LATEST CRETACEOUS WOODS OF THE CENTRAL NORTH SLOPE, ALASKA

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ABSTRACT. Coniferous woods from the Kogosukruk Tongue of the Prince Creek Formation (Campanian-Maastrichtian), central North Slope, Alaska (U.S.A.) have narrow growth rings, abundant false rings, and high ratios of late wood to early wood. These characteristics are the same across several taxa, and suggest that summers were cool and growing conditions variable. When compared with woods from the middle Cretaceous Nanushuk Group of the North Slope, the growth-ring characteristics of the Kogosukruk Tongue support conclusions that climate deteriorated substantially on the North Slope during the Late Cretaceous.

ALTHOUGH the total data set is still small, the analysis of growth rings in ancient (pre-Quaternary) woods is proving to be of considerable use in interpreting palaeoclimate, particularly when used in conjunction with other data. Analyses to date include those of Creber (1977), Jefferson (1982), Francis (1984, 1986), Creber and Chaloner (1984, 1985, 1987), and Parrish and Spicer (1988a). All of these workers used standard techniques of growth-ring analysis (Fritts 1976; Creber 1977). These techniques were originally established for dendrochronological, as well as palaeoclimatic, studies of Holocene and Quaternary woods (Fritts 1976). However, they are proving useful for understanding more ancient palaeoclimates, particularly when used in conjunction with other data, such as vegetational physiognomic analysis (Spicer and Parrish 1986; Parrish and Spicer 1988b).

The purpose of this paper is to present new data on growth-ring characteristics of fifteen specimens of well-preserved fossil wood collected from the upper part of the Kogosukruk Tongue of the Prince Creek Formation, which crops out along the Colville River, North Slope, Alaska (text-fig. 1). The trees were small, rarely exceeding 20 cm in diameter; the largest was 50 cm in diameter (Spicer and Parrish 1987). The specimens comprise six taxa (Table 1), including *Xenoxylon latiporosum* (Cramer) Gothan, which is widespread at northern high latitudes (Arnold 1952) and also is found in Cenomanian-age rocks of the North Slope (Parrish and Spicer 1988a). This taxon occurs in the upper part of the section, from probable Maastrichtian-age rocks. The remaining taxa are from the Campanian part of the section (see below). To our knowledge, the remaining five taxa have not yet been described. We do not attempt to name them in this paper, although we provide brief descriptions and illustrations.

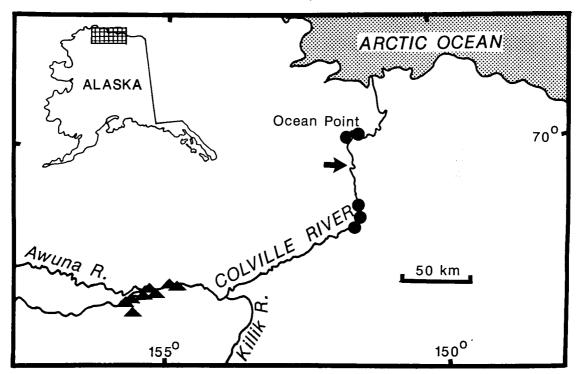
GEOLOGY AND DEPOSITIONAL ENVIRONMENTS

The Kogosukruk Tongue (Gryc et al. 1951) is the upper member of the Prince Creek Formation, which is the terrestrial portion of the Late Cretaceous (Turonian to Maastrichtian) Colville Group (see also Molenaar et al. 1987; text-fig. 2). In the northeastern portion of the lower Colville River region, the unit is divided into two parts by the marine Sentinel Hill Member of the Schrader Bluff Formation, which is marine and partly equivalent to the Prince Creek Formation. The lower part of the Kogosukruk Tongue is conglomeratic and very thin along the Colville River, and did not yield any useful plant megafossils, although the unit contains thin coal beds, and wood and plant fragments are abundant (Brosgé and Whittington 1966; this study).

The upper part of the Kogosukruk Tongue is a fluvio-deltaic unit, dated Campanian to Maastrichtian on the basis of marine fossils from over- and underlying beds (Brosgé and Whittington 1966; Marincovich et al. 1985; McDougall 1986), pollen (Frederiksen 1986; Frederiksen et al. 1986), and ostracodes (Brouwers 1988). The unit includes thin coal beds that decrease in thickness and rank toward the top (Spicer et al. 1988). The coals also become less woody toward the top, which may reflect a decrease in the proportion of trees in the

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TEXT-FIG. 1. Map showing fossil wood localities. Triangles: Nanushuk Group (Parrish and Spicer 1988 a). Circles: Kogosukruk Tongue (this paper). Arrow indicates position of the Campanian Maastrichtian boundary (at Sentinel Hill) with Campanian rocks occurring southward of this point.

mire environment (Spicer and Parrish 1987). Plant megafossils generally are found in the overbank mudstones and lacustrine (pond) claystones, although the wood specimens were collected from channel sandstones and levée deposits as well. None of the wood was found in life position.

