FOSSIL FORESTS FROM THE LOWER CRETACEOUS OF ALEXANDER ISLAND, ANTARCTICA

by TIMOTHY H. JEFFERSON

ABSTRACT. Fossil forests and forest floors have been found in the Lower Cretaceous part of the Fossil Bluff Formation in south-east Alexander Island, Antarctica. These grew at an apparent palaeolatitude of 65° to 75° S., within the Cretaceous polar circle. Analyses of the well-preserved growth patterns have yielded important information about periodicity of growth, and the effect of rapid burial on trees. Increments of annual growth were very variable and growth rates were high. These growth characteristics are very different from those of modern high-latitude trees. They compare most closely with some species of living trees growing in warm temperate areas with a long growing season. The palaeoclimatic information is apparently inconsistent with the high palaeolatitudes proposed in most existing palaeocontinental reconstructions.

THE Upper Jurassic–Lower Cretaceous Fossil Bluff Formation crops out as a coastal strip of well-exposed cliffs and nunataks on the east side of Alexander Island, Antarctica (text-fig. 1a, b). Fluviatile and lacustrine sedimentary rocks occur in the southern part of this formation and are of Aptian–Albian age (Taylor, Thomson, and Willey 1979). Within this part of the succession occur abundant fossil leaf floras (Jefferson 1981 and in prep.) and several fossil coniferous forests. The sediments which now constitute the rocks of the Fossil Bluff Formation accumulated in a fore-arc basin (Suárez 1976). Most of it was derived from a volcanic-arc source 20–40 km to the east and has a high volcaniclastic component. The silicification of the secondary wood of conifers within the fossil forest can be attributed to early diagenesis of these sediments, decomposition of volcanic material, and release of free silica. The processes of decay and mineralization of the fossil wood, together with the taxonomy, are discussed in detail in Jefferson (1981), and will be the subject of a forthcoming paper.

PALAEOGEOGRAPHY

Reconstructions of Early Cretaceous palaeogeography position south-eastern Alexander Island within the Cretaceous polar circle. The most recent reconstruction with the largest data base is that of Smith, Hurley, and Briden (1981), in which south-east Alexander Island is at 74° S. Lesser Antarctica, however, is now considered to be made up of at least three plates, the Antarctic Peninsula, Ellsworth, and Thurston plates (Baker and Griffiths 1977; DeWit 1977). Text-fig. 2 is a combination of a 110 ma reconstruction produced by Dr. A. Smith (computer program as in Smith et al. 1981) with the possible range of positions of the Antarctic Peninsula plate. Palaeolatitude varies from 69° to 75° S. A limited amount of palaeomagnetic data from the Antarctic Peninsula gives a 110 ma palaeolatitude of 65° S, but this involves an error margin of ± 10 degrees (Kellogg 1980). The palaeomagnetic control for the stable continental blocks of South America and East Antarctica is much better. The range of positions of the Antarctic Peninsula relative to these is limited by the structural continuity of the southern Andes and the Antarctandes and by geological and palaeomagnetic evidence. This evidence fixes the northern end of the Antarctic Peninsula close, or adjacent, to the southern tip of South America (Dalziel and Elliott 1973; Barker and Burrell 1977). Reconstructions involving a wide separation between the Antarctic Peninsula and South America
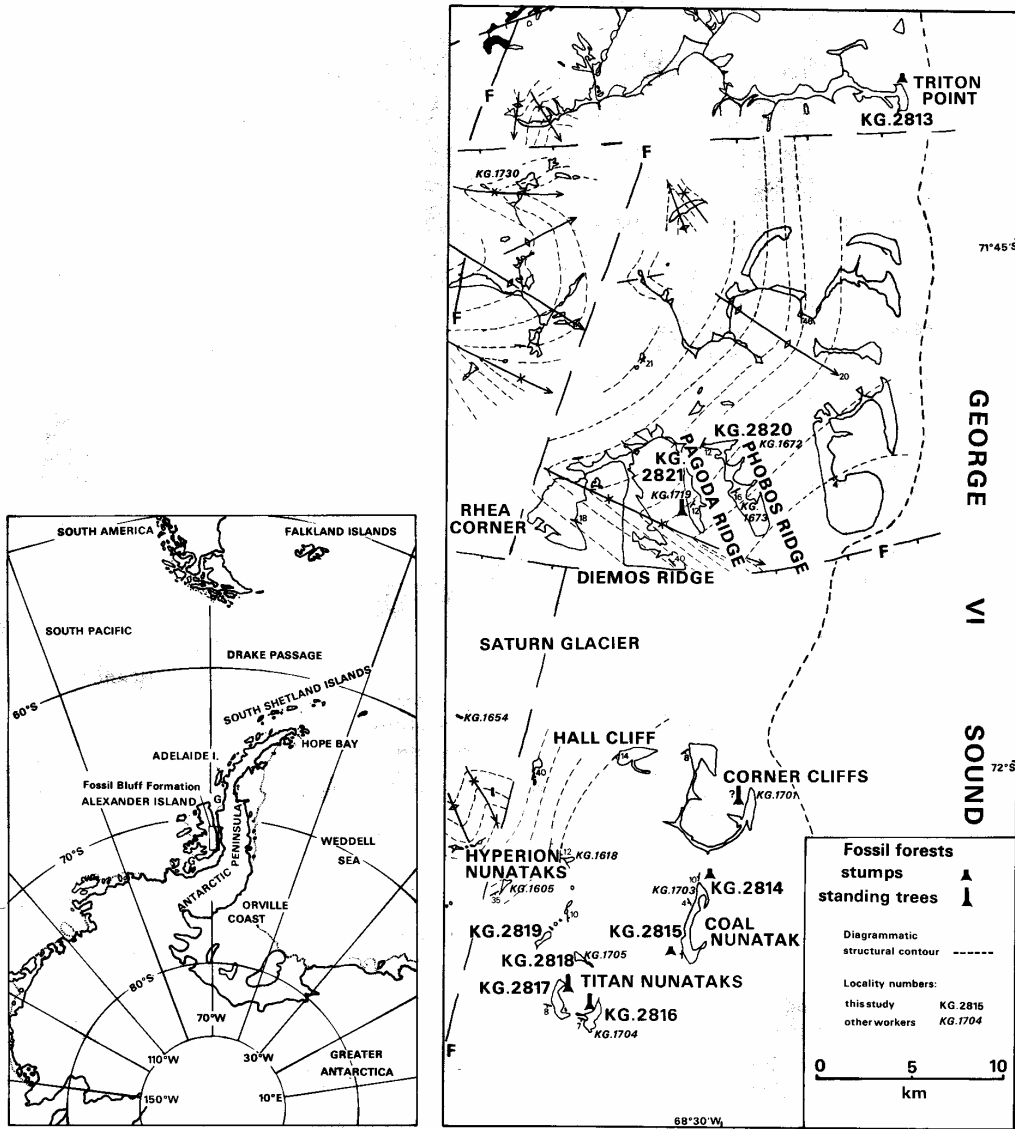
TEXT-FIG. 1. (a) Map of Lesser Antarctica showing localities used in text. Position of text-fig. 1b indicated. (b) Map of south-eastern Alexander Island showing positions of fossil forest floors and standing-tree fossil forests.
