MIDDLE CRETACEOUS WOOD FROM THE NANUSHUK GROUP, CENTRAL NORTH SLOPE, ALASKA

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ABSTRACT. Analysis of growth rings in Albian and Cenomanian (late Cretaceous) coniferous wood from the North Slope of Alaska (74-85° N. palaeolatitude) has shown that tree growth was rapid and steady during the growing season, resulting in wide growth rings and few false rings, that narrow late wood, as little as one cell wide, indicates that tree growth ceased abruptly at the end of the growing season owing to rapid onset of winter darkness, and that inter-annual growth was variable. Water being in abundant supply, this variability was likely to have been caused by fluctuations in soil drainage or in summer mean temperatures.

IN mid-Cretaceous times, the North Slope of Alaska was situated 75-85° N. (Smith and Briden 1977; Ziegler *et al.* 1983) and was probably the nearest land to the North Pole. The mid-Cretaceous South Pole was in Antarctica, but no part of the continent that was within 5° of the pole is currently accessible. Mid-Cretaceous global climate generally is regarded to have been warm relative to the present, particularly at high latitudes (Savin 1977; Barron 1983). Therefore, the North Slope is a critical region for Cretaceous climatic studies.

The Albian-Cenomanian Nanushuk Group of the North Slope contains a rich leaf megafossil flora (Smiley 1966, 1967, 1969a, b; Scott and Smiley 1979; Spicer 1983) and abundant fossil wood. In 1985 we collected 45 samples of this wood from several localities along the Colville River (text-fig. 1; Spicer and Parrish 1986). They are coniferous and comprise three taxa, *Xenoxylon latiporosum* (Cramer) Gothan and two previously undescribed taxa. Thirteen were preserved well enough to yield some anatomical information, and seven yielded sequences of seven or more measurable growth rings. Certain characteristics of the growth rings provide information about the palaeoclimate. Although this information is not conclusive by itself, analysis of the growth rings supports our previous conclusions about the polar climate during the mid-Cretaceous.

PREVIOUS WORK

Fossil woods. Studies on the palaeoclimatic implications of growth rings are few for wood older than Pleistocene, although many pre-Pleistocene fossil woods, including those from northern Alaska (Arnold 1952), have been described and named (Jefferson 1982; Creber and Chaloner 1984, 1985). Palaeoclimate-orientated studies include Francis (1984) on Purbeck wood, Isle of Portland, England, Jefferson (1982) on early Cretaceous wood, Alexander Island, off the Antarctic Peninsula, Francis (1986) on Cretaceous and early Tertiary wood of the Antarctic Peninsula, and Creber and Chaloner (1984, 1985) who surveyed Cretaceous and Tertiary wood worldwide.

Polar palaeoclimatology. Until recently, only qualitative information existed on Cretaceous polar temperatures. Based on the leaf megafossil assemblages and noting particularly the presence of cycads, Smiley (1969a) implied a warm-temperate climate for the North Slope but did not define 'warm-temperate'. A similar conclusion was reached by May and Shane (1985), using palynofloral assemblages, and Roehler and Stricker (1984), based on the presence of dinosaurs and wide growth rings in fossil woods. Following Savin (1977), Barron (1983) estimated mean annual polar temperatures of 0-15 °C, based on extrapolations from seawater temperatures at lower palaeolatitudes as determined from isotopic analyses. This estimate encompasses the range of climates from subpolar to subtropical (cf. Wolfe 1979), but was the most reasonable quantitative estimate at the time.
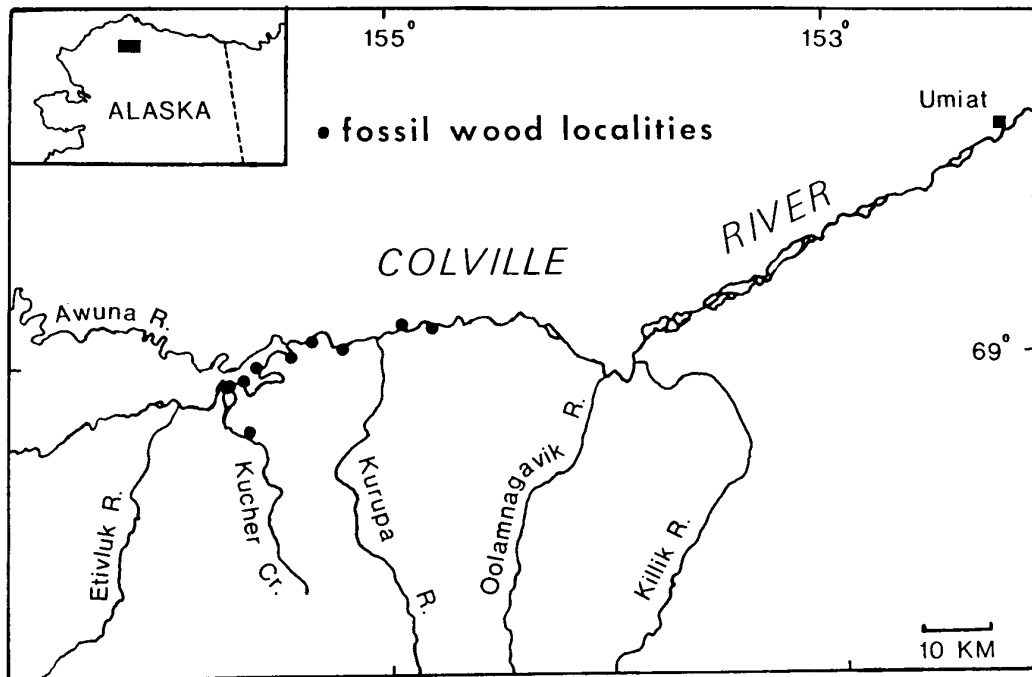
TEXT-FIG. 1. Map showing fossil wood localities.

Subsequently, we added to and reassessed the leaf megafossil data of the Cretaceous North Slope (Spicer and Parrish 1986). Using leaf-margin analysis of the angiosperms, we concluded that the mean annual temperature in the Cenomanian was $10 \pm 3\,°C$, or cool temperate in Wolfe's (1979) scheme.

