

Leaf phenology of some mid-Cretaceous polar forests, Alexander Island, Antarctica

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(Received 30 March 2000; accepted 10 October 2000)

Abstract – The leaf longevity and seasonal timing of leaf abscission within a plant community is closely related to climate, a phenomenon referred to as leaf phenology. In this paper the leaf phenology of some mid-Cretaceous (late Albian) forests which grew at latitude of 75° S on Alexander Island, Antarctica, is analysed. Five independent techniques for determining leaf longevity are applied to the fossil remains of each of the canopy-forming trees. These techniques utilize: (1) the anatomical character of growth rings in trunk woods, (2) leaf trace persistence in juvenile branch and stem woods, (3) leaf physiognomy, (4) comparison with nearest living relatives, and (5) leaf taphonomy. The application of techniques 1–5 suggests that the araucarian and podocarp conifers, which comprised more than 90% of the canopy-forming vegetation, were evergreen with leaf retention times in excess of 5–13 years. The application of techniques 3–5 to rare taxodioid conifers indicates the existence of both evergreen and deciduous habits in this group, whilst both ginkgos and taeniopterids, which are locally abundant, are interpreted as possessing a deciduous habit. The polar forests of Alexander Island were therefore dominantly evergreen. Preliminary analysis of five other mid-Cretaceous polar forests suggests the presence of dominantly evergreen vegetation in Australia and Antarctica, and mixed evergreen–deciduous vegetation in Alaska, northern Russia and New Zealand. Cold month mean temperature probably exerted the largest influence on the leaf phenology at each of these forest sites.

1. Introduction

Fossil forests occur at multiple horizons in the mid-Cretaceous (late Albian) Triton Point Formation, Fossil Bluff Group of southeast Alexander Island, Antarctic Peninsula (Jefferson, 1982; Moncrieff & Kelly, 1993; Nichols & Cantrill, unpub. data) (Fig. 1). This formation accumulated within a fore-arc basin and is divided in two members; the lower Citadel Bastion Member consists of braided alluvial plain deposits and the upper Coal Nunatak Member consists of coastal plain deposits characterized by more laterally restricted (probably meandering) river channels (Cantrill & Nichols, 1996; Nichols & Cantrill, unpub. data). Upright, coniferous tree trunks (up to seven metres high) occur in both facies associations where they are rooted in carbonaceous palaeosols and buried by coarse-grained sandstone units interpreted as major flood deposits (A. C. M. Moncrieff, unpub. British Antarctic Survey Field Report AD6/2R/1988/G4, 1989). Transported logs and wood fragments occur in siltstone and sandstone units variously interpreted as river channel deposits, flood deposits and crevasse splay deposits. Abundant foliage remains occur on palaeosols (e.g. Cantrill & Nichols, 1996) and in fine-grained overbank deposits (Jefferson, 1982).

Quantitative analysis of 68 wood fragments from this formation has revealed the presence of araucarian (*Araucarioxylon* Kraus and *Araucariopitys* Jeffrey; 13%

of specimens), podocarp (*Podocarpoxyton* Gothan sp. 1 and sp. 2; 85% of specimens) and taxodioid conifers (*Taxodioxylon* Hartig; 2% of specimens). This conifer diversity is mirrored in the foliage record that includes *Araucaria* Juss. and *Araucarites* Presl. (Araucariaceae); *Podocarpites* Unger (Podocarpaceae); *Athrotaxites* Andra (Taxodiaceae); *Brachyphyllum* Brongniart, *Elatocladus* Halle, *Pagiophyllum* Heer, and *Podozamites* (Brongniart) Braun (Incertae Familae) (Cantrill & Falcon-Lang, unpub. data). Estimates of tree height based on stump diameter suggest that these conifers were tall trees up to 29 m high (Falcon-Lang & Cantrill, 2000). Other plant fossils present include liverworts, lycopsids, sphenopsids, ferns, ginkgophytes, taeniopterids, bennettitaleans and angiosperms (Cantrill & Nichols, 1996).

Preliminary palaeoecological reconstructions based on the distribution of plant remains on exposed palaeosol surfaces indicate that the braidplain was dominated by shrubby taeniopterids interspersed with stands of podocarp and taxodioid conifers (Cantrill & Nichols, 1996). On the coastal plain, open canopy forests dominated by podocarp and araucarian conifers occurred in some regions (Jefferson, 1982; Chaloner & Creber, 1989) and graded into broken conifer woodlands and fern thickets on more immature substrates (Cantrill, 1995a,b; Cantrill & Nichols, 1996; Falcon-Lang & Cantrill, 2000). This temperate rainforest vegetation grew well within the Southern Hemisphere polar circle (palaeolatitude of 75° S) during the mid-Cretaceous thermal optimum (Creber & Chaloner, 1985; Spicer, Rees & Chapman, 1993;

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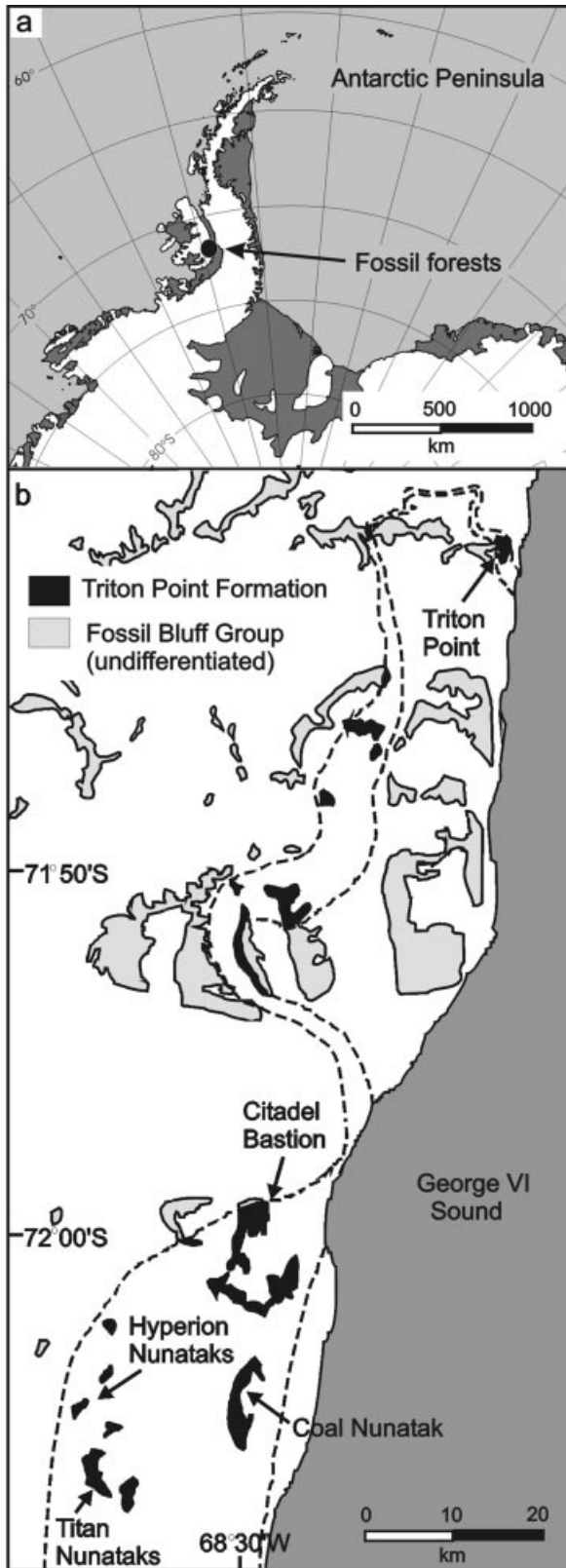


Figure 1. Location details of study area. (a) Map of Antarctic Peninsula showing the position of the Alexander Island fossil forests; (b) detailed outcrop map of southeast Alexander Island showing the outcrop of the Albian Triton Point Formation, a stratigraphic unit within the Fossil Bluff Group. Dashed line delimits inferred extent of Triton Point Formation (Moncrieff & Kelly, 1993). Principal localities mentioned in the text where the fossil wood was collected are shown.