On the basis of pollen, Frederiksen (1986) provisionally drew the Campanian-Maastrichtian boundary within the Kogosukruk Tongue just north of Sentinel Hill. Thus, thirteen of our wood specimens (7·1 to 80·5; Table 1) are probably Late? Campanian age whereas the remaining two (272·1 and 336·1) are Maastrichtian age.

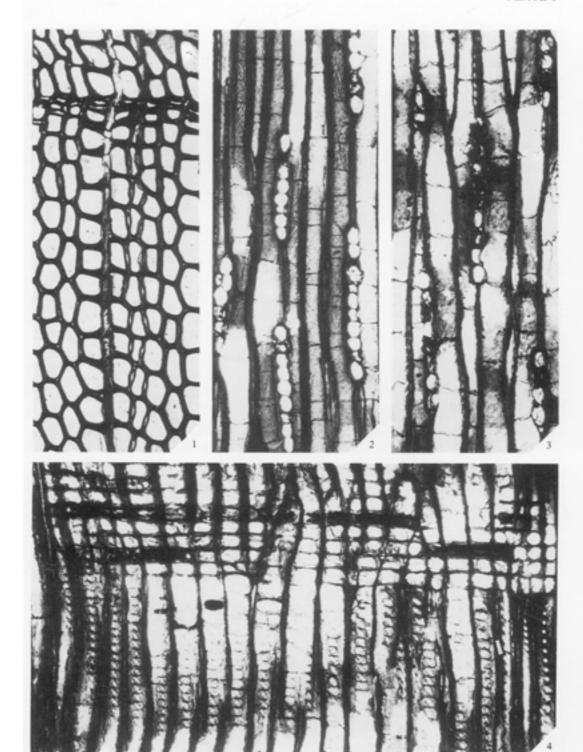
PREVIOUS WORK

We recently reported an analysis of growth rings in woods from middle Cretaceous rocks of the Nanushuk Group (Chandler Formation) of the North Slope of Alaska (U.S.A.; Parrish and Spicer 1988a). These rings showed the following: (1) moderate to high variability in ring width, suggesting variable growth conditions from year to year; (2) wide growth rings with rare false rings, suggesting favourable conditions during the growing seasons; and (3) very narrow late wood, suggesting abrupt cessation of otherwise rapid growth. We interpreted these data to mean the following:

1. The Nanushuk Group trees grew in a shifting sedimentological and hydrological environment. This conclusion is consistent with the fluvial setting interpreted from the rocks.

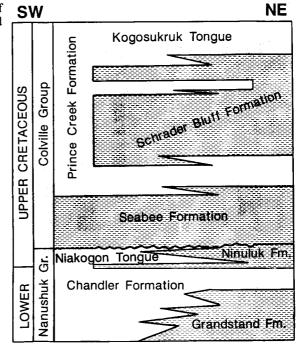
EXPLANATION OF PLATE 1

Figs. 1-4. Xenoxylon latiporosum. 1, specimen 272·1, transverse section, ×177. 2, specimen 272.1, tangential longitudinal section, ×177. 3, specimen 336·1, tangential longitudinal section, ×177. 4, specimen 336·1, radial longitudinal section, ×177.



SPICER and PARRISH, Xenoxylon

TEXT-FIG. 2. Generalized Cretaceous stratigraphy of the Colville River region (modified from Brosgé and Whittington 1966). Shading: marine units.



- 2. Conditions during each growing season were favourable for rapid and continuous growth. This is consistent with equable climate during the growing season. The high-latitude positions of northern Alaska during the Late Cretaceous (77°-85° N; Smith et al. 1981; Ziegler et al. 1983) would have resulted in continuous daylight during the summer, and the fossil leaf flora supports the interpretation that climate was relatively warm (Spicer and Parrish 1986).
- 3. Growth ceased abruptly at the end of the growing season, consistent with the rapid change in photoperiod at high latitudes. Seasonality of light also is supported by the leaves (Spicer and Parrish 1986), which show that all plants were deciduous (angiosperms, taxodiaceous conifers, cycadophytes, ginkgophytes), could die back every winter (sphenophytes, ferns), or could become dormant (cupressaceous conifer).