## GEOLOGY AND DEPOSITIONAL ENVIRONMENTS OF THE WOOD

The fossil plants are found in nonmarine rocks of the Nanushuk Group (text-fig. 2), although associated marine rocks contain rare leaf remains and abundant finely disseminated carbonaceous debris that was derived from terrestrial vegetation. The Nanushuk Group consists of a fluvial-deltaic assemblage (Ahlbrandt et al. 1979; Huffman et al. 1985) and comprises several depositional facies along the Colville River. These and the environments of the wood and associated fossil plant material are described in Table 1.

DESCRIPTION OF THE WOOD

1. *Xenoxylon latiporosum* (Cramer) Gothan (Pl. 5, figs. 1-5)

Transverse section. Secondary wood consists of tracheids and parenchymatous rays only. Cross-sectional area of early-wood tracheid lumina typically is 2100 μm^2. Transition from early wood to late wood is abrupt; late-wood zone is narrow. Tracheids tend to be rectangular in cross-section with early-wood walls 5 μm thick. Rays are uniseriate, 10–12 μm wide. Resin ducts are absent.

Radial longitudinal section. Bordered pits on the radial sides of the tracheids are vertically flattened, uniseriate, and contiguous, measuring 15 μm vertically and 20–23 μm horizontally. Pit apertures are round or slightly elliptical and typically 8 μm in diameter (or 4 × 8 μm where elliptical). Pits are not uniformly distributed along the tracheid wall but are in groups of variable number separated by more or less smooth tracheid walls. Transverse septae within the tracheids are common and spaced at intervals typically ranging from 60 μm to 90 μm. The rays
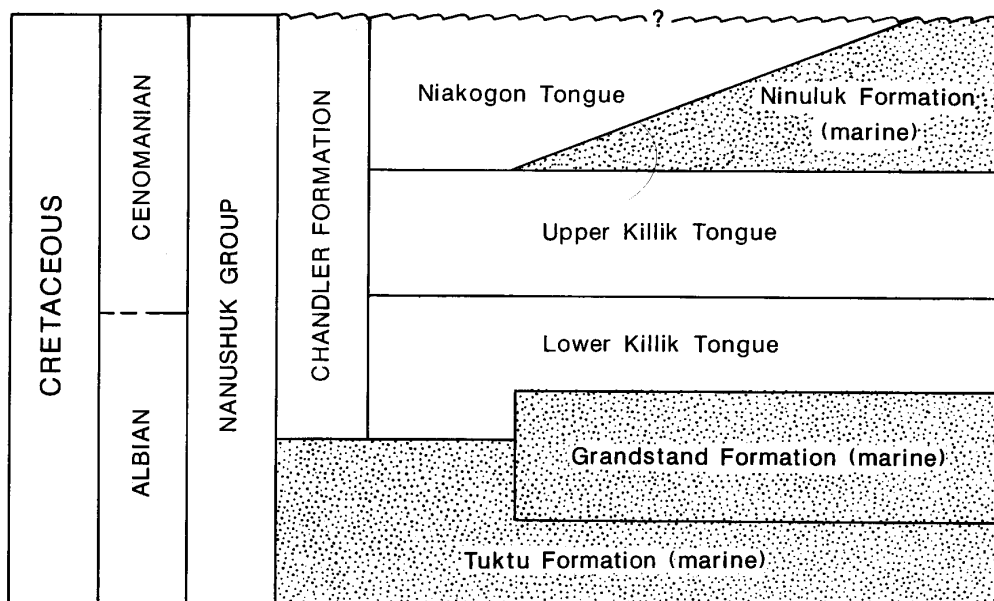
TEXT-FIG. 2. The Nanushuk Group, North Slope, Alaska (modified from Huffman 1985). Position of Albian–Cenomanian boundary based on Foraminifera (Sliter 1979) and palaeobotanical evidence (Spicer and Parrish 1986). The Grandstand and Tuktu Formations contain Albian molluscs and the Ninuluk Formation contains the Cenomanian bivalve, *Inoceramus dunveganensis* (Detterman *et al.* 1963; Chapman *et al.* 1964; Brosgé and Whittington 1966).

TABLE 1. Depositional environments, lithologies, and palaeontology of the Nanushuk Group.

Depositional environments	Lithology	Palaeontology
Fluvial channels: distributaries	Very fine to fine, broad, lenticular sandstone occasionally cross-bedded, ripple-marked	Wood; G, platanoid A, E
main channels	Narrow, lenticular very fine sandstone to pebble conglomerate	Wood, commonly flow orientated
Overbank deposits	Very poorly bedded, mottled brown, grey, yellow mudstone; thin coal lenses; dark red, fossiliferous ironstone concretions, nodular or tabular, probably representing wetter areas	Abundant root casts, rhizome systems of *Equisetites*, diverse leaf assemblages including Co, G, Cy, F, A; wood, including stumps in growth position; clams, turtle
Swamps	Coal, few cm to > 3 m thick	Wood; impressions of *Podozamites* leaves in paper coal; seat earths contain *Equisetites* rhizomes
Ponds	Poorly consolidated to indurated grey claystones, weathering light yellow	Abundant leaves, including entire abscissed Co shoots, cones, twigs, A, G

Leaves: A, angiosperms; G, ginkgophytes; Co, conifers; Cy, cycadophytes; F, ferns; E, *Equisetites*.

appear to be entirely parenchymatous. Cross-field pits are large and fenestrate with more or less square to rhombic outlines. Usually only one pit per cross field exists but rarely two are present.

Tangential longitudinal section. Rays are uniseriate, typically 12-15 cells high (but extremely variable from 1 to 30 cells high), each cell measuring 20-21 μm in height. Pits on the tangential side of the tracheids are rare and somewhat smaller than on the radial side.

Comments. Wood of this kind is widespread at high northern latitudes in the Mesozoic. Although the wood possesses pineoid cross-field pitting, it cannot be assigned to any living family of conifers (Arnold 1952).

2. *Taxon A* (Pl. 6, figs. 1-3)

Transverse section. Secondary wood consists of tracheids and ray parenchyma. Transition from early wood to late wood is abrupt with minimal late wood. Early-wood cell lumina typically are 50 μm across, usually more or less square in section. Cell walls typically are 8-10 μm thick. Resin ducts apparently are absent.

Radial longitudinal section. Tracheid pitting is mixed uniseriate and biseriate. Uniseriate pits typically measure 23 μm in height and 26-28 μm in width (occasionally up to 38 × 23 μm) with apertures of 7·5 μm, commonly separated from one another. Biseriate pits are close packed and alternate, pit diameters typically are 18-21 μm and aperture diameters 5-6 μm. Pitting apparently is confined to discrete zones. Rays consist of parenchyma cells typically 18-23 μm in height. Cross-field pitting is large, fenestrate, 31-33 μm in length and 13-15 μm in height. Pitting is absent on horizontal and transverse walls of ray cells. Tracheids have numerous transverse septae separated at intervals of 180 μm to 230 μm.