Clarke & Jenkyns, 1999). In this environment, plant growth was subject to conditions of extreme light seasonality characterized by up to 70 days of unbroken darkness each winter and a humid climate (Parrish, Ziegler & Scotese, 1982; Read & Francis, 1992).

Despite this broad understanding of the nature of the Alexander Island ecosystem, it is still not known whether these forests were dominantly evergreen or deciduous. It is particularly important to understand this palaeoecological dimension because the leaf longevity and seasonal timing of leaf abscission in a plant community is closely related to climate, a phenomenon referred to as leaf phenology (Woodward, 1987). Analyses of the leaf phenology of fossil plant communities could yield valuable palaeoclimatic data needed to test and refine numerical models of past global climates, vegetation and environments (Wolfe & Upchurch, 1987; Otto-Bliesner & Upchurch, 1997; Upchurch, Otto-Bliesner & Scotese, 1999; Falcon-Lang, 2000a). In addition, the presence or absence of winter vegetation has important implications for the ecology of terrestrial faunas described from the Cretaceous polar circle, such as theropod, sauropod, and ornithomimid dinosaurs (Dettman *et al.* 1992). In this paper we make a systematic attempt to analyse the leaf longevity of the most common trees in the mid-Cretaceous fossil forests of Alexander Island. These data are then discussed in relation to palaeoclimate models to interpret the leaf phenology of the Alexander Island forests, and compared with preliminary analyses of leaf phenology from other mid-Cretaceous polar forest sites in Alaska, Australia, New Zealand and northern Russia.

2. Analysis of the leaf longevity of the Alexander Island trees

There is no single, simple way of determining the leaf longevity of a fossil plant. In an earlier paper one of us (Falcon-Lang, 2000a) reviewed some of the techniques available for such analysis but stressed the need to utilize as many techniques as possible in order to test and refine the interpretation. Here we critically describe five independent techniques for analysing fossil leaf longevity and apply each of them to the remains of the canopy-forming vegetation on Alexander Island, the conifers, ginkgos and taeniopterids.

2.a. Growth rings in trunk woods

2.a.1. Method

The first technique, developed by Falcon-Lang (2000a,b), utilizes the anatomical characteristics of growth rings in coniferopsid trunk woods. In transverse section, growth rings are composed of parallel rows of tracheid cells which decrease in diameter across the ring. The larger cells are produced in the early part of the growing season (earlywood) and the smaller cells are formed towards the end of the grow-

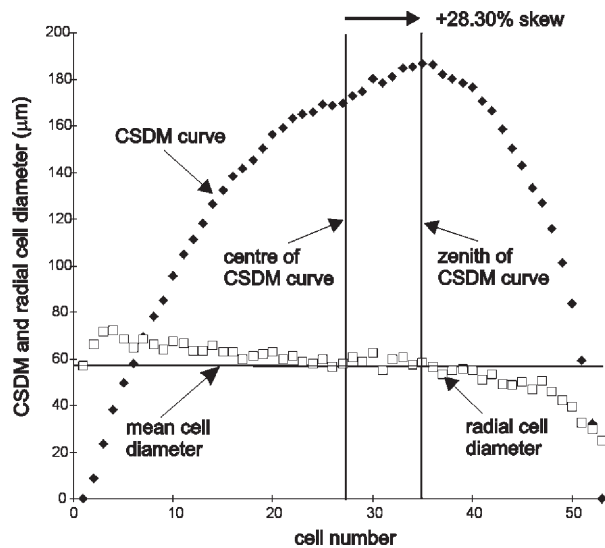


Figure 2. Diagram illustrating how percentage skew is calculated (see text for explanation; after Falcon-Lang, 2000a).

ing season (latewood). In this technique the radial diameters of individual tracheid cells (viewed using standard transverse thin sections) are measured across each ring increment with the aid of a calibrated scale mounted in the eye-piece of the transmitted light microscope. Five adjacent rows of cells are measured for each ring increment and averaged (cf. Falcon-Lang, 1999a). The cumulative sum of each cell's deviation from the mean of this data is then calculated (Creber & Chaloner, 1984) and plotted as a zero-trending curve (the CSDM curve). For each growth ring increment the percentage skew of the zenith of the CSDM curve relative to the centre of the plot is ascertained (Falcon-Lang, 2000a) (Fig. 2). Only growth rings lacking subtle false rings, growth interruptions or any other growth abnormalities can be used in this analysis because the presence of these features gives rise to CSDM curves with multiple zeniths.

Falcon-Lang (2000a,b) showed that the percentage skew of the zenith of the CSDM curve is closely related to the leaf longevity of the parent tree in modern coniferosids. Only deciduous species possess CSDM skews of less than -10% and only evergreen species have skews of greater than $+10\%$. Of the woods which yielded skew values between -10% and 0% , 81% were from deciduous conifers and 19% from evergreen conifers, whilst between 0% and $+10\%$ skew, 46% were from deciduous conifers and 54% from evergreen species. Woods that possess growth rings with CSDM skews in the range from -10% to $+10\%$ therefore cannot be unambiguously assigned evergreen or deciduous status, although the majority with a negative percentage are likely to be deciduous. Nevertheless, in many cases the woods produced by deciduous and evergreen conifers may be distinguished from one another on the basis of percentage skew values.

2.a.2. Data and interpretation

Poor preservation meant that the only *Araucarioxylon* wood specimen could not be analysed by the present technique. However, two specimens of *Araucariopitys*, eight specimens of *Podocarpoxylon* sp. 1, four specimens of *P.* sp. 2 and one specimen of *Taxodioxylon* possessed sufficiently well-preserved growth rings for the study. The former two genera possessed growth rings with subtle ring boundaries continuous around the stem circuit (Fig. 3a,b); the latter genus possessed

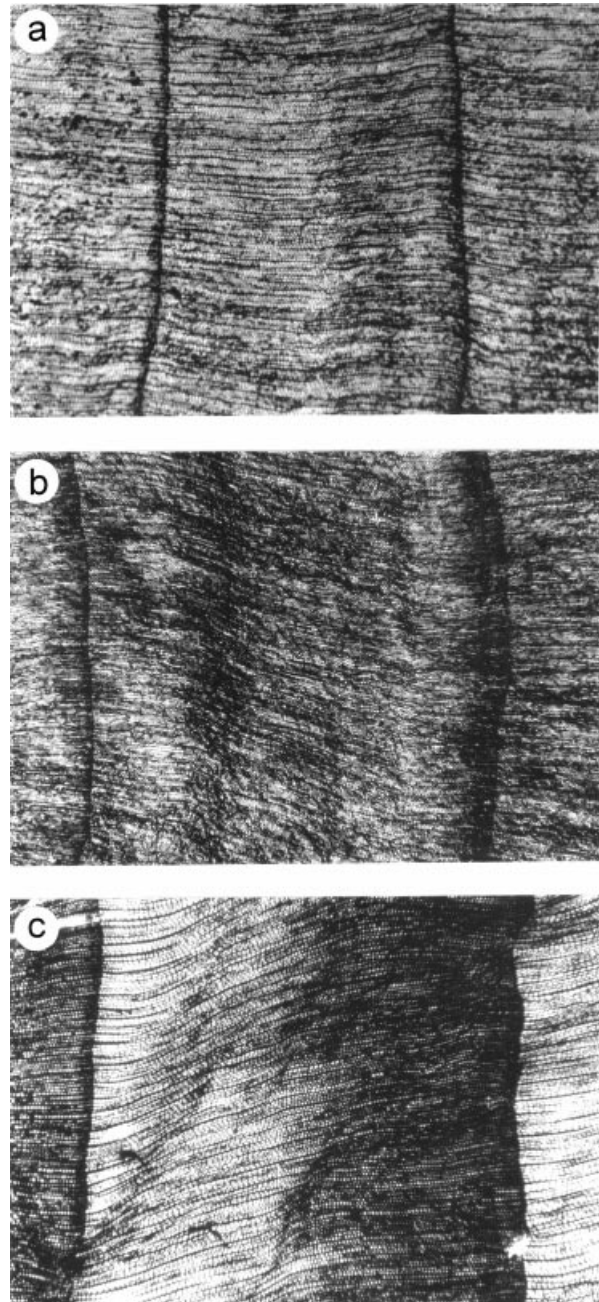


Figure 3. Transverse sections of conifer woods, (a) *Podocarpoxylon* sp. 1 exhibiting subtle growth rings, mag. $\times 25$, KG. 4710.1; (b) *Araucariopitys* exhibiting subtle growth rings, mag. $\times 25$, KG. 4740.11; (c) *Taxodioxylon* exhibiting marked growth rings, mag. $\times 25$, KG. 4626.1.

