the more nutrient efficient evergreens or there may have been very little disturbance allowing the evergreens to become established, overtopping and out-competing deciduous conifers for light.

The reasons for the pattern produced below 80° seem to vary from place to place due to the microenvironments produced within the grid-squares favouring one leaf life-span over another. When a warmer climate was used (as suggested by some fossil-based reconstructions) the leaf habit in the model depended on the result of two competing forces: the ability of the trees to colonise land and the ability to grow taller. Trees with shorter LLSs put most of their energy into growth rather than leaf production on soils that are rich in nutrients compared to evergreens which construct thick, strong, long-lasting leaves. But in areas of frequent disturbance deciduous trees put most of their effort into reproduction and are therefore better able to reproduce and grow quickly to colonize areas that are affected by small scale, frequent disturbances. The model includes disturbance as a fire return interval which produces more frequent forest fires in drier climates. A good modern analog to this is Siberia where frequent fires have created forests dominated by deciduous larch (personal communication S. Brentnall, University of Sheffield).

However, trees with long LLSs are able to grow taller on nutrient-poor soil, therefore if the disturbance interval is long enough for them to get well established they will survive and overtop trees with shorter LLSs and out-compete with them for light (Brentnall *et al.*, 2005). A good modern analogue for this is Patagonia where Monkey Puzzle and podocarp conifers with long LLSs are dominant in areas of massive but infrequent disturbance, mainly by volcanic activity or landslides (Armesto *et al.*, 1995).

In the lower latitudes (below 60°) the model predicts areas with particularly long LLSs (48-96 months) such as the Antarctic Peninsula, Australia and Greenland. This may be because these coastal regions were mild enough, under the influence of the maritime climate, for trees with long LLSs to grow well and damp enough for the fire return interval to be long, allowing evergreens to dominate. However there is also a large part of the Northern Hemisphere in what is now Canada and North America which also has very long LLSs. This area is clearly continental therefore cannot have been influenced by a maritime climate and other reasons must have been responsible for these long LLSs such as a long fire return interval.

Overall it is felt that, following minor improvements, the USCM will provide an accurate interactive representation of the vegetation present in the high latitude regions during the Cretaceous. It is hoped that when the USCM is fully coupled to global climate models it will resolve the detailed distribution of high latitude conifer forests and allow investigation of underlying climatic and biogeochemical controls on the biogeography of the forests, as well as the influence on regional and global climate. It is hoped that the inclusion of the USCM in global climate models will provide more realistic simulations of high latitude palaeoclimates, without the seasonal extremes of climate that are predicted by models at present.

Chapter 7 Discussion

7.1. Introduction

This research presents the first comprehensive study of the leaf habit and leaf life-spans of mid-Cretaceous conifer forests from Svalbard, the Canadian Arctic, Antarctica and Australia used to validate the new University of Sheffield Conifer Model.

In this chapter modern high latitude floral composition is compared to the fossil evidence from this and previous research in order to investigate changes in composition and diversity over time and differences between hemispheres (Section 7.2). The new method used to determine leaf habit from wood growth rings is discussed and the data from its application to modern wood analyzed in order to assess the implications for its use in fossil wood studies (Section 7.3). The evidence of the leaf habit of fossil polar conifer forests is assessed to determine if there is any advantage to being evergreen or deciduous in warm greenhouse climates (Section 7.4). The evidence from Nearest Living Relative and growth ring analyses is used to determine the palaeoenvironments present to provide information on the palaeoclimates that existed in the polar regions during the mid-Cretaceous (Section 7.5). The fossil data collected during this research is compared to the outputs of the University of Sheffield Conifer Model to assess its validity and possible impacts on palaeoclimate modelling (Section 7.6). Finally, a new painting of the reconstructed palaeoenvironment of the forests of Svalbard is presented (Section 7.7).

7.2. Composition of mid-Cretaceous high latitude forests

Modern high latitude regions constitute some of the harshest environments for life on Earth today. In the Northern Hemisphere, modern Svalbard contains only arctic tundra vegetation (Elven, 2004) comprising algae, cyanobactera, lichens, fungi, mosses and pteridophytes alongside approximately 160 species of flowering plants (angiosperms) occupying low ground as the snow cover recedes in the short summer (Harland, 1997). Dwarf birch and willow grow to 15cm in height. On Ellesmere and Axel Heiberg islands in the Canadian Arctic the climate is now so dry and cold that continuous vegetation is generally limited to sheltered valleys; well-watered margins of lakes, ponds and streams; and gentle slopes below slow-melting snow drifts (In-Cho, 1984). Few species of plants are present but, Purple Saxifrage (*Saxifraga oppositifolia*) and Arctic Willow (*Salix arctica*) are able to grow in protective prostrate mats (In-Cho, 1984 see also survival strategies in Chapter 1, Section 1.2.2). On the Dryas tundra near to the sea *Saxifraga* and *Salix* are mixed with associated herbs (*Pedicularis*, *Carex*, *Cerastium* and *Draba*) and lichens (In-Cho, 1984). Within slight depressions and among rocks Arctic heather (*Cassiope*) and Alpine Bilberry (*Vaccinium*) may also be found (In-Cho, 1984). No conifers species (gymnosperms) are present in either Svalbard or the Canadian Arctic (Harland, 1997).

In the Southern Hemisphere the mainland of Australia currently only reaches ~36°S therefore does not have a cold climate flora, except on remote southern islands.

The flora of Antarctica, like Svalbard, is currently dominated by lichens (~200 species), mosses (~85 species) and algae which are present in both inland and maritime locations (Longton, 1985). In the comparatively mild maritime areas these form substantial closed stands with widespread liverworts, macrofungi, *Deschampsia Antarctica,* a grass that forms low mats, and *Colobanthus quiltensis* which forms compact cushions up to 25cm wide. The latter two species are the only angiosperms present, occurring locally on the Antarctic Peninsula up to 68°S (Moore, 1982; Longton, 1985). Continental Antarctica however contains only sparse vegetation with mosses and lichens having been recorded on nunataks beyond 84 and 86°S respectively (Longton, 1985). As in the northern high latitudes there are no gymnosperms on Antarctica at present (Longton, 1985).

However, the discovery of fossilized wood on the Antarctic Peninsula by James Eights in 1829 (Walton and Bonner, 1985), on Australia by Charles Darwin in 1836 (Nicholas and Nicholas, 1989), on Svalbard by Oswald Heer in 1876 (Harland, 1997) and on Ellesmere Island by Otto Sverndrup's Norwegian Polar Expedition in 1901 (Kalkreuth *et al.*, 1996) indicates that the present day vegetation and climate of these regions are atypical (Chapter 1, Section 1.2). The fossil wood present in the mid-Cretaceous high latitude regions is dominated by conifers with *in situ* stumps, suggesting that they would have formed large, dense forests (Chapter 1, Section 1.2.2). This wood is therefore of immense value in providing a substantial record of the high latitude mid-Cretaceous forest composition and growth.

Fossil wood from the Northern Hemisphere (Svalbard and the Canadian Arctic) identified during this project shows that the conifer forests were composed of *Piceoxylon, Laricioxylon, Cedroxylon, Taxodioxylon, Pinuxylon, Palaepiceoxylon, Taxoxylon, Juniperoxylon, Protocedroxylon, Araucariopitys, Xenoxylon* and *Cupressinoxylon* (Chapter 2, Section 2.5). In the Southern Hemisphere (Australia and Antarctica) the forests were composed of *Podocarpoxylon, Taxodioxylon, Araucariopitys, Cupressinoxylon, Agathoxylon, Protophyllocladoxylon, Sciadopityoxylon* and *Circoporoxylon* (Chapter 2, Section 2.6). In the Canadian Arctic the dominant conifer genus was *Pinuxylon,* in Svalbard and Antarctica *Taxodioxylon* and in Australia the entire sample set was represented by *Podocarpoxylon*. Only *Araucariopitys* and *Taxodioxylon* appear in both hemispheres and the Northern Hemisphere appears to have had slightly more diverse conifer flora than the Southern Hemisphere.

The forest compositions identified during this research were compared to previous studies to ascertain if there was any supporting evidence for the presence of these tree types (Chapter 1, Section 1.2). It was found that very little work has previously been carried out on the Cretaceous floras of Svalbard and the Canadian Arctic. However Harland (1997) reported that the flora of Spitsbergen, Svalbard was dominated by *Ginkgo, Elatides, Podozamites, Pinites* and *Pseudotorellia* with rare cycadophytes during the early part of the mid-Cretaceous. Gothan (1910) described Jurassic and Tertiary conifer wood with affinities to *Dadoxylon*, *Protopiceoxylon*, *Piceoxylon*, *Xenoxylon*, *Protocedroxylon*, *Cedroxylon*, *Taxodioxylon* and *Cupressinoxylon*. This is a very similar combination of conifers to those found in this study, suggesting that these conifer genera were also present in the intervening Cretaceous period. A study by Bannan and Fry (1957) found that the Canadian Arctic (Axel Heiberg and Amund Ringnes islands) was dominated by coniferous trees during the Albian, in particular *Cedroxylon* and *Piceoxylon*, as also represented in the present study. No other conifer wood has been reported from the islands of the Canadian High Arctic of mid-Cretaceous age.

Albian to Cenomanian wood and foliage has, however, been found at slightly lower latitudes on the continental margin of the North Slope of Alaska (Spicer and Parrish, 1986; Spicer, 2003). The foliage represented *Podozamites* (possibly related to *Podocarpus* conifers), *Pityophyllum*, *Athrotaxopsis*, *Cephalotaxopsis*, *Sequoia* and *Elatocladus* with remains also being found of *Taxodium*, *Parataxodium* and *Metasequoia*, suggesting that the Taxodiaceae were dominant in terms of species numbers (Smiley, 1966; 1969; Spicer and Parrish, 1986; Francis and Frakes, 1993; Spicer *et al.*, 1994; Spicer and Herman, 2001; Spicer, 2003). Several authors have also described wood and leaves of Early Tertiary (Eocene) age from Axel Heiberg and Ellesmere islands representing *Metasequoiaoxylon*, *Glyptostroboxylon*, *Pinus*, *Larix*, *Picea* and *Cupressus* (Basinger, 1991; Francis, 1991; Greenwood, 1993; Basinger *et al.*, 1994; Greenwood and Basinger, 1994; Kumagai *et al.*, 1995; Williams *et al.*, 2003). This diverse combination of conifers is very similar to that described within this study, suggesting that these genera were already established within the forests of the Canadian Arctic during the Cretaceous. In northeastern Russia during the late Albian the Taxodiaceous conifers, including *Sequoia*, increased in dominance with *Elatocladus*, *Araucarites* and *Cephalotaxopsis* also present (Spicer and Herman, 2001; Spicer, 2003).

In all of the Albian to Cenomanian studies it was noted that the dominant conifer type was Taxodiaceous, either *Metasequoia* or *Taxodium*, suggesting that there had been some change in forest composition from evergreen dominated forests to deciduous dominated forests during the mid-Cretaceous. Angiosperms appear to have been rare in all of these sites, with first occurrences in Alaska during the late Albian and in northeastern Russia in the early-middle Albian (Spicer and Herman, 2001).

In the Northern Hemisphere there appears to have been remarkable similarity of floras right across the region, embracing the Canadian Arctic, Alaska, Franz Josef Land and north-eastern Russia (Vakhrameev, 1991; Spicer and Herman, 2001).

Previous studies of the Southern Hemisphere indicate that it was also occupied by conifer-dominated forests. In the Victoria area of Australia the forests were composed of Araucariaceae, Cheirolepidiaceae, Podocarpaceae and to a lesser extent *Ginkgoales* during the mid-Cretaceous, with a diverse understorey of ferns, lycophytes, equisetaleans and bryophytes (Douglas and Williams, 1982; Tosolini *et al.*, 2002). Although these previous studies indicate a much more diverse flora than that described in the current research, it confirms the presence of podocarps. On Antarctica the mid-Cretaceous flora is described as being composed of dominantly araucarian and podocarp conifers with rare taxodiaceous forms, supporting the findings of this study, in addition to an understorey of cycadophytes, ginkgoes and diverse ferns including *Alamatus* and *Aculea* (Cantrill, 1996; Francis, 1996; Falcon-Lang and Cantrill, 2000; Falcon-Lang and Cantrill, 2001; Howe, 2003).

As with the Northern Hemisphere, there seem to be remarkable similarity in floral composition across the whole Southern Hemisphere region. The araucarian and podocarp conifers dominant everywhere, with minor Cheirolepidiaceae and taxodiaceous types also present. Angiosperms were rare but present on Antarctica by the late Albian, especially *Nothofagus* and some magnoliids (Francis, 1986; Howe and Cantrill, 2001; Eklund, 2003).

There are no modern analogues for these Cretaceous high latitude forests. The modern tree line in the Northern Hemisphere does not extend far beyond latitude 70°N, primarily determined by wind, temperature, moisture and land availability (Figure 7.1, Krebs, 1972; Wilmking and Juday, 2005). In the Southern Hemisphere the modern treeline is at ~55°S, with vegetation being restricted to this latitude by the presence of the Southern Ocean. These modern tree-line forests have a higher proportion of angiosperms than inferred for the mid-Cretaceous when the conifers appear to have been dominant.

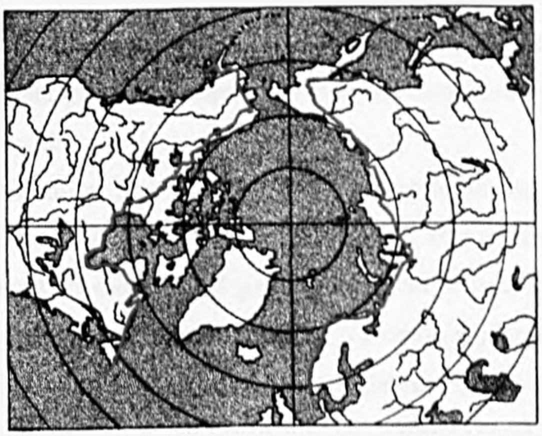


Figure 7.1. Northern Hemisphere polar limit to tree-like conifers (green line), irrespective of species. Some dwarf forms may occur beyond this limit (Krebs, 1972).

In the Northern Hemisphere the conifers that grow close to the treeline today are *Larix* (Larch) in Siberia, and *Picea* (Spruce), *Abies* (Fir) and *Pinus* (Pine) in Canada, western North America, Scandinavia and Russia (including within the Arctic Circle) (Krebs, 1972; Vidakovic, 1991). In the Southern Hemisphere the highest latitude modern forests are dominated by *Araucaria* in South America and Australia, and *Podocarpus* in Australia, New Zealand, South Africa and South America (Vidakovic, 1991). All of these modern tree-line conifers are represented in the fossil record in high latitudes (with the exception of *Abies* which is absent in the current research), indicating that during the Cretaceous these trees were not restricted to lower latitudes by temperature, wind or moisture availability.

The presence of the same fossil genera of araucarian and podocarp conifers across the whole of the Southern Hemisphere seems to suggest that the continents were not entirely separated by the Southern Ocean during the mid-Cretaceous (see palaeogeographic map Chapter 1, Section 1.2.1; Smith *et al.*, 1994; Markwick *et al.*, 2000; Scotese, 2004). Antarctica, Australia and New Zealand may still have been joined together supporting the interpreted palaeogeography or may have only recently separated at that time allowing the dispersal of seeds and pollen between them. The same may also be true of the Northern Hemisphere high latitude region with a possible land route being present across the Bering Land Bridge that created a link between Alaska and Russia during the mid-Cretaceous (see palaeographic map Chapter 1, Section 1.2.1). However, the conifers of Svalbard appear to have been more diverse and did not contain *Pinuxylon* which was dominant in the Canadian Arctic, suggesting that Svalbard may have been separated from the Northern Hemisphere landmass some time previous to the mid-Cretaceous. This is supported by the Harland's (1997) suggestion that the Canadian Basin has already opened up by the mid-Cretaceous.

7.3. Leaf habit of extant conifers

The LLS and seasonal timing of leaf abscission within conifers is closely related to climate (Schoettle, 1994; Reich *et al.*, 1995; Falcon-Lang and Cantrill, 2001a). The LLS of high latitude conifer forests is therefore an important feature in investigations of the palaeoclimate that has not previously been explored but may yield valuable information for inclusion in climate models.

In 2000(a) Falcon-Lang devised the Ring Markedness Index (RMI) calculation in order to establish the factors influencing growth ring style, that is, whether it is purely related to environmental factors in the area of growth or if there is a genetic element to their formation. This innovative method also provided a means of quantitatively determining the trees' LLS from the structure of the wood, therefore eliminating the need to rely on leaf trace and nearest living relative analysis, both of which are problematical (see Chapter 3, Sections 3.2.1 and 3.2.2). However, there were several problems with Falcon-Lang's initial work. He used a very small sample set of conifers, all of which were derived from cultivated sites, and employed methods of data collection that made the research unrepeatable and added substantial errors to the results (see Chapter 3, Section 3.3.4). Falcon-Lang's (2000a) method of determining leaf life-span using Ring Markedness Index was therefore developed further here in order to make it repeatable, reduce errors and produce less variable, therefore more reliable, results (Chapter 3, Section 3.3.4.1).

A much larger dataset of extant conifer wood was examined during this research than has previously been used, in total thirty six specimens representing twenty eight species of conifer were included. This database was generated to include more species of extant conifers with a wide range of known LLSs and including wood from branches and trunks, damaged wood, a high latitude tree, and trees from cultivation as well as natural stand settings (Chapter 3, Section 3.4). This was undertaken in order to produce a comprehensive database that could be used in the derivation of the leaf life-spans of fossil wood.

It was found that deciduous species produced high values of RMI (>40) whilst evergreen species produced low values (<40). Although these results were obtained from a much larger dataset than that used by Falcon-Lang (2000a) in his initial trial and a modified method was applied (Chapter 3, Section 3.3.4), these results are similar to his original findings. Therefore this study confirms that the principal of ring markedness holds true over a larger range of conifers (Chapter 3, Section 3.3.3).

Concerns have been raised as to whether intra-tree differences in wood structure between branches and the trunk wood distort the results produced from quantitative analyses such as RMI (Chapman, 1994; Falcon-Lang, 2005a). In this research there was no significant difference found between the wood structure and values of RMI produced in branch or trunk wood or between those of damaged or undamaged wood, indicating that all types of wood produce the same underlying signal for the species in question (Chapter 3, Sections 3.4.3 and 3.4.4). Therefore, although it has been shown that there are intra-tree differences in wood structure, when ratios rather than absolute values are applied they can produce valid, reliable results that are comparable across studies (Chapman, 1994; Falcon-Lang, 2005).

The analysis of wood from a variety of altitudes and latitudes carried out during the current research produced inconclusive results, showing no trend in increasing or decreasing LLS with altitude or latitude, despite observational studies of leaf fall having shown that LLS increases with increasing altitude and latitude (Schweingruber, 1996; Oleksyn *et al.*, 2003 see also Chapter 3, Section 3.4.5). This may be due to the small sample set used here or to differences in altitude of the samples not being substantial enough to produce distinct differences in growing conditions.

One sample was analysed during this research to assess the effect of growth at high latitudes on wood structure because this has proved a controversial point with some authors who have suggested that the light regime during past greenhouse climates may have forced the conifers to be deciduous in habit (Chaney, 1947; Wolfe, 1980; Spicer and Parrish, 1986). Although modern conifers no longer grow at the extreme high latitudes as they did during the Cretaceous, they do grow under conditions of long winter darkness at up to 70° latitude in the Northern Hemisphere (Krebs, 1972) which may at least provide an indication of their reaction to the light in these areas. The conifer sample examined in the current research is from 66°N in the Komi Republic, Russia and appeared to show that percentage diminution is elevated for trees grown under these conditions. This may be due to the rapid expansion of the cells early in the summer light season and the rapid cessation of cell inflation at the end of the growing season. The same signal, of elevated Percentage Diminution, was produced by the fossil samples examined in this thesis. Therefore further investigations need to be carried out using extant conifers to verify whether this is a reaction to the unusual light regime at high latitudes alone or whether temperature also plays a part. This effect may also be an artifact of elevated CO_2 levels in the fossil wood, therefore further work should also be carried out on fossil wood from lower latitudes to determine if elevated Percentage Diminution is also seen in these samples.

Very few modern conifers have a deciduous leaf habit but these needed to be included as end members for the extant sample set used here and ultimately for use in the derivation of the fossil LLSs therefore all possibilities must be included. Three genera known to be deciduous today were obtained to include within this project: *Larix, Metasequoia* and *Taxodium. Larix* and *Metasequoia* both produced high RMI signals, confirming that they are deciduous as expected in this analysis (Chapter 3, Section 3.4.1). However *Taxodium distichum*, which is widely accepted to be a deciduous conifer species today, produced an anomalously evergreen signal in the extant wood examined for this project (Chapter 3, Section 3.4.2). It was initially thought that this was because the first sample examined was from wood of a tree growing outside of its natural range at Tapton Experimental Gardens, Sheffield, UK. Therefore further samples were obtained from Alabama and Florida in the USA, within the natural range of *Taxodium distichum* to determine if these did produced a deciduous signal (see Appendix A, Section A1.1.6). However these samples also produced anomalously evergreen results. Investigations showed that this is probably because a small proportion of the leaves are perennial with LLSs of 12 to 24 months which are often overlooked as they are unimportant in terms of horticulture and timber production (personal communication Friederike Wagner, Utrecht University). *Taxodioxylon* is thought to be the ancestral form of *Taxodium*, and *Taxodioxylon* is one of the few fossil form-genera that have been found to form a major part of the flora in mid-Cretaceous age sediments from both the northern and southern hemispheres. Therefore despite these apparently anomalous results, *T. distichum* is important to include within the modern dataset for completeness because this behaviour may not be restricted to extant forms.

The results of this analysis show that there is a strong underlying genetic signal of deciduous or evergreenness produced within the wood structure of modern conifers that is specific to each genus (supporting the findings of Falcon-Lang (2000a)). However variations in LLS observed within each genus are probably produced by variation in environmental conditions suggesting that there is also a subsidiary climatic signal (Schoettle, 1994; Reich *et al.*, 1995 and 1999; see also Chapter 3). It is suggested that where possible large datasets should be used for leaf life-span analysis in order to be able to account for the natural variations within species.