Tangential longitudinal section. Rays are uniseriate; fusiform rays apparently are absent.

3. *Taxon B* (Pl. 6, figs. 4 and 5)

Transverse section. Secondary wood consists of tracheids and ray parenchyma. Transition from early wood to late wood is abrupt with minimal late wood. Early-wood cell lumina typically are 1400 μm^2; cell walls are 6 μm thick.

Radial longitudinal section. Tracheid pitting is uniseriate and bordered. Pits commonly are isolated, pit diameters typically are 15-23 μm; aperture diameters are 7·5 μm. Rays are composed of parenchyma cells with pitting on horizontal and transverse, as well as radial, walls. Radial wall pitting consists of 2-3 slightly elliptical pits per cell measuring 13 × 10 μm.

Tangential longitudinal section. Rays are uniseriate and typically 20-25 cells high, but may be as small as 3 or 4 cells high; fusiform rays apparently are absent. Tracheids have numerous transverse septae that are irregularly spaced.

GROWTH-RING ANALYSIS

Growth rings were measured from thin sections and polished blocks; we used both where feasible (Table 2). Because most of the samples are silicified, rather than calcified, we elected not to make acetate peels, although etching usefully emphasized the rings in one sample. Some diagenetic alteration, consisting of cracks, recrystallization, and crush zones, had occurred in some samples. Crush zones are common in fossil wood (Jefferson 1982; Creber and Chaloner 1985). However, in all the samples measured, each ring in some part of the sample field was minimally altered. Cracks and recrystallized zones were avoided entirely. No attempt was made to measure rings with crush zones unless the individual cells could be distinguished and the amount of crushing therefore estimated (Pl. 5, fig. 2).

EXPLANATION OF PLATE 5

Figs. 1, 4, 5. *Xenoxylon latiporosum*, specimen 132.1. 1, transverse section showing minimal late wood, × 39. 4, radial longitudinal section, × 183. 5, tangential longitudinal section, × 120.

Fig. 2. *X. latiporosum*, specimen 96.1. Transverse section showing crush zone in early wood, × 39.

Fig. 3. *X. latiporosum*, specimen 129.1. Transverse section showing false rings, × 48.

PLATE 5
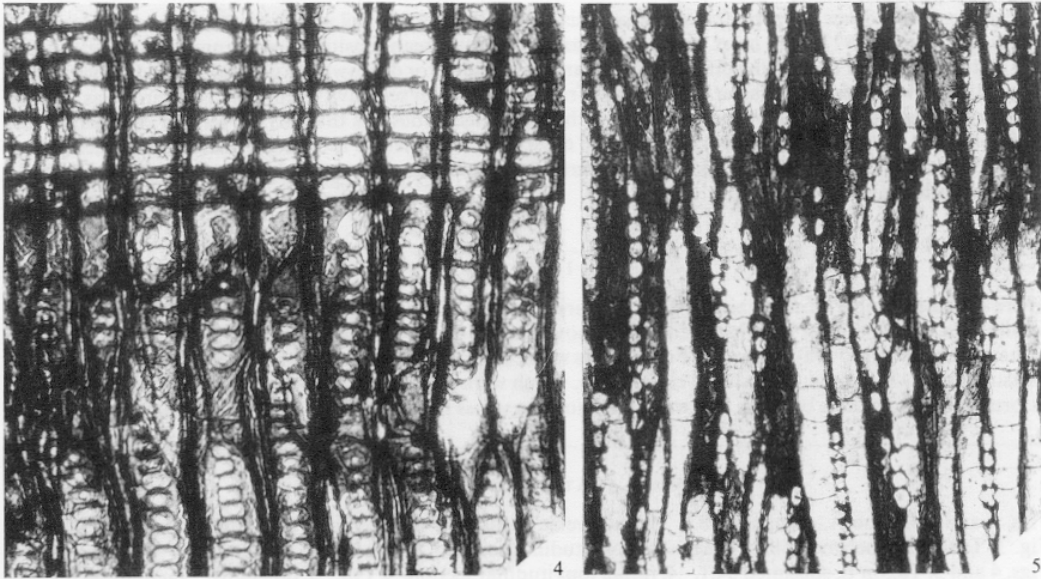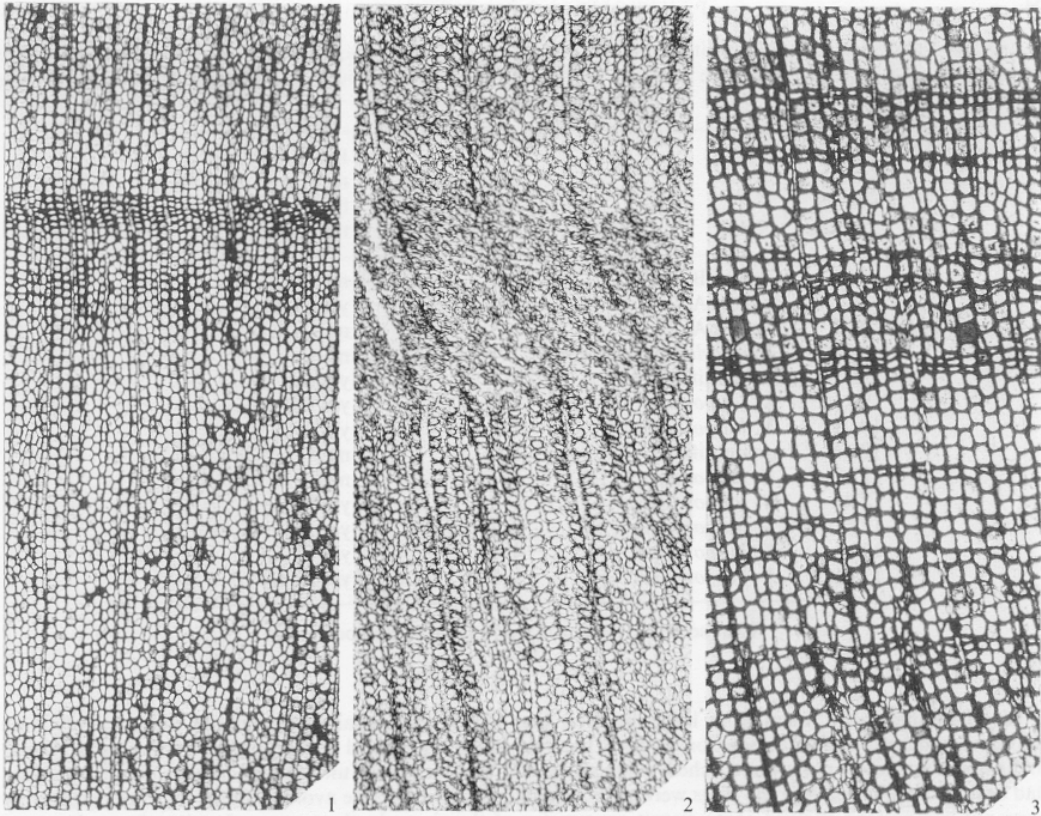
PARRISH and SPICER, *Xenoxylon*