Table 1. Results of the application of Falcon-Lang's (2000a) 'percentage skew technique' to the Alexander Island coniferous woods

Wood taxon (Specimen number)	Locality	Facies association	Number of cells per ring	Percentage skew	Interpretation of leaf phenology
<i>Araucariopitys</i>					
KG. 4740.11	Coal Nunatak	Coastal plain	135	+51.1	Evergreen
KG. 4740.11	Coal Nunatak	Coastal plain	52	+34.6	Evergreen
KG. 4740.11	Coal Nunatak	Coastal plain	136	+61.8	Evergreen
KG. 4702.17	Coal Nunatak	Coastal plain	30	+40.0	Evergreen
KG. 4702.17	Coal Nunatak	Coastal plain	46	+52.2	Evergreen
Mean			79.8	+47.9	Evergreen
<i>Podocarpoxylon sp. 1</i>					
KG. 4657.9	Titan Nunataks	Braided alluvial plain	30	+66.7	Evergreen
KG. 4657.9	Titan Nunataks	Braided alluvial plain	24	+58.3	Evergreen
KG. 4660.4	Citadel Bastion	Braided alluvial plain	39	+43.6	Evergreen
KG. 4710.2	Triton Point	Braided alluvial plain	21	+38.1	Evergreen
KG. 4717.42	Titan Nunataks	Braided alluvial plain	51	+52.9	Evergreen
KG. 4717.44	Titan Nunataks	Braided alluvial plain	20	+40.0	Evergreen
KG. 4717.45	Titan Nunataks	Braided alluvial plain	67	+76.1	Evergreen
KG. 4717.45	Titan Nunataks	Braided alluvial plain	41	+41.4	Evergreen
KG. 4717.46	Titan Nunataks	Braided alluvial plain	51	+69.8	Evergreen
KG. 4719.4	Titan Nunataks	Braided alluvial plain	45	+64.4	Evergreen
Mean			38.9	+55.1	Evergreen
<i>Podocarpoxylon sp. 2</i>					
KG. 2814.256	Coal Nunatak	Coastal plain	83	+83.1	Evergreen
KG. 2814.256	Coal Nunatak	Coastal plain	84	+54.2	Evergreen
KG. 4660.1	Citadel Bastion	Braided alluvial plain	41	+61.0	Evergreen
KG. 4710.3	Triton Point	Braided alluvial plain	44	+59.1	Evergreen
KG. 4747.13	Coal Nunatak	Coastal plain	33	+51.5	Evergreen
Mean			57	+61.8	Evergreen
<i>Taxodioxylon</i>					
KG. 4626.1	Hyperion Nunataks	Braided alluvial plain	128	-11.7	Deciduous
KG. 4626.1	Hyperion Nunataks	Braided alluvial plain	74	+4.1	Evgrn/Decid.
KG. 4626.1	Hyperion Nunataks	Braided alluvial plain	97	+4.6	Evgrn/Decid.
KG. 4626.1	Hyperion Nunataks	Braided alluvial plain	134	-6.0	Evgrn/Decid.
KG. 4626.1	Hyperion Nunataks	Braided alluvial plain	47	+6.4	Evgrn/Decid.
Mean			96	-0.5	Deciduous?

much more marked ring boundaries continuous around the stem circuit (Fig. 3c). Five ring increments were measured for *Araucariopitys*, *Podocarpoxylon sp. 2* and *Taxodioxylon*, and ten ring increments were measured for *P. sp. 1*. The results were as follows: *Araucariopitys* gave percentage skew values ranging from +34.6% to +61.8%, for *Podocarpoxylon sp. 1* values ranged from +38.1% to +76.1%, and for *P. sp. 2* values ranged from +51.5% to +83.1% (Table 1; Figs 4, 5). Compared with the modern data in Falcon-Lang (2000a) and summarized above, these skew values are consistent with woods produced by evergreen conifers with long leaf retention times, probably more than five years. For example, modern specimens of *Araucaria araucana* (Molina) K. Koch, which retain leaves for 3–15 years, give a mean skew value of +66.7% (Falcon-Lang, 2000a). *Taxodioxylon* percentage skew values range from -11.7% to +6.38% (Table 1; Figs 4, 5). Compared with modern data, these values straddle the deciduous and the evergreen fields with short leaf retention times. Therefore the leaf longevity of the parent tree cannot be interpreted with certainty; it may have been deciduous or evergreen with a short leaf retention time.

2.b. Leaf traces in juvenile branch and stem woods

2.b.1. Method

The second technique utilizes the leaf traces in juvenile stem or branch coniferopsid wood. Leaf traces are bundles of vascular tissue which join the living leaf to the primary vascular cylinder at the centre of the young stem. In deciduous plants, the onset of secondary growth and the centripetal addition of a layer of secondary wood by the vascular cambium, buries the proximal part of the leaf trace and ruptures away the distal portion: leaf traces thus are only encountered embedded in the first ring increment of such stems (Eames & McDaniels, 1947; Esau, 1977). In evergreen plants, leaf traces are extended by a type of secondary growth which increases them in length by addition of new tissue. As the woody plant stem increases in diameter by secondary growth, the phloem is progressively stripped away from the leaf trace, so that the buried portion of the trace consists only of a xylem strand (Eames & McDaniels, 1947; Esau, 1977). Thus, where a tree has a high leaf retention time, as in *Araucaria araucana*, the leaf trace may be very long, passing through many growth ring