7.4. Leaf habit of polar fossil conifers

In the past researchers have thought that the polar plants, including conifers, were all deciduous (Wolfe, 1978; 1980; Axelrod, 1984; Spicer and Parrish, 1986; Parrish and Spicer, 1988; Basinger *et al.*, 1994; Spicer *et al.*, 1994; Parrish *et al.*, 1998). The hypothesis proposed was that polar plants would have been deciduous in response to the unusual light regime in a greenhouse world when the polar regions were warm. It was argued that the winter darkness would have favoured respiration over photosynthesis. So evergreenness would have not been favoured due to carbon loss from leaves (Chaney, 1947; Wolfe, 1980; Axelrod, 1984; Royer *et al.*, 2003; 2005).

This seems to be supported by the presence of thick leaf mats and leaf physiognomy that suggests a deciduous habit (Spicer and Parrish, 1986; Basinger *et al.*, 1994; Parrish *et al.*, 1998). The presence of well preserved leaves in thick mats may indicate seasonal leaf fall because if leaves fell year round they would be more likely to show a range of sizes and biological degradation and be more widely dispersed within sediment (Wolfe, 1978; Spicer and Parrish, 1986; Pigg and Taylor, 1993). However Falcon-Lang and Cantrill (2001a) have argued that leaf mats can also be the product of random sedimentary processes because *Cordaites,* known to have been evergreen, have been found in thick, well preserved leaf-mats in the Upper Carboniferous sediment of Nova Scotia therefore it is suggested that there should not be too much emphasis placed on taphonomic data.

The leaves would also suggest the presence of deciduousness because shoot droppers, such as modern *Metasequoia* and *Taxodium*, lose complete shoots and tend to have expanded bases to the petioles on their leaves, as seen in some fossil assemblages (Spicer and Parrish, 1986). The presence of these elements may, however, only indicate that there was a deciduous element to the forests, which would inevitably produce more leaves over a short period of time that would be more likely to be preserved *en masse* than the small numbers of evergreen leaves shed over a longer period. It has also been suggested that the presence of *Podozamites* leaves attached to stems of various sizes may not indicate shoot droppers, losing shoots each year, but mechanical damage to the tree with stems of various ages being broken off the parent plant (Falcon-Lang and Cantrill, 2001a). The presence of *Araucaria alexanderensis* leaves of at least two sizes (7 and 40mm long) attached to individual stems is very similar to modern *Araucaria bidwillii* and *Wollemia nobilis* and suggests evergreenness on mid-Cretaceous Alexander Island because in the modern trees this type of foliage represents at least two growing seasons-worth of growth (Falcon-Lang and Cantrill, 2001a).

The results from this project, based on physiognomic analysis of growth ring characteristics in wood, show that the conifers in the polar regions were dominantly evergreen, with only a few deciduous samples at some sites. Several of the fossil samples, particularly in the Southern Hemisphere, also appear to have had very long LLSs (Chapter 4). Therefore this indicates that deciduousness was not likely to have been a response to high latitude light regimes.

Given the lack of comparable modern high latitude forests to test the hypothesis that deciduousness was not necessary for growth in high latitude light regimes, greenhouse experiments have been carried out in order to determine past polar leaf habits. Beerling and Osborne (2002) suggested that high concentrations of atmospheric CO_2 during the mid-Cretaceous made it more efficient (in terms of carbon gain) for conifers to be evergreen and respire during the mild dark polar winters rather than be deciduous and lose their leaves. Experiments were carried out by Royer *et al.* (2003) using genera that have close taxonomic affinity to some fossil genera, three deciduous (*Metasequoia glyptostroboides*, *Taxodium distichum* and *Ginkgo biloba*) and two evergreen (*Sequoia sempervirens* and *Nothofagus cunninghamii*) species. They were grown in environmentally-controlled growth rooms at the University of Sheffield UK that simulated Cretaceous high latitude climate in order to test Beerling and Osborne's (2002) suggestion that an evergreen habit would be more efficient than a deciduous habit at high latitudes under elevated CO_2 conditions. Royer *et al.* (2003) therefore carried out two CO_2 treatments, one at 400 p.p.m.v (ambient) and the other at 800 p.p.m.v (elevated), in order to determine if elevated CO_2 under high latitude conditions made any difference at all in terms of leaf habit and if so, whether elevated CO_2 made evergreen or deciduous leaf habit more efficient (Royer *et al.*, 2003; 2005).

The results of these experiments showed that evergreen trees lost, on average, eight times more carbon than the deciduous species in winter. This was due to loss of carbon caused by canopy respiration continuing in the evergreens when deciduous trees had shed their leaves and were in a near-dormant state with very low respiration rates. This effect is shown in terms of grams of carbon lost per plant per winter in the histogram in Figure 7.2a. However deciduous trees lost, on average, twenty times more carbon by losing it in the leaves they shed in autumn whilst the evergreen trees keep their leaves and only lost minimal amounts of carbon through canopy respiration over the winter period. This effect is shown graphically as grams of carbon lost per plant per year through litter production (leaf loss) in the histogram shown in Figure 7.2b. When these two effects (carbon loss due to winter respiration and leaf shedding) were added together the carbon cost for leaf production in deciduous trees far outweighed that of respiration in evergreen trees. The combined cost for evergreens was only a ninth of the total cost for deciduous trees, irrespective of the concentration of CO_2 in the atmosphere. These combined effects are shown as the canopy carbon cost in grams of carbon per plant in the histogram in Figure 7.2c.

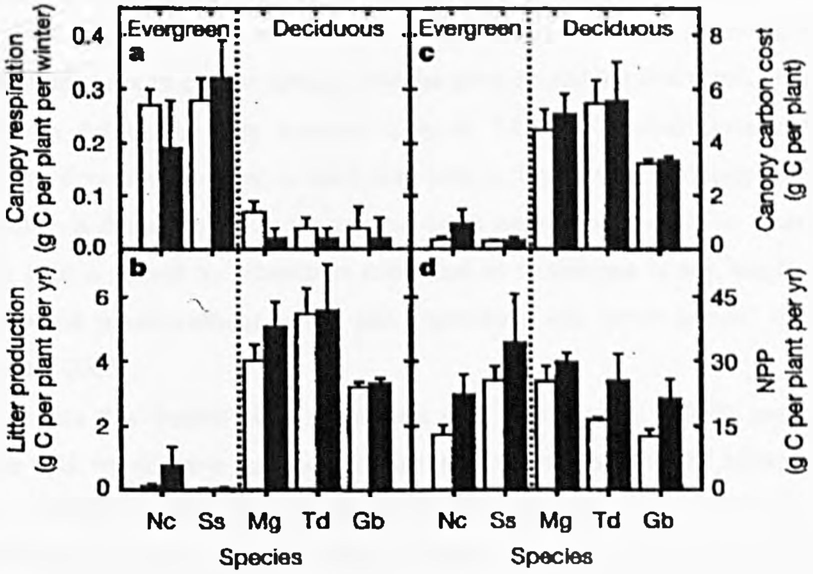


Figure 7.2. Results of experimental analysis of carbon costs of high latitude leaf habit for two atmospheric CO_2 levels. Open bars, 400 p.p.m.v.; closed bars, 800 p.p.m.v. a) Canopy respiration during the 6-week period of continuous darkness winter 2002-2003. b) Litter production in 2002. c) Total carbon cost of the polar winter, defined as the sum of a) and b). d) Annual net primary production (NPP). Values are means of four replicates for NC, *Nothofagus cunninghamii*, Ss, *Sequoia sempervirens*, Mg, *Metasequoia glyptostroboides*, Td, *Taxodium distichum* and Gb, *Ginkgo biloba* (Royer *et al.*, 2005).

As well as confirming Beerling and Osborne's (2002) suggestion that evergreen trees are more efficient than deciduous trees in terms of carbon gain under high CO_2 conditions, it also appears that they are more efficient than deciduous trees at high latitudes in general, whatever the CO_2 concentration. These results continued to hold true when the observations were scaled up to the mature forest level using process-based models of forest biogeochemistry. Although the difference was diminished, because the calculations more accurately account for the carbon losses incurred by leaf fall from the evergreen canopy, the deciduous forests still lost approximately double the amount of carbon compared to evergreen forests (Royer *et al.*, 2003; 2005). It was, however, found that both deciduous and evergreen trees produced similar values of Net Primary Productivity (NPP), suggesting that the deciduous trees somehow compensated for their greater carbon loss during the winter by gaining higher levels of carbon during another interval of the year (Figure 7.2d).

This may have been due to the pattern of carbon uptake throughout the year because further work by Royer *et al.* (2005) showed that the deciduous taxa produced a second pulse of carbon gain during the late summer to early autumn (Figure 7.3). It can be seen from Figure 7.3. that the deciduous species *Metasequoia glyptostroboides*, *Taxodium distichum* and *Ginkgo biloba* all display marked second pulses of growth between the 27th of July and the 13th of October. However the evergreen angiosperm *Nothofagus cunninghamii* displays only a slight increase in carbon uptake over the same period but this is below the initial peak of uptake in spring to early summer (Figure 7.3). The evergreen conifer *Sequoia sempervirens* however shows no second peak with carbon uptake declining steadily until mid October when it drops rapidly as the tree becomes dormant (Figure 7.3). This second pulse of carbon gain is caused by a complex combination of changes in day length, canopy area, leaf area-based photosynthetic rates, and night-time and below-ground respiration rates (Royer *et al.*, 2005).

Despite this double pulse of carbon gain Royer *et al.* (2005) suggested that the deciduous taxa would have still suffered greater carbon losses at the highest latitudes and therefore would have been disadvantaged in these regions. This is because at the higher latitudes the late-summer growth window is shorter than at lower latitudes because there is a rapid transition from summer sunlight to winter darkness therefore shortening the time in which the deciduous trees have to gain their additional carbon. These findings therefore challenge the hypothesis that only deciduous trees could have survived the winter darkness. Indeed they suggest that evergreen trees were far from being disadvantaged by the high latitude light regime but appear to have had the competitive advantage poleward of 69° over deciduous forms (Osborne *et al.*, 2004).

The University of Sheffield Conifer Model predicts that in both hemispheres at the highest latitudes (above ~80°) the forests during the mid-Cretaceous would have been entirely evergreen although with short leaf life-spans (~12-18 months). However a band of deciduousness then occurs between ~80 and 60° before evergreenness returns below 60° with particularly long leaf life-spans recorded (48-96 months) (Brentnall *et al.*, 2005). In the Northern Hemisphere these two zones are separated by a narrow band of mixed evergreen and deciduous conifers not seen in the Southern Hemisphere (Brentnall *et al.*, 2005). The reason for evergreenness at the poles within the model appears to vary from place to place but may be because deciduous species were restricted by climate and carbon uptake, light supply or due to disturbance, all of which have been shown to influence LLS (Reich *et al.*, 1995; Ennos, 2001; Royer *et al.*, 2003; 2005).

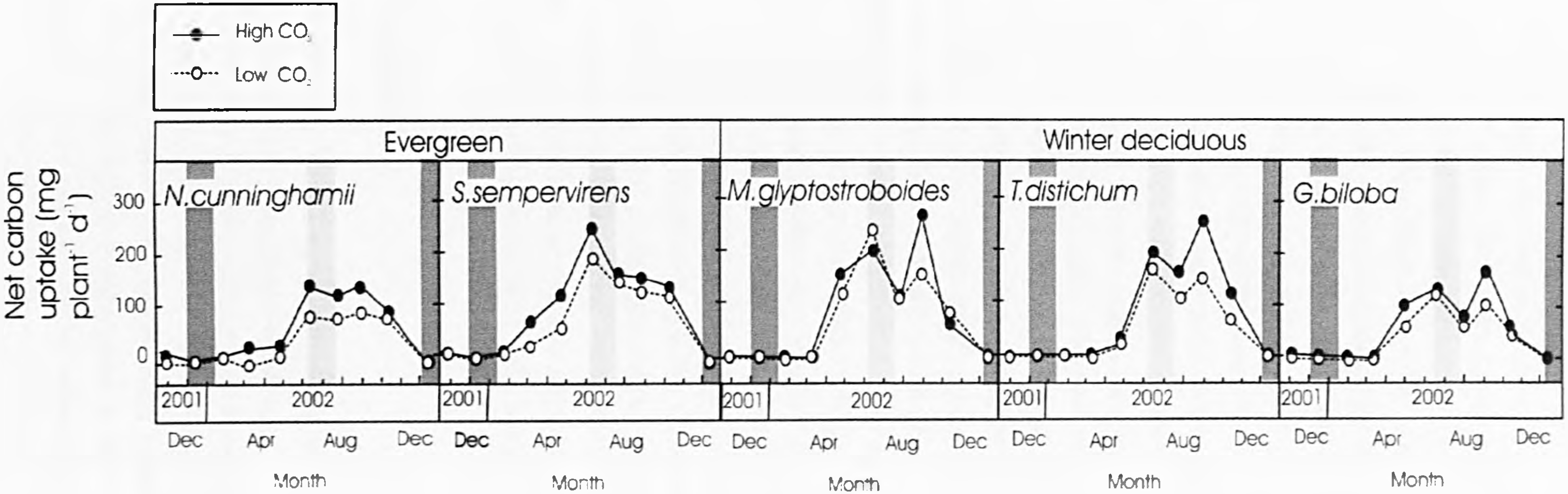


Figure 7.3. Seasonal patterns of whole-tree CO_2 uptake for five ancient taxa. Light gray vertical bands correspond to intervals of continuous daylight (polar summer), and dark gray bands correspond to intervals of continuous darkness (Royer *et al.*, 2005). Deciduous species *Metasequoia glyptostrobus*, *Taxodium distichum* and *Ginkgo biloba* all show two peaks of net carbon uptake whilst evergreen *Nothofagus cunninghami* and *Sequoia sempervirens* only show one peak.

At lower latitudes disturbance appears to have played a large part in whether the model predicted deciduous- or evergreenness as being dominant. Trees with long LLSs are able to grow taller and produce thick, strong leaves. Therefore if the fire return interval is long enough for them to become well established they will overtop trees with shorter LLSs and out-compete them for light (Reich *et al.*, 1999). If the fire return interval is long enough the thick bark produced by species like modern *Araucaria araucana* also enables these trees with long-lived foliage to survive in fire-prone areas (Veblen, 1982). These effects are thought to have been important in the lower latitudes (below 60°) where the model predicts areas with particularly long LLSs (48-96 months) in areas such as the Antarctic Peninsula, Australia and Greenland. These coastal regions may be mild enough, under the influence of the maritime climate, for trees with long LLSs to grow well and damp enough for the fire return interval to be long, allowing evergreens to dominate (personal communication S. Brentnall, University of Sheffield, UK). However if the fire return interval is short, trees with short LLSs (between 60 and 80 ° in the model) that can put all of their effort into reproduction and initially grow quicker by putting resources into growth rather than thick solid leaf production will have the advantage. A good example of this is in modern Siberia where deciduous Larch (*Larix*) dominates the forests due to frequent disturbance by fire from lightning strikes (personal communication S.Brentnall).

The fossil data, experimental results and computer models therefore do not support the hypothesis that deciduousness was a botanical response to the light regime at high latitudes in the past. Indeed the results from all of these approaches seem to show that whether evergreen- or deciduousness is dominant depends on complex interactions of several components including the genetics of the tree (this research and Falcon-Lang 2000a), carbon gain efficiency (Lusk, 2001; Beerling and Osborne, 2002; Royer *et al.*, 2003 and 2005), nutrient cycling efficiency (Schoettle and Fahey, 1994; Reich *et al.*, 1995; Lusk, 2001) and disturbance frequency (Brentnall *et al.*, 2005). Genetics however appears to be the dominant factor because the trees will either adapt to the prevailing conditions or will be selected against.

7.5. Palaeoclimate

Several lines of evidence have been used within this project to determine the climate of the high latitude regions during the mid-Cretaceous.

Nearest Living Relative (NLR) analysis assumes that fossil flora had the same ecological tolerances to similar types of flora found today, therefore it is often used to determine what the climate would have been like in the past (Beerling, 1998; Mosbrugger, 1999). Although this method is problematical in that it assumes that all of the trees functioned in the same way in the past as their modern equivalents do now and because there are no modern analogues for the warm, high CO_2 environments of the Cretaceous, it was used here in order to compare the results with previous studies (see Chapter 3, Section 3.2.1).

In the current research, for the Northern Hemisphere, NLR analysis indicates that comparing the forest composition of the fossils in Svalbard to that of modern counterparts suggests a moist upland cool temperate area containing genera such as *Cupressinoxylon* and *Juniperoxylon* with mild, sheltered warm temperate areas with rivers and/or swamps present in the lowlands dominated by *Taxodioxylon* (Moore, 1982; Vidakovic, 1991; Moss *et al.*, 2005). In the Canadian Arctic the dominance of *Pinuxylon* with relatively narrow growth rings suggests moderate warmth although the presence of *Pinuxylon* in combination with the other genera suggests that these specimens may be from a cool temperate upland area. Frakes and Francis (1988) report ice-rafted deposits in both of these Northern Hemisphere sites suggesting that there was sea ice present for at least part of the year. This would support the cool temperate climate suggested for the Canadian Arctic but seems to be cold for Svalbard where *Taxodioxylon* are present in the lowlands. However it has been shown that modern *Taxodium,* thought to be the nearest living relative of *Taxodioxylon,* can withstand temperatures as low as -30°C therefore these conifers could have survived low temperatures in winter (Vidakovic, 1991).

In the Southern Hemisphere in Australia the dominance of *Podocarpoxylon* is not diagnostic as its modern equivalent *Podocarpus* occurs in several habitats including warm-temperate areas similar to small areas of the Drakensburg mountains of Africa and a narrow strip along the south coast where there is sufficient moisture for them to survive, or in the frequently disturbed cool-temperate rainforests of northern Patagonia (Heusser, 1974; Moore, 1982; Veblen, 1982; Armesto *et al.*, 1995; Lusk, 2001). *Podocarpus* is also present in Australia and in New Zealand in sub-alpine and warm-temperate rainforests (Patel, 1967a; 1967b; Vidakovic, 1991; Gibson *et al.*, 1995; Ogden and Stewart, 1995). Therefore although it may be assumed that the climate of Australia was probably temperate during the mid-Cretaceous it is not possible to say if it was cool- or warm-temperate from nearest living relative analysis of forest composition alone (Moore, 1982). However, Frakes and Francis (1990) have suggested that the climate would have been very seasonal during the mid-Cretaceous (Aptian-Albian) of Australia, the presence of ice-rafted boulders indicating the presence of seasonal ice formed on rivers draining into the Eromanga Basin. This is supported by the lack of false rings in the wood due to frost damage during the growing season, indicating that the summers were warm and any ice was only present during the winter. Frakes and Francis (1988) also reported that evidence from fossils and the sedimentology on Australia indicate that the climate would have been humid with cool temperatures and short periods of winter freezing supporting the interpretation of these forests having been similar to the cool-temperature rainforests of northern Patagonia.

On James Ross Island on the eastern side of the Antarctic Peninsula the *Podocarpoxylon* and araucarian dominated mid-Cretaceous forests suggest similarities to the modern warm-temperate rainforests of New Zealand, Chile and north-east Australia, with mean monthly summer temperatures of 16-22°C, in winter 3-8°C and mean annual temperature of 15 °C (Moore, 1982; Armesto *et al.*, 1995; Baxter *et al.*, 1998; Lusk, 2001; Hildebrand-Vogel, 2002). However the modern conifer types to those represented on James Ross Island prefer a range of altitudes, representing specimens from high mountainous areas (>1000m araucarioid conifers) and lower slopes (400-900m *Podocarpus* and the Cupressaceae). The range of these conifers suggest temperate conditions like those of the northern Chilean and Argentine rainforests with mean annual temperatures of 10-12°C rather than the warm temperate conditions that may, never the less, have been present in valleys (Veblen, 1982; Diehl *et al.*, 2003). On Alexander Island to the west of the Antarctic Peninsula very few of the specimens could be identified but the combination of *Podocarpus* and *Taxodium* types suggest that the climate would have been warm temperate indicated by modern *Taxodium* preferring mean annual temperatures >13°C (Moss *et al.*, 2005). Falcon-Lang and Cantrill (2001a) also indicated that Araucariaceae were present, suggesting that Alexander Island may have been warm-temperate similar to modern Chile or New Zealand. Recent work by Howe (2003) suggest that Alexander Island had well-drained mollisols that were rich and fertile for growth in a climate that was warm temperate to semi-arid with seasonal precipitation, intermittent wet phases and long growing seasons that allowed rapid growth on Alexander Island during the mid-Cretaceous.

Creber and Chaloner (1984b) suggested that araucarian and podocarp conifers in particular may produce rings that are more genetically controlled than environmentally influenced. Studies on living members of the araucarian and podocarp conifer families having been used in dendrochronology suggesting that there is sufficient environmental influence for them to be useful in this type of study (Lamarche *et al.*, 1979; Francis, 1986). However it has been shown by Falcon-Lang (2005b) that ring width series are significant in all species and display variations that are predominantly climatically rather than genetically controlled.

Therefore growth ring widths of the fossil specimens were measured and annual and mean sensitivity values calculated in order to obtain detailed information about seasonality, annual growing conditions and water availability (Fritts, 1965; 1976; Creber and Francis, 1999). All fossil wood examined contains growth rings indicating that the climate in both northern and southern polar regions was probably seasonal during the mid-Cretaceous with trees becoming dormant for some period of the year. This finding is supported by several previous studies in both the northern and southern hemispheres (Jefferson, 1982; Francis, 1986; Parrish and Spicer, 1988; Francis and Poole, 2002).

In the Northern Hemisphere in Svalbard and the Canadian Arctic growth rings varied in mean width from 0.36 to 5.55mm with a mean for Svalbard and the Canadian Arctic of 1.7 and 1.27mm respectively, indicating that the trees had the potential for quite high growth rates but that in some cases the environment may not have been entirely favorable and hence growth rate was slow (Table 7.1). The average mean sensitivities of 0.29 for Svalbard and 0.27 for the Canadian Arctic shows that the growth response was complacent, suggesting that the trees grew under equable conditions in areas with adequate water supply. In Svalbard annual sensitivity values show that some trees appear to have suffered adverse affects from the climate for at least part of their lives, probably due to intermittent or restricted water supply. No previous growth-ring analyses of fossil wood from Svalbard could be found for comparison.

Table 7.1. Comparison of growth ring analysis for the Northern Hemisphere from Parrish and Spicer (1988) and this study.