TABLE 2. Wood samples providing data on growth rings. Parts of rings were preserved more commonly than were measurable ring sequences. In such samples, thickness of late wood could be determined where other ring characteristics could not.

Sample number	Name	Thickness of late wood (no. of cells)	Ring sequence measured (b: from block; ts: from thin section)
54.1	Taxon B	1-5	no
58.1	Taxon A	3-7	yes (b, ts)
58.2	Taxon A	1	no
89.1	*Xenoxylon latiporosum*	2-5	no
95.1	unidentified*	2-3	yes (b)
96.1	*X. latiporosum*	2-3	yes (ts)
101.1	*X. latiporosum*	1-4	yes (b)
125.1	unidentified*	1-4	no
127.1	*X. latiporosum*	1-3	no
128.1	*X. latiporosum*	1-2	yes (ts)
129.1	*X. latiporosum*	1-3	yes (b)
132.1	*X. latiporosum*	4-15	yes (b, ts)
139.1	*X. latiporosum*	1-3	yes (b, ts)

* Thin sections were not made from these specimens.

Wood samples were taken from large-diameter logs (25-50 cm), small-diameter logs that possibly were branches, and tree bases in life position. Some of the logs, which lay parallel to bedding, were compressed. Wood in the upper and lower parts was crushed, whereas the sides were relatively undistorted. Where lateral expansion had occurred, splits between the rings were obvious and could therefore be avoided. Some logs that apparently were not compressed showed some circuit asymmetry of the rings. In these cases, the site of sampling was controlled by preservation.

Statistical procedures appropriate for the analysis of growth rings in fossil woods have been described in Fritts (1976) and Creber (1977). The most useful are mean ring width, mean sensitivity, and annual sensitivity. Mean ring width is useful for comparing different woods and as an indicator of growth; in general, the wider the ring, the longer the growing season or faster the growth (Fritts 1976). Mean sensitivity generally is regarded as the best indicator of variability in growth rate. Woods with mean sensitivities less than 0·3 are termed complacent and probably grew in relatively constant and equable environments, whereas those with mean sensitivities greater than 0·3 are regarded as sensitive and probably grew in variable environments. Mean sensitivity is calculated using the following expression:

$$\text{m.s.} = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1}-x_t)}{x_{t+1}+x_t} \right|$$

where n is the number of rings and x_t and x_{t+1} are adjacent rings, counted from oldest to youngest. Annual sensitivities, that is, the last term in the equation above, may be grouped for each sample to give a graphic display of the variability in growth-ring width. For samples with crush zones, calculations were performed using both the measured ring widths and the restored ring widths, which were derived by using the upper limit of the estimated deformation. Differences between the two calculations were less than 10% in all cases. We did not attempt to use

EXPLANATION OF PLATE 6

Figs. 1 and 2. Taxon A, specimen 58.1. 1, transverse section, × 48. 2, radial longitudinal section, × 120.
Fig. 3. Taxon A, specimen 58.2. Tangential longitudinal section, × 120.
Figs. 4 and 5. Taxon B, specimen 54.1. 4, radial longitudinal section, × 190. 5, tangential longitudinal section, × 120.