DESCRIPTION OF THE WOODS

Xenoxylon latiporosum (Cramer) Gothan (Pl. 1, figs. 1-4; Pl. 5, fig. 3)

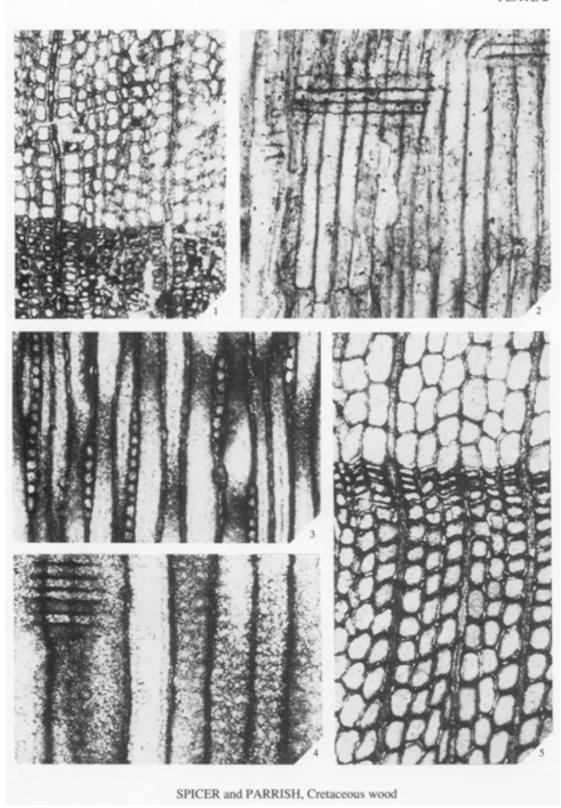
Transverse section. Secondary wood consists of tracheids. Early wood tracheid lumina typically are 900 μ m² in cross-sectional area. Resin canals apparently are absent.

Radial longitudinal section. Bordered pits are uniseriate, contiguous, oval, and 25 μ m wide by 15–18 μ m high, with apertures $5 \times 7.5 \mu m$. Tracheids have numerous septa (resin plates?), typically 13–25 μm apart. Cross-field pits are fenestriform. Ray cells are 25 μ m high.

EXPLANATION OF PLATE 2

Figs. 1 and 2. Taxon A. 1, specimen 7.1, transverse section, ×177. 2, specimen 7.1, radial longitudinal section, ×177. Figs. 3-5. Taxon B. 3, specimen 46·1, tangential longitudinal section, ×177. 4, specimen 46·1, radial

longitudinal section, $\times 177$. 5, specimen 80·1, transverse section, $\times 177$.



Transverse longitudinal section. Rays are uniscriate, very rarely biseriate, and generally short (usually less than 22 cells high) and 15 μ m wide.

Taxon A (Pl. 2, figs. 1 and 2)

Transverse section. Secondary wood consists of tracheids and parenchymatous rays only. Resin canals are absent. Cross-sectional area of early wood tracheid lumina is typically 550 μ m².

Radial longitudinal section. Axial tracheids only are present; no axial parenchyma is visible. Bordered pits are irregularly uni- and biseriate, not always contiguous, and typically 12 μ m in diameter, with apertures 3-4 μ m diameter. Cross-field pits are 6-8 μ m in diameter. Ray cells are 20-24 μ m wide in a vertical direction and 70-190 μ m long, with mostly vertical or sometimes oblique walls.

Transverse longitudinal section. Rays are uniseriate, typically 5–20 cells high. Areas of ray cell lumina typically measure 400 μ m² in vertical section.

Taxon B (Pl. 2, figs. 3-5)

Transverse section. Secondary wood consists of tracheids and parenchymatous rays only. Resin canals are absent. Early wood tracheid cell lumina typically are $2000-2300~\mu\text{m}^2$ in cross-section area; overall cell dimensions are $20-25~\mu\text{m}$ diameter.

Radial longitudinal section. Tracheid bordered pits are biseriate, opposite, contiguous, and 20 μ m in diameter. Cross-field pits are circular, 2 per cross-field area, and 10 μ m in diameter. Ray tracheid walls are oblique. Ray cell height is typically 15 μ m.

Transverse longitudinal section. Rays are uniseriate, typically 2–30 cells high. Ray cells are typically 10–12 μ m broad.

Taxon C (Pl. 3, figs. 1-4)

Transverse section. Secondary wood consists of tracheids and ray cells only. Early wood tracheids typically are $2000 \ \mu\text{m}^2$ in cross-sectional area. Resin canals and axial parenchyma apparently are absent.

Radial longitudinal section. Tracheid bordered pits are uniseriate, not necessarily contiguous and often irregularly distributed. Cross-field areas are not preserved.

Transverse longitudinal section. Rays are uniseriate, with cells in long files (> 20 is common). Ray cells are $12-15 \mu m$ wide. Highly multiseriate areas occur rarely.