Study	Age	Location	Average mean ring width (mm)	Average mean sensitivity
Parrish and Spicer (1988)	Latest Albian-Cenomanian	North Slope of Alaska	2.8	0.42
This study	Aptian-Albian	Svalbard	1.78	0.29
This study	Aptian-Albian	Canadian High Arctic	1.27	0.27

The only other work carried out on growth rings from fossil wood of mid- to early Late Cretaceous age is from the Nanushuk Group at slightly higher latitudes on the North Slope of Alaska (Parrish and Spicer, 1988; Spicer and Parrish, 1990) show that there are some differences between this continental margin site and the maritime High Arctic sites of this study (Table 7.1). The growth rings are wider than found in this study, ranging from 1.1mm to 4.6mm with a mean of 2.8mm. This finding would suggest that the trees grew well and should have been complacent like those of the High Arctic sites. However 71% of the North Slope of Alaska trees were sensitive with the average mean sensitivity being 0.42 (Table 7.1). The wider rings in this area may be due to the presence of abundant water in humid conditions, as suggested by the thick coals and bog deposits in this area producing fewer effects due to drought than at higher latitudes with thin soils. The high mean sensitivity may be due to several factors, including the small size of the sample set, the short ring sequences used or the samples being close to a large continental mass (Parrish and

Spicer, 1988).

In the Southern Hemisphere the Australian wood had growth rings that varied in mean width but were all moderately narrow (0.56 to 2.45mm) with a mean for the sample set of 1.25mm indicating that growth was quite slow in this area (Table 7.2). The values produced for Australia are encompassed by those found by Frakes and Francis (1990) in the Aptian-Albian sediments of the Eromanga Basin, Australia, who found rings which were much wider, up to 4.53mm.

Table 7.2. Comparison of growth ring analysis for the Southern Hemisphere from Francis (1986), Francis and Poole (2002), Jefferson (1982) and this study.

Study	Age	Location	Average mean ring width (mm)	Average mean sensitivity
This study	Aptian-Albian	Australia	1.25	0.25
Frakes and Francis (1990)	Aptian-Albian	Eromanga Basin, Australia	(range 0.34-4.53)	(range 0.10-0.37)
This study	Turonian-Coniacian	James Ross Island Antarctic Peninsula	1.76	0.32
Francis and Poole (2002)	Early Albian	Antarctic Peninsula	1.53	0.15
Francis and Poole (2002)	Late Coniacian to latest Campanian	Antarctic Peninsula	2.28	0.25
This study	Barremian-Albian	Alexander Island Antarctica	1.42	0.36
Jefferson (1982)	Aptian-Albian	Alexander Island	1.40	0.42

The ring widths in wood from Antarctica were wider than in Australian woods ranging from 0.58 to 4.16mm with the average for Alexander Island being slightly lower at 1.42mm than on James Ross Island at 1.76mm (Table 7.2). Therefore some of the Antarctic trees appear to have had the potential for moderate growth but most were quite slow growing, indicating that one or more factor in the environment may have been unfavourable. However, these findings are comparable to modern *Araucaria araucana* ring widths from 37-43°S in Argentina where the trees grow in areas ranging from sub-alpine to warm mild

Mediterranean type climates that can produce mean ring widths ranging from 0.38 to 3.33mm wide (see Table 7.2., Lamarche *et al.*, 1979; Veblen, 1982). These findings are also in line with measurements collected by Francis and Poole (2002) from the early Albian with a mean ring width for woods from James Ross Island of 1.53mm, which falls between the values here for James Ross and Alexander islands. However Jefferson (1982) reported growth rings from the Aptian-Albian of Alexander Island up to 9.55mm wide, much wider than any in other studies, and he argued that this rapid growth suggested that the trees were producing similar growth patterns to modern *Phyllocladus* growing in warm-temperate climates with a long growing season. It could also be argued however that these anomalously wide rings may have been produced by a tree growing in a particularly favourable microenvironment.

The only Southern Hemisphere site to produce complacent mean sensitivity values was Australia (MS = 0.25), indicating that this was the only area where trees were growing in equable conditions with adequate water supply (Table 7.2). Annual sensitivity values indicate that there was only slight variation in environmental conditions from year to year.

These findings appear to be supported by those of Frakes and Francis (1990) in their dataset for the Eromanga Basin which also produced complacent values. Both the James Ross and Alexander Island wood produced sensitive values of mean sensitivity, 0.32 and 0.36 respectively, indicating that the trees were growing under variable climatic conditions from one year to the next. These sites appear to show moderate variation in environmental conditions therefore they may represent several microenvironments e.g. some growing on dry, exposed hillsides whilst others grew in moist, sheltered areas, therefore it is difficult to compare these results with those found from NLR analysis. These variations also make it difficult to compare the results here to previous growth ring analysis unless inferences are made about the particular microenvironment of growth. The findings here contrast with those of Francis (1986) and Francis and Poole (2002) who obtained complacent values from the wood they examined from James Ross Island (Table 7.2). The maximum values for Francis (1986) and Francis and Poole's (2002) datasets did overlap with the mean values obtained in this study therefore indicating that there is some comparability and the results are not unreasonable. Francis (1986) suggests that the complacent value and wide rings in her study may have been produced by the trees having grow in moist warm to cool temperate forest interior settings, suggesting that they represented a warmer moist lowland microenvironment similar to that suggested for some of the samples in this dataset.

The values for mean sensitivity for Alexander Island are similar to those obtained by Jefferson (1982) of 0.42 for the mid-Cretaceous (Albian) (Table 7.2). Therefore both studies indicate the trees were growing reasonably close to their ecological limits. Several of the rings present in the Alexander Island wood also pinch out completely suggesting that the trees may have been growing in dense stands which would also explain the presence of false rings, as the trees would have been competing with each other for water during the summer months (Fritts, 1976). The only conifers that consistently produce values near to or above 0.4 are those growing in semi-arid environments where there is variation in the availability of water (Fritts and Schatz, 1975).

Compilation maps, produced by the Geological Institute of the Russian Academy of Science, of the geological evidence for climate during the mid-Cretaceous, indicate that at this time the northern high latitude sites were within the Northern High-latitude Temperate Humid (NHT) zone (Chumakov *et al.*, 1995; translated in Spicer and Skelton, 2003). This is inferred from the presence of abundant coal-bearing beds and moderately thermophilic (warmth-loving) plants (Vakhrameev, 1991; Herman and Spicer, 1996). Other geological climatic indicators for the mid-Cretaceous produce mean annual temperatures of 10 ±3°C (from leaf margin analysis) with a lower limit of -14°C (from NLR analysis of turtle remains) for the North slope of Alaska (Spicer and Parrish, 1986, 1990; Spicer *et al.*, 1994; Spicer, 2003). These temperatures seem to be a reasonable match to the forest composition and growth ring analysis data for the Canadian Arctic (cool temperate, temperatures between ~ 3 and 10°C) but may be a little low for Svalbard (cool to warm temperate, temperatures between ~3 and 20 °C) (Figure 7.4).

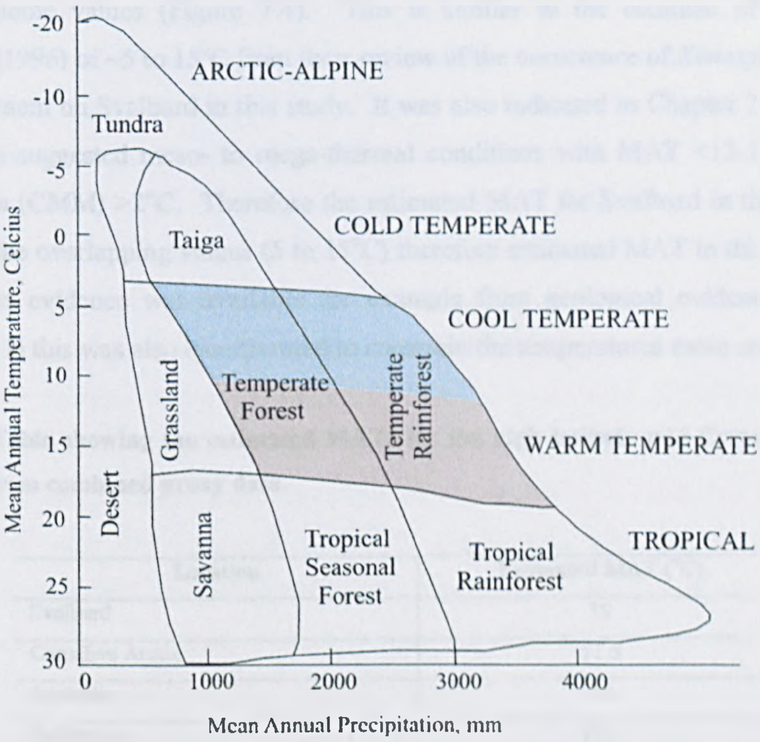


Figure 7.4. Diagram showing the world biome-types in relation to climatic humidity and temperature (adapted from Whittaker, 1975). All samples in this project fall either within the green (cool temperate) area, the pink (warm temperate) area or could occur in both.

In the Southern Hemisphere the geological evidence indicates that Australia and Antarctica would have been in the Southern High-latitude Temperate Humid (SHT) belt due to the presence of moderately thermophilic vegetation, dinosaur remains and rare coals. During the Aptian the temperatures on Australia have been predicted to have been between 10 and 30°C due to the presence of *Ceratus* (the lungfish) with vegetation during the Albian suggesting that mean annual temperatures were between 5 and 8 °C. On Antarctica during the Albian NLR analysis of *Hausmannia* suggests that the mean annual temperature would have been between 13 and 27 °C. If the palaeotemperature predictions from forest composition and growth ring analysis for Australia and Antarctica are compared to the world biome-type plot (Figure 7.4) it can be seen that both fall between the temperatures predicted by the geological data. Australia is predicted to be cool temperate therefore in Figure 7.4 falls between ~ 3 and 10°C and Antarctica temperate rainforest which places it between ~3 and 20 °C.

By combining the previously predicted mean annual temperatures with estimates from the forest composition in this study, estimates of mean annual temperature for each site were made (Table 7.3). For example Svalbard is predicted to have been cool to warm temperate from the NLR analysis (Chapter 2) and growth rings analysis (Chapter 5) in the present study and is therefore predicted to have MAT between ~3 and 20°C from the range of world biome values (Figure 7.4). This is similar to the estimate of Philippe and Thevenard (1996) of ~5 to 15°C from their review of the occurrence of *Xenoxylon* which was found to present on Svalbard in this study. It was also indicated in Chapter 2 that the forest composition suggested meso- to mega-thermal conditions with MAT <13-24°C with cold month mean (CMM) >2°C. Therefore the estimated MAT for Svalbard in this study is the average of the overlapping values (5 to 15°C) therefore estimated MAT in this case is 10 °C. Where other evidence was available for example from geological evidence (Chapter 1, Section 1.4.1) this was also incorporated to constrain the temperatures more accurately.

Table 7.3. Table showing the estimated MATs for the high latitude mid-Cretaceous locations calculated from combined proxy data.

Location	Estimated MAT (°C)
Svalbard	10
Canadian Arctic	11.5
Australia	16
Antarctica	19.5

When the estimated MATs from the combined proxy data were compared to the predicted MATs from the most recent mid-Cretaceous computer climate simulations of Price *et al.* (1998) it was found that the models produced temperatures in the high latitudes that were between 4 and 13.5°C lower than the proxy data estimates. This suggests that there is a problem with the computer models presently in use.

7.6. Contribution of fossil data to climate models

Climate models were developed as a means of understanding the mechanisms, interactions and feedbacks that control global climate (Deconto *et al.*, 2000a, 2000b; Beerling and Woodward, 2001; Bergengren *et al.*, 2001; Blackmon *et al.*, 2001). Researchers have used models to simulate globally warm greenhouse climates. However, these models have consistently produced climate simulations that are too extreme, in particular making the polar regions too cold in winter to be comparable with the proxy data. This suggests that something is missing from the models (see Section 7.5 above Barron and Washington, 1982; Crowley, 1993; Sloan and Pollard, 1998). We know that vegetation was present in these high latitude areas during the Cretaceous from the extensive fossil record (Chapter 1, Section 1.2 and Chapter 2). However, vegetation is not often included within climate models even though it is known to affect albedo, land surface roughness, surface hydrology and the partitioning of sensible and latent heat (Deconto *et al.*, 2000b; Osborne and Beerling, 2002; Beringer *et al.*, 2005). Therefore vegetation may have played an important role in warming the high latitude continental interiors during greenhouse intervals and truly interactive climate-vegetation models should be included within global climate models (Beerling, 2000; Deconto *et al.*, 2000b).

When vegetation has been included in climate models in the past the distribution of vegetation has been prescribed, having used just one fixed vegetation type as a global default (Barron *et al.*, 1992) or a best guess distribution based on reference points from proxy data that do not provide a realistic representation of the terrestrial ecosystems present (Otto-Bliesner and Upchurch, 1997). In an attempt to make the vegetation component of climate models more realistic, dynamic predictive models have been developed to improve interaction with climate models. The Equilibrium Vegetation Ecology (EVE) model has been used to describe the physical characteristics of vegetation as a function of climate and ecological principles (Deconto *et al.*, 2000a; 2000b; Bergengren *et al.*, 2001). This much more complex model does not however include physiological processes such as photosynthesis, respiration, water cycle effects or the effect of soil heterogeneity, which are particularly important factors in high latitude areas.

The LEAF portion of this model is unable to simulate the range of LLSs produced by evergreen species, but gives the evergreen conifers constant leaf area. This makes their contribution to other canopy properties constant, potentially over- or under-estimating their contribution to these properties e.g. leaf area index, leaf albedos and canopy height. The Top-down Representation of Interactive Foliage and Flora Including Dynamics (TRIFFID) model made further improvements by allowing plant functional types to compete within individual gridboxes using a carbon balance approach (Cox, 2001). Unlike the combined EVE and LEAF approach, TRIFFID included photosynthesis, respiration, water fluxes and soil state (Cox, 2001). Leaf death varies in TRIFFID with temperature, so that leaf turnover increases when the temperature drops, but it is not able to produce realistic phenology.

The Sheffield University Conifer Model (USCM) was therefore developed in order to produce a realistic vegetation model of these high latitude forests to investigate the controls on the distribution of evergreen and deciduous conifer forests between hemispheres and their feedback on polar climate (Chapter 6). The dominant leaf habits and leaf life-spans determined from fossil high latitude conifer wood allowed comparison with the values produced by the USCM to determine if the model produced reliable results.

In the Northern Hemisphere the predicted values for Svalbard produce a reasonable match to the fossil data with the slightly higher proportion of deciduousness predicted in the model possibly due to the relatively short fire return interval of 80 years (Chapter 6). The model predictions are a better match for the Canadian Arctic matching the mixed but predominantly evergreen data from the fossils. In the Southern Hemisphere the model matches the fossil evidence suggesting that Australia and James Ross Islands were predominantly evergreen but predicts that Alexander Island should have of mixed leaf type whilst the fossils say it is entirely evergreen. On Alexander Island the model produces a much lower maximum leaf life-span (96 months) than the fossils predict (151 months) however the model was programmed only to produce leaf life-spans up to 96 months therefore if this upper limit was extended it may produce a better match for the Alexander Island fossils. Overall it is felt that the USCM will provide a much more accurate representation of the vegetation that was present in the high latitude regions than those previously used within global climate models.

Various studies have previously been carried out to test the contribution of vegetation models to climate models (Otto-Bliesner and Upchurch, 1997; Upchurch *et al.*, 1998; 1999; Deconto *et al.*, 2000). Early prescriptive vegetation models, were coupled to the GENESIS v1.02 Global Climate Model with CO_2 levels set at x2 pre-industrial levels (580ppm), represented BESTGUESS vegetation, a best estimate of global vegetation during the Cretaceous (Otto-Bliesner and Upchurch, 1997; Upchurch *et al.*, 1998). Although these were basic models they were able to produce high latitude land surfaces that were warm year round (annual mean warming 2.2 - 4.2°C), with above freezing temperatures for two additional months as well as warming of the high latitude oceans by 4.0°C in the Northern Hemisphere and 3.5°C in the Southern Hemisphere (although Upchurch *et al.*, 1998 suggest the high latitudes may have been up to 12°C warmer). This reduced the extent and duration of sea ice (Otto-Bliesner and Upchurch, 1997; Upchurch *et al.*, 1998). These projects indicated that even basic vegetation can make a huge contribution to climate models and aid in making them produce more realistic representations of past climate.

When the more complex, predictive rather than prescribed, interactive EVE vegetation model was first coupled to the GENESIS v2.0 GCM with CO_2 set at 1680ppm (effective concentration of 1500ppm) it showed that the predicted biomes at high latitude (needleleaf forests in continental Antarctica, North America and Asia) played an important role in maintaining low meridional thermal gradients and warmed continental interiors, as shown by prior, non-interactive models such as that of Otto-Bleisner and Upchurch (1997) and Deconto *et al.* (2000a). This was due to the evergreen linear-leaf rainforests at high latitudes lowering albedo, particularly in late autumn and early spring (Deconto *et al.*, 2000a). Snow is easily blow off evergreen trees and hidden on the ground beneath them, resulting in low albedos due to light and heat being absorbed by the dark foliage on the trees (snow-masking effect). This causes a warming that increases tree migration poleward. However, the presence of deciduous or fewer trees would lead to higher albedo due to light and heat being reflected off the snow accumulated under the trees through bare branches hence there is no means of absorbing the incoming radiation, and the subsequent cooling leads to even less trees being present. These processes continue within the model until equilibrium is reached. The results of these advanced models produce much closer matches to the fossil data, producing *Araucaria* and *Podocarpus* type forests on the Antarctic Peninsula (Deconto *et al.*, 2000a), and highlighting that not just the presence and absence of the trees but their leaf life-span is important in the climatic effects.

Further studies with the EVE/LEAF model coupled to the GENESIS v1.02 General Circulation Model with x2 present CO_2 (680ppm) by Bergengren *et al.* (2001) confirmed the finding that evergreen trees lower albedo and boreal forests moved northwards as climate warmed to replace tundra vegetation. This is due to the snow-masking effect. It was found that the boreal forest-tundra snow-masking albedo feedback was the largest feedback effect in these simulations of temperature response to CO_2 doubling, with this feeding southwards to enhance the poleward migration of grasslands at the southern limit to the boreal forest (Bergengren *et al.*, 2001). These findings suggest that high latitude forests would have played a significant role in regulating the climate during greenhouse periods and reiterates that realistic representations of the vegetation should always be included within climate models (Otto-Bliesner and Upchurch, 1997; Upchurch *et al.*, 1998; Bergengren *et al.*, 2001).

S.Brentnall at the University of Sheffield, UK is currently working on incorporating the USCM in global climate models. The present situation is that P. Valdes at the University of Bristol, UK has completed a calibration run of the climate model to be used. This was carried out in order to improve the heat fluxes to correct the sea surface temperatures. When the USCM is fully coupled to global climate models it will resolve the detailed distribution of high latitude conifer forests and allow investigation of underlying climatic and biogeochemical controls on the forests' biogeography, as well as their influence on regional and global climate. Therefore the next step will be to use the new boundary conditions in the climate model to run the USCM for several iterations to determine the impact of the vegetation on the climate model. It is predicted that the inclusion of the USCM in global climate models will produce the warm climate of high latitude continental interiors shown by proxy data. This mechanism has been suggested by the previous climate-vegetation model outputs of Upchurch *et al.* (1998) and observations of modern vegetation by Beringer *et al.* (2005).

7.7. Painting of Cretaceous forests of Svalbard

The picture in Figure 7.5 is a reconstruction of the mid-Cretaceous fossil forests of Spitsbergen, Svalbard painted by Robert Nichols. The painting is a scientific reconstruction, primarily based on the information contained within this thesis. The forest was reconstructed using evidence about the composition and leaf life-span of the trees discussed in Chapters 2 and 4. The environment in which the trees are growing in the painting was reconstructed using the information on palaeoclimate from growth rings and forest composition within Chapters 2 and 5, from elevations taken from Figure 1.2. (Markwick *et al.* 2000), survival strategies for high latitude trees discussed in Chapter 1 and the evidence from the geological record discussed in Chapter 2.

The painting represents a forest on Svalbard during the early autumn when the shadows are particularly long due to the low angle of the light at high latitudes. The deciduous trees in the forest are just about to start losing their leaves. In the foreground of the painting are deciduous *Laricioxylon* trees with their leaves starting to turn yellow. The dinosaur represented in the clearing behind these trees is *Iguanodon*, the presence of which is suggested by footprints found at Festningsodden (Harland, 1997). The tree in the right hand foreground is a *Piceoxylon,* similar to a modern spruce. The tree with orange-coloured foliage is *Taxodioxylon,* similar to a modern Swamp Cypress which loses most of its leaves in autumn but keeps a small percentage of them throughout the winter. Other trees represented in the forest are *Juniperoxylon*, *Piceoxylon*, *Cupressinoxylon* and *Taxoxylon*. The presence of these dense forests would have increased evapotranspiration, adding water vapour into the atmosphere to form the clouds seen in the background. There is an understorey dominated by cycadophytes and ferns in moist areas close to a stream and the main river channel (Harland, 1997). In the midground there is a log jam shown adjacent to the river channel, representing the remains of trees that will eventually be washed out on to the shallow marine shelf.