PLATE 6
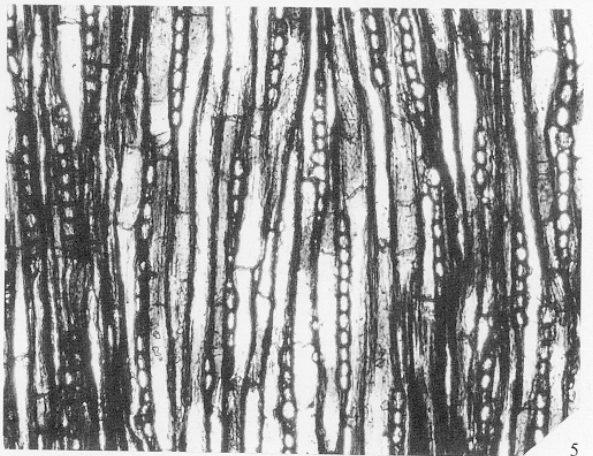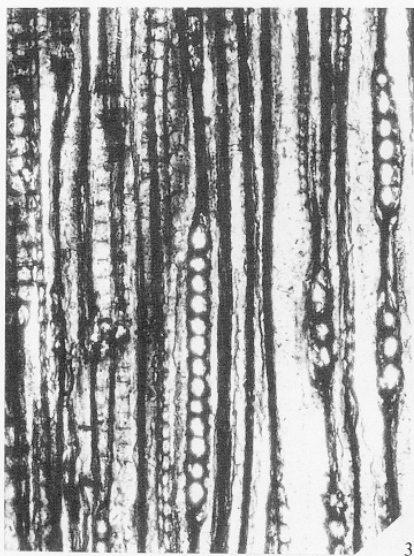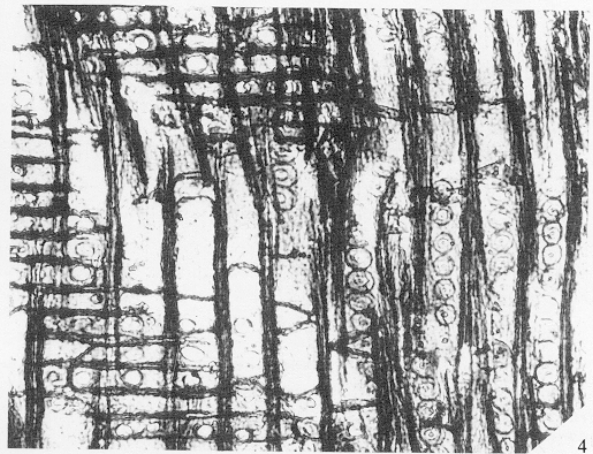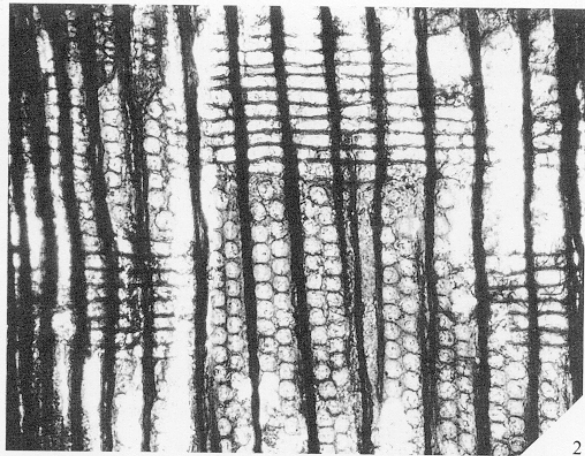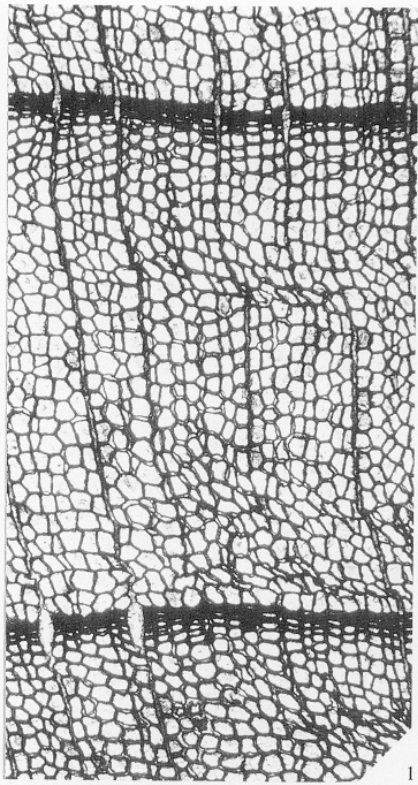
TABLE 3. Growth-ring data. The first numbers are measurements from blocks, the numbers in parentheses from thin section (except 96.1, 128.1); early wood cell counts from thin section only. Rings are listed from oldest to youngest. For explanation of deformation, see text.

Ring width (mm)	Late wood (no. cells)	Early wood (no. cells)	Deformation (% diminution)
SAMPLE 58.1			
2·1			5-10
1·1			< 5
1·5			0
1·3			0
2·1			0
1·1			0
1·4			0
—2 rings disrupted by cracking—			
1·1 (1·3)	4	20	5-10 (0)
1·5 (1·3)	4	20	0 (0)
2·2 (1·9)	4	28	0 (0)
1·7 (1·6)	4	27	0 (0)
1·2 (1·1)	3	19	5 (0)
0·8 (0·8)	4	12	10-15 (0)
0·7 (0·7)	4	14	20-25 (5-10)
0·5 (0·6)	3	9	20-30 (5)
(0·7)	4	13	(15-25)
(0·9)	6-7	23	(30-40)
SAMPLE 96.1. Measurements from thin section only; first ring ring was partial			
> 4	2	not counted	none
6·2	3	133	5
7·9	3	170	5

Ring width	Deformation	Ring width	Deformation
SAMPLE 95.1		**SAMPLE 101.1** (*cont.*)	
0·5	10-15	2·5	10-15
1·2	10-15	4·7	5-10
3·2	0	3·8	5-10
3·2	15-20	2·9	5-10
2·7	5	2·5	5-10
2·6	0	1·7	5-15
1·5	5	2·3	5-10
		2·3	5-15
SAMPLE 101.1		3·1	5-10
5·9	10-15	2·0	5-10
7·2	10-20	1·8	5-10
4·6	10-20	3·8	5-10
3·5	15-25		
2·8	10-15	**SAMPLE 139.1**	
3·5	10	4·7	5
4·9	5	5·2	5
5·2	10-15	2·0	5-10
4·9	10·20	6·3 (6·1)	5 (5-10)
6·0	10-15	4·6 (3·9)	> 5 (5)
6·1	15-20	4·8 (4·5)	5-10 (5-10)
4·1	10	4·6	10-20

TABLE 3 (cont.)

Ring width	Late wood (no. cells)	Ring width	Late wood (no. cells)	Early wood (no. cells)
SAMPLE 129.1. Only one ring (number 10, 0·6 mm wide) had significant deformation (10–20%)		SAMPLE 132.1. First ring in thin section is partial		
		3·6	1–2	
4·4	1	12·9 (> 10·1)	8 (15)	> 222
1·2	1	3·9 (4·2)	1 (4)	87
0·8	2–3	7·3 (6·9)	5 (7)	165
0·8	1–2	2·2	1–2	
1·7	1	3·8	5	
0·8	1–2	1·4	1–2	
0·4	1	3·2	1	
0·6	2	4·3	1	
0·6	1–2	2·6	1	
0·6	1	5·6	1	
1·0	1			
0·9	1			
0·5	1–2			

Ring width	Ring width	Ring width
SAMPLE 128.1. Measurements from thin section only. Thickness of late wood is 1–2 cells; early wood not measured. Deformation < 5%		
1·2	1·0	2·1
0·9	1·8	2·6
1·4	1·7	1·1
1·6	ring broken up	3·6
1·0	ring broken up	

a densitometer because crush zones, uneven mineralization, and other diagenetic effects would give spurious results, as observed by Jefferson (1982).

RESULTS

Growth-ring data for the fossil wood samples are presented in Tables 3 and 4. Late wood, easily distinguished as an abrupt diminution of cell lumen size and thickening of cell walls (Pl. 6, fig. 1), is generally less than 5 cells thick. None of the woods showed the distinct band of late wood that is typical of modern temperate woods, and we observed in only one sample a gradual diminution of cell size that might be interpreted as being similar to the pattern in modern temperate woods (132.1; Pl. 5, fig. 1). Most of the woods do show a slight diminution of cell size through the entire ring, particularly after the initial early wood in samples with wide rings. However, this change is uneven in all the samples, and cells with large lumina are nearly as common near the late wood as in the early wood. In some samples, the earliest early wood appears to have been a zone of weakness, within which crushing tended to occur (Pl. 5, fig. 2); this also was observed by Jefferson (1982).