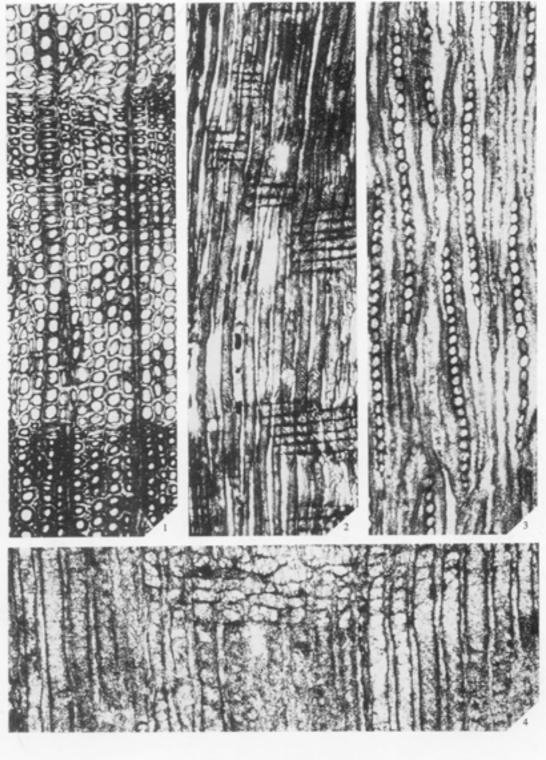
Taxon D (Pl. 4, figs. 1-5)

Transverse section. Secondary wood consists of tracheids; resin canals and parenchyma apparently are lacking. Early wood tracheid cross-sectional areas are variable, between 750 μ m² and 2900 μ m², but usually about 2300 μ m².

Radial longitudinal section. Bordered pits are small, 12–18 μ m in diameter, with apertures 4–6 μ m in diameter, and are numerous, irregularly distributed, and often isolated. Cross-field pits are poorly preserved, and may be circular, with several per cross-field area. Ray cells are approximately 20 μ m high.

EXPLANATION OF PLATE 3

Figs. 1—4. Taxon C. 1, specimen 46·8, transverse section showing false ring in early wood ×177. 2, specimen 46·8, radial longitudinal section, ×177. 3, specimen 46·2, tangential longitudinal section, ×177. 4, specimen 80.5, radial longitudinal section, ×177.



SPICER and PARRISH, Cretaceous wood

Transverse longitudinal section. Rays are mostly uniseriate, but may be bi- or multiseriate in places, 5-30 cells high, $15 \mu m$ wide.

Taxon E (Pl. 5, figs. 1 and 2)

Transverse section. Secondary wood is composed of tracheids and ray parenchyma only. Resin canals apparently are absent. Early wood tracheid lumina are typically $1500-2000 \, \mu \text{m}^2$ in cross-sectional area.

Radial longitudinal section. Bordered pits are uniseriate and contiguous, with borders typically 15 μ m in diameter and apertures 5 μ m in diameter. Cross-field pits are not preserved. Ray parenchyma cells are typically 25 μ m high. Ray tracheids are 20 μ m high. Axial parenchyma is abundant and associated with the rays.

Transverse longitudinal section. Rays are uniseriate, typically 30 μ m wide. Axial parenchyma cells are typically 100 μ m × 45 μ m.

METHODS

Methods of growth-ring analysis have been explained in detail elsewhere (Fritts 1976; Creber 1977; Parrish and Spicer 1988a), so only a brief summary will be included here. Characteristics of growth rings that are useful for studying the climatic signal in pre-Quaternary woods are (1) ring width, (2) interannual variability in ring width, (3) proportion of late wood to early wood, and (4) presence or absence of false rings.

Growth rings wider than about 0.5 cm are regarded as indicative of favourable conditions during the growing season, that is, enough light, water and warmth to permit rapid and continuous growth. However, because ring width is also dependent on other factors, such as genetics, no quantitative climatic information may be drawn from this parameter, and it is most useful for comparing woods from different times and/or localities.

Interannual variability in ring width is termed 'mean sensitivity' and quantified using the equation

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 x_t is width of ring t and x_{t+1} is the width of the adjacent younger ring. Woods with mean sensitivities less than 0·3 are termed 'complacement' and are interpreted to have grown under conditions that were stable from year to year. Woods with mean sensitivities greater than 0·3 are termed 'sensitive', suggesting variable conditions from year to year. Sensitive trees of a particular taxon live at the edges of the range of that taxon (e.g. LaMarche 1974; Kay 1978), and the sensitivity is generally linked to climatic effects, although other factors, such as waterlogging of roots, also can affect sensitivity (Fritts 1976).