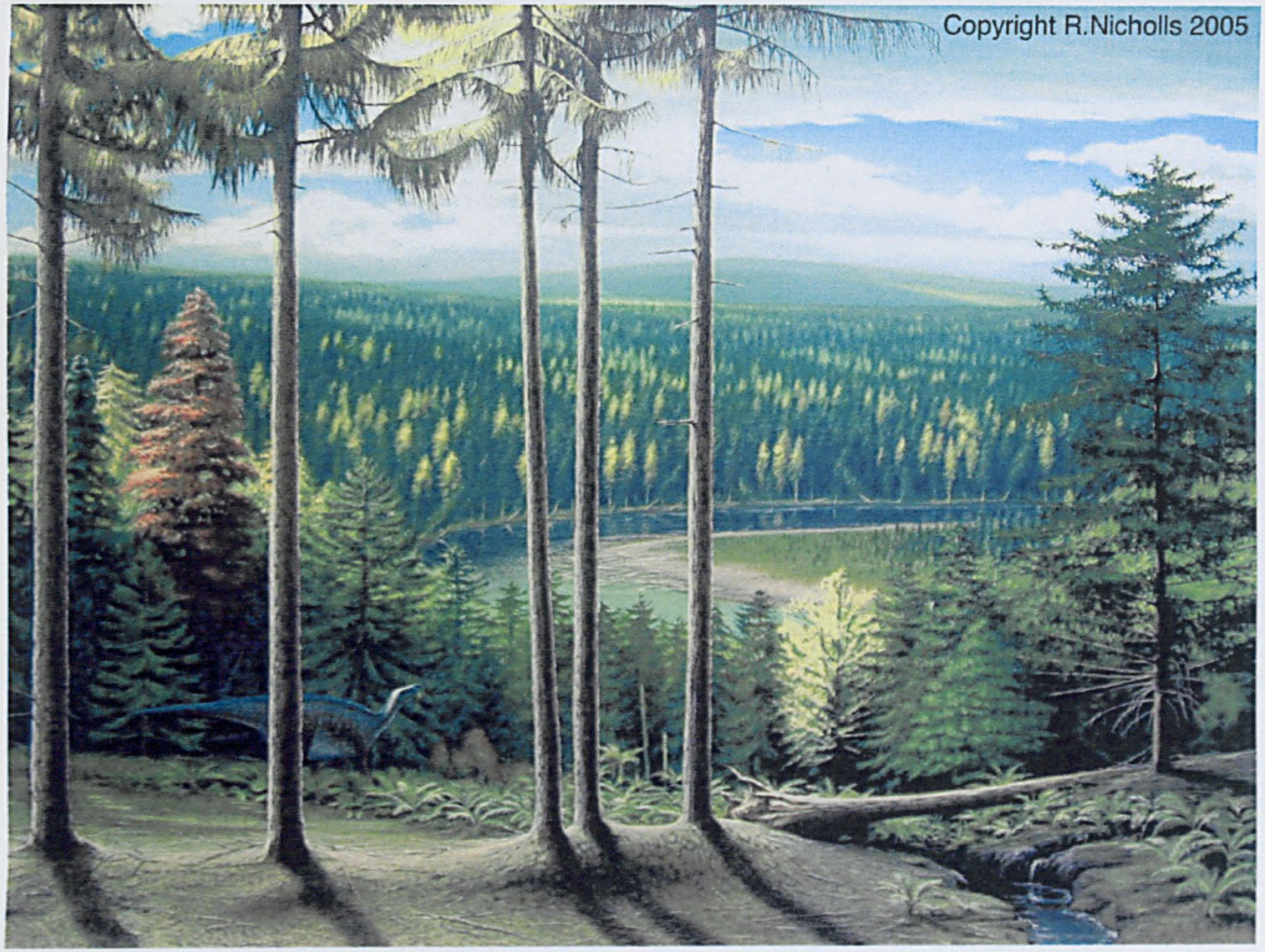


Figure 7.5. **A reconstruction of the mid-Cretacouse fossil forests of Svalbard by Robert Nichols (Paleocreations).**

Chapter 8 Conclusions

8.1. Conclusions

- Fossil wood is abundant within mid-Cretaceous sediments in both the northern and southern hemisphere polar regions, representing the remains of vegetation that was able to grow at high latitudes when the climate was much warmer.
- In the Northern Hemisphere (Svalbard and the Canadian Arctic) the high latitude conifer forests were composed of *Piceoxylon, Laricioxylon, Cedroxylon, Taxodioxylon, Pinuxylon, Palaepiceoxylon, Taxoxylon, Juniperoxylon, Protocedroxylon, Araucariopitys, Xenoxylon* and *Cupressinoxylon*. In Svalbard the dominant genus was *Taxodioxylon* and in the Canadian Arctic *Pinuxylon*.
- In the Southern Hemisphere (Australia and Antarctica) the high latitude conifer forests were composed of *Podocarpoxylon, Taxodioxylon, Araucariopitys, Cupressinoxylon, Agathoxylon, Protophyllocladoxylon, Sciadopityoxylon* and *Circoporoxylon*. On Antarctica the dominant genus was *Taxodioxylon* and on Australia *Podocarpoxylon*.
- A new method has been developed to determine the evergreen or deciduous habit of conifers, based on cell proportions within growth rings in wood. This method, called Ring Markedness Index (RMI), is the relationship between cell dimensions (Percentage Diminution) across growth rings and Percentage Latewood. RMI values are high in deciduous wood and low in evergreen wood. RMI analysis of extant conifer wood shows that there is a strong underlying genetic signal of deciduous or evergreenness produced within the wood structure of conifers that is specific to each genus. The underlying signal of leaf life-span is reproduced in branch, trunk, damaged and undamaged wood and wood collected from a variety of altitudes and latitudes therefore all wood can be included in this type of study.
- Variations in RMI values within species are probably caused by subsidiary environmental effects.
- One-way ANOVA analysis confirmed the strong relationship between LLS and RMI to the 95% confidence level by producing two population groupings, one evergreen and the other deciduous.
- Modern *Taxodium distichum* is widely known as a deciduous species. However, it consistently produced an evergreen signal from its wood with LLSs of 12-24 months. This is probably due to a small proportion of the leaves being perennial. Despite this, *T.*

distichum was included within the modern dataset as this behaviour may not be restricted to extant forms.

- The Percentage Skew method (Falcon-Lang, 2000b) of leaf life-span determination was found to be unreliable when used on a large sample set of extant conifers.
- Fossil wood contains the same structural features as extant wood therefore Ring Markedness Index was applied to fossil wood in order to determine the leaf life-span of Cretaceous conifer trees.
- In the Northern Hemisphere in Svalbard the mid-Cretaceous conifers were found to be predominantly evergreen (85%), with only 15% deciduous. In the Canadian Arctic the conifers were again predominantly evergreen with only 10% of samples deciduous. The dominant leaf life-span for both areas was ~33 months.
- In the Southern Hemisphere in Australia the mid-Cretaceous conifers were entirely evergreen with a dominant leaf life-span of ~63 months. On the eastern side of the Antarctic Peninsula (James Ross Island) the conifers were predominantly evergreen with only 11% being deciduous. The dominant leaf life-span was ~48 months. On the western side of the Antarctic Peninsula the conifers were entirely evergreen with an exceptionally long dominant leaf life-span of ~151 months.
- All Cretaceous high latitude woods were predominantly evergreen therefore a deciduous habit in the polar forests appears not to have been such a crucial adaptation for reducing canopy respiratory CO_2 losses, as previously suggested by experiments carried out on "living fossil" conifers (Beerling and Osborne, 2002).
- The leaf life-spans of the Southern Hemisphere conifers were consistently longer than those of the Northern Hemisphere conifers. This may be due to the disturbance in these Southern Hemisphere areas having been low allowing trees with long leaf life-spans to become established and to overtop and out-compete trees with shorter leaf life-spans. This is also suggested by the output of the USCM which shows that the climate was mild enough to allow high growth rates but damp enough, in the maritime setting, to keep the fire return interval low. It may also be due to the genetics of the trees involved, because many of the modern Southern Hemisphere conifer genera thought to be related to the fossil types described here, have particularly long leaf-life spans e.g. *Araucaria*.
- Analysis of growth rings and comparison to modern counterparts of the fossil genera in the Northern Hemisphere show that trees on Svalbard probably grew in moist cool upland areas and warm temperate areas probably with rivers and/or swampy areas present in the lowlands. In the Canadian Arctic the same analysis shows that the climate was similar to that of Svalbard but the dominance of *Pinuxylon* indicates that it would have been slightly cooler, probably similar to northern Canada today.

- Environmental analysis of growth rings and comparison to modern counterparts of the fossil genera in the Southern Hemisphere show that the conifers of Australia could have grown in either warm-temperate forests like those of modern Australia and New Zealand or cool-temperate forests similar to those in northern Patagonia. The absence of frost rings suggest that the summer growing period was warm, however narrow rings observed in this study suggests that growth was slow and this, coupled with the presence of ice-rafted deposits reported by Frakes and Francis (1990), suggests that the climate was probably strongly seasonal, cool-temperate.
- On James Ross Island environmental analysis suggests that the forests seem to have been growing in cool-temperate forests like those of the northern Chilean rainforests. On Alexander Island the climate was probably warm, temperate to semi-arid with annual rainfall and intermittent wet phases.
- High values of Percentage Diminution within extant and fossil wood specimens suggest that this may be a signal of growth under high latitude light regimes. Further work is needed to confirm this finding.
- Comparison of the compiled mean annual temperatures from the fossil data in this thesis and other proxy data with previous computer palaeoclimate models shows that the models consistently produce temperatures that are too low for the high latitude areas by as much as 13.5°C in some areas.
- The University of Sheffield Conifer Model produces reasonable values and distributions of predicted leaf habit and leaf life-span for some areas, James Ross Island and Svalbard, when compared to the values calculated from the fossil wood. However in other areas Alexander Island, Australia and the Canadian Arctic further refinements are needed before the USCM can be used as a tool in assessing the affects of high latitude conifer forests in both regional and global climate models.

8.2. Future work

- To carry out Ring Markedness Index analysis on mid-Cretaceous wood from Russia. The wood available from Russia covers a range of latitudes (Vakhrameev, 1991) which would provide an opportunity to determine whether the University of Sheffield Conifer Model is accurate in its prediction of deciduousness over this region.
- To carry out Ring Markedness Index analysis on Tertiary wood from high latitude regions in order to determine whether the signal produced and forest composition is different to that of the mid-Cretaceous.
- To carry out an investigation of modern and fossil wood from the tropical regions in order to determine whether it is of climatic significance. Modern tropical wood can produce drought

induced rings within their wood (personal communication A. O'Dea, Smithsonian Tropical Research Institute, Panama; Creber and Francis, 1999) and if this is found to be reproduced in fossil wood it may give some indication of water availability and temperature during past greenhouse periods. This would provide a means of testing whether the palaeotemperature gradient was flattened during the Cretaceous, as has been suggested, relative to the steep gradient seen today.

- Carry out investigations on modern high latitude conifers to establish whether high values of Percentage Diminution in the wood is an artifact of growth under high latitude light regimes.

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Appendix A – Extant wood

A1.1. Sample Methodology

A1.1.1. Introduction

This appendix presents additional data and information on the extant wood used in this study. The methods of collection, preparation and preservation of extant wood specimens are presented. Sections A1.1.2 and A1.1.3 discuss field trials carried out at the University of Leeds, UK and Tapton Experimental Gardens, Sheffield, UK respectively for the collection of extant wood samples. Section A1.1.4 presents the various techniques trialed for the sectioning and preservation of samples and finally Section A1.1.5 presents the set up of the Leitz Wetzler binocular microscope for analysing the samples.

A1.1.2. Field trial and sample preparation, University of Leeds, UK

The University of Leeds, UK, allowed access to three mature *Metasequoia glyptostroboides* trees growing on campus to carry out a field trial of the coring procedure and to allow the sample preparation methods to be tested (Figure A1.1). The School of Geography at the University of Leeds, UK, supplied a Sunnto increment borer for an initial sampling period (23 July to 1 September 2002).

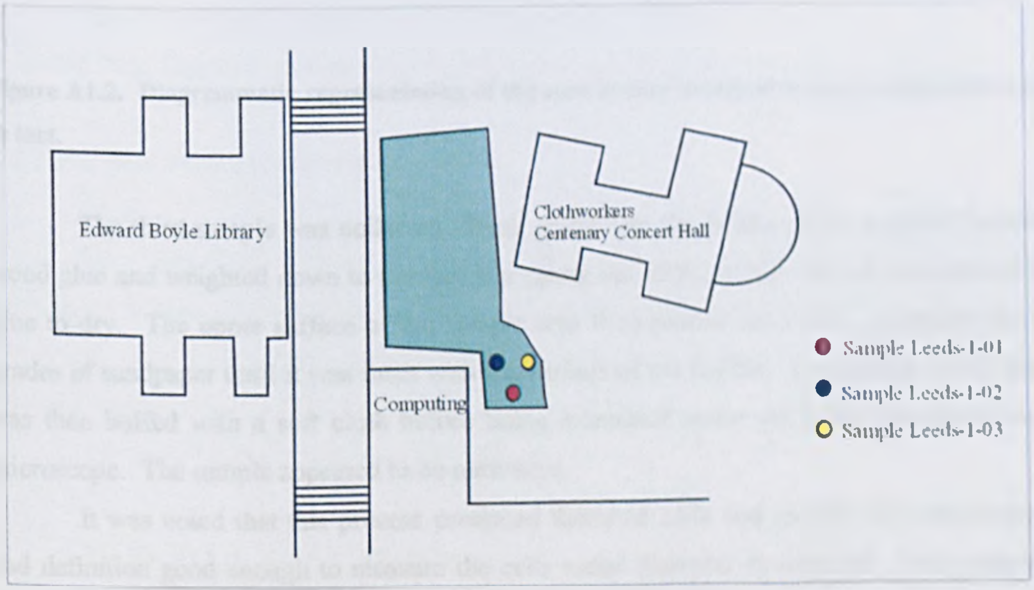

Figure A1.1. Location of samples taken at University of Leeds.

Using the Sunnto incremental borer, Sample Leeds-1-01 was collected on 25 July 2002. On removal from the tree the core broke up into small pieces (~0.5cm long) these were kept in the correct order within the extractor and it was possible to use a marker pen to mark way up whilst the sample was still in the corer. However, when the pieces were removed from the extractor to be placed sequentially into a straw for storage it was noted that the sample twisted, shifting the marked line by ~180° then flipping back several times along the length of the core.

A second sample was taken (Leeds-1-02) in an attempt to correct this problem. Although this sample again broke up into small pieces it was not seen to twist. Both of these samples were short being between 7 and 10 cm. It was found that it was not possible to section these samples as they were too small to work on. After consulting colleagues at the Univeristy of Sheffield, it was decided to collect a third sample (Leeds-1-03) that would be dried before being sectioned. The workshop at the University of Leeds, School of Earth Sciences, made a prototype holder onto which the dried sample could be glued to make it more manageable (Figure A1.2.).

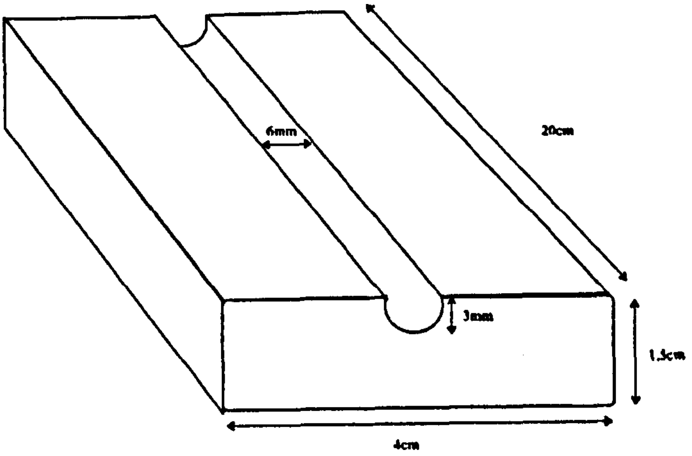

Figure A1.2. Diagrammatic representation of the core holder designed to store and preserve cores in tact.

The third sample was collected, dried, glued into the holder using standard household wood glue and weighted down to prevent it popping out of the holder the left overnight for the glue to dry. The upper surface of the sample was then sanded with three progressively finer grades of sandpaper until it was flush with the surface of the holder. The surface of the sample was then buffed with a soft cloth before being examined under the Leitz Wetzler binocular microscope. The sample appeared to be untwisted.

It was noted that this process produced distorted cells and in only one ring increment had definition good enough to measure the cells radial diameter as required. Data analysis of this sample showed that distortion of the cells had occurred during this process and accurate results were not possible using this method.

It was decided that the collection of larger, more manageable blocks of wood might produce better sections, and so the methods described in Section A1.1.3 were used.

A1.1.3. Field trial Tapton Experimental Gardens, University of Sheffield, UK

Tapton Experimental Gardens in Sheffield, UK, gave permission to collect samples from 18 different species of conifers (for sample list see Table A1.1 below). Although in almost all cases there is only one sample of each species it was envisaged that this would be sufficient to allow comparison with observed leaf retention times.

Samples from branches and one small trunk (*Taxus baccata* TAP-01-19) were collected using a domestic saw and cut into blocks of ~1cm^2 and placed into 35mm film cases for storage prior to sectioning. Each film case was labeled with the date of collection, specimen number, species name and the location. The blocks were immediately immersed in a solution of :-

Methylated spirits	100ml
Formalin	5ml

(40% solution of formaldehyde).

This solution prevents shrinkage of the wood and distortion of the cells. The cases were then left for several weeks to allow the wood to absorb the solution.

A1.1.4. Sectioning and sample preservation

The following sections discuss the methods used to section and preserve the samples collected from Tapton Experimental Gardens following the guidelines of Ives (2001).

A1.1.4.1. Microtome sectioning method

The School of Biology, University of Leeds, UK, provided a Beck 3880/A288 microtome to section the samples. The thickness of the sections is dependent on the hardness of the wood, with softer wood requiring thicker sectioning to prevent disintegration, but the average is approximately 20-30 microns.

The standard technique used for section preparation was followed:-

1 Set the sample block in the vice.

2 Set the block until it touches the blade, flood the knife with cutting fluid (soluble

oil 15ml, mild detergent e.g. washing up liquid 15ml, methylated spirit 125ml and water up to 250ml) and trim the surface until a full section is cut.

3 Two sections should be cut and discarded as they may be damaged by the surface trimming, then slide the third one on to a wet microslide. Wetting helps to prevent crinkling. Dry and flatten with a paper towel and view under x40 or x100 magnification.

4 Examine the cells to see if they are broken.

5 Check other areas to see if they are complete and or distorted. All these defects can only be seen under a moderately high magnification.

6 Check to see if there are "tramlines" across the section indicating a nick in the knife edge.

7 If all is satisfactory continue cutting sections.

9 Wash sections with water to which a little mild detergent is added to remove debris then rinse.

10 Sandwich sections between microslides and clip or bind together and label. Store in water (with a little disinfectant added if it is to remain in water more than a day or so), until sufficient are cut and ready for staining.

This method was tested using sample TAP-01-1, *Taxodium distichum* and was found to be very inefficient. The sample had a tendancy to split horizontally whilst sections were being cut, the knife was not long enough to get a full sample from across the block and it proved impossible to get a section that was thin enough to use under the microscope. A second sample was tested, sample TAP-01-2 *Cedrus deodara*, to confirm that this was not because of the wood type in the first sample being difficult to handle. It was found that the same problems occurred with the second sample.

A.1.1.4.2. Band saw method

As problems had been encountered with other methods a new way of sectioning the samples had to be devised. A test sample TAP-01-3, *Pinus rigida* was sanded on one end using fine sandpaper, then buffed with a soft cloth. This was then taken to the workshop at the School of Earth Sciences, University of Leeds, UK where the technicians cut a transverse section from the sanded/buffed end which was approximately 2mm in thickness. This section was then glued to a thin section slide (sanded/buffed side down) using Eukitt™ acrylic medium. The sample was left for several days to dry then was sanded down manually using fine sandpaper then buffed with a soft cloth. The sample was checked under the microscope as in section A.1.1.4.1 and was found to give very good results. This method was therefore employed to section the full set of modern specimens.

A1.1.4.3. Staining and clearing

Once the samples had been sectioned as in A1.1.4.2 above, the following method was used to stain and clear them (Ives, 2001).

By using a combination of stains that attach themselves to different wood tissues, it is possible to differentiate between the general mass of woody fibers and the parenchyma and ray cells. It was decided that the samples should be stained individually in tubs to prevent them being mixed up. Stain was made up according to the following formulas.

Safranin (sometimes spelt safranine), stains nearly all wood a reddish colour.

Safranin	3gms
Methylated Spirit	100ml
Distilled Water	100ml
Formaldehyde 40% Solution	2ml

The Safranin is mixed with the methylated spirit, then the other ingredients are added before the mixture is shaken. The solution was left for a minimum of one day before use.

Alcian Blue stains young parenchyma and bark tissue.

Alcian Blue	1.5gms
Distilled Water	125ml
Glacial Acetic Acid	3 drops
Formaldehyde 40% Solution	2 ml

The solution was mixed and left for a minimum of one day before use.

The procedure followed is detailed in Figure A1.3 and discussed below. Tubs were set out as shown in Figure A1.3 and each was filled with the required reagent. The following sequence was then followed.

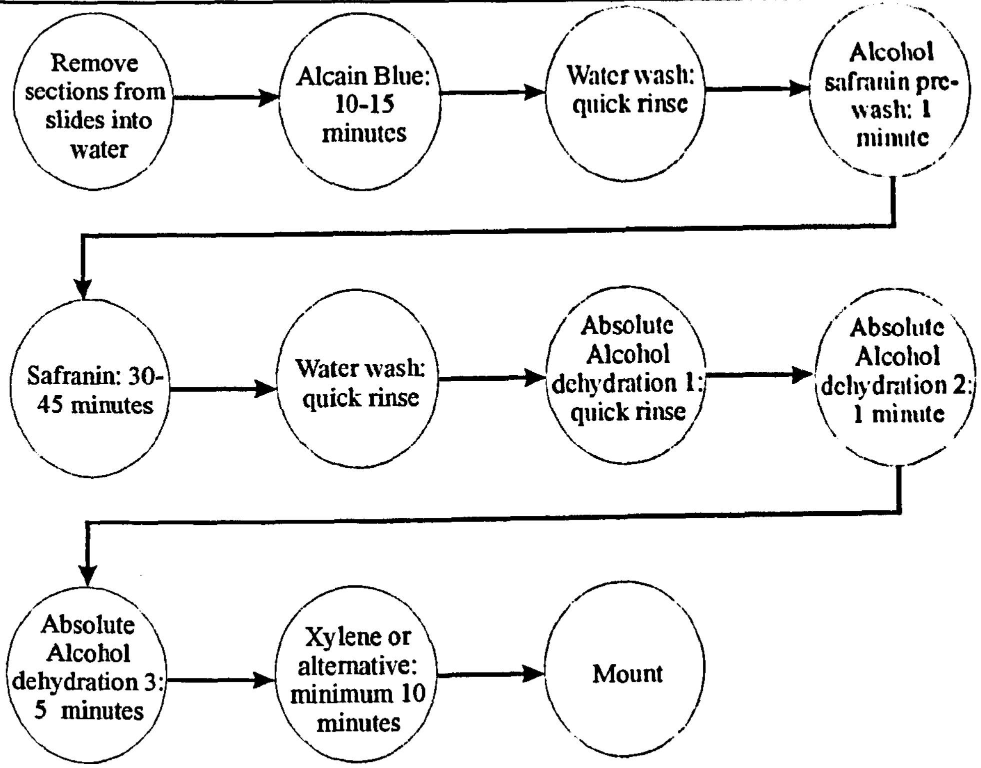

Figure A1.3. Staining and mounting sequence (Ives, 2001).

(i) The sample, still attached to the slide, was gently washed in water.

(ii) The sample was removed from the water and placed in the Alcian Blue and stained for 10-15 minutes, or as long as required of the individual sample. It should be noted that not all wood sections take the blue stain. Often Safranin adds to the Alcian Blue changing it to a darker purple colour.