Most samples (54.1, 58.1, 101.1, 128.1, 129.1, 132.1) have very narrow late wood, consisting of only one or two small cells (text-fig. 3), in many or all of their rings. In all cases, these rings are contiguous

TABLE 4. Summary of statistics on growth-ring characteristics. Numbers in parentheses are corrected for deformation of rings (upper estimate; see text and Table 3).

Sample	Mean ring width (mm)	Mean sensitivity	Variance
58.1[1]	1·3	0·30[2]	0·21
95.1	2·1 (2·3)	0·41 (0·45)	1·13 (1·32)
101.1	3·8[3]	0·28[3]	2·35
128.1	1·7	0·40[2]	0·63
129.1	1·1	0·44	1·1
132.1[4]	4·6	0·76	10·14
139.1[4]	4·6 (4·9)	0·40 (0·42)	1·68 (1·86)

[1] Excludes last two rings and includes thin section measurements where the samples overlap (see Table 3).
[2] Ring pairs are $n-2$ because of the breaks (see Table 3).
[3] Uncorrected (see Table 3).
[4] Statistics from measurement on block.
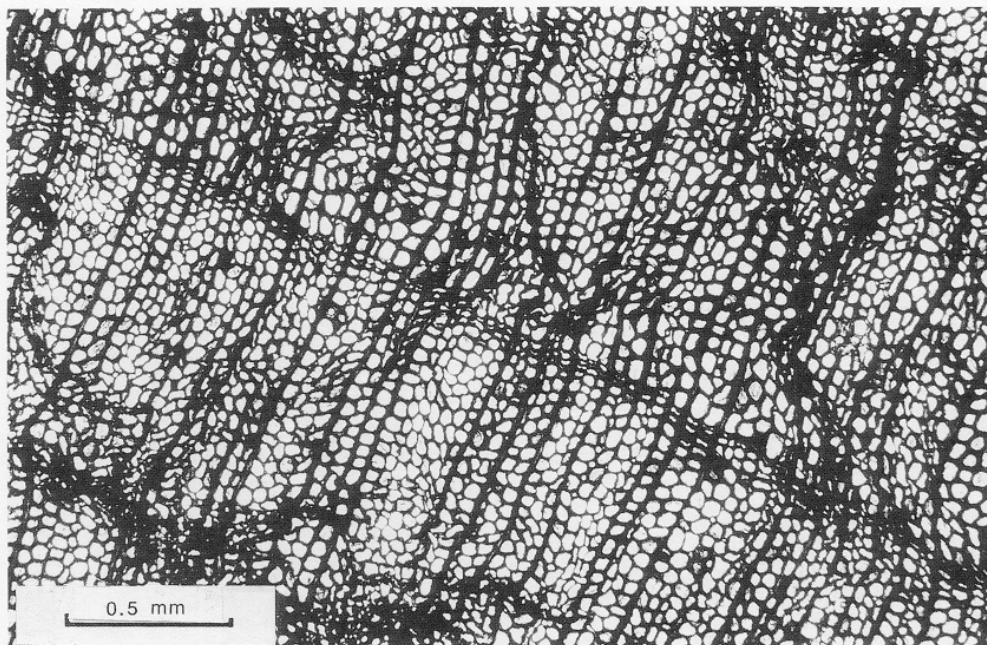
TEXT-FIG. 3. Taxon B, specimen 54.1. Transverse section showing thin late wood of a true growth ring.

within the sample and are unlikely to be false rings. False rings were observed in three samples (95.1, 96.2, 129.1; Pl. 5, fig. 3) and were clearly distinguishable from the true growth rings.

Mean ring widths range from 1·1 mm (129.1) to 4·6 mm (4·9 mm corrected mean, 139.1). The overall mean ring width is 2·8 mm, excluding sample 96.1, which has only two, very wide rings (3·4 mm, including 96.1). The narrowest ring observed is 0·4 mm (undeformed ring, 129.1) and the widest
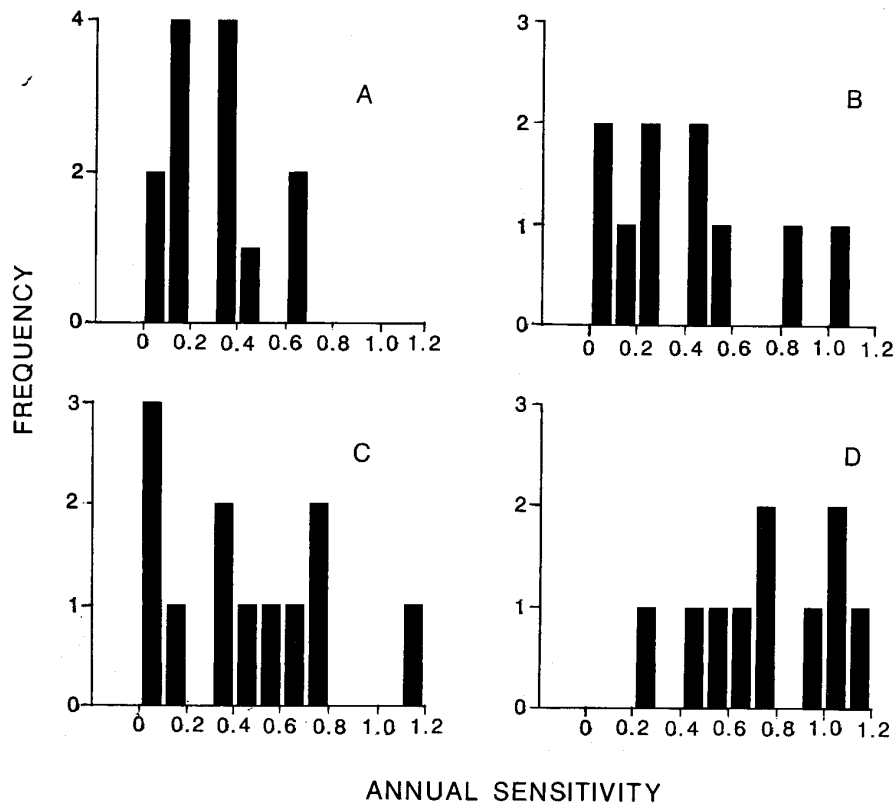
TEXT-FIG. 4. Histograms of annual sensitivities. A, specimen 58.1; B, specimen 128.1; C, specimen 129.1; D, specimen 132.1.