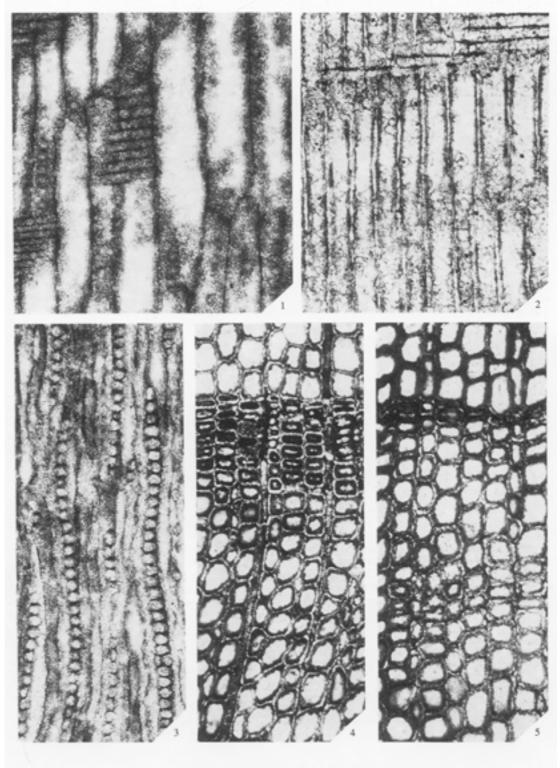
The proportion of late wood to early wood which, like ring width, is qualitative and most useful in a comparative sense, can reflect the nature of seasonality. A high proportion of late wood to early wood is typical of temperate-forest trees, where growing conditions gradually become less favourable as the summer wanes. Narrow late wood, on the other hand, is suggestive of rapid cessation of growth owing to abrupt change in growing conditions such as light (Parrish and Spicer 1988a) or water (Francis 1984).

False rings are formed during temporary slowing or cessation of growth during the growing season. False rings indicate that the tree grew under conditions that became temporarily inimical, owing, for example, to fire, drought, freezing or insect attack. The climatic significance of false rings, must, therefore, be supported with other, such as sedimentological, evidence.

Preservation of the woods was generally good. Only one specimen, 80·3, showed crushing of the growth rings during compaction. Interestingly, the crushing was not in the early wood, as observed by Jefferson (1982) and

EXPLANATION OF PLATE 4

Figs. 1–5. Taxon D. 1, specimen 80·4, radial longitudinal section, × 177. 2, specimen 46·9, radial longitudinal section, × 177. 3, specimen 80·4, tangential longitudinal section, × 177. 4, specimen 46·9, transverse section, × 177. 5, specimen 46·5, transverse section, × 177.



SPICER and PARRISH, Cretaceous wood

TABLE 1. Wood samples providing data on growth rings and thickness of late wood.

Sample number	Name		Thickness of late wood-number of cells or percentage of total ring width
272-1	Xenoxylon latiporosum		2–4 cells
336-1	Xenoxylon latiporosum	* .	1–5 cells
7 ·1	Taxon A		5–12 cells
46-1	Taxon B		2–4 cells
80-1	Taxon B		3–9 cells
46.2	Taxon C		2–5 cells
46.8	Taxon C		6–26 cells
80.3	Taxon C		not measured (see text)
80.5	Taxon C	Taxon C	
46.5	Taxon D		
46.9	Taxon D		
80.4	Taxon D		
46 ·7	Taxon E		5–8 cells up to 58%
46.13	Taxon E		1–8 cells
46.4	unident., branch (see tex	unident., branch (see text)	

Parrish and Spicer (1988a), but in the late wood, making measurement of the late wood impossible (Table 1). However, overall the average diminution of ring width in this specimen was only about 10%; corrected values were used in the statistics (Tables 2 and 3).

RESULTS

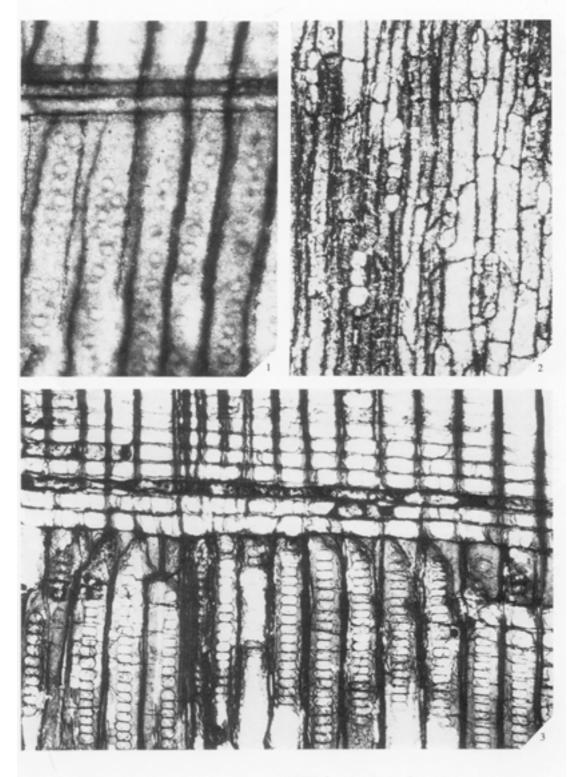
Growth rings in fifteen specimens were measured from thin sections and/or polished blocks (Table 2). The blocks provide longer ring sequences on which to perform the statistics, so in the discussion below and in Table 3, we use measurements taken from polished blocks in preference to those taken from thin sections. However, both data sets for the relevant samples are presented in Table 2. The longest ring-width series, one from each taxon, are presented in text-figs. 3 and 4. Raw measurements are available from J.T.P. on request; the material is lodged with R.A.S. at Oxford University Museum. All of the growth-ring characteristics reported below were observed in woods collected from widely separated localities.