(iii) The sample was transferred to a tub of water and rinsed until free of surplus Alcian Blue.

(iv) The sample was rinsed with pre-Safranin alcohol to prevent contamination of the Safranin with Alcian Blue. This alcohol is one having previously been used as the second and third dehydration alcohols and is heavily contaminated with washed out Safranin.

(v) The sample was transferred directly to the Safranin and stained for 30-45 minutes or as long as required for individual samples (many only need 2 minutes). Overstaining can be reduced by increasing the times in the rinse water or alcohol 1.

(vi) The sample was quickly rinsed in water to remove surplus stain.

(vii) The sample was then dehydrated through the three alcohols. Weaker alcohols remove much of the Safranin stain. The sample was left in alcohol 2 for about 1 minute and at least several minutes in alcohol 3.

(viii) The sample was then cleared in Xylene to remove any remaining water for 10 minutes which reacted with the Eukitt™ to unstick the sample from the slide.

The samples were now ready to be mounted using the following methods.

A1.1.4.4. Mounting

Eukitt™ acrylic resin medium was used to mount the sections. It hardens at the coverglass edges in 20 minutes but slides should be left for at least two days before cleaning.

The following procedure was used to mount the slides:

(i) Rubber gloves were used as Xylene is readily absorbed into the skin and bloodstream.
(ii) A clean microslide was placed on a mounting card.
(iii) Mountant was spread evenly and fairly thickly over the mounting area with a dropper.
(iv) The section was removed from the Xylene with stamp forceps/tweezers. It was drained on a paper towel and arranged on the microslide.
(v) The sample was checked under the microscope for debris or folded corners.
(vi) The cover slip was placed gently on one end of the slide touching the Eukitt™, lightly pressing down with the fine forceps or an eraser of a pencil placed about 2mm from the balsamed edge of the cover whilst at the same time opening the stamp forceps so that the cover is resting on the lower leg only.
(vii) The cover slip was lowered gradually on the stamp forceps until they could be slid out from under the cover slip.
(viii) The edges were pressed down with the stamp forceps and then slid towards the centre to force out any air bubbles.
(ix) The slide was left at room temperatures for 10-15 minutes, then was checked for air bubbles. Any bubbles that had formed were removed by gently pressing the coverglass with the eraser of a pencil.

At the end of the drying period cleaning was carried out in two stages:

(i) Removal of surplus mountant.
(ii) Cleaning and polishing of the surface.

A scalpel was used for removing the surplus resin. When surplus resin was scraped off the surface was scrubbed with a small brush lubricated with an alcohol solution and dipped in an abrasive. The surface was then polished with a soft cloth. Clear nail varnish was then applied around the edges of the cover slips to seal them. However, it was found that the nail varnish melted the Eukitt™ allowing air bubbles to form under the glass therefore this method was abandoned. Several samples were prepared and stored in this way, however, It was noted upon examination after a few days that several of the samples had developed air bubbles whether or not nail varnish was applied. It was still possible to use these samples however it was decided not to apply cover slips to any further samples prepared.

A1.1.5. Leitz Wetzler binocular microscope

A Leitz Wetzler binocular microscope located in the Optics Laboratory at the School of Earth Sciences, University of Leeds, UK was used to examine both extant and fossil samples used within this project.

All measurements were carried out using a x25 eyepiece graticule with a x40 objective making the total magnification x1000. The scale of the graticule was calculated as per Figure A.1.4 below.

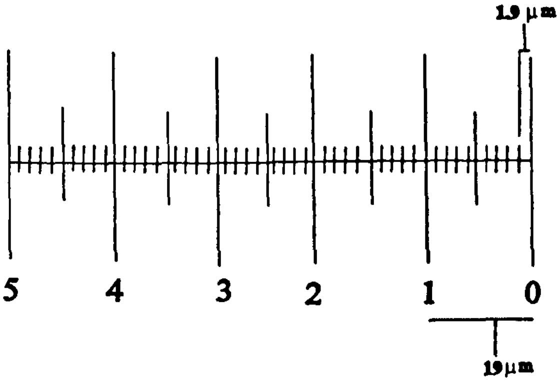

Figure A1.4. Scale of eyepiece graticule, one small increment equals 1.9µm, therefore each measurement was multiplied by 1.9 to convert to microns.

The estimated error on each measurement is calculated to be ~0.48µm (1/4 of a small increment in Figure A1.4).

A.1.1.6. Selection of extant conifer samples used

Extant conifer wood was examined from seven sources (Table A1.1.).

Seven samples were examined from a collection belonging to Jane Francis, School of Earth and Environment at the University of Leeds which were already thin sectioned and mounted. These samples had no numerical filing system therefore were given sample numbers as shown on Table A1.1 in order to aid referencing. The provenance within Australia of these samples is unknown and it is also unknown whether they originated from natural stands or cultivation. All of the samples are of large diameter, as indicated by the growth ring boundaries being straight in transverse section (in contrast to those of juvenile stems, which show pronounced curvature).

The one sample of *Araucaria araucana* provided by Paul Wignall (School of Earth and Environment, University of Leeds) was from a 12 year old tree grown in Leeds prepared using the methods outlined within Appendix A. This sample was important to include as there are very few genera with the long LLS of *Araucaria* and it could be used as an end member in the sample set. However it was noted that this may give anomalous results as it is from a juvenile tree and it is known that growth within the first few years of a trees life is erratic due to the tree putting all of its resources into increasing height before diverting energy into reproduction (Chapman, 1994). Therefore only the outer ring increments were used.

Eighteen samples of branch material and one sample of a small trunk (*Taxus baccata*, TAP-01-19) were collected from Tapton Experimental Gardens in Sheffield. All of these samples were sectioned and prepared at the University of Leeds (Appendix A). Being branch material of small diameter only the outer rings could be measured as with juvenile wood. The reason for collecting branch wood was twofold. Firstly, this collection of trees is an important resource for many research projects and it was important not to cause irreparable damage to the trees. Secondly, it is not always possible to determine whether fossil wood samples originated from a branch or the trunk of a tree. Various authors have expressed concern that there are important differences between wood anatomy in samples taken from different areas within the tree that require accounting for in any research on wood (Chapman, 1994; Falcon-Lang, 2005a). Chapman (1994) showed that within branches the cells are small and the transition from early to latewood is gradual whereas the cells in trunk wood are larger with less latewood being present in the upper trunk than the lower trunk and stump, however these differences are not easy to distinguish in isolated sections of wood. Therefore it needed to be established that the calculations used would hold true for both branch and trunk material. Two samples collected (*Metasequoia glyptostroboides* (TAP-01-11) and *Araucaria araucana* (TAP-01-06)) were not used in this study as it was found that all of the rings present were less than 30 cells in width. Sample TAP-01-17 (*Sequoia sempervirens*) was taken from a pruned branch collected in order to compare the results with an un-pruned branch of the same species (TAP-01-16) to establish if damage to the tree made any significant difference to the results obtained. The wide range of samples from a single climatic regime were selected in order to assess whether there was a clear genetic signal within the samples, as it is unusual for conifers with such a large range of leaf retention times to grow within a single natural community therefore only a cultivated stand could be used for this purpose.

A *Taxodium distichum* sample obtained from Brian Axsmith from the University of Southern Alabama campus, USA was prepared at the University of Leeds (Appendix A). This sample was obtained as it represents a species of the few conifers which are deciduous and could thus be used as an end member within the sample set.

Thirteen samples obtained fromVanessa Thorn at the University of Wellington, New Zealand were from natural stands, cultivation and a range of altitudes within New Zealand. All samples were sectioned and prepared at the University of Leeds (Appendix A). Four of these samples were not used within this study. *Dacrydium cupressinum* NZ-03-1/5 were not used as they contained false rings and it was not clear where true ring boundaries occurred. *Phyllocladus trichomanoides* NZ-03-8 was not used as all rings were <30 cells wide and

Cupressus macrocarpa NZ-03-11 was not used as it was not possible to obtain a known leaf life-span for this species. These samples were obtained in order to assess whether the same species showed differences in wood anatomy when grown under different climatic regimes or altitudes therefore representing a climatic control to wood growth. They were also obtained in order to have more representatives of the Southern Hemisphere species.

One sample of *Taxodium mucronatum* from Mexico was examined at the Royal Botanic Gardens at Kew, UK as this represents the only recognized extant evergreen *Taxodium* species. It was not possible to establish what its leaf life-span is at present as no work in this area has been carried out therefore it is not included within the calibration dataset. However, as both evergreen and deciduous forms occur today either or both forms may have occurred in the fossil record, it was felt that the values obtained could be used as a comparison should evergreen fossil *Taxodioxylon* (most similar to modern *Taxodium*) wood be found within the fossil sample set. One sample of *Taxodium distichum* from Florida was examined following prior examination of the sample obtained from Brian Axsmith as this appeared to be producing anomalous results therefore it was felt that at least one further sample should be examined in order to establish whether these results were an accurate representation of the species. One sample of *Metasequoia glyptostroboides* from China was examined as it is thought to be the NLR of *Metasequoiaoxylon* in the fossil record which appears to be very common in previous work on High Arctic fossil wood and it also represented a further example of a rare deciduous conifer for inclusion in the database. All of these samples are from mature stems.

One *Picea obovata* sample was obtained from Eugene Lopantin from the University of Joensuu, Finland as it represents a modern high-latitude species from the northern forest-tundra transition zone in the Komi Republic, Russia at 66°N. This sample is from a mature stem of a visibly healthy tree with no signs of near-neighbour competition or forest management and was from an area that experiences the most extreme light conditions of all modern conifers of large, non-prostrate form. The known leaf life-span of this species was not specifically found, however, it is classified in several publications as being a subspecies of *Picea abies* with a leaf life-span of 5-7 years and this has been assumed to be its habit within this thesis (Nisbet, 1893; Vidakovic, 1991).

Table A1.1. Table showing full dataset for extant samples (^{C} = cultivated stand material, ^{N} = natural stand material and $^{?}$ = unknown origin).

Species/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Percentage Skew
Branch Material					
Taxodium distichum					
TAP-01-1^{C}	5	88	29	26	+22
TAP-01-1^{C}	6	90	28	25	+36
Mean		89	29	25	+29
Range of Values		88-90	28-29	25-26	+22-36
Cedrus deodara					
TAP-01-2^{C}	1	67	15	10	+27
TAP-01-2^{C}	10	64	25	16	+12
Mean		65	20	13	+20
Range of Values		64-67	15-25	10-16	+12-27
Pinus rigida					
TAP-01-3^{C}	2	69	37	24	+16
Mean		69	37	24	+16
Range of Values		69	37	24	+16
Larix leptolepis					
TAP-01-4^{C}	13	77	52	40	-8
Mean		77	52	40	-8
Range of Values		77	52	40	-8
Cedrus libani					
TAP-01-5^{C}	8	73	19	14	+54
Mean		73	19	14	+54
Range of Values		73	19	14	+54
Sequoia dendron					
TAP-01-7^{C}	7	78	36	28	+23
TAP-01-7^{C}	8	71	39	28	+6
Mean		74	38	28	+15
Range of Values		71-78	36-39	28	+6-23
Abies veitchii					
TAP-01-8^{C}	3	71	30	22	+34
TAP-01-8^{C}	4	72	20	15	+12
Mean		71	25	18	+23
Range of Values		71-72	20-30	15-22	+12-34
Pseudotsuga menziesii					
TAP-01-9^{C}	3	70	30	21	-17
TAP-01-9^{C}	6	62	20	12	+48
Mean		66	25	16	+15
Range of Values		62-70	20-30	12-21	-17-+48
Pinus strobus					
TAP-01-10^{C}	9	66	33	22	+13
TAP-01-10^{C}	10	76	18	14	+18
TAP-01-10^{C}	11	74	22	16	+8
Mean		72	24	17	+13
Range of Values		66-76	18-33	14-22	+8-18

Continued ....

Species/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Percentage Skew
Pinus banksiana					
TAP-01-12^{C}	3	77	25	19	+43
TAP-01-12^{C}	4	66	21	14	+9
Mean		71	23	17	+26
Range of Values		66-77	21-25	14-19	+9-43
Saxegotheae conspicua					
TAP-01-13^{C}	2	66	19	12	+20
TAP-01-13^{C}	5	74	26	20	+34
TAP-01-13^{C}	6	70	14	10	+68
Mean		70	20	14	+44
Range of Values		66-74	14-26	10-20	+30-68
Larix decidua					
TAP-01-14^{C}	1	87	48	41	-22
TAP-01-14^{C}	2	76	53	40	-12
Mean		82	50	41	-17
Range of Values		76-87	48-53	40-41	-22- -12
Larix decidua					
TAP-01-15^{C}	3	79	50	40	-10
TAP-01-15^{C}	4	82	64	52	-8
TAP-01-15^{C}	5	82	51	42	-34
TAP-01-15^{C}	2	82	52	43	-15
Mean		81	54	44	-17
Range of Values		79-82	50-64	40-52	-34- -8
Picea abies					
TAP-01-18^{C}	2	78	35	27	-36
TAP-01-18^{C}	4	71	29	21	-40
TAP-01-18^{C}	5	77	36	28	-12
TAP-01-18^{C}	6	73	47	35	-13
Mean		75	37	27	-25
Range of Values		71-78	29-47	21-35	-40- -12
Prumnopitys taxifolia					
NZ-03-2^{N}	7	87	14	12	+52
NZ-03-2^{N}	11	86	14	12	+21
Mean		87	14	12	+36
Range of Values		86-87	14	12	+21-52
Prumnopitys taxifolia					
NZ-03-6^{N}	57	90	21	19	+39
Mean		90	21	19	+39
Range of Values		90	21	19	+39
Sequoia sempervirens					
TAP-01-16^{C}	6	59	28	16	+19
TAP-01-16^{C}	4	67	22	15	+6
Mean		63	25	16	+13
Range of Values		59-67	22-28	15-16	+6-19
Damaged Branch Material					
Sequoia sempervirens					
TAP-01-17^{C}	4	72	26	19	+26
TAP-01-17^{C}	5	66	24	17	+19
TAP-01-17^{C}	7	74	26	19	-1

Continued ....

Species/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Percentage Skew
Mean		71	25	19	+15
Range of Values		66-74	24-26	17-19	-1-+26
Trunk Material					
Tsuga canadensis					
A1-1	2	88	32	28	+21
A1-1	3	81	34	27	+19
A1-1	4	81	33	27	+21
Mean		83	33	28	+20
Range of Values		81.88	32.34	27.28	+19.21
Pinus strobus					
A1-2	5	86	32	28	+26
A1-2	6	91	31	28	+33
Mean		88	31	28	+29
Range of Values		86-91	31-32	28	+26-33
Larix occidentalis					
A1-3	1	87	50	44	-4
A1-3	2	94	51	47	-4
A1-3	3	93	48	45	+2
A1-3	4	91	51	46	-1
A1-3	5	90	54	49	-10
A1-3	6	86	59	51	-21
Mean		90	52	47	-6
Range of Values		86-94	48-59	44-51	-21-+2
Pseudotsuga menziesii					
A1-4	1	78	41	32	+9
A1-4	2	80	39	31	+10
A1-4	3	80	44	35	+5
A1-4	4	79	43	34	+9
Mean		79	42	33	+8
Range of Values		78-80	39-44	31-35	+5-10
Picea sitchensis					
A1-5	1	89	29	26	+27
A1-5	2	85	33	28	+28
A1-5	3	87	37	33	+15
A1-5	4	87	34	29	+17
Mean		87	33	29	+22
Range of Values		85-89	29-37	26-33	+15-28
Pinus contorta					
A1-6	1	82	42	35	+9
A1-6	2	80	40	32	+16
A1-6	3	76	41	31	+5
A1-6	4	79	33	26	+30
A1-6	5	80	34	27	+27
A1-6	7	78	35	28	+23
A1-6	8	78	38	30	+15
Mean		79	38	30	+18
Range of Values		76-82	33-42	26-35	+5-30
Juniperus virginiana					
A1-7	1	82	30	25	+21
A1-7	2	81	33	27	+15

Continued ....

Species/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Percentage Skew
A1-7	3	85	25	21	+25
Mean		83	29	24	+21
Range of Values		81-85	25-33	21-27	+15-25
Araucaria araucana					
LEEDS-02-1^{C}	1	70	27	19	+27
LEEDS-02-1^{C}	2	68	26	18	+32
LEEDS-02-1^{C}	3	66	19	13	+26
LEEDS-02-1^{C}	5	65	27	18	+26
Mean		67	25	17	+28
Range of Values		65-70	19-27	13-19	+26-32
Taxus baccata					
TAP-01-19^{C}	2	61	16	10	+56
TAP-01-19^{C}	3	67	22	15	-1
Mean		64	19	12	+28
Range of Values		61-67	16-22	10-15	-1-+56
Taxodium distichum					
AME-05-1^{N}	2	96	31	30	+36
AME-05-1^{N}	3	96	33	32	+32
AME-05-1^{N}	4	96	30	29	+33
AME-05-1^{N}	7	93	33	30	+26
AME-05-1^{N}	8	95	27	25	+45
AME-05-1^{N}	10	96	40	38	+17
AME-05-1^{N}	12	96	30	29	+37
Mean		95	32	30	+32
Range of Values		93-96	27-40	25-38	+17-45
Pseudotsuga menziesii					
NZ-03-9^{C}	3	82	44	37	+4
NZ-03-9^{C}	4	81	41	33	-5
NZ-03-9^{C}	5	83	43	35	+11
NZ-03-9^{C}	6	86	37	32	-1
NZ-03-9^{C}	7	88	44	38	-5
Mean		84	42	35	+1
Range of Values		81-88	37-44	32-38	-5-+11
Podocarpus totara					
NZ-03-3^{N}	1	93	16	15	+51
NZ-03-3^{N}	2	93	23	21	+33
NZ-03-3^{N}	3	87	13	11	+32
NZ-03-3^{N}	8	92	15	20	+53
NZ-03-3^{N}	9	92	19	17	+31
NZ-03-3^{N}	11	93	15	14	+31
NZ-03-3^{N}	21	94	14	13	+64
NZ-03-3^{N}	29	94	18	17	+39
NZ-03-3^{N}	30	93	22	21	+47
NZ-03-3^{N}	31	94	16	15	+53
Mean		93	17	16	+43
Range of Values		87-94	13-23	11-21	+31-64
Pinus radiata					
NZ-03-4^{C}	2	95	18	17	+31
NZ-03-4^{C}	1	94	14	13	+21
Mean		94	16	15	+26
Range of Values		94-95	14-18	13-17	+21-31

Continued ....

Species/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Percentage Skew
Prumnopitys ferrugina					
NZ-03-7^N	4	93	17	15	+37
NZ-03-7^N	6	92	26	24	+9
Mean		93	21	20	+23
Range of Values		92-93	17-26	15-24	+9.37
Pinus radiata					
NZ-03-10^C	2	82	31	25	-36
NZ-03-10^C	3	89	30	27	-35
NZ-03-10^C	5	90	31	28	+27
NZ-03-10^C	7	88	27	23	-3
Mean		87	30	26	-12
Range of Values		82-90	27-31	23-28	-36-+27
Podocarpus totara					
NZ-03-12^N	4	94	29	27	+21
NZ-03-12^N	19	92	13	12	+35
NZ-03-12^N	21	94	18	17	+26
NZ-03-12^N	22	94	9	8	+49
NZ-03-12^N	23	94	9	9	+27
NZ-03-12^N	24	91	19	18	+36
NZ-03-12^N	1	91	14	13	+22
NZ-03-12^N	2	95	17	16	+46
Mean		93	16	15	+33
Range of Values		91-95	9-29	8-27	+21-49
Agathis australis					
NZ-03-13^C	17	93	16	15	+43
NZ-03-13^C	19	94	18	17	+6
Mean		93	17	16	+24
Range of Values		93-94	16-18	15-17	+6-43
Metasequoia glyptostroboides					
KEW-06-1^N	1	92	56	51	-15
KEW-06-1^N	2	95	47	45	+3
Mean		93	52	48	-6
Range of Values		92-95	47-56	45-51	-15-+3
Taxodium distichum					
KEW-06-3^N	1	95	32	31	-4
KEW-06-3^N	2	93	45	42	-7
KEW-06-3^N	3	95	41	39	+12
Mean		94	39	37	+1
Range of Values		93-95	33-45	31-42	-7-+12
Picea obovata					
RUSS-07-1^N	28	85	29	25	+33
RUSS-07-1^N	29	87	33	29	+30
RUSS-07-1^N	30	86	30	26	+27
RUSS-07-1^N	47	89	36	32	+12
RUSS-07-1^N	48	89	35	31	+21
RUSS-07-1^N	3	89	26	23	+28
RUSS-07-1^N	4	89	36	32	+20
RUSS-07-1^N	5	90	31	28	+33
RUSS-07-1^N	6	89	32	28	+33
RUSS-07-1^N	7	87	38	33	+22

Continued ....

Species/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Percentage Skew
Mean		88	32	29	+26
Range of Values		85-90	26-38	23-33	+12-33
Trunk Material (No LLS)					
Taxodium mucronatum					
KEW-06-2^{N}	1	82	8	7	+57
Mean		82	8	7	+57
Range of Values		82	8	7	+57

Appendix B – Fossil wood

Table B1.1. Table showing fossil conifer wood samples examined. Sample numbers were given by the collector of the samples. Those from Antarctica are British Antarctic Survey catalogue numbers. * This is the number of rings used for palaeoenvironmental analysis, more may be present but were not included either because they were badly damaged or unclear

Sample N°	Form Genus	Location	Approximate distance from centre of trunk/branch (mm)	Presumed Material Type Branch (B) Trunk (T)	N° of Growth Rings Present *	N° of Growth Rings Measured	Notes
SVALBARD							
LD101	Type G (*Juniperoxylon*)	Lumdstromdalen, Spitsbergen	1.97	B	6	1	Compression wood present. Close to centre of stem. Poor preservation. One false ring in summer wood (ring 6 @0.35mm).
LD102	Type D (*Cedroxylon*)	Lumdstromdalen, Spitsbergen	90	T	5	4	High proportion of split rings.
LD105	Type B (*Piceoxylon*)	Lumdstromdalen, Spitsbergen	65	T	13	5	Good preservation but some bending within rings.
LD108	Type I (*Araucariopitys*)	Lumdstromdalen, Spitsbergen	80	T	36	5	Poor preservation with a majority of split rings. One definite false ring (ring 5 @ 1.32mm) in autumn wood and possibly more .
LD120	Type H (*Protocedroxylon*)	Lumdstromdalen, Spitsbergen	0.95	B	35	4	Close to centre of stem. False rings present in summer wood (ring 16?, ring 17 @0.09mm, ring 18 @ 0.09mm, ring 26 @0.16mm, rings 27-31?). Possibly compression wood.
LD123	Type C (*Laricioxylon*)	Lumdstromdalen, Spitsbergen	1	B	49	5	Close to centre of stem. Contains compression wood and possibly one false ring (ring 43 @0.32mm).