12·9 mm (about 5% diminution owing to crushing, 132.1). Mean sensitivities range from 0·28 (101.1) to 0·76 (132.1).

Ideally, only long ring sequences should be used for plotting annual sensitivities, but such sequences were not available to us. Samples 58.1, 128.1, 129.1, and 132.1 had sequences of more than 10 ring pairs. The histograms for these samples are presented in text-fig. 4. The complacent samples (m.s. < 0·3), 58.1 and 101.1, have annual sensitivities clustered near the low end of the scale, indicating small changes in ring width from year to year. The histograms for the other samples (m.s. > 0·3), are much more spread out. Particularly striking is sample 132.1, which shows clustering at the higher end of the scale, indicating large changes in ring width from year to year. This sample also has the highest mean sensitivity by far, 0·76. We should emphasize that the annual sensitivities are not indicative of total variability, which could be considerable as the tree ages, but of the difference in growth between successive years. A tree with wide inner rings and narrow outer rings may still be complacent.

DISCUSSION

Several features of the growth rings in the Alaskan fossil wood are notable and climatically significant. These are wide growth rings, narrow latewood, paucity of false rings, and moderately high mean sensitivities.

Wide growth rings. These indicate rapid growth or a long growing season or both. Implicit in this is the presence of favourable conditions for growth. Creber and Chaloner (1984, 1985) sought to demonstrate latitudinal gradients in ring width in fossil woods. Such gradients might be expected because the growing season is shorter at high latitudes than at low latitudes. Creber and Chaloner (1984, 1985) cited Cretaceous wood from high northern palaeolatitudes in which the widest rings were 4·0 mm (northern Alaska), 6·5 mm (Amund Ringnes Island, Canadian Arctic), and 3·0 mm (Ellesmere Island). Thus, our results seem particularly significant, as some of the mean values in the woods we collected are greater than 4·0 mm. Creber and Chaloner's (1984, 1985) data showed that the expected latitudinal gradient in ring width as weak at best; our data show that such a gradient now cannot be demonstrated.

Narrow late wood. The amount of late wood is controlled by a variety of factors. Among the reported causes of relatively large proportions of late wood in modern trees are increasing age of the tree, increasing ecological suppression in the community, lower temperature during the growing season, decreasing latitude, and the timing of precipitation during the growing season (Creber 1977). Narrow late wood is common. For example, Alvin *et al.* (1981) and Creber and Chaloner (1984) illustrated coniferous wood from the early Cretaceous and Jurassic of southern England that show similar thin late wood, although Francis's (1984) data indicate that the rings in the Jurassic wood tend to be narrower (mean ring width 0·5 mm to 2·3 mm) than those in the Alaskan wood. A Permian wood from Brazil, illustrated by Creber and Chaloner (1984), similarly has thin late wood. Narrow late wood indicates very rapid cessation of growth, either through the onset of unfavourable conditions or through normal seasonal change. For modern trees at high latitudes, cessation of growth at the end of the growing season may occur even if the environmental conditions seem favourable (Fritts 1976, p, 86). In the Jurassic and early Cretaceous of southern England, the unfavourable condition was aridity, indicated by the presence of evaporites or mudcracks; rainfall may have been highly seasonal.

In discussions fomented by the suggestion that the Earth's obliquity might have been lower during times of warm polar temperatures (Wolfe 1980; Douglas and Williams 1982), several authors have pointed out that the polar regions receive more than enough light annually to support the growth of some low-latitude species (Jefferson 1982; Creber and Chaloner 1984, 1985; Axelrod 1984; Barron 1984). We now know that the entire middle Cretaceous flora of the North Slope consisted of plants that were either deciduous or could die back or go into dormancy every winter (Spicer and Parrish 1986), thus obviating the need to invoke obliquity changes to explain the presence of high biomass vegetation. However, the striking feature of the annual distribution of light at high latitudes is the very rapid change in day length. We suggest that, like most trees, the mid-Cretaceous trees of northern Alaska responded to threshold light levels for onset and cessation of growth. As these thresholds would be passed very quickly at high latitudes, changes in growth rate might be expected to follow accordingly.

False rings. These represent a temporary slowing or cessation of growth during the growing season and are commonly formed by trees that live in unstable growing conditions. False rings are characterized by diminution of cell size, followed by a gradual return to normal cell size, and are commonly irregular and discontinuous. False rings can be caused by severe insect attack to the foliage, freezing, and drought (Fritts 1976). The paucity of false rings in the Alaskan wood suggests that the trees did not suffer sudden adverse conditions. This is in contrast, for example, to the arid-climate woods of the Jurassic of southern England (Francis 1984), which have abundant false rings.

Moderately high mean sensitivities. Five of the seven wood specimens with measurable ring sequences have mean sensitivities greater than 0·3; of these, four have values of 0·4 or greater. The average mean sensitivity is 0·42 (0·43 with corrected measurements). By comparison, the average mean sensitivity is 0·53 for Purbeckian trees (Francis 1984), 0·42 for early Cretaceous trees of Alexander Island (Antarctic Peninsula; Jefferson 1982), 0·17 for early Cretaceous trees and 0·20 for Campanian–Maastrichtian

trees of the Antarctic Peninsula (Francis 1986, table 2a), and 0·30 for modern black spruce in Arctic forest outliers at about 63° N. (Kay 1978). Our average is raised considerably by sample 132.1 (Table 4). Without this sample, the average mean sensitivity of our woods is 0·37. This illustrates the problems with the relatively small sample size and short ring sequences available to us. Comparisons with other work and, indeed, the statistics on the Alaskan wood themselves are less rigorous because of these constraints.

Ring width and, thus, ring-width variability are controlled by the length of the growing season, genetics, water supply, and temperature. In modern trees, temperature is more important than water supply only for trees at high altitudes or latitudes where very cold temperatures are reached (LaMarche 1974; Fritts 1976). With milder Cretaceous temperatures, one would expect water supply to be the dominant factor controlling growth of the North Slope woods. That water was plentiful is indicated by the numerous and thick coals (Sable and Stricker 1985) and by the abundant pond and bog deposits. The presence of possible freshwater clams, a turtle (Parrish et al. in press), large angiosperm leaves (Spicer and Parrish 1986), and the absence of desiccation features further support the conclusion that water probably was not limiting to plant growth. Finally, most of the forty-five wood samples we collected were not only compressed, but had a swirly, smeared appearance, suggesting that the wood was waterlogged, partly rotted, and plastic when it was buried.