Mean ring widths in woods from the Kogosukruk Group ranged from 0·39 mm to 3·67 mm, with a mean of 1·76 mm. The narrowest ring measured was 0·14 mm (specimen 46·4). The widest 'normal' growth ring measured was 5·88 mm (specimen 46·5). This was the innermost ring of the specimen. Ring width normally decreases as the tree ages, although it should be noted that, in this particular specimen, the adjacent and all subsequent rings were much narrower. A growth ring 13·6 mm wide was measured in specimen 46·1, and was the first ring in a five-year sequence of wood generated in response to injury. The injury is apparent as a longitudinal scar in the trunk, around which the rings grew. The response, as indicated by the contrast with the normal rings, was dramatic (Table 4), but typical. Mean sensitivities of the Kogosukruk woods were 0·10–0·77, with a mean of 0·40.

EXPLANATION OF PLATE 5

Figs. 1 and 2. Taxon E. 1, specimen 46.7, radial longitudinal section, ×177. 2, specimen 46.7, tangential longitudinal section. ×177.

Fig. 3. Xenoxylon latiporosum, specimen 272.1, radial longitudinal section, ×177.



SPICER and PARRISH, Cretaceous wood

TABLE 2. Data on growth-ring characteristics of woods from the Kogosukruk Tongue of the Prince Creek Formation. Samples are in order by taxon (see Table 1).

Sample	Number of rings	Mean ring width (mm)	Variance	Mean sensitivity
272-1	15	2.23	1.00	0.52
336-1	31	1.46	1.31	0.53
7.1	7	1.94	0.87	0.77
46.1	20	0.87	0.03	0.12
46.1*	30	o·77	0.02	0.15
80.1†	46	1.14 (1.02)	0.24	0.41
46.2	13	3.04	0.82	0.10
46.8	6	1.18	0.31	0.49
80.3†	6	3.67 (3.51)	0.75	0.32
80.5	47	0.53	0.18	0.42
46.5:	transect 1**			
	9	1.35	0.99	0.66
	transect 2, (2 thin sections)			
	17	1.86	1.62	0.48
46-9	14	2.87	1.30	0.39
46.9*	15	3.32	1.56	0.34
80.4	6	3.94	0.29	0.17
80.4*	16	2.96	0.41	0.25
46.7	13	0.97	0.25	0.48
46.13	10	0.98	0.23	0.39
46.4	35	0.39	0.03	0.32

^{*} Measured from block

TABLE 3. Comparison of growth-ring characteristics of woods from the Kogosukruk Tongue and the Nanushuk Group. For samples measured from blocks and thin sections, the measurements from the blocks are used in the combined statistics.

	Kogosukruk woods	Nanushuk woods			
Ring width (mm)					
Range	0·14-5·88	0.4–12.9			
Range of means	0.39-3.67	1·1-4·9			
Means of means	1·76	2.81			
Mean sensitivity					
Range	0.10-0.77	0.28-0.76			
Mean	0.40	0.44			
Late wood					
Number of cells	1 - > 30	1–15			
Ratio to early wood	max. 0·83	max. 0·30			
False rings	abundant multiple false rings per growth ring	rare (1 sample), 1 false ring per growth ring			

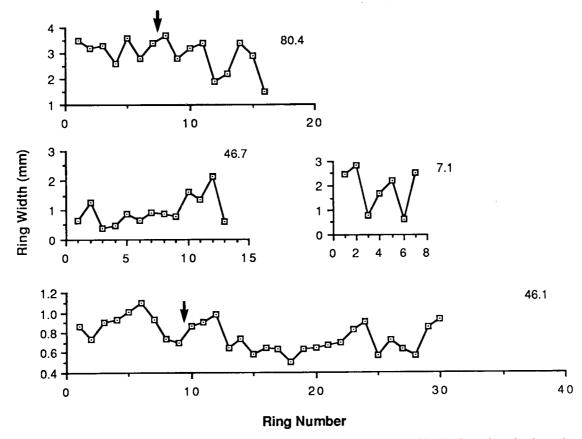
^{**} This portion sustained injury during growth; the measurements are provided for information only and not included in statistics.

[†] Number in parentheses is uncorrected for crushing (see text).