Continued .....

Sample N°	Form Genus	Location	Approximate distance from centre of trunk/branch (mm)	Presumed Material Type Branch (B) Trunk (T)	N° of Growth Rings Present *	N° of Growth Rings Measured	Notes
LD126	Type C (*Lariciaxylon*)	Lumdstromdalen, Spitsbergen	0.61	B	48	5	Very narrow rings close to centre of stem. Outer edge poorly preserved. False rings present (ring 11 @ 0.30mm, ring 13 @ 0.28mm, ring 17 @ 0.30mm, ring 44 @ 0.35mm) appearing to have formed in late summer.
LD129	Type F (*Taxodiaxylon*)	Lumdstromdalen, Spitsbergen	1.77	B	16	5	Close to centre of stem. False rings present (ring 5 @ 1.11mm and ring 9 @ 0.73mm) appearing to have formed in late summer/early winter.
LD130	Type J (*Xenoxylon*)	Lumdstromdalen, Spitsbergen	95	T	11	5	Contains a lot of bent and split rings.
LD131	Type F (*Taxodiaxylon*)	Lumdstromdalen, Spitsbergen	Unclear	T	21	5	Contains a high proportion of deformed and split rings.
LD132	Type L (*Cupressinoxylon*)	Lumdstromdalen, Spitsbergen	1.14	T	27	5	Small trunk. Poor preservation with deformed and split cells. Rings close to centre of stem.
LD133	Type F (*Taxodioxylon*)	Lumdstromdalen, Spitsbergen	2.29	T	12	1	Close to centre of stem. High proportion of rot and deformation present.
SN25 4	Type K (*Taxoxylon*)		4.09	B	20	5	This sample is close to the centre of the branch. There is some minor splitting and bending present. There may be compression wood also present. False rings present (ring 2 @ 0.06mm, ring 8 @1.11mm and ring 10 @0.53mm) in spring, summer and autumn.

Continued .....

Sample N°	Form Genus	Location	Approximate distance from centre of trunk/branch (mm)	Presumed Material Type Branch (B) Trunk (T)	N° of Growth Rings Present *	N° of Growth Rings Measured	Notes
CANADIAN ARCTIC							
RR102	Type B (*Piceoxylon*)	Roll Rock Valley	60	T	6	3	Good preservation but some splitting.
RR111	Type A (*Pinuxylon*)	Roll Rock Valley	20	T?	63	5	This sample has mainly well preserved rings however there is a high proportion of false rings present (~15 of the 63) that appear to have formed in all seasons. Some rings split or slightly bent.
RR113	Type B (*Piceoxylon*)	Roll Rock Valley	1.30	B	43	4	Close to centre of stem. False rings present in several rings but preservation is poor making them difficult to identify. Some narrow rings. One ring (18) appears to have two sets of false rings @ 0.29mm and 0.45mm in spring and summer wood.
RR121	Type D (*Cedroxylon*)	Roll Rock Valley	102	T	37	3	This sample contains a lot of deformation (bending, shearing and splitting).
RR122	Type A (*Pinuxylon*)	Roll Rock Valley	68	T	49	1	This sample has some rot patches. Four rings display false rings in the spring and summer wood (9,10, 13 and 38) and one that appears to have formed in autumn (5).
RR123	Type D (*Cedroxylon*)	Roll Rock Valley	48	T	22	1	This sample contains a lot of deformation (bending, shearing and splitting). Some rot present also.
BL125	Type E (*Palaepiceoxylon*)		47	T	59	5	There is a lot of rot, splitting and bent rings in this sample. Only one possible false ring was identified (ring 31 @ 0.13mm) within spring wood although this may be a band of crushed cells.

Continued .....

Sample N°	Form Genus	Location	Approximate distance from centre of trunk/branch (mm)	Presumed Material Type Branch (B) Trunk (T)	N° of Growth Rings Present *	N° of Growth Rings Measured	Notes
E137	Type L (*Cupressinoxylon*)		1.26	B?	77	5	Close to centre of branch? Contains a lot of deformation (bending, splitting and rot).
E139	Type A (*Pinuxylon*)		0.79	B?	49	3	Close to centre of stem. Variable ring widths. A high proportion of rot and splitting.
E140	Type A (*Pinuxylon*)		85	T	29	5	There is a lot of rot and splitting present.
AUSTRALIA							
872/W16	Type R (Unidentified conifer)		4	B?	67	2	Irregular ring widths. Possibly branch but could be damaged trunk. Very poorly preserved with rot present. Large amount of compression wood (rings 23-35) and some false rings (ring 32 @ 0.19mm, late summer, ring 54 @ 0.71mm spring).
872/W17	Type M (*Podocarpoxylon*)		4	T	27	5	Poorly preserved with rot and bent rings present.
872/W104	Type R (Unidentified conifer)		Unclear	B	75	3	Poor preservation with rot and split rings present.
872/W128	Type R (Unidentified conifer)		Unclear	T	30	3	Contains a lot of deformation, rot patches and bent rings.
872/W149	Type R (Unidentified conifer)		2	B?	40	2	Contains a lot of rot and splits.
872/W166	Type M (*Podocarpoxylon*)		5	B?	14	5	Irregular ring boundaries, possibly due to preservation but could indicate branch material. Possibly false rings present. High proportion of rot and splits.
872/W167	Type M (*Podocarpoxylon*)		0.82	?	29	5	High proportion of rot present.

Continued .....

Sample N°	Form Genus	Location	Approximate distance from centre of trunk/branch (mm)	Presumed Material Type Branch (B) Trunk (T)	N° of Growth Rings Present *	N° of Growth Rings Measured	Notes
872/W168	Type R (Unidentified conifer)		5	?	46	1	Poor preservation with rot and deformed rings. False rings present (ring 24 @ 0.28mm, spring and ring 42 @ 0.26mm, spring)
ANTARCTICA							
5215	Type I (*Araucariopitys*)	Long Valley south side near Station II. James Ross Island	Unclear	T?	15	2	Contains a bent rings and rot. False rings present (ring 2 @ 0.97mm, ring 4 @ 2.82mm and ring 14 @ 4.58mm) in summer wood.
D421	Type S (Unidentified Araucarioid)	Lachmann Crags. South James Ross Island	3.17	B	45	5	Only transverse and radial slides available. Contains a lot of deformation, rot and bending. Close to centre of stem. Poor preservation with splitting in places. A high proportion of false rings predominantly in the summer wood but a small amount also in autumn wood.
DJ135.3	Type T (Unidentified Non Araucarioid)	Slope near moraine lake, east of Lachmann Crags, James Ross Island	19	T	15	5	Poor preservation with rot and splitting. A high proportion of crushing and bending.
DJ137.6	Type L (*Cupressinoxylon*)	South facing slope ~6km east of Cape Lamb. Vega Island	36	?	21	5	Contains split and bent rings. Some patches of rot also present.
DJ137..8	Type N (*Agathoxylon*)	South facing slope ~6km east of Cape Lamb. Vega Island	Unclear	T	27	5	Radial section poorly preserved. Straight ring boundaries. Contains rot and some splitting. False rings present (ring 4 @ 0.38mm and ring 15 @ 0.21mm) in autumn wood.

Continued …..

Sample N°	**Form Genus**	**Location**	**Approximate distance from centre of trunk/branch (mm)**	**Presumed Material Type Branch (B) Trunk (T)**	**N° of Growth Rings Present ***	**N° of Growth Rings Measured**	**Notes**
DJ141.3	Type N (*Agathoxylon*)	East side Lachmann Crags, James Ross Island	Unclear	T	22	2	Contains some crushing in cells at ring boundaries. False rings present (ring 2 @ 0.44mm and ring 4 @ 0.46mm) in summer wood.
DJ141.6	Type O (*Protophyllocladoxylon*)	East side Lachmann Crags, James Ross Island	19	B?	40	5	Contains crushing, bending and splitting.
DJ141.7	Type T (Unidentified Non Araucarioid)	East side Lachmann Crags, James Ross Island	Unclear	T?	8	1	Poor preservation with a lot of bending and splitting present. Straight ring boundaries.
DJ141.8	Type R (Unidentified conifer)	East side Lachmann Crags, James Ross Island	33	T	62	5	Transverse section only. Contains crushed and bent rings. One false ring present (ring 35 @ 0.31mm) in spring/summer wood. Ring width variable.
DJ141.13	Type M (*Podocarpoxylon*)	East side Lachmann Crags, James Ross Island	1.45	?	18	1	Close to centre of stem. Contains a lot of split rings and the boundaries are very feint in places.
DJ141.14	Type M (*Podocarpoxylon*)	East side Lachmann Crags, James Ross Island	12	T	27	5	Ring boundaries feint and high proportion of splitting and crushing.
DJ141.16	Type R (Unidentified conifer)		3	T	16	2	Transverse section only. Ring boundaries feint. Small amount of bending present. False ring present (ring 13 @ 1.5mm) in the autumn wood.
DJ144.2	Type M (*Podocarpoxylon*)	North west side of San Jose Pass, James Ross Island	1.48	T?	22	5	Close to centre of stem. High proportion of bending present.
DJ144.3	Type R (Unidentified conifer)	North west side of San Jose Pass, James Ross Island	29	B	32	5	Transverse section only. Ring widths variable. Contains some bending and areas of rot but generally good preservation. Two false rings present (ring 9 @ 0.46mm, spring summer; ring 23 @ 0.68mm, autumn).

Continued .....

B7

Sample N°	Form Genus	Location	Approximate distance from centre of trunk/branch (mm)	Presumed Material Type Branch (B) Trunk (T)	N° of Growth Rings Present *	N° of Growth Rings Measured	Notes
DJ144.5	Type P (*Sciadopityoxylon*)	North west side of San Jose Pass, James Ross Island	0.87	B	68	5	Ring widths variable. Close to centre of stem. High proportion of bent rings, some split and areas of rot. Two false rings present (ring 23 @ 0.43mm, ring 27 @ 0.26mm) in spring wood.
DJ144.7	Type I (*Araucariopitys*)	North west side of San Jose Pass, James Ross Island	2.48	T?	26	2	Poor preservation with a lot of bending and rot. Close to centre of stem.
DJ366.7	Type S (Unidentified Araucarioid)		2	?	11	4	Contains some bending and splitting of rings but well preserved. Three false rings present (ring 5 @ 0.37, summer; ring 8 @ 0.70mm autumn and ring 11 @ 0.40mm, autumn).
DJ451.3	Type T (Unidentified Non Araucarioid)	Knoll near San Jose Pass (N W side), James Ross Island	Unclear	T?	16	4	Straight boundaries. Contains some bending and splitting. Small patches of rot also present. Three false rings present (ring 8 @ 3.17mm, summer; ring 11 @ 0.33mm spring/summer and ring 13 @0.49mm, spring).
DJ451.4	Type F (*Taxodioxylon*)	Knoll near San Jose Pass (N W side), James Ross Island	15	T	8	2	Contains a lot of bending and splitting.
DJ455.1	Type F (*Taxodioxylon*)	South west side Abernethy Flats, Brandy Bay, James Ross Island	17	T	11	3	Contains some bending and a high proportion of splitting.
DJ455.3	Type Q (*Circoporoxylon*)	South west side Abernethy Flats, Brandy Bay, James Ross Island	3.5	B?	15	4	Contains rot, splitting and bending.
DJ458.1	Type F (*Taxodioxylon*)	South west side Abernethy Flats, Brandy Bay, James Ross Island	Unclear	T?	23	1	Poor preservation with straight boundaries. Contains a lot of rot, splitting and bending.

Continued .....

Sample N°	Form Genus	Location	Approximate distance from centre of trunk/branch (mm)	Presumed Material Type Branch (B) Trunk (T)	N° of Growth Rings Present *	N° of Growth Rings Measured	Notes
DJ462.2	Type Q (*Circoporoxylon*)	South west side Abernethy Flats, Brandy Bay, James Ross Island	6	T	22	5	Contains a lot of rot, bending and splitting.
DJ462.3	Type Q (*Circoporoxylon*)	South west side Abernethy Flats, Brandy Bay, James Ross Island	Unclear	T?	7	3	Straight boundaries. Contains a lot of rot and bending.
DJ462.5	Type F (*Taxodioxylon*)	South west side Abernethy Flats, Brandy Bay, James Ross Island	Unclear	T?	9	5	Straight boundaries. Contains bending and splitting.
DJ463.5	Type F (*Sciadopityoxylon*)	North west side of Stickle Ridge, James Ross Island	Unclear	Unclear	5	1	Poor preservation. Contains a lot of rot, bending and splitting.
DJ465.1	Type R (Unidentified conifer)	East Lachmann Crags, James Ross Island	8.67	?	9	3	Contains rot, bending and splitting.
DJ466.2	Type R (Unidentified conifer)	South west side of Abernethy Flats, James Ross Island	5	B	7	1	Contains bent rings. There are two false rings (ring 1 @ 0.60mm, ring 2 @ 0.24mm) in spring wood.
KG1703.23	Type M (*Podocarpoxylon*)	Alexander Island	Unclear	B	40	5	Rings pinch out. At least three false rings are present, two which appear to have two sets (rings 15, 16 and 34) formed in the summer. High proportion of deformation (bending, crushing, shearing).
KG1719.3b	Type R (Unidentified conifer)	Alexander Island	Unclear	T?	23	3	Only transverse section available as an acetate peel. This sample has some splitting, bending and rot within rings.

Continued .....

Sample N°	**Form Genus**	**Location**	**Approximate distance from centre of trunk/branch (mm)**	**Presumed Material Type Branch (B) Trunk (T)**	**N° of Growth Rings Present ***	**N° of Growth Rings Measured**	**Notes**
KG2814.252	Type R (Unidentified conifer)	Alexander Island	0.45	B	51	3	Transverse section only. Close to centre of stem. High proportion of false rings in spring, summer and autumn wood. A lot of crushing and bending of rings.
KG2814.256	Type R (Unidentified conifer)	Alexander Island	Unclear	B	32	1	Transverse section only. Very deformed containing crushed and sheared rings. Four obviously have false rings that appear to have formed in the summer, autumn and winter.
KG2817.20	Type R (Unidentified conifer)	Alexander Island	Unclear	?	32	2	Transverse section only. High proportion of deformation including crushing and shearing.
KG4626.1	Type F (*Taxodioxylon*)	Alexander Island	69	T	12	3	Identified at British Antarctic Survery. Transverse section only. False rings present. High proportion of deformation (bending, crushing and shearing).
KG4672.6	Unidentified	Alexander Island	0.74	B	38	4	Transverse section only. Close to the centre of the stem and poorly preserved. Rot obscuring some ring boundaries.
KG4710.1	Type R (Unidentified conifer)	Alexander Island	Unclear	B	26	4	Transverse section only. Very deformed with crushing, bending and shearing throughout. Some false rings in summer, autumn and winter wood.
KG4717.43	Type R (Unidentified conifer)	Alexander Island	2.34	B?	44	2	Transverse section only. Sample contains a deep wound. Close to the centre of the stem. Deformation obscuring some ring boundaries. High proportion of false rings in spring, summer and autumn wood.

Table B1.2. Database of previously published work on fossil conifer wood.

Form Genera	References
Abietoxylon Houlbert (1910)	Roy and Hills, 1972
Agathoxylon Greguss (1952:160, 169) [non Hartig 1848]	Greguss, 1970; Garcia, 1998; Ottone and Medina, 1998; Philippe *et al.*, 1999; 2004; Torres and Philippe, 2002
Araucariopitys Jeffrey (1907)	Kraüsel, 1949; Shilkina, 1967; Falcon-Lang and Cantrill, 2000; Poole and Cantrill, 2001
Araucarioxylon Kraus in Schimper (1870)	Kraüsel, 1949; Ilic, 1995 – modern hoop and bunya pine; Bamford, 2000; Falcon-Lang and Cantrill, 2000, 2001b; Francis, 2000; Poole and Cantrill, 2001; Heady *et al.*, 2002 – modern Wollemia pine
Arctoxylon Kraüsel (1949)	Kraüsel, 1949
Baieroxylon Greguss (1961)	Prasad and Lele, 1984; Torres and Philippe, 2002
Brachyoxylon Jeffrey in Hollick and Jeffrey (1909)	Kraüsel, 1949; Garcia, 1998; Philippe *et al.*, 2004
Cedroxylon Kraus (1872)	Gothan, 1907, 1910; Kraüsel, 1949; Arnold, 1953; Bannan and Fry, 1957; Shilkina, 1967
Circoporoxylon Kraüsel (1949)	Kraüsel, 1949;
Cupressinoxylon Goeppert (1850)	Gothan, 1907; Kraüsel, 1949; Shilkina, 1967; Poole *et al.*, 2001; Falcon-Lang, 2003
Dadoxylon Gothan (1910)	Gothan, 1910; Pant, 1965
Dammaroxylon Schultze-Motel (1966)	Meijer, 2000
Glyptostroboxylon Conwentz (1884)	Kraüsel, 1949; Suss and Schultka 2001; Fairon-Demaret, 2003; Visscher and Jagels, 2003 – modern wood
Ginkgo Linnaeus	Scott *et al.*, 1962
Juniperoxylon Houlbert (1910) em. Kraüsel, 1949	Kraüsel, 1949
Laricioxylon Greguss (1963)	Roy and Hills, 1972; Blokhina, 1985; Philippe *et al.*, 1999
Metapodocarpoxylon (Edwards) Dupéron-Laudoueneix and Pons, 1985	Bamford *et al.*, 2002
Metasequoiaoxylon Greguss (1967)	Basinger, 1981; Philippe *et al.*, 1999; Stockey *et al.*, 2001; Visscher and Jagels, 2003 – modern wood
Palaepiceoxylon Kraüsel (1949)	Kraüsel, 1949
Phyllocladoxylon Greguss (1953)	Gothan, 1907; Kraüsel, 1949; Francis, 2000; Cantrill and Poole, 2004
Piceoxylon Gothan (1905) em. Roy and Hills, 1972	Gothan, 1910; Kraüsel, 1949; Bannan and Fry, 1957; Roy and Hills, 1972
Pinuxylon Gothan (1905) em. Roy and Hills, 1972	Kraüsel, 1949; Shilkina, 1967; Roy and Hills, 1972; Meijer, 2000
Planoxylon Stopes (1916)	Kraüsel, 1949
Platyspiroxylon Greguss (1961)	Ramanujam, 1971; Philippe *et al.*, 1999

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Form Genera	References
Podocarpoxylon Gothan (1905)	Kraüsel, 1949; Patel, 1967a, 1967b – modern *Dacrydium* and *Podocarpus* respectively; Shilkina, 1967; Ramanujam, 1971; Falcon-Lang and Cantrill, 2000, 2001b; Cesari, 2001; Poole and Cantrill, 2001; Poole *et al.*, 2001; Cantrill and Poole, 2004
Protocedroxylon Gothan (1910)	Gothan, 1910; Medlyn and Tidwell, 1986
Protocupressinoxylon Eckhold (1921)	Kraüsel, 1949; Francis, 1983
Protojuniperoxylon Eckhold (1972)	Kraüsel, 1949
Protophyllocladoxylon Kraüsel (1939)	Kraüsel, 1949
Protopiceoxylon Gothan (1907)	Gothan, 1907, 1910
Protopinuxylon Eckhold (1922)	Kraüsel, 1949; Bamford, 2000
Protopodocarpoxylon Eckhold (1921)	Kraüsel, 1949; Bamford, 2000; Philippe, 2002
Protosciadopityoxylon Zhang, Zheng et Ding (1999)	Zhang *et al.*, 1999
Prototaxoxylon Walton (1925) em. Kraüsel and Dolianiti, 1958	Bamford, 2000
Sahnioxylon Bose and Sah (1954)	Falcon-Lang and Cantrill, 2001b; Poole and Cantrill, 2001; Cantrill and Poole, 2005
Sequoiaoxylon R.E.Torr (1923)	Basinger, 1981; Philippe *et al.*, 1999
Sciadopityoxylon Schamhausen (1877) em. Jurasky, 1928	Kraüsel, 1949
Spiroxylon Walton (1925)	Prakash and Srivastava, 1959
Taxaceoxylon Kraüsel and Jain (1964)	Roy, 1972
Taxodioxylon Hartig (1848) em. Gothan, 1905	Gothan, 1910; Kraüsel, 1949; Ramanujam and Stewart, 1969; Ramanujam, 1971; Falcon-Lang and Cantrill, 2000; Meijer, 2000; Fairon-Demaret *et al.*, 2003; Yang and Zheng, 2003
Taxoxylon Houlbert (1910)	Kraüsel, 1949
Xenoxylon Gothan (1905)	Gothan, 1907, 1910; Kraüsel, 1949; Arnold, 1953; Shilkina, 1967; Medlyn and Tidwell, 1975; Parrish and Spicer, 1988
General Papers	Phillips, 1941 – Gives identifying features for each genera of modern wood Kraüsel, 1949 – Initial identification key for fossil conifer wood Greguss, 1955 – Gives general wood characteristics for all modern gymnosperms Barefoot and Hankins, 1982 – Has useful details for key on modern and fossil wood Wilson and White, 1986 – Useful general information on wood structure Baas *et al.*, 2004 – List of microscopic features for softwood identification, modern but good for seeing what fine detail should look like.

Table B1.3. Table showing full dataset of calculated values of Percentage Diminution, Percentage Latewood and Ring Markedness Index for fossil samples plus the calculated leaf life-span.

Form Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
SVALBARD					
Juniperoxylon					
LD101	3	72	34	24	35
Mean		72	34	24	35
Range of Values		72	34	24	35
Cedroxylon					
LD102	4	77	19	15	126
LD102	5	80	25	20	60
LD102	8	79	15	12	177
LD102	3	81	19	16	110
Mean		79	20	16	110
Range of Values		77-81	15-25	12-20	60-177
Piceoxylon					
LD105	3	78	24	19	73
LD105	5	79	38	30	18
LD105	10	81	32	26	30
LD105	7	84	36	30	18
LD105	8	82	29	24	38
Mean		81	32	26	30
Range of Values		78-84	24-38	19-30	18-73
Araucariopitys					
LD108	2	77	22	17	90
LD108	3	79	20	15	115
LD108	5	80	31	25	33
LD108	14	84	25	21	58
LD108	21	86	22	19	77
Mean		81	24	19	69
Range of Values		77-86	20-31	15-25	33-115
Protocedroxylon					
LD120	17	86	40	34	10
LD120	18	87	40	35	9
LD120	14	72	25	18	85
LD120	13	82	32	27	27
Mean		82	34	28	21
Range of Values		72-87	25-40	18-35	9-85
Laricioxylon					
LD123	21	84	43	36	8
LD123	7	87	46	38	6
LD123	8	85	39	33	11
LD123	9	92	49	45	2
LD123	11	90	46	41	4
Mean		88	45	39	6
Range of Values		84-92	39-49	33-45	2-11
Laricioxylon					
LD126	22	80	56	45	3
LD126	21	82	50	40	4
LD126	20	74	51	38	6

Continued .....