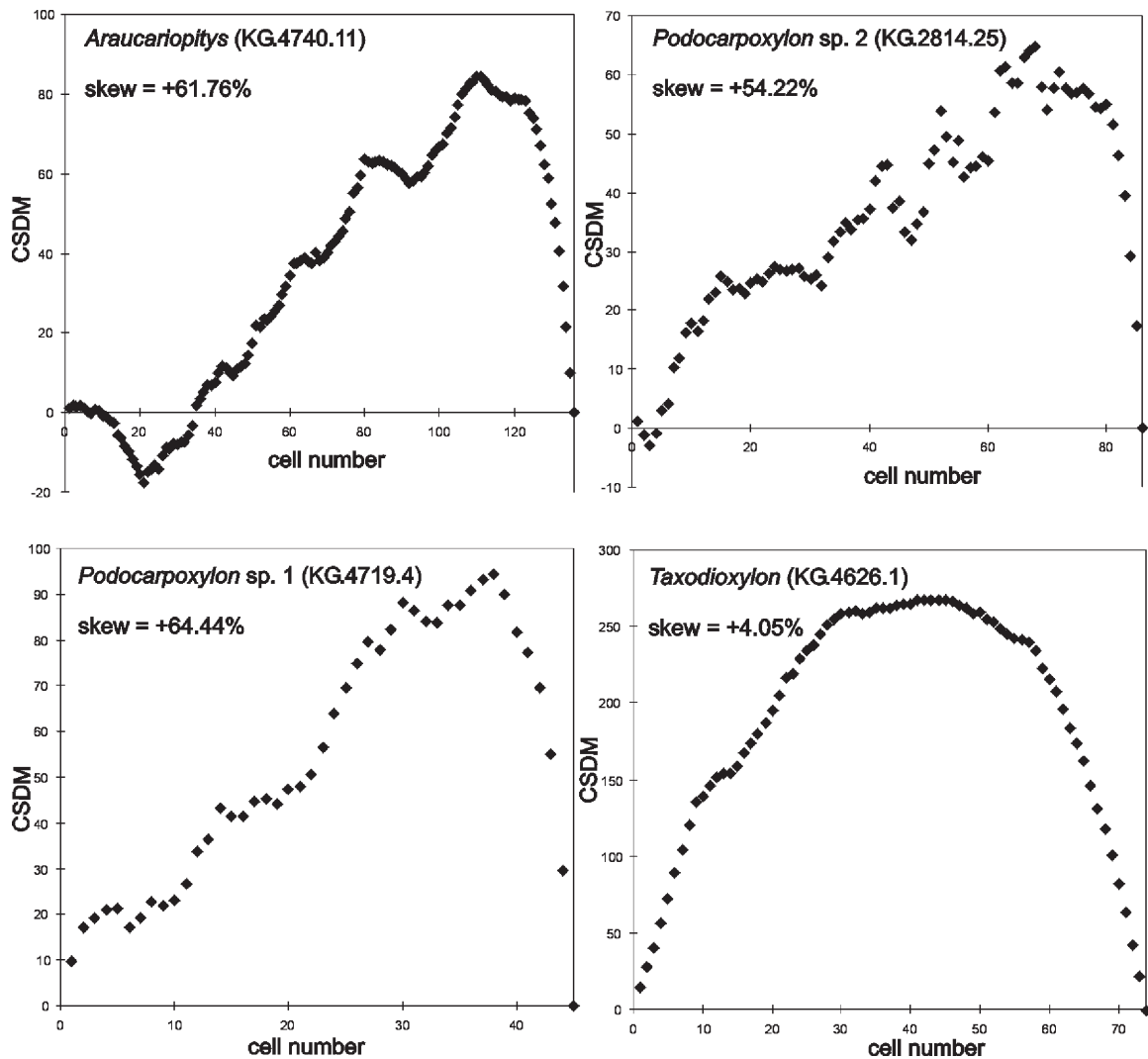
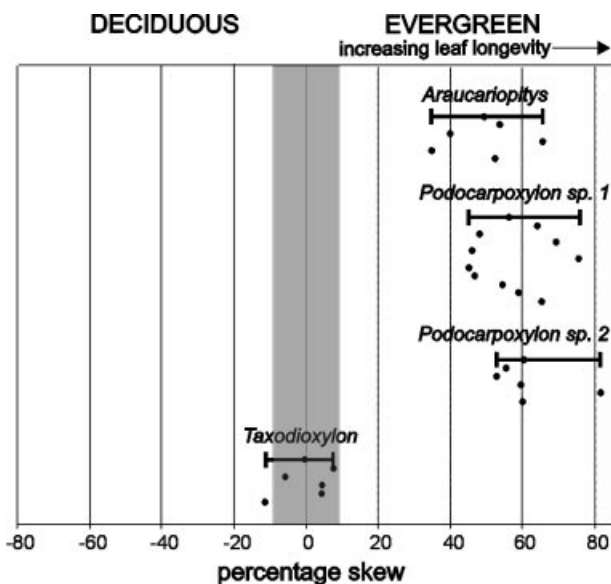


Figure 4. Example graphs showing the Cumulative Sum of the Deviations from the Mean (CSDM) for four measured growth rings in the Alexander Island woods. Note that *Araucariopitys* and the two *Podocarpoxylon* species possess CSDM curves with high positive skew values whilst the CSDM curve of *Taxodioxyton* is almost symmetrical.



increments before being occluded by parenchyma (Eames & McDaniels, 1947). By counting the number of growth ring increments through which a leaf trace passes before being occluded, a very precise estimate of the leaf longevity of the parent plant can be made (Fig. 6a; W. G. Chaloner, pers. comm., 1997; Falcon-Lang, 1999a). However, this technique is difficult to apply to fossil specimens because leaf traces, due to their small size and widely spaced distribution around the stem circumference, are rarely intersected in the plane of thin sections; only a very few examples have

Figure 5. Results of analysis of Alexander woods using Falcon-Lang's (2000a) new technique. The grey area represents the zone of overlap between the deciduous and evergreen fields based on data in Falcon-Lang (2000a). The results imply that *Araucariopitys* and the two *Podocarpoxylon* species were evergreen with long leaf retention times whilst *Taxodioxyton* may have been deciduous or evergreen with a short leaf retention time.

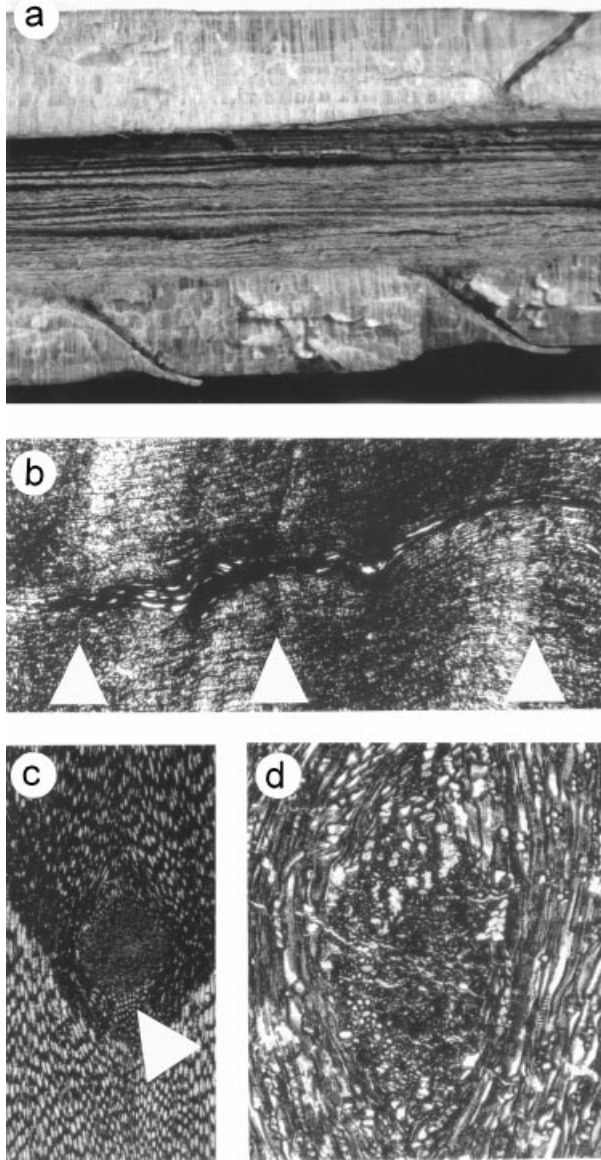


Figure 6. Leaf traces. (a) Longitudinal section through modern specimen of branch of *Araucaria araucana* (19 mm diameter) showing three persistent leaf traces. The traces, which pass through 11 growth ring increments, were attached to living leaves when the specimen was collected; they indicate that leaf longevity was > 11 years in this specimen. (b) Leaf trace departing through juvenile stem of *Araucariopitys*, transverse section. Arrows mark ring boundaries intersected by leaf trace, mag. $\times 25$, KG. 4740.11. (c) Cross-section of circular leaf trace in latewood of *Podocarpoxylon* sp. 1. Arrow marks strand of secondary xylem on the underside of the trace, oblique tangential section, mag. $\times 25$, KG. 4719.4. (d) Cross-section of oval leaf trace in *Araucarioxylon*, tangential section, mag. $\times 100$, KG. 4702.4.

been described in the literature with sufficient detail to apply the technique (e.g. Gordon, 1935; Galtier & Scott, 1994; Falcon-Lang & Cantrill, 2000). In addition, the technique is dependent on the ring increments in young woods representing annual periods of growth, a questionable assumption for some fossil wood assemblages (Falcon-Lang, 1999a).