Abundant water does not necessarily imply high rainfall. The Brooks Range, which was a major topographic feature a short distance to the south (e.g. Mull 1985) could have induced rainfall, supplying the fluvial system that formed the Nanushuk Group. Wind directions predicted from global circulation models favour precipitation on the north side of the mountains (Parrish and Curtis 1982). In addition, the cool temperatures suggested by the leaf flora mean that evaporation would have been low.

Thus variability in ring width in the Alaskan wood may reflect either relatively minor fluctuations in annual water supply or changes in the local growth environment for each plant. Such changes include variations in soil drainage, which have been shown to affect ring widths in modern plants (Fritts 1976). High soil moisture can actually result in drought conditions so far as the plants are concerned by reducing soil aeration and, consequently, root growth. The presence of coals, ponds, and bogs, besides indicating the presence of abundant water, also indicates that areas of poor drainage were common.

General considerations. The most comparable studies to ours are those of Jefferson (1982) and Francis (1986) in that their samples also included Cretaceous coniferous wood and were from relatively high palaeolatitudes and humid palaeoenvironments. Like the Alaskan wood, Jefferson's (1982) had moderately high mean sensitivities, for which he did not suggest an explanation other than to state that such values are typical of modern woods from warm temperate environments and inconsistent with the apparent high-latitude position of the fossil growth site. From this, he seemed to conclude that the errors were likely to lie in the palaeogeographic reconstructions, either in the position of the Antarctic Peninsula relative to the major cratonic areas or in the palaeomagnetic data. Jefferson's (1982) reservations about the palaeogeography are justified; alternate reconstructions (e.g. Ziegler et al. 1983) place the Antarctic Peninsula as far north as 50-55° S. The position of northern Alaska, on the other hand, is more certain. Although reconstructions of the Arctic region vary greatly (e.g. Churkin and Trexler 1980; Jones 1980; Ziegler et al. 1983; Smith 1985), most workers agree that by the middle Cretaceous, northern Alaska was in its present position relative to North America and that western North America was further north than it is today.

The results of our growth-ring analyses and those of Francis (1986) and Jefferson (1982) are summarized in Table 5. All of Francis's (1986) wood were more complacent than either Jefferson's (1982) or ours, supporting her suggestion that the trees in her samples were from the forest interior (Fritts et al. 1965). In addition, the tip of the Antarctic Peninsula would have had an extremely constant palaeoclimate, well away from any continental climatic influence (e.g. Ziegler et al. 1983). By contrast, both Jefferson's (1982) forest and the North Slope were further poleward and closer to large continental masses.

TABLE 5. Comparison of growth-ring analyses of Jefferson (1982), Francis (1986), and this study.

Study	Age	Average mean ring width	Maximum ring width (mm)	Average mean sensitivity
This study	latest Albian–Cenomanian	2·8[1]	12·9	0·42
Jefferson (1982)	Aptian–Albian	1·4	9·6	0·42
Francis (1986)	Aptian–Albian[2]	1·5	2·4	0·16
	all early Cretaceous	2·5	6·9	0·17
	Campanian–Maastrichtian (conifers only)	1·9	7·8	0·21

[1] Excluding sample 96.1.
[2] Two samples.
NB: The equation for mean sensitivity was misprinted in Francis (1986); we assume that her calculations were correct.

Interestingly, although the Alaskan wood had higher mean sensitivities than Francis's (1986) and the same or slightly lower mean sensitivities than Jefferson's (1982), the ring widths in the Alaskan wood were much greater (Table 5), despite the fact that they grew at the highest palaeolatitudes. Thus, no latitudinal gradient in growth-ring characteristics can be demonstrated for the Cretaceous from the small amount of information available from this study, nor from Jefferson (1982) and Francis (1986).

It is important to emphasize that the environmental parameters encoded in wood sensitivity are not always climatic. This is illustrated, for example, by black spruce sampled in the Canadian Arctic at the forest edge, tree line, and in forest outliers (Kay 1978). Kay correlated thirty-year climatic and dendrochronologic records at these sites. Although the outlying trees had the narrowest growth rings and highest mean sensitivities, the per cent variation that could be attributed to temperature and precipitation was the lowest of the three sites. Outliers occur in sites where the climate is locally ameliorated, so that edaphic and topographic factors, for example, become proportionately more important. Given the mild climate suggested by the wide growth rings and the plentiful water supply indicated by the geology, it is likely that the high mean sensitivities of the Cretaceous Alaskan woods are related to local water table, flooding, and so on.

As Jefferson (1982) discussed, sensitivity also can have a strong genetic control. He apparently had only one taxon represented in his samples, and Francis (1986) had two taxa of conifers (podocarp- and araucaria-like woods) but did not distinguish between the taxa in the growth-ring data presented. Our sample 58.1 was the one identified sample that was not *Xenoxylon latiporosum* and which had measurable growth rings, and its growth-ring characteristics were within the range established by the other samples. Clearly one sample is not enough to prove consistency among different taxa, but it does not suggest any great difference.

Cretaceous polar forests have no modern analogue. High-latitude floras today are strongly affected by extremely low temperatures. Creber and Chaloner (1984) and Jefferson (1982) regarded low winter light levels and the restriction of modern evergreen conifer forests to much lower latitudes than fossil ones as the crucial problems presented by high-palaeolatitude forests. Modern plants can be shown to be limited by temperature, not light (Creber and Chaloner 1984; Axelrod 1984). However, with the high temperatures of the Cretaceous, evergreen plants such as the modern conifers could not survive months of darkness. In the warmth, they would continue to respire, rapidly depleting energy reserves

unless they had extraordinary organs for storage; no evidence for such structures exists. Thus, with sufficient water supply, the seasonal control in high latitudes in the Cretaceous would have been light. Our finding (Spicer and Parrish 1986) that the northern Alaska Cretaceous flora was deciduous, including all but one of the conifers (a microphyllous cupressaceous form that probably was capable of entering dormancy), removes the problem of explaining the existence of coniferous forests at high latitudes. Unfortunately, the wood data do not solve the question of whether the dark polar winter in the Cretaceous also was cold.

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