Form Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
Laricioxylon cont.					
LD126	29	72	67	49	1
LD126	30	82	56	46	2
Mean		78	56	44	3
Range of Values		72-82	50-67	38-49	1-6
Taxodioxylon					
LD129	8	90	40	36	8
LD129	9	91	33	30	17
LD129	10	89	24	21	54
LD129	11	84	27	23	44
LD129	2	90	36	32	13
Mean		89	32	28	21
Range of Values		84-91	24-40	21-36	8-54
Xenoxylon					
LD130	2	91	16	15	128
LD130	3 bottom	94	13	12	172
LD130	5	93	22	21	58
LD130	7	92	13	12	170
LD130	3 top	94	29	27	25
Mean		93	19	17	89
Range of Values		91-94	13-29	12-27	25-172
Taxodioxylon					
LD131	11	91	26	24	40
LD131	12	93	40	37	7
LD131	14	92	25	23	44
LD131	15	91	26	24	39
LD131	18	94	28	26	30
Mean		92	29	27	25
Range of Values		91-94	25-40	23-37	7-44
Cupressinoxylon					
LD132	20	93	39	36	8
LD132	21	89	23	21	58
LD132	22	94	26	24	36
LD132	24	92	27	25	33
LD132	23	89	19	17	90
Mean		91	27	25	35
Range of Values		89-94	19-39	17-36	8-90
Taxodioxylon					
LD133	4	93	15	14	137
Mean		93	15	14	137
Range of Values		93	15	14	137
Taxoxylon					
SN25 4	9	88	15	14	144
SN25 4	10	88	9	8	290
SN25 4	12	93	19	17	89
SN25 4	22	92	12	11	206
SN25 4	24	91	11	10	246
Mean		90	13	12	180
Range of Values		88-93	9-19	8-17	89-290

CANADIAN ARCTIC

Continued .....

Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
Piceoxylon					
RR102	2	94	14	14	147
RR102	3	95	18	18	87
RR102	5	95	25	23	41
Mean		95	19	18	80
Range of Values		94-95	14-25	14-23	41-147
Pinuxylon					
RR111	4	93	27	25	34
RR111	10	93	38	36	8
RR111	21	93	17	16	110
RR111	26	94	22	20	62
RR111	36	94	27	26	30
Mean		93	26	24	36
Range of Values		93-94	17-38	16-36	8-110
Piceoxylon					
RR113	4	95	33	31	15
RR113	6	95	25	23	40
RR113	7	95	26	25	34
RR113	10	90	38	33	12
Mean		94	30	28	22
Range of Values		90.95	25-38	23-33	12-40
Cedroxylon					
RR121	4	96	36	35	9
RR121	7	96	34	32	13
RR121	15	92	32	30	18
Mean		95	34	32	13
Range of Values		92-96	32-36	30-35	9-18
Pinuxylon					
RR122	11	96	27	26	30
Mean		96	27	26	30
Range of Values		96	27	26	30
Cedroxylon					
RR123	11	95	35	33	11
Mean		95	35	33	11
Range of Values		95	35	33	11
Palaepiceoxylon					
BL125	22	94	21	20	64
BL125	23	93	28	26	30
BL125	27	94	21	19	68
BL125	30	93	17	16	108
BL125	31	92	31	28	22
Mean		93	23	22	50
Range of Values		92-94	17-31	16-28	22-108
Cupressinoxylon					
E137	10	88	29	26	30
E137	12	89	20	18	80
E137	6	94	16	15	122
E137	3	94	29	28	23
E137	2	94	38	36	8
Mean		92	27	25	35
Range of Values		88-94	16-38	15-36	8-122

Continued .....

Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
Pinuxylon					
E139	41	91	24	22	48
E139	42	91	43	39	5
E139	46	92	26	24	40
Mean		92	31	28	22
Range of Values		91-92	24-43	22-39	5-48
Pinuxylon					
E140	9	96	22	21	55
E140	18	95	26	25	34
E140	13	92	19	18	84
E140	10	95	28	26	28
E140	17	96	19	18	84
Mean		95	23	22	52
Range of Values		92-96	19-28	18-26	28-84
AUSTRALIA					
Type R (Unidentified conifer)					
872/W16	15	91	13	11	194
872/W16	16	91	15	17	95
Mean		91	14	14	136
Range of Values		91	13-15	11-17	95-194
Podocarpoxylon					
872/W17	1	92	24	22	46
872/W17	3	93	26	24	38
872/W17	4	94	26	25	34
872/W17	5	91	30	28	23
872/W17	7	86	24	20	60
Mean		91	26	24	38
Range of Values		86-94	24-30	20-28	23-60
Type R (Unidentified conifer)					
872/W104	21	85	28	24	39
872/W104	22	85	18	15	116
872/W104	50	84	25	21	53
Mean		85	24	20	62
Range of Values		84-85	18-28	15-24	39-116
Type R (Unidentified conifer)					
872/W128	2	92	17	16	112
872/W128	7	89	14	13	165
872/W128	12	92	13	12	171
Mean		91	15	14	147
Range of Values		89-92	13-17	12-16	112-171
Type R (Unidentified conifer)					
872/W149	27	90	20	18	78
872/W149	26	86	25	21	55
Mean		88	22	20	66
Range of Values		86-90	20-25	18-21	55-78
Podocarpoxylon					
872/W166	3	93	12	11	204
872/W166	4	94	14	13	156
872/W166	7	94	13	12	168
872/W166	8	95	12	11	197
872/W166	9	95	8	7	330

Continued .....

Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
872/W166 cont					
Mean		94	12	11	204
Range of Values		93-95	8-14	7-13	156-330
Podocarpoxylon					
872/W167	9	94	20	18	78
872/W167	11	94	26	24	38
872/W167	14	95	25	24	37
872/W167	17	96	21	21	59
872/W167	18	95	25	23	41
Mean		95	23	22	48
Range of Values		94-96	20-26	18-24	37-78
Type R (Unidentified conifer)					
872/W168	3	94	13	13	165
Mean		94	13	13	165
Range of Values		94	13	13	165
JAMES ROSS ISLAND ANTARCTICA					
Araucariopitys					
5215	1	90	14	12	171
5215	11	87	5	5	463
Mean		88	10	9	282
Range of Values		87-90	5-14	5-12	171-463
Type S (Unidentified Araucarioid)					
D421	19	80	7	5	430
D421	20	88	14	13	165
D421	21	92	13	12	187
D421	23	83	20	15	123
D421	24	92	13	12	176
Mean		87	13	11	196
Range of Values		80-92	7-20	5-15	123-430
Type T (Unidentified Non Araucarioid)					
DJ135.3	1	92	40	37	7
DJ135.3	3	91	32	30	18
DJ135.3	4 top	88	33	29	20
DJ135.3	4 bottom	90	29	27	26
DJ135.3	5	93	33	30	16
Mean		91	33	30	16
Range of Values		88-93	29-40	27-37	7-26
Cupressinoxylon					
DJ137.6	2	94	31	29	19
DJ137.6	9	89	24	21	53
DJ137.6	12	92	33	30	17
DJ137.6	13	94	33	31	16
DJ137.6	14	91	39	35	9
Mean		92	32	29	19
Range of Values		89-94	24-39	21-35	9-53
Agathoxylon					
DJ137.8	5	89	26	23	42
DJ137.8	9	92	26	24	40
DJ137.8	10	88	30	26	29

Continued .....

Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
DJ137.8 cont	11	93	25	23	42
DJ137.8	12	85	15	13	162
Mean		90	24	22	50
Range of Values		85-93	15-30	13-26	29-162
Agathoxylon					
DJ141.3	8	96	30	29	20
DJ141.3	10	95	33	31	14
Mean		96	31	30	17
Range of Values		95-96	30-33	29-31	14-20
Protophyllocladoxylon					
DJ141.6	1	72	26	19	76
DJ141.6	5	93	15	14	147
DJ141.6	12	93	17	16	107
DJ141.6	13	83	16	14	147
DJ141.6	14	83	9	8	314
Mean		84	17	14	141
Range of Values		72-93	9-26	8-19	76-314
Type T (Unidentified Non Araucarioid)					
DJ141.7	5	91	16	15	123
Mean		91	16	15	123
Range of Values		91	16	15	123
Type R (Unidentified conifer)					
DJ141.8	26	78	27	22	51
DJ141.8	27	77	31	24	37
DJ141.8	28	77	27	20	60
DJ141.8	1 bottom	82	34	28	22
DJ141.8	22 bottom	84	34	29	20
Mean		80	31	25	35
Range of Values		77-84	27-34	20-29	20-60
Podocarpoxylon					
DJ141.13	7	88	8	7	349
Mean		88	8	7	349
Range of Values		88	8	7	349
Podocarpoxylon					
DJ141.14	3	79	8	7	367
DJ141.14	4	87	16	14	147
DJ141.14	5	83	13	10	229
DJ141.14	6	89	24	21	56
DJ141.14	7	89	20	18	83
Mean		85	16	14	142
Range of Values		79-89	8-24	7-21	56-367
Type R (Unidentified conifer)					
DJ141.16	2	88	16	14	143
DJ141.16	3	91	13	12	188
Mean		89	14	13	164
Range of Values		88-91	13-16	12-14	188-143
Podocarpoxylon					
DJ144.2	4	82	16	14	146
DJ144.2	5	83	13	11	210
DJ144.2	6	90	23	20	61

Continued .....

Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
DJ144.2 cont	7	93	21	20	65
DJ144.2	9	86	23	20	64
Mean		87	19	17	95
Range of Values		82-93	13-23	11-20	61-210
Type R (Unidentified conifer)					
DJ144.3	3	94	32	30	17
DJ144.3	4	90	21	19	76
DJ144.3	6	85	18	15	119
DJ144.3	12	88	32	28	21
DJ144.3	16	82	28	22	48
Mean		87	26	23	44
Range of Values		82-94	18-32	15-30	17-119
Sciadopityoxylon					
DJ144.5	17	94	18	17	96
DJ144.5	18	94	15	14	139
DJ144.5	19	94	23	21	52
DJ144.5	3	92	22	20	65
DJ144.5	4	90	26	23	41
Mean		93	21	19	71
Range of Values		90-94	15-26	14-23	41-139
Araucariopitys					
DJ144.7	~7	87	24	21	53
DJ144.7	~13	91	21	19	68
Mean		89	23	20	60
Range of Values		87-91	21-24	19-21	53-68
Type S (Unidentified Araucarioid)					
DJ366.7	10	87	22	19	73
DJ366.7	14	93	28	26	30
DJ366.7	15	93	21	19	69
DJ366.7	16	92	15	14	136
Mean		91	21	20	67
Range of Values		87-93	15-28	14-26	30-136
Type T (Unidentified Non Araucarioid)					
DJ451.3	5	96	24	23	42
DJ451.3	7	90	19	16	100
DJ451.3	10	96	17	16	103
DJ451.3	11	97	14	14	140
Mean		95	18	17	88
Range of Values		90-97	14-24	14-23	42-140
Taxodioxylon					
DJ451.4	6	92	10	9	267
DJ451.4	8	86	11	9	253
Mean		89	10	9	260
Range of Values		86-92	10-11	9	253-267
Taxodioxylon					
DJ455.1	4	94	35	33	12
DJ455.1	5	94	45	42	4
DJ455.1	10	95	43	40	4
Mean		94	41	39	6
Range of Values		94-95	35-45	33-42	4-12

Continued .....

Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
Circoporoxylon					
DJ455.3	10	92	18	17	95
DJ455.3	11	93	17	16	110
DJ455.3	12	94	26	24	37
DJ455.3	13	88	39	35	9
Mean		92	25	23	43
Range of Values		88-94	17-39	16-35	9-110
Taxodioxylon					
DJ458.1	17	90	39	36	8
Mean		90	39	36	8
Range of Values		90	39	36	8
Circoporoxylon					
DJ462.2	3	93	22	20	59
DJ462.2	5	94	22	21	58
DJ462.2	6	83	19	15	117
DJ462.2	7	94	28	27	27
DJ462.2	8	92	26	24	39
Mean		91	23	21	53
Range of Values		83-94	19-28	15-27	27-117
Circoporoxylon					
DJ462.3	1	87	20	18	86
DJ462.3	2	91	21	19	73
DJ462.3	3	89	16	15	129
Mean		89	19	17	93
Range of Values		87-91	16-21	15-19	73-129
Taxodioxylon					
DJ462.5	2	88	17	15	121
DJ462.5	3	92	33	31	16
DJ462.5	4	92	27	25	35
DJ462.5	5	92	39	36	8
DJ462.5	6	92	27	25	32
Mean		91	29	26	28
Range of Values		88-92	17-39	15-36	8-121
Sciadopityoxylon					
DJ463.5	4	81	15	12	179
Mean		81	15	12	179
Range of Values		81	15	12	179
Type R (Unidentified conifer)					
DJ465.1	1	91	55	50	1
DJ465.1	2	89	56	50	1
DJ465.1	3	93	47	44	3
Mean		91	53	48	2
Range of Values		89-93	47-56	44-50	1-3
Type R (Unidentified conifer)					
DJ466.2	2	94	7	6	377
Mean		94	7	6	377
Range of Values		94	7	6	377
ALEXANDER ISLAND ANTARCTICA					

Continued .....

Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
Podocarpoxylon					
KG1703.23	6	87	20	19	87
KG1703.23	7	85	14	12	192
KG1703.23	8	86	11	10	243
KG1703.23	9	87	7	6	380
KG1703.23	18	89	26	23	41
Mean		87	16	14	145
Range of Values		85-89	7-26	6-23	41-380
Type R (Unidentified conifer)					
KG1719.3b	5	92	14	13	162
KG1719.3b	6	91	18	17	99
KG1719.3b	7	92	23	21	56
Mean		92	18	17	96
Range of Values		91-92	14-23	13-21	56-162
Type R (Unidentified conifer)					
KG2814.252	9	80	7	5	420
KG2814.252	10	74	12	9	275
KG2814.252	11	81	8	7	366
Mean		78	9	7	348
Range of Values		74-81	7-12	5-9	275-420
Type R (Unidentified conifer)					
KG2814.256	27	87	15	13	151
Mean		87	15	13	151
Range of Values		87	15	13	151
Type R (Unidentified conifer)					
KG2817.20	1	81	4	3	553
KG2817.20	2	87	14	12	176
Mean		84	9	8	312
Range of Values		81-87	4-14	3-12	176-553
Taxodioxylon					
KG4626.1	2	89	33	30	18
KG4626.1	3	93	27	25	32
KG4626.1	9	91	27	25	35
Mean		91	29	27	27
Range of Values		89-93	27-33	25-30	18-35
Type R (Unidentified conifer)					
KG4672.6	31	87	13	11	194
KG4672.6	32	92	15	14	146
KG4672.6	33	92	24	22	49
KG4672.6	34	83	5	4	520
Mean		89	14	13	164
Range of Values		83-92	5-24	4-22	49-520
Type R (Unidentified conifer)					
KG4710.1	2	90	14	12	177
KG4710.1	4	86	18	16	110
KG4710.1	16	78	18	14	141
KG4710.1	17	83	14	11	195
Mean		84	16	13	152
Range of Values		78-90	14-18	11-16	110-195

Continued .....

Genus/ Sample Number	Ring Number	Percentage Diminution	Percentage Latewood	Ring Markedness Index	Leaf Life Span (months)
Type R (Unidentified conifer)					
KG4717.43	15	88	20	18	84
KG4717.43	~47	82	26	22	52
Mean		85	23	20	66
Range of Values		82-88	20-26	18-22	52-84

Table B1.4. Table showing ring diameters, number of rings and false rings and annual sensitivity data for fossil conifer wood samples examined.

Specimen N°	Wood Type	Total Diameter of Sample (mm)	N° of False Rings	Total N° of Rings	AS values from Each Measureable Ring
Svalbard					
LD101	*Juniperoxylon*	11.13	1	6	0.23, 0.54, 0.23, 1.20, 0.59
LD102	*Cedroxylon*	37.11	0	5	0.05, 0.29, 0.00, 0.08
LD105	*Piceoxylon*	51.15	0	13	0.08, 0.28, 0.05, 0.76, 0.65, 0.33, 0.05, 0.05, 0.12, 0.18, 0.21, 0.13
LD108	*Araucariopitys*	49.71	1	36	0.32, 0.04, 0.27, 0.31, 0.49, 0.00, 0.22, 0.11, 0.09, 0.26, 0.05, 0.06, 0.06, 0.16, 0.35, 0.26, 0.80, 0.40,0.93, 0.23, 0.61, 0.51, 0.02, 0.32, 0.67, 0.80, 0.07, 0.27, 0.03, 1.06, 0.21, 0.05, 0.25, 0.10, 0.08
LD120	*Protocedroxylon*	18.95	9	35	0.16, 0.11, 0.97, 0.36, 0.14, 0.34, 0.11, 0.05, 0.21, 0.19, 0.38, 0.25, 0.36, 0.04, 1.09, 0.64, 0.18, 0.04, 0.04, 0.52, 0.05, 0.82, 0.82, 0.33, 0.40, 1.00, 0.07, 0.22, 0.29, 0.17, 0.27, 0.08, 0.04, 0.20
LD123	*Laricioxylon*	55.11	1	49	0.17, 0.48, 0.64, 0.27, 0.90, 0.58, 0.57, 0.68, 0.23, 0.03, 0.43, 0.02, 0.57, 0.43, 0.42, 0.14, 0.28, 0.31, 0.07, 0.37, 0.50, 0.56, 0.00, 0.62, 0.03, 0.10, 0.31, 0.47, 0.61, 1.16, 0.19, 0.25, 0.06, 0.32, 0.23, 0.79, 0.67, 0.03, 0.08, 0.38, 0.47, 0.24, 0.43, 0.04, 0.58, 0.15, 1.23, 0.91
LD126	*Laricioxylon*	43.29	4	48	0.81, 0.05, 0.38, 0.07, 0.00, 0.51, 0.34, 0.02, 0.23, 0.28, 0.29, 0.57, 0.88, 0.13, 0.34, 1.13, 0.02, 0.58, 0.28, 0.63, 0.23, 0.07, 0.06, 0.28, 0.14, 0.26, 0.32, 0.06, 0.06, 0.05, 0.42, 0.00, 0.06, 0.34, 0.71, 0.20, 0.10, 0.16, 0.16, 0.68, 0.05, 0.13, 0.16, 0.09, 0.28, 0.47, 0.01
LD129	*Taxodioxylon*	16.26	2	16	0.03, 0.29, 0.22, 0.63, 0.08, 0.14, 0.08, 0.11, 0.60, 0.57, 0.24, 1.04, 0.16, 0.04, 0.80
LD131	*Taxodixoylon*	33.88	0	21	0.37, 0.17, 0.36, 0.07, 0.19, 0.24, 0.08, 0.24, 0.16, 0.35, 0.02, 0.13, 0.46, 0.08, 0.49, 0.36, 0.05, 0.36, 0.40, 0.03
LD130	*Xenxoylon*	34.39	0	11	0.31, 0.13, 0.21, 0.26, 0.09, 0.34, 0.18, 0.22, 0.33, 0.12
LD132	*Cupressinoxylon*	26.10	0	27	0.62, 0.11, 1.13, 0.27, 0.46, 0.51, 0.04, 0.13, 0.33, 0.56,

Continued .....

Specimen N°	Wood Type	Total Diameter of Sample (mm)	N° of False Rings	Total N° of Rings	AS values from Each Measureable Ring
LD132 continued	*Cupressinoxylon*	26.10	0	27	0.24, 0.07, 0.05, 0.01, 0.03, 0.20, 0.04, 0.10, 0.13, 0.09, 0.08, 0.20, 0.16, 0.24, 0.06
LD133	*Taxodioxylon*	33.56	0	12	0.07, 0.69, 0.27, 0.03, 0.22, 0.35, 0.76, 0.88, 0.45, 0.19, 0.03
SN25 4	*Taxoxylon*	35.35	3	20	0.19, 0.01, 0.34, 0.44, 0.18, 0.23, 0.04, 0.47, 0.38, 0.65, 0.17, 0.05, 0.73, 0.08, 0.11, 0.40, 0.58, 0.40, 0.02
Canadian Arctic					
RR102	*Piceoxylon*	18.46	0	6	0.22, 0.38, 0.18, 0.39, 0.18
RR113	*Piceoxylon*	25.33	3	43	0.32, 0.28, 0.17, 0.34, 0.02, 0.23, 0.30, 0.61, 0.06, 0.68, 0.47, 0.71, 0.10, 0.53, 0.43, 0.22, 0.69, 0.14, 0.21, 0.69, 0.58, 1.18, 0.49, 0.00, 0.29, 0.89, 0.09, 0.80, 0.37, 0.26, 0.20, 0.03, 0.44, 0.13, 0.07, 0.13, 0.00, 0.03, 0.00, 0.64, 0.05, 0.24
RR111	*Pinuxylon*	73.81	15	63	0.80, 0.18, 0.26, 0.65, 0.73, 0.26, 0.28, 0.11, 0.85, 0.99, 0.41, 0.12, 0.03, 0.34, 0.39, 0.40, 0.36, 0.38, 0.08, 0.43, 0.09, 0.54, 0.64, 0.08, 0.39, 1.10, 0.07, 0.10, 0.00, 0.42, 0.06, 0.39, 0.01, 0.28, 0.25, 0.08, 0.07, 0.05, 0.35, 0.69, 0.17, 0.11, 0.23, 0.27, 0.30, 0.48, 0.73, 0.46, 0.50, 0.63, 0.42, 0.03, 0.14, 0.16, 0.31, 0.22, 0.34, 0.09, 0.23, 0.03, 0.39, 0.19
RR122	*Pinuxylon*	45.99	5	49	0.37, 0.33, 0.20, 0.09, 0.68, 0.12, 0.37, 0.81, 0.69, 0.05, 0.51, 0.27, 0.30, 0.04, 0.20, 0.17, 0.29, 0.19, 0.84, 0.58, 0.36, 0.04, 1.17, 0.06, 0.49, 0.26, 0.05, 0.19, 0.11, 0.11, 0.22, 0.14, 0.45, 0.83, 0.14, 0.22, 0.19, 0.04, 0.34, 0.26, 0.20, 0.00, 0.38, 0.47, 0.06, 0.30, 0.10
E139	*Pinuxylon*	32.96	0	49	0.35, 0.16, 0.31, 0.51, 0.21, 0.08, 0.07, 0.10, 0.07, 0.07, 0.47, 0.32, 0.21, 0.54, 0.16, 0.74, 0.00, 0.27, 0.07, 0.58, 0.10, 0.07, 0.13, 0.12, 0.62, 0.04, 0.20, 0.14, 0.22, 0.13, 0.44, 0.32, 0.64, 0.18, 0.24, 0.06, 0.06, 0.39, 0.25, 0.17, 0.23, 0.11, 0.05, 0.33, 0.09, 0.06, 0.08, 0.06

Continued .....