2.b.2. Data and interpretation

In two specimens of *Araucariopitys*, vascular traces 290–415 μm in diameter (up to 0.140 mm^2 in cross-sectional area; $n=8$), and composed of scalariform or reticulate thickened tracheids of 6–8 μm diameter were found. The first specimen (KG. 4702.28) consisted of a 45 mm diameter woody cylinder surrounding a parenchymatous pith and was interpreted as part of a small vertical stem because reaction wood was absent (Creber, 1975). This fossil specimen possessed two vascular traces which passed through five ring increments before disappearing out of the plane of section. The second specimen (KG. 4740.11) consisted of a 65 mm diameter, strongly asymmetric woody cylinder surrounding a parenchymatous pith. Marked asymmetry in stem cross-section is most commonly found in branches (where it is termed reaction wood) and is due to the influence of gravity on wood formation. In gymnosperms the widest stem radius occurs on the underside of the branch (Creber, 1975). On the basis of this observation, specimen KG. 4740.11 is interpreted as a lateral branch. Six vascular traces extended from the lower side of this fossil branch and passed through up to 13 ring increments before disappearing from the plane of section; one such trace is 31 mm in length (Fig. 6b). Vascular traces were also noted in one specimen of *Podocarpoxylon* sp. 1. This specimen (KG. 4719.4) consisted of a woody cylinder (90 mm in diameter), surrounding a poorly preserved pith and was interpreted as a small vertical stem because reaction wood was absent. Four large leaf traces, up to 475 μm in diameter (up to 0.178 mm^2 cross-sectional area) occurred close to the pith region and extended through the first five growth increments (Fig. 6c).

There are three pieces of evidence which suggest that all these persistent vascular traces are leaf traces and not small branch traces. First, the vascular traces are almost identical in cross-sectional area (Fig. 6c,d) to the leaf traces of modern araucarian conifers such as *Agathis australis* (D. Don) Laudon (0.134 mm^2 : Lacey, 1953) and *Araucaria araucana* (0.095 mm^2 : H. J. Falcon-Lang, pers. obs., 1997). Second, the vascular traces are composed entirely of cells with scalariform to reticulate wall ornamentation, uncharacteristic of the more mature tissue one would expect to encounter in branches (Esau, 1977). Third, small branch traces are also present in the *Araucariopitys* specimens; they are more than 2 mm in diameter (an order of magnitude larger than the leaf traces), and exhibit a concentric outer layer of secondary xylem, a feature not seen in leaf traces.

The Alexander Island conifers grew in a polar environment. In this setting, the onset of the cool, dark winter would be the most likely trigger of cambial dormancy and growth ring formation, and individual ring increments in the woods therefore probably

represent an annual growth period (Francis, 1986). Furthermore, in the closest modern analogues to the vegetation of the Triton Point Formation, the cool temperate podocarp forest of South Island, New Zealand, conifers usually only make one growth ring per annum (Franklin, 1969). Assuming that growth rings were formed annually, the fossil leaf trace data indicate that *Araucariopitys* and *Podocarpoxyton* sp. 1 were both evergreen with long leaf retention times, at least five years in *Podocarpoxyton* sp. 1 and at least 13 years in the case of *Araucariopitys*. However, there is limited evidence that the leaf traces of present-day araucarian conifers may continue to extend in length even after leaf fall (Eames & McDaniels, 1947); if this is confirmed, then the estimates of leaf longevity for the *Araucariopitys* plant may be too high.

2.c. Leaf physiognomy

2.c.1. Method

In the third technique, the form and structure of fossil leaves (leaf physiognomy) are examined for clues that may suggest leaf habit. In angiosperms, evergreen leaves are usually thicker with a smaller surface area than their deciduous counterparts and possess a thick cuticle, sunken stomata and an array of sclerophyllic characteristics such as spines or hairs to avoid winter herbivore predation (Chabot & Hicks, 1982; Wolfe & Upchurch, 1987; McElwain & Chaloner, 1996). However, interpretation of the leaf physiognomy of non-angiosperms is more difficult and has only been attempted to a limited degree (Chaloner & Creber, 1990). For example, Pigg & Taylor (1993) interpreted the presence of an abscission scar on the leaf petiole of a glossopterid to indicate a deciduous habit.

2.c.2. Data and interpretation

The coniferous foliage of Alexander Island can be broken down into three classes; there are (1) large broad leaves, (2) small appressed scale leaves, and (3) linear dorsiventrally flattened leaves that are often twisted to lie in one plane (Cantrill & Falcon-Lang, unpub. data). The large, broad leaves are either broadly attached at the base and strongly imbricate (e.g. *Araucaria*; Fig. 7a), or are constricted basally and almost petiolate (e.g. *Podozamites*; Fig. 7b). The leaves of *Araucaria alexanderensis* Cantrill show evidence of seasonal variation in leaf size; a transition from large leaves (40 mm long) to small leaves (7 mm long) and then back to larger leaves (40 mm) again occurs in KG. 4745.15. This type of growth pattern is seen in many extant conifers including araucarian species such as *A. bidwillii* Hook. (Stockey, 1982, plate III, 7) and *Wollemia nobilis* W. G. Jones *et al.* (Chambers, Drinnan & McLoughlin, 1998, fig. 1) where the variation in size relates to the growing season. The fluctuation in leaf size seen in KG.

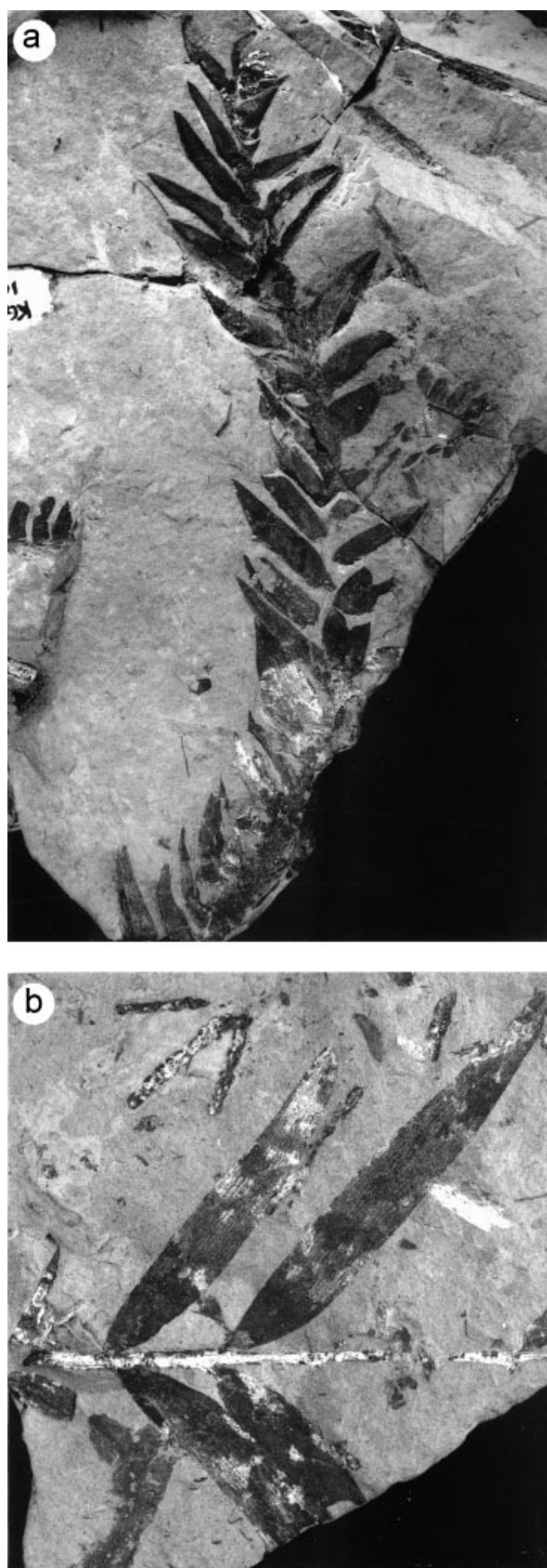


Figure 7. (a) Broad-leaved *Araucaria alexanderensis* Cantrill, mag. $\times 1$, KG. 2815.165, and (b) broad-leaved *Podozamites binatus* Cantrill with scaly taxodiaceous conifer leafy shoot (*Brachyphyllum*) in top-left corner, mag. $\times 1$, KG. 1704.5a.