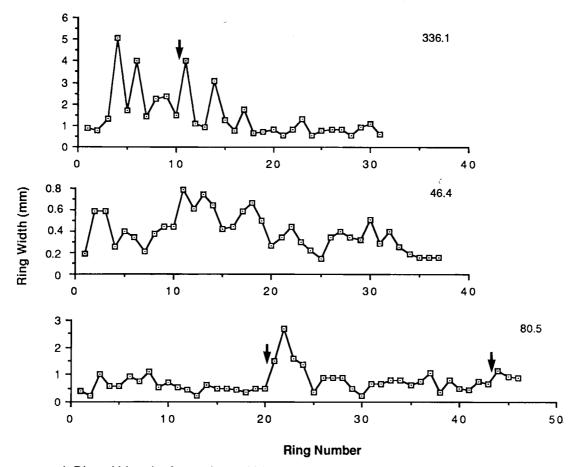
TABLE 4. Growth response to injury in specimen 46·1. Only the last few normal rings of a 31-ring sequence are listed.

Ring type	Ring width (mm)
normal	0.9
normal	1.0
normal	0.8
normal	0.7
response	
1st year	13.6
2nd year	11.1*
3rd year	11.6*
4th year	6.6
5th year	5.2
bark	ina) y

* False ring present.



TEXT-FIG. 3. Ring-width series for specimens 7·1, 46·1 (block), 46·7, and 80·4 (block). Locations in the series where rings were unmeasurable are marked by arrows. Note that vertical scales are not equivalent.



TEXT-FIG. 4. Ring-width series for specimens 46·4, 80·5, and 336·1. Locations in the series where rings were unmeasurable are marked by arrows. Note that vertical scales are not equivalent.

Late wood in growth rings from woods of the Kogosukruk Tongue was rarely narrower than three cells and, where counted, ranged as high as twenty-six cells (Table 1). In many rings, counting late wood cells was not possible because the cells diminished in size gradually over a substantial width of the ring; all the late wood in specimen 80.5 was of this nature. Where a distinct zone of late wood was present, its width was as much as 83% of the total ring width. The thickness of late wood was independent of the total width of the ring.

False rings were observed in nine of the specimens of wood from the Kogosukruk Tongue (specimens 7·1, 46·4, 46·5, 46·7, 46·9, 80·1, 80·5, 272·1, 336·1). As many as four false rings were observed in a single growth ring (specimen 46·5); two false rings per growth ring were common (specimens 7·1, 46·5, 46·7, 80·5, 336·1).

No difference in growth-ring characteristics exists between *Xenoxylon latiporosum*, which occurred in the Maastrichtian part of the section, and the other taxa, which occurred in the Campanian part.

INTERPRETATION AND COMPARISON WITH WOODS FROM THE NANUSHUK GROUP

Ring width and mean sensitivity

Growth-ring characteristics of woods of the Kogosukruk Tongue are compared with those of the Nanushuk Group in Table 3. Growth rings in woods from the Nanushuk Group were wider, with means ranging $1\cdot1-4\cdot9$ mm, against $0\cdot39-3\cdot67$ mm in woods from the Kogosukruk Tongue. This difference is statistically significant at $P \le 0\cdot01$. The narrowest ring measured from Nanushuk woods was $0\cdot4$ mm, versus $0\cdot14$ mm in the Kogosukruk woods, and the widest rings were $12\cdot9$ mm versus $5\cdot88$ mm.

Woods from both the Nanushuk Group and Kogosukruk Tongue were sensitive (Table 3). Mean sensitivities in woods from the Nanushuk Group were 0.28-0.76 with a mean of 0.44, against 0.10-0.77 and a mean of 0.40 in woods of the Kogosukruk Tongue. This difference in means is statistically significant at $P \le 0.05$.

Although climate is most important in determining mean sensitivity, it is not the only factor, and we (Parrish and Spicer 1988a) interpreted the sensitivity of the Nanushuk woods to a shifting sedimentological and hydrological environment, rather than to climate. The woods generally lacked other characteristics, such as significant late wood and false rings, that would have indicated a stronger climatic effect on the growth of the trees. The sensitivity of most of the Kogosukruk woods also could be due to variations in sedimentology and hydrology, as the Kogosukruk Tongue and Chandler Formations (the unit of the Nanushuk Group from which the woods were collected) were deposited in similar environments. However, the Kogosukruk woods exhibit additional characteristics that indicate a somewhat severer climate than that encountered by the woods from the Nanushuk Group. Nevertheless, many of the woods in the Kogosukruk Tongue were complacent, suggesting that, although climate might have been severer overall, the interannual variability was not great.

Late wood and false rings

The major difference between the two sets of woods was in the amount of late wood and the number of false rings. Late wood in woods from the Nanushuk Group was rarely wider than three cells, with a maximum of fifteen cells in one ring. By contrast, late wood in woods from the Kogosukruk Tongue was usually wider than three cells and, because the rings were narrower, constituted a substantially higher proportion of the wood than in woods from the Nanushuk Group. Growth of the Kogosukruk trees did not cease abruptly, as it did in the Nanushuk trees, but rather slowed during the latter part of each growing season, much as occurs in temperate-region trees today. Thus, the cessation of growth in the Kogosukruk woods was not due just to light, as we interpreted from the Nanushuk woods, but also was influenced by temperature.