Specimen N°	Wood Type	Total Diameter of Sample (mm)	N° of False Rings	Total N° of Rings	AS values from Each Measureable Ring
E140	*Pinuxylon*	61.92	2	29	0.34, 0.49, 0.10, 0.14, 0.22, 0.30, 0.32, 0.19, 0.01, 0.61, 0.22, 0.36, 0.06, 0.27, 0.28, 0.05, 0.05, 0.13, 0.35, 0.42, 0.03, 0.56, 0.48, 0.19, 0.24, 0.35, 0.13, 0.18
RR121	*Cedroxylon*	48.90	0	37	0.51, 0.54, 0.00, 0.10, 0.15, 0.08, 0.15, 0.56, 0.67, 0.30, 0.21, 0.03, 0.19, 0.02, 0.30, 0.32, 0.35, 0.08, 0.43, 0.09, 0.04, 0.06, 0.19, 0.22, 0.11, 0.05, 0.49, 0.04, 0.41, 0.08, 0.48, 0.15, 0.33, 0.05, 0.11, 0.34
RR123	*Cedroxylon*	38.10	0	22	0.23, 0.12, 0.02, 0.14, 0.11, 0.37, 0.72, 0.26, 0.01, 0.19, 0.30, 0.40, 0.00, 0.43, 0.33, 0.35, 0.20, 0.20, 0.28, 0.24, 0.31
BL125	*Palaepiceoxylon*	67.51	1	59	0.18, 0.67, 0.30, 0.24, 0.46, 0.57, 0.12, 0.02, 0.37, 0.30, 0.15, 0.22, 0.21, 0.47, 0.15, 0.10, 0.26, 0.51, 0.02, 0.09, 0.20, 0.85, 0.79, 0.51, 0.50, 0.18, 0.05, 0.44, 0.04, 0.27, 0.03, 0.08, 0.06, 0.18, 0.01, 0.11, 0.12, 0.03, 0.08, 0.01, 0.21, 0.02, 0.15, 0.03, 0.88, 0.34, 0.50, 0.03, 0.13, 0.20, 0.04, 0.04, 0.16, 0.24, 0.17, 0.10, 0.00, 0.25
E137	*Cupressinoxylon*	59.63	0	77	0.09, 0.11, 0.11, 0.39, 0.07, 0.03, 0.28, 0.27, 0.10, 0.44, 0.37, 0.27, 0.08, 0.08, 0.04, 0.21, 0.07, 0.42, 0.29, 0.10, 0.07, 0.10, 0.14, 0.07, 0.31, 0.36, 0.88, 0.00, 0.04, 0.58, 0.54, 0.52, 0.00, 0.00, 0.21, 0.13, 0.37, 0.24, 0.05, 0.05, 0.00, 0.22, 0.22, 0.27, 0.15, 0.10, 0.02, 0.07, 0.24, 0.07, 0.03, 0.29, 0.08, 0.08, 0.15, 0.06, 0.03, 0.04, 0.30, 0.03, 0.06, 0.03, 0.01, 0.35, 0.13, 0.38, 0.20, 0.09, 0.31, 0.10, 0.16, 0.28, 0.29, 0.19, 0.13, 0.08
Australia					
872/W17	*Podocarpoxylon*	32.66	0	27	0.00, 0.21, 0.10, 0.02, 0.06, 0.15, 0.25, 0.17, 0.29, 0.33, 0.05, 0.19, 0.46, 0.12, 0.18, 0.14, 0.13, 0.16, 0.20, 0.44, 0.48, 0.24, 0.10, 0.14, 0.26,

Continued .....

Specimen N°	Wood Type	Total Diameter of Sample (mm)	N° of False Rings	Total N° of Rings	AS values from Each Measureable Ring
872/W166	*Podocarpoxylon*	38.09	0	14	0.09, 0.23, 0.13, 0.24, 0.35, 0.11, 0.38, 0.24, 0.16, 0.07, 0.43, 0.25, 0.30
872/W167	*Podocarpoxylon*	25.95	0	29	0.44, 0.45, 0.08, 0.11, 0.07, 0.31, 0.32, 0.11, 0.12, 0.34, 0.10, 0.01, 0.50, 0.06, 0.11, 0.32, 0.26, 0.17, 0.12, 0.49, 0.51, 0.10, 0.27, 0.05, 0.10, 0.05, 0.02, 0.04
872/W16	Type R (Unidentified conifer)	38.19	2	67	0.20, 0.27, 0.19, 0.53, 0.55, 0.32, 0.42, 0.17, 0.03, 0.22, 0.46, 0.27, 1.11, 0.18, 0.86, 0.64, 0.73, 0.75, 0.18, 0.08, 0.39, 0.60, 0.00, 0.84, 1.17, 0.25, 0.34, 0.10, 0.46, 0.27, 0.31, 0.04, 0.04, 0.50, 0.56, 0.24, 0.05, 0.03, 0.25, 0.50, 0.29, 0.29, 0.82, 0.38, 0.30, 0.49, 0.03, 0.23, 0.30, 0.13, 0.49, 0.19, 0.98, 0.70, 0.36, 0.57, 0.00, 0.19, 0.08, 0.08, 0.20, 0.22, 0.15, 0.13, 0.21, 0.07
872/W104	Type R (Unidentified conifer)	65.65	0	75	0.41, 0.09, 0.10, 0.45, 0.31, 0.22, 0.13, 0.19, 0.16, 0.18, 0.10, 0.56, 0.12, 0.23, 0.17, 0.08, 0.00, 0.11, 0.51, 0.02, 0.05, 0.34, 0.01, 0.15, 0.24, 0.10, 0.74, 0.19, 0.08, 0.52, 0.02, 0.53, 0.07, 0.16, 0.15, 0.17, 0.16, 0.10, 0.43, 0.06, 0.16, 0.00, 0.18, 0.46, 0.10, 0.15, 0.02, 0.40, 0.27, 0.07, 0.29, 0.35, 0.02, 0.02, 0.43, 0.29, 0.05, 0.74, 0.48, 0.18, 0.08, 0.10, 0.28, 0.27, 0.24, 0.18, 0.31, 0.12, 0.33, 0.05, 0.17, 0.17, 0.14, 0.08
872/W128	Type R (Unidentified conifer)	76.68	0	30	0.34, 0.30, 0.26, 0.10, 0.21, 0.33, 0.00, 0.02, 0.04, 0.05, 0.08, 0.27, 0.13, 0.65, 0.71, 0.07, 0.08, 0.05, 0.25, 0.05, 0.23, 0.14, 0.01, 0.12, 0.05, 0.23, 0.49, 0.30, 0.19
872/W149	Type R (Unidentified conifer)	44.42	0	40	0.32, 1.33, 0.07, 0.02, 0.16, 0.14, 0.09, 0.07, 0.27, 1.29, 0.91, 0.23, 0.19, 0.09, 0.10, 0.23, 0.31, 0.09, 0.41, 0.15, 0.11, 0.22, 0.36, 0.29, 0.04, 0.21, 0.01, 0.31, 0.03, 0.46, 0.74, 0.55, 0.01, 0.97, 0.22, 0.50, 0.27, 0.48, 0.12
872/W168	Type R (Unidentified conifer)	58.08	2	46	0.11, 0.01, 0.44, 0.43, 0.35, 0.19, 0.13, 0.02, 0.30, 0.13, 0.21, 0.14, 0.30, 0.57, 0.41, 0.26, 0.24, 0.12, 0.68, 0.27, 0.25, 0.05, 0.26, 0.40, 0.07,

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Specimen N°	**Wood Type**	**Total Diameter of Sample (mm)**	**N° of False Rings**	**Total N° of Rings**	**AS values from Each Measureable Ring**
872/W168 continued	Type R (Unidentified conifer)	58.08	2	46	0.02, 0.21, 0.29, 0.45, 0.40, 0.10, 0.12, 0.44, 0.22, 0.15, 0.10, 0.51, 0.52, 0.15, 0.18, 0.76, 0.76, 0.48, 0.57, 0.63
James Ross Island Antarctica					
5215	*Araucariopitys*	37.84	3	15	0.06, 0.52, 0.40, 0.74, 0.08, 0.01, 0.08, 0.36, 0.32, 0.22, 0.42, 0.28, 1.22, 1.03
DJ144.7	*Araucariopitys*	48.20	0	26	0.30, 0.70, 0.38, 0.58, 0.04, 0.19, 0.36, 0.12, 0.19, 0.45, 0.28, 0.17, 0.29, 0.78, 0.44, 0.17, 0.05, 0.66, 0.48, 0.14, 0.23, 0.28, 0.20, 0.20, 0.45
DJ137.6	*Cupressinoxylon*	23.89	1	21	0.23, 0.16, 0.01, 0.50, 0.23, 0.02, 0.06, 0.09, 0.11, 0.70, 0.73, 0.99, 0.15, 0.18, 0.18, 0.50, 0.40, 0.61, 0.03, 0.22, 0.05
DJ137.8	*Agathoxylon*	19.59	2	27	0.07, 0.16, 0.33, 0.95, 1.11, 0.30, 0.26, 0.21, 0.13, 0.36, 0.43, 0.33, 0.18, 0.09, 0.29, 0.69, 0.04, 0.22, 0.55, 0.70, 0.29, 0.06, 0.05, 0.23, 0.08, 0.67
DJ141.3	*Agathoxylon*	26.51	2	22	0.17, 0.29, 0.26, 0.15, 0.12, 0.06, 0.05, 0.10, 0.77, 0.07, 0.30, 0.22, 0.55, 0.16, 0.13, 1.05, 0.10, 0.26, 0.03, 0.29, 0.16
DJ141.6	*Protophyllocladoxylon*	51.06	4	40	0.26, 0.48, 0.18, 0.23, 0.23, 0.30, 0.36, 0.21, 0.21, 0.27, 0.63, 0.22, 0.25, 0.48, 0.38, 0.06, 0.59, 0.51, 0.01, 0.26, 0.38, 0.23, 0.14, 0.08, 0.22, 0.62, 0.43, 0.76, 0.56, 0.22, 0.14, 0.12, 0.20, 0.01, 0.84, 0.03, 0.84, 0.52, 0.11
DJ141.13	*Podocarpoxylon*	24.67	0	18	0.40, 0.17, 1.11, 0.36, 0.95, 0.14, 0.24, 0.57, 0.52, 0.16, 0.12, 0.39, 0.28, 0.61, 0.10, 0.08, 0.43

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Specimen N°	Wood Type	Total Diameter of Sample (mm)	N° of False Rings	Total N° of Rings	AS values from Each Measureable Ring
DJ141.14	*Podocarpoxylon*	36.60	0	27	0.16, 0.53, 1.32, 0.69, 0.02, 0.10, 0.05, 0.14, 0.19, 0.50, 0.02, 0.02, 0.45, 0.12, 0.78, 0.31, 0.21, 0.02, 0.22, 0.13, 0.25, 0.29, 0.03, 0.17, 0.33, 0.03
DJ144.2	*Podocarpoxylon*	28.87	0	22	0.40, 0.71, 0.21, 0.40, 0.33, 0.31, 0.56, 0.29, 0.20, 0.25, 0.23, 0.45, 0.26, 0.20, 0.18, 0.34, 0.40, 0.30, 0.01, 0.13, 0.32
DJ451.4	*Taxodioxylon*	27.57	0	8	0.65, 0.30, 0.60, 0.35, 0.00, 0.33, 0.14
DJ455.1	*Taxodioxylon*	34.58	0	11	0.25, 0.01, 0.01, 0.55, 0.18, 0.23, 0.01, 0.14, 0.42, 0.29
DJ458.1	*Taxodioxylon*	52.39	0	23	0.26, 0.10, 0.06, 0.11, 0.48, 0.07, 0.11, 0.04, 0.05, 0.06, 0.20, 0.02, 0.26, 0.24, 0.22, 0.21, 0.15, 0.46, 0.02, 0.11, 0.03, 0.13
DJ462.5	*Taxodioxylon*	22.98	0	9	0.33, 0.19, 0.11, 0.40, 0.52, 0.45, 0.32, 0.11
DJ463.5	*Sciadopityoxylon*	23.44	0	5	0.21, 0.39, 0.36, 0.01
DJ144.5	*Sciadopityoxylon*	53.59	2	68	0.43, 0.06, 0.45, 0.18, 0.37, 0.40, 0.21, 0.06, 0.38, 0.34, 0.21, 0.05, 0.15, 0.30, 0.36, 0.29, 0.00, 0.50, 0.25, 0.16, 0.29, 0.18, 0.28, 0.38, 0.25, 0.06, 0.31, 0.58, 0.52, 0.23, 0.24, 0.13, 0.09, 0.59, 0.73, 0.11, 0.44, 0.05, 0.07, 0.04, 0.38, 0.13, 0.19, 0.19, 0.08, 1.04, 0.00, 0.34, 0.38, 0.17, 0.47, 0.00, 0.16, 0.23, 0.08, 0.13, 0.15, 0.11, 0.49, 0.04, 0.34, 0.27, 0.23, 0.46, 0.40, 0.93, 0.15
DJ455.3	*Circoporoxylon*	23.44	0	15	0.32, 0.22, 0.38, 0.20, 0.04, 0.16, 0.85, 0.15, 0.62, 0.26, 0.01, 0.03, 0.21, 0.06
DJ462.2	*Circoporoxylon*	47.43	0	22	0.19, 0.07, 0.54, 0.03, 0.36, 0.09, 0.17, 0.06, 0.23, 0.04, 0.15, 0.27, 0.39, 0.06, 0.25, 0.39, 0.21, 0.42, 0.19, 0.19
DJ462.3	*Circoporoxylon*	23.26	0	7	0.08, 0.19, 0.58, 0.26, 0.52, 1.00

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Specimen N°	Wood Type	Total Diameter of Sample (mm)	N° of False Rings	Total N° of Rings	AS values from Each Measureable Ring
D421	Type S (Unidentified Araucarioid)	39.87	6	45	0.36, 0.23, 0.12, 0.40, 0.08, 0.46, 0.39, 0.01, 0.56, 0.55, 0.11, 0.07, 0.04, 0.04, 0.23, 0.48, 0.67, 0.38, 0.50, 0.42, 0.54, 0.44, 0.13, 0.41, 0.12, 1.08, 1.28, 0.11, 0.29, 0.85, 0.41, 0.39. 0.18, 0.20, 0.55, 0.31, 0.22, 0.35, 0.70, 0.52, 0.34, 0.00, 0.34, 0.00
DJ366.7	Type S (Unidentified Araucarioid)	19.76	3	11	0.20, 0.78, 0.02, 0.59, 0.33, 0.01, 0.08, 0.89, 0.05, 0.38
DJ135.3	Type S (Unidentified Araucarioid)	52.90	0	15	0.05, 0.19, 0.80, 0.64, 0.07, 0.71, 0.01, 0.10, 0.43, 0.78, 1.01, 0.07, 0.23, 0.05
DJ141.7	Type T (Unidentified Non Araucarioid)	42.47	1	8	0.10, 0.09, 0.26, 0.15, 0.03, 0.18, 0.03
DJ451.3	Type T (Unidentified Non Araucarioid)	58.69	3	16	0.40, 0.39, 0.01, 0.56, 0.14, 0.24, 0.19, 0.10. 0.52, 0.84, 0.90, 0.29, 0.92, 0.80, 1.46
DJ141.16	Type R (Unidentified conifer)	31.13	1	16	0.08, 0.61, 0.12, 0.06, 0.05, 0.31, 0.71, 1.15, 0.02, 0.40, 0.23, 0.53, 0.28, 0.09, 0.45
DJ141.8	Type R (Unidentified conifer)	49.10	1	62	0.37, 0.59, 0.22, 0.20, 0.42, 0.49, 0.56, 0.05, 0.70, 0.65, 0.21, 0.38, 0.14, 0.20, 0.04, 0.59, 0.53, 0.88, 0.06, 0.52, 0.32, 0.12, 0.15, 0.63, 0.21, 0.35, 0.15, 0.54, 0.71, 0.58, 0.76, 0.08, 0.44, 0.76, 0.25, 0.53, 0.39, 0.02, 0.29, 0.20, 0.42, 0.24, 0.94, 0.30, 0.33, 0.32, 0.37, 0.58, 0.00, 0.18, 0.34, 0.39, 0.47, 0.63, 0.79, 0.86, 0.35, 0.00, 0.75, 0.55, 0.70
DJ144.3	Type R (Unidentified conifer)	36.43	2	32	0.34, 0.27, 0.10, 0.38, 0.32, 0.00, 0.16, 0.07, 0.09, 0.26, 0.32, 0.06, 0.05, 0.23, 0.11, 0.04, 0.28, 0.13, 0.24, 0.03, 0.28, 0.49, 0.32, 0.38, 0.04, 0.29, 0.06, 0.16, 0.55, 0.34, 0.00
DJ465.1	Type R (Unidentified conifer)	26.57	0	9	1.07, 0.09, 0.73, 0.62, 0.49, 0.56, 0.99, 0.08
DJ466.2	Type R (Unidentified conifer)	23.92	2	7	0.14, 0.21, 0.01, 0.25, 0.71, 0.88

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Specimen N°	Wood Type	Total Diameter of Sample (mm)	N° of False Rings	Total N° of Rings	AS values from Each Measureable Ring
Alexander Island Antarctica					
KG1703.23	*Podocarpoxylon*	55.43	3	40	0.88, 0.52, 0.69, 0.47, 0.76, 1.06, 0.54, 0.06, 0.51, 0.47, 0.26, 1.37, 0.74, 0.61, 0.68, 0.30, 0.41, 0.38, 0.88, 0.19, 0.38, 0.35, 0.08, 0.08, 0.63, 0.34, 0.89, 0.16, 0.37, 0.21, 0.50, 0.41, 0.10, 0.29, 0.70, 0.15, 0.27, 0.06, 0.08
KG1719.3b	Type R (Unidentified conifer)	37.66	0	23	0.53, 1.23, 0.53, 0.56, 0.44, 0.48, 0.10, 0.53, 0.42, 0.32, 0.92, 0.69, 0.14, 0.45, 0.38, 0.25, 0.41, 0.07, 0.49, 0.03, 0.30, 0.08
KG2814.256	Type R (Unidentified conifer)	49.75	4	32	0.29, 0.63, 0.46, 0.18, 0.64, 0.17, 0.63, 0.14, 0.19, 0.18, 0.58, 0.03, 0.14, 0.12, 0.42, 0.24, 0.67, 0.19, 0.22, 0.33, 0.28, 0.64, 0.55, 0.25, 0.47, 0.80, 1.04, 0.13, 0.66, 0.06, 0.79
KG2817.20	Type R (Unidentified conifer)	44.99	0	32	0.73, 0.26, 0.20, 0.23, 0.21, 0.08, 0.21, 0.01, 0.25, 0.75, 0.26, 0.24, 0.05, 0.16, 0.63, 0.28, 0.03, 0.13, 0.39, 0.13, 0.27, 0.08, 0.47, 0.46, 0.02, 0.52, 1.00, 0.37, 0.30, 0.24, 0.09
KG4626.1	*Taxodioxylon*	36.24	1	12	1.02, 0.10, 0.23, 0.02, 0.62, 0.38, 0.21, 0.19, 0.03, 0.39, 0.29
KG4672.6	Type R (Unidentified conifer)	46.61	2	38	0.22, 0.69, 0.09, 1.16, 0.54, 1.03, 0.09, 1.20, 0.13, 0.30, 0.91, 0.63, 0.41, 0.58, 0.15, 0.12, 0.92, 0.17, 0.55, 0.19, 0.54, 0.00, 0.10, 0.14, 0.13, 0.71, 0.12, 0.15, 0.18, 0.35, 0.69, 0.11, 0.25, 0.14, 0.08, 0.22, 0.20
KG4710.1	Type R (Unidentified conifer)	63.53	5	26	0.43, 0.16, 0.42, 0.15, 0.58, 0.04, 0.23, 0.23, 0.13, 0.36, 0.24, 0.30, 0.29, 0.04, 0.02, 0.21, 0.11, 0.55, 0.76, 0.40, 0.73, 0.88, 0.19, 0.56, 0.14

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Specimen N°	Wood Type	Total Diameter of Sample (mm)	N° of False Rings	Total N° of Rings	AS values from Each Measureable Ring
KG2814.252	Type R (Unidentified conifer)	39.58	11	51	0.15, 0.18, 0.13, 0.40, 0.66, 0.45, 0.44, 0.01, 0.21, 0.54, 0.56, 0.30, 0.29, 0.10, 0.00, 0.02, 0.06, 0.08, 0.26, 0.04, 0.10, 0.51, 0.08, 0.46, 0.50, 0.02, 0.19, 0.61, 0.98, 0.23, 0.96, 0.79, 0.63, 0.04, 0.97, 0.22, 0.46, 0.88, 0.14, 0.02, 0.49, 0.00, 0.01, 0.38, 0.16, 0.26, 0.54, 1.00, 0.07, 0.26
KG4717.43	Type R (Unidentified conifer)	31.43	10	44	0.47, 0.62, 0.03, 0.09, 0.14, 0.07, 0.22, 0.33, 0.25, 0.02, 0.11, 0.15, 0.09, 0.58, 1.02, 0.13, 0.32, 0.56, 0.03, 0.10, 0.40, 0.70, 0.02, 0.24, 0.02, 0.14, 0.81, 0.55, 0.26, 0.16, 0.31, 0.96, 0.51, 0.83, 0.50, 0.12, 0.12, 0.17, 0.27, 0.42, 0.21, 0.39, 0.60