4745.15 indicates that this foliage is evergreen and represents two seasons of growth.

Podozamites leaves are always found attached to stems and never as isolated leaves (Fig. 7b). Stems range from those with two to three leaves to larger stems with up to 20 leaves. This suggests that the foliage preserved does not represent seasonally determinate shoots that abscised in the autumn, but rather portions of the plant that have been broken off. Further support for this interpretation is seen in the stem bases that lack an abscission zone or expanded base, a feature often seen in deciduous shoots. In addition, deciduous foliage units typically have small leaves at the base that grade into mature leaves more distally. All the leaves seen in *Podozamites* are of a uniform size. Thus the combined evidence supports an evergreen interpretation.

Both these broad foliage types occur in the upper part of the Triton Point Formation associated with the woody stems, *Araucariopitys* and *Podocarpoxyton*. Lacey (1953) noted that the cross-sectional area of a leaf trace shows a positive correlation with leaf area. For example *Agathis australis* possesses leaf traces with a large cross-sectional area (0.134 mm²) and possesses large leaves of dimensions 7 × 4 cm (Lacey, 1953). The Alexander Island woody conifer stems *Araucariopitys* and *Podocarpoxyton* sp. 1, which possess leaf traces of a similar size to *Agathis australis*, therefore may have borne equally large broad leaves. On this basis, the two Alexander Island foliage types attributed to *Araucaria* and *Podozamites* (maximum leaf dimensions: 4 × 1.2 cm and 8.2 × 1.1 cm respectively) are the most likely taxa borne by these two wood genera (Cantrill & Falcon-Lang, unpub. data).

The small appressed scale-like leaves are represented by the foliage of *Athrotaxites titanensis* Cantrill and *Brachyphyllum* (Fig. 7b). It is suggested that most of this foliage is also evergreen because foliage units are not determinate and do not appear to be shed as foliage units. However, there is limited evidence that one species of *Brachyphyllum* may have been deciduous; these shoots are of similar dimensions suggesting a initially determinate habit, and that the plant may have shed foliage units like extant deciduous taxodiaceous conifers. These *Brachyphyllum* foliage units occur in the braided river systems at a similar stratigraphic level to the *Taxodioxyton* wood, which may also have been derived from a deciduous taxodiaceous conifer (cf. Section 2.a.2).

The linear lanceolate leaves in the Alexander Island foliage assemblage possess a single midvein and occur attached in a helical fashion with the leaves oriented into two planes (e.g. *Elatocladus*). Comparison with the foliage of the deciduous conifers *Taxodium* Rich and *Metasequoia* Hu & W.C. Cheng, allows the leaf habit of *Elatocladus* to be interpreted. In these two extant genera a resting bud surrounded by scale leaves overwinters, and in the spring produces a determinate

shoot with linear lanceolate, helically inserted leaves. In the autumn these foliage units are shed, except where the long shoots become indeterminate; resting buds form in the leaf axils of this latter shoot and the leaves are shed. Consequently deciduous conifers have a distinctive morphology when compared to conifers with longer leaf retention times. The foliage shoots are characterized by distinct basal buds and scale leaves. Non-deciduous forms lack these features. The linear lanceolate foliage seen in the Alexander Island material lacks this morphology and therefore is considered to be evergreen also.

Other foliage of linear lanceolate leaves such as *Podocarpites wileyii* Cantrill possesses resting buds with scale leaves and leafy shoots with longer leaves. However, these are rarely found as isolated foliage units but rather as isolated branches with short lateral shoots. This suggests that these small shrubby podocarps were not deciduous but produced resting buds that presumably overwintered prior to leaf and shoot expansion in the spring (Cantrill & Falcon-Lang, unpub. data).

Finally, specimens of *Ginkgoites* Seward are characterized by the long shoot–short shoot syndrome seen in fossil *Ginkgo* (Zhou & Zhang, 1989) and other extant (e.g. *Larix* Mill., *Malus*) and fossil (e.g. *Glossopteris* Brongniart and *Nilsoniocladius* Kimura & Sekido) deciduous plants. On this basis *Ginkgoites* was almost certainly deciduous. A similar shoot morphology is observed in *Taeniopteris* Brongniart and it is also considered to be deciduous.

2.d. Nearest Living Relatives

2.d.1. Method

In the fourth method, the Nearest Living Relative technique, the assumption is made that related modern and fossil groups have similar leaf longevity. Clearly, the closer the taxonomic relationship between the two groups in question, the more accurate the interpretation of leaf life span possible. This method becomes increasingly difficult to apply for pre-Tertiary floras where only family-level taxonomic affinity may be assumed (Chaloner & Creber, 1990). In addition, axiomatic to the method is that the ecological and climatological requirements of taxa were constant throughout geological time and were not affected by evolutionary changes; this assumption is questionable for floras of Cretaceous age (A. B. Herman, pers. comm., 2000)

2.d.2. Data and interpretation

Three conifer families, the Araucariaceae, Podocarpaceae and Taxodiaceae, occur in the Alexander Island forest assemblage together with ginkgopsids (Falcon-Lang & Cantrill, 2000; Cantrill & Falcon-

Lang, unpub. data). Today, all members of the Podocarpaceae and Araucariaceae are evergreen, usually with long leaf retention times. For example, amongst the Araucariaceae, *Araucaria araucana* growing in Chile retains leaves for 15 years (Vidakovic, 1982) whilst the podocarp conifers *Halocarpus bififormis* (Hook) Quinn and *Halocarpus bidwillii* (Hook. F. ex Kirk) Quinn growing in New Zealand may hold leaves for 10 and 20 years respectively (Wardle, 1963; Odgen & Stewart, 1995). Alexander Island Araucariaceae and Podocarpaceae may therefore also have been evergreen with long leaf retention times. In contrast, present-day Taxodiaceae possess the greatest number of deciduous genera of any conifer family; of the eight extant genera, *Taxodium*, *Glyptostrobus* Endl. and *Metasequoia* are all deciduous (Vidakovic, 1982), whilst the remaining genera are evergreen with short leaf retention times. The only taxodiaceous foliage found on Alexander Island was assigned to *Athrotaxites*, a form genus that bears some similarity to the extant evergreen conifer genus *Athrotaxis* D. Don, endemic to Tasmania (Cantrill & Falcon-Lang, unpub. data). The interpretation of *Athrotaxites* as evergreen seems plausible given its shoot morphology discussed above. Finally, the only living relative of the foliage genus *Ginkgoites* is *Ginkgo biloba*, which is deciduous.

2.e. Leaf taphonomy

2.e.1. Method

The fifth technique relies on the interpretation of the transport and depositional history of plant parts (plant taphonomy), based on the distribution of fossil plant remains in sedimentary facies. One might expect that deciduous leaves which are synchronously shed at a particular time in the year would tend to accumulate in discrete layers (leaf mats), whilst evergreen leaves shed throughout the year would occur randomly within a sequence (Spicer & Parrish, 1986). This idea has been developed to good effect by Retallack (1980), who correlated the occurrence of glossopterid leaves with the autumn–winter component of Permian lacustrine varved units, thus demonstrating autumnal abscission and a deciduous habit. Interpretation of leaf habit is more problematic, however, where leaves occur in sequences with no intra-annual temporal framework such as floodbasin mudstone units. For example, Parrish *et al.* (1998) recorded discrete leaf mats of *Agathis* Salsib. from the Cretaceous of New Zealand; all leaves were well preserved which suggested to the authors that they were synchronously shed in the autumn by a deciduous plant. However, similar well-preserved leaf mats of *Cordaites* Unger are found in the Upper Carboniferous of Nova Scotia (Falcon-Lang, 1999b; Falcon-Lang & Scott, 2000); it is known that cordaitaleans were evergreen so these

leaf accumulations must merely represent the product of random sedimentary processes. As a consequence it is important not to place too much emphasis on taphonomic data.