The resiliency lent to the Kogosukruk woods by the high proportion of late wood is probably partially responsible for the generally good preservation; about half the samples collected were well enough preserved to be useful for analysis. Crushing was much more prevalent in woods from the Nanushuk Group and, indeed, only a fraction of the samples collected from the Nanushuk (seven of forty-five) were sufficiently well preserved to permit growth-ring analysis (Parrish and Spicer 1988a).

False rings were abundant in the woods from the Kogosukruk Tongue, whereas only one specimen of wood from the Nanushuk Group had false rings. Multiple false rings within a single growth ring were not observed in woods from the Nanushuk Group. We tentatively rule out insect attack as the cause of false rings in the Kogosukruk woods because we found no evidence for insect attack in either the woods or the leaves, and because many growth rings have more than one false ring. Insects in seasonal climates tend to have rigid life cycles and attacks on trees by a given species of insect will occur during a relatively constrained time period. Thus, if the false rings were formed during the stress of insect attack, several species of insects would have to have been involved. No evidence for even temporary drought has been found in Kogosukruk sediments; indeed, the system

was very wet (Phillips 1987). Fire and freezing both are plausible explanations for growth disruption in Kogosukruk woods. Charcoal is abundant in Kogosukruk Tongue (indeed, the presence or absence of charcoal can be useful in distinguishing these rocks in core; J. T. Parrish and R. A. Spicer, unpublished data). However, freezing is an equally likely explanation, given the low temperatures suggested by the thick late wood and the vegetational physiognomy (Parrish and Spicer 1988b).

Vegetation

The fossil leaf flora changed dramatically between the Nanushuk Group and the Kogosukruk Tongue (Spicer and Parrish 1987; Parrish and Spicer 1988b). The flora of the Nanushuk Group is very diverse, including sixty-seven forms of angiosperm leaves; several taxa each of ferns and conifer leaves and cones; and ginkgophytes, sphenophytes and cycadophytes (Spicer and Parrish 1986). By Kogosukruk time, total diversity of megafossils other than wood was ten forms, including the sphenophyte *Equisetites*, two ferns, two conifer leaf forms, a fruit, two angiosperm leaf forms and two types of small seed (Spicer and Parrish 1987; Parrish and Spicer 1988b). Quantitative estimates of mean annual temperature, derived from angiosperm leaf-margin analysis (Wolfe 1979), were 10°C for the latest Albian and Cenomanian and 13°C for the Coniacian (Parrish and Spicer 1988b). The angiosperm megaflora was too depauperate in the Kogosukruk Tongue for leaf-margin analysis, but we interpreted the drastic drop in diversity as indicative of cooling. Based on the overall physiognomy of the flora, we estimated the mean annual temperature to be 2–6°C. In such a climate, cold snaps seem likely (Parrish *et al.* 1987).

Frederiksen et al. (1988) reported a relatively high diversity of angiosperm pollen from the Kogosukruk Tongue. The discrepancy between the diversity of the megaflora and that of the palynoflora would appear to indicate that the angiosperm component of the vegetation was principally herbaceous. This is consistent with the cooler and more variable climate indicated by the woods. Such a climate would favour opportunistic taxa with annual life cycles.

The question of whether freezing occurred is critical to understanding the presence of dinosaurs in the Kogosukruk Tongue (Clemens 1985; Brouwers et al. 1987; Parrish et al. 1987; Paul 1988). The palaeobotanical data suggest that winter temperatures were likely to have been close to freezing. In addition, the presence of glendonites, which form in seawater near freezing, in older and younger marine sediments of the North Slope (Kemper 1987) suggests that the Arctic Ocean was likely to have been cool throughout the Cretaceous.

Although the vegetation suggests cool temperatures, the morphology of the tracheids in the woods may provide evidence against prolonged freezing. Tracheid cross-sectional areas are related to exposure to water stress. Where water stress is experienced, thick tracheid walls (and therefore small lumina) are necessary to prevent tracheid collapse as tension builds up in the water column. Conversely thin-walled tracheids and large lumina are correlated with stress-free environments. Although some Kogosukruk early wood tracheid cross-sectional areas are as small as $550 \, \mu \text{m}^2$ (specimen 7·1) most are greater than $2000 \, \mu \text{m}^2$. This figure is comparable to modern conifers growing in highly mesic environments where water stress is never experienced (Carlquist 1975). Thus, it is unlikely that the Kogosukruk trees experienced freezing of the root zone, which could have induced severe water stress, particularly during the early spring growth. It appears that periglacial conditions were not experienced at sea level, even at northern latitudes greater than 80° N.

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