2.e.2. Data and interpretation

Only a few observations pertinent to this paper can be made with regard to the taphonomy of the Alexander Island floras. First, *Ginkgoites* leaves, which are widespread within the sequence, often form prominent leaf mats. These leaf mats are characterized by leaves of a uniform size class and preservational state suggesting they were synchronously shed. *Taeniopteris* also forms similar leaf mats at a number of localities (e.g. KG. 4737). These data indicate that both these taxa may have been deciduous.

3. Discussion

Data acquired using the five independent techniques above strongly suggest that the canopy-forming vegetation of Alexander Island that included conifers, ginkgos and taeniopterids was dominantly evergreen. The araucarian and podocarp conifers that composed more than 90% of the forest canopy were evergreen with leaf retention times of at least 5–13 years. Some rare taxodiaceous conifers were also evergreen but with much shorter leaf retention times; other taxodiaceous conifers may have been deciduous as were all the ginkgos and taeniopterids. The understorey vegetation, dominated by ferns, was probably mainly deciduous. For example, pteridophytes such as *Phyllopteroides* Medwell (Osmundaceae) frequently occur as isolated pinnules; this may imply that this fern died down during the winter months as do extant *Osmunda* L. Some of the understorey angiosperms may have been evergreen, however (Cantrill & Nichols, 1996).

3.a. Southern Hemisphere polar vegetation

Forest vegetation is also known to have grown in the Southern Hemisphere polar region at two other sites during the mid-Cretaceous (Fig. 8a). In New Zealand, late Albian–Cenomanian vegetation grew at a latitude of 70° S. One of the dominant elements of this flora was the foliage of *Agathis*, a canopy-forming araucarian conifer. On the basis of cuticle thickness and taphonomic data, Parrish *et al.* (1998) interpreted one *Agathis* species as being deciduous whilst another was assigned evergreen status. Other plants present were liverworts, ferns, sphenopsids, taeniopterids, cycads, bennettites, pentoxylaleans, ginkgophytes, podocarp conifers and angiosperms which probably included a mixture of evergreen and deciduous plants (Stopes, 1914, 1916; Parrish *et al.* 1998).

In southeastern Australia, abundant Albian fossil floras have been studied in the Otway Basin; these

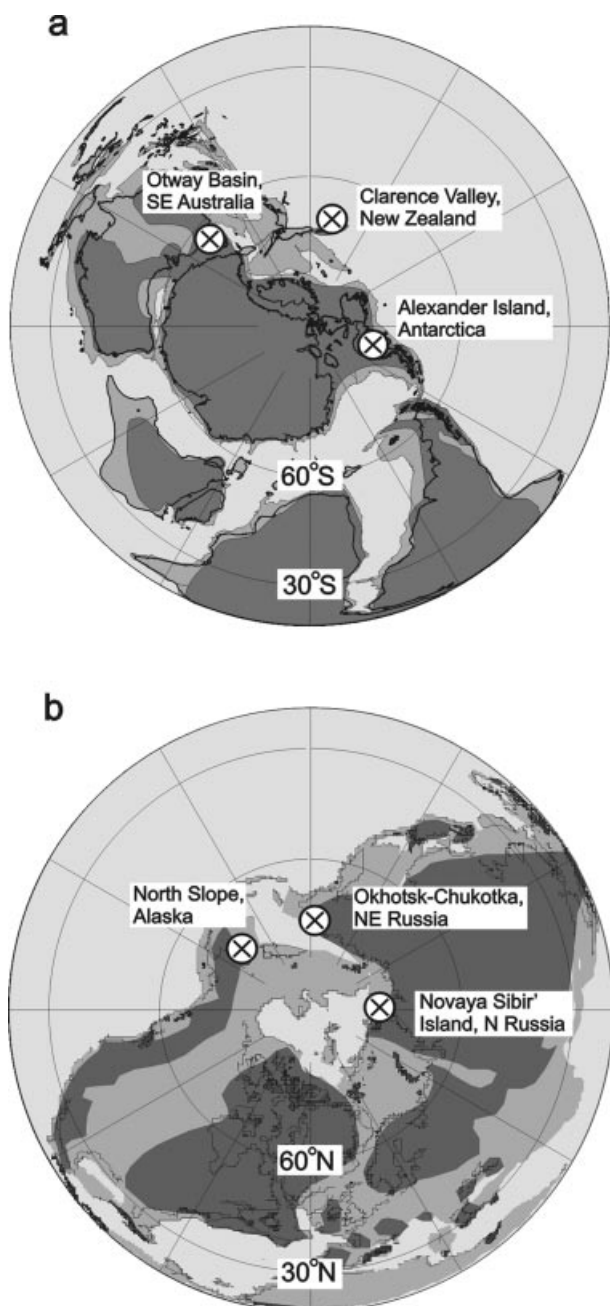


Figure 8. Mid-Cretaceous polar-centred geographies showing the position of fossil forests mentioned in the text. (a) Southern Hemisphere, late Albian stage, 105 Ma, and (b) Northern Hemisphere, Albian–Cenomanian stages, 95 Ma (Palaeo-coastlines from Smith, Smith & Funnell, 1994, and R. Livermore, BAS). Light grey – deep ocean; medium grey – continental marine shelf; dark grey – land.

represent vegetation which grew at a latitude of 66° S. Floras are dominated by the wood and foliage of evergreen araucarian and podocarp conifers which would have formed the forest canopy; taxodiaceous conifers which may also have been evergreen occur rarely (Cantrill & Webb, 1987; Cantrill & Douglas, 1988; Cantrill, 1991, 1992; Dettman *et al.* 1992). The understorey comprised a mixed evergreen–deciduous vegetation which included cycads, gymnosperms, ferns,

ginkgophytes and angiosperms (Douglas & Williams, 1982).

In summary, the Southern polar forests of Alexander Island and southeastern Australia appear to have been composed of an almost exclusively evergreen coniferous canopy with a mixed evergreen–deciduous understorey, but New Zealand forests from a similar latitude appear to have contained a larger deciduous component.

3.b. Northern Hemisphere polar vegetation

Vegetation patterns have also been reconstructed for several mid- to Late Cretaceous sites in the northern polar region (Fig. 8b). Spicer & Parrish (1986) described a number of floras from the Albian–Cenomanian Nanushuk Group of northern Alaska which grew at a latitude of more than 75° N. These were largely composed of deciduous plants including angiosperms, ginkgophytes, ferns, vine-like cycads and conifers (Axelrod, 1984; Spicer & Parrish, 1990; Spicer & Herman, 1996). The dominant conifers were probably deciduous because they possessed foliage morphotypes comparable to that of modern taxodiaceous shoot-dropping species. Some other conifers such as the broad-leaved *Podozamites* which grew in Alaskan peat mire environments have also been assigned deciduous status but this interpretation is based on equivocal taphonomic grounds; microphyllous conifers such as *Brachyphyllum* were almost certainly evergreen (Spicer & Parrish, 1986). In the same vicinity, Coniacian and Campanian–Maastrichtian plant assemblages have been described from the Colville Group and were also dominantly deciduous being composed of angiosperms, ginkgophytes, ferns and sphenopsids. Some of these conifers, particularly the cupressaceous forms, were probably evergreen whilst other more dominant taxodiaceous forms were deciduous (Parrish & Spicer, 1988).

Finally, mid- to Late Cretaceous forest vegetation is also known from many sites in northern and north-eastern Russia where it flourished at latitudes of 65–82° N (Spicer & Herman, 1998). These forests were composed of deciduous caytonealeans, ginkgos, czezanowskialeans, vine-like cycads, and many conifers and angiosperms. Some of the conifers were of the taxodiaceous shoot-dropping species, but many others were of araucarian or cupressaceous affinity, and possessed evergreen scale-like leaves (Herman, 1999; Kelley, Spicer & Herman, 1999). Considered in totality, the Northern Hemisphere polar forests of Alaska and northern Russia appear to have contained a much larger deciduous component than the Southern forests of Antarctica, Australia and New Zealand (Wolfe & Upchurch, 1987). This conclusion conflicts with early studies which suggested that both Northern and Southern Hemisphere polar forests were equally deciduous (Spicer, Rees & Chapman, 1993).

3.c. Mid-Cretaceous polar environments

Why did Northern Hemisphere polar forests contain a much larger number of deciduous trees than the Southern Hemisphere forests? Growing within the polar circles (palaeolatitude $>66^\circ$), all these floras would have had to adapt to conditions of extreme light seasonality including a protracted period of permanent darkness during the winter months (Read & Francis, 1992). The employment of different ecological strategies in these two coeval polar communities suggests that environmental conditions differed between the Northern and Southern Hemisphere poles. In this section we explore the nature of the Cretaceous polar environments and attempt to relate these environmental conditions to the observed patterns of leaf phenology.

In the Northern Hemisphere, the Alaskan and Russian polar forests both grew on maritime peninsulas almost entirely surrounded by ocean or on islands. Multivariate analyses of foliar physiognomic data from these regions suggest that the cold month mean temperature never fell very low, being in the region of $+6.2^\circ\text{C}$ at 75°N in Alaska, -0.6°C at 82°N in northern Russia, and $+5.5^\circ\text{C}$ at 70°N in northeast Russia during the late Albian–Coniacian stages, and that Arctic Ocean temperature was warm year-round, never falling much below 5.7°C (Herman & Spicer, 1996; Spicer & Herman, 1998). These figures compare reasonably well with the results of climate computer models run by Valdes, Sellwood & Price (1996). Although dropstone evidence suggests that seasonal sea-ice may have formed adjacent to continental high northern latitude regions such as Spitsbergen in the Albian (Frakes & Francis, 1988; Francis & Frakes, 1993), there is no widespread evidence for sea-ice in the Arctic Circle; permanent ice was probably only present at high altitude in Alaska and Russia (Spicer & Parrish, 1990). Collectively these data suggest a mild, maritime climate during the Arctic winter months.

In contrast, the polar floras of the Southern Hemisphere grew along the palaeo-Pacific coast of the Gondwanan supercontinent in New Zealand and the Antarctic Peninsula, and in a more continental setting in southeast Australia (Fig. 8a). Numerical computer climate models predict cold month mean temperatures to have been around $+4^\circ\text{C}$ for maritime New Zealand but much lower (down to -8°C) for Antarctica and southeast Australia (Valdes, Sellwood & Price, 1996). More primitive terrestrial climate models have predicted that Australia–Antarctica would have experienced cold month mean temperatures as low as -18°C (Barron & Washington, 1984). Freezing winter conditions are implied by the presence of Aptian ikaite pseudomorphs (glendonites nodules) in central Australia which develop under cold bottom water conditions (Dettman *et al.* 1992; Francis & Frakes, 1993), and Aptian–Albian dropstones in northern Australia suggest that seasonal sea-ice periodically extended

as far north as 55°S (Frakes & Krassay, 1992). The presence of a small permanent Early Cretaceous Antarctic ice sheet has also been inferred by Stoll & Schrag (1996) to explain rapid sea-level changes during this interval. All these data suggest that Southern Hemisphere polar vegetation in Australia and Antarctica grew under a climate characterized by cold, dark winter conditions whilst New Zealand floras existed in a maritime setting where winter temperatures were milder.

3.d. Mid-Cretaceous polar leaf phenology

As noted in the introduction, the leaf phenology of plants is ‘finely tuned’ to the growing environment in order to achieve the highest possible annual carbon gain. The largest problem facing plants growing well within the polar circle relates to the high levels of dark respiration incurred during the winter darkness. This may not have been such a severe problem during the Cretaceous greenhouse phase as it would be today, because it is known that whole-canopy dark respiration is reduced under conditions of elevated carbon dioxide (Barker *et al.* 2000). Nevertheless, physiological adaptation to prolonged periods of dark respiration may have been one of the main factors influencing leaf phenology.

For example, in polar regions with warm dark winters like those of the Cretaceous Northern Hemisphere (e.g. $+6^\circ\text{C}$ cold month mean temperature), a deciduous habit would probably be favoured because the presence of winter leaves would permit high rates of dark respiration and quickly lead to etiolation of seedlings (Spicer & Corfield, 1992). Creber & Chaloner (1985) have suggested that some evergreen plants may have been able to survive in such warm winter dark conditions by altering their physiology so that optimum respiration temperature was set a few degrees higher than ambient temperature. Another option would be to evolve scale-like, xeromorphic foliage which could effectively close stomata and minimize dark respiration carbon-loss; this strategy appears to have been utilized by some araucarian and cupressacean conifers from the northern Russian sites (Herman, 1999).

In contrast, in polar regions with cold dark winters like those of mid-Cretaceous Australia and Antarctica (perhaps as low as -8°C), an evergreen habit would probably have been favoured. Here, temperatures would be sufficiently low to suppress metabolic activity during the winter darkness, therefore minimizing respiration losses (Gower & Richards, 1990). Under such circumstances, an evergreen habit would be advantageous as it would permit photosynthesis to begin as soon as light and temperature levels exceeded the necessary threshold, whilst at the same time reducing the carbon-expenditure in making a new leaf canopy (Chabot & Hicks, 1982). In contrast New

Zealand floras existed under a milder maritime climate, and as in the Northern Hemisphere, plants with a deciduous habit were more competitive.

This thesis for explaining mid-Cretaceous phenological patterns is supported by the work of Read & Francis (1992). They examined the response of some seedlings to ten weeks of permanent darkness at both 4 °C and 15 °C. In general evergreen conifer species such as *Dacrycarpus cinctus* (Pilg.) de Laub., *Lagarostrobos franklinii* (Hook.) Quinn, *Microstrobos niphophilus* J. Garden & L.A.S. Johnson and *Phyllocladus aspleniifolius* Hook. f. survived 70 days of darkness without long-term damage at the lower temperature but were more severely affected at the higher temperature. In contrast, deciduous taxa such as *Ginkgo biloba* L. and *Nothofagus antarctica* were apparently unaffected by either the warm or cold dark treatment.

4. Conclusions

(1) A systematic study of the leaf phenology of a fossil forest is presented for the first time. Five independent lines of evidence are drawn upon to strongly suggest that the mid-Cretaceous (late Albian) forest vegetation of Alexander Island consisted of a dominantly evergreen canopy with a mixed evergreen–deciduous understorey.

(2) Preliminary analysis of all known polar forests implies the existence of a rather complex ecophysiological mosaic during mid- to Late Cretaceous times; Antarctic and Australian forests were dominantly evergreen whilst Alaskan, Russian and New Zealand forests possessed a rather larger deciduous component.

(3) These two ecological strategies represent responses to different polar environments. In Alaska, Russia and New Zealand, forests experienced mild dark winter climates; these conditions favoured a deciduous strategy which acted to minimize dark-respiration carbon loss. In Antarctica and Australia, forests experienced cold, dark winter conditions; these forests developed an evergreen strategy to efficiently exploit the short summer growing season whilst low winter temperatures thermally depressed metabolic rates and minimized dark-respiration losses.

Acknowledgements. This paper was prepared as part of a post-doctoral project examining Cretaceous polar forests and was funded by the British Antarctic Survey (BAS). Chris Gilbert and Pete Bucktrout (BAS) are thanked for preparing the photographs. Discussion with Chris Page improved our grasp of conifer ecology, whilst thorough and thoughtful reviews by W. G. Chaloner and A. B. Herman greatly tightened up our arguments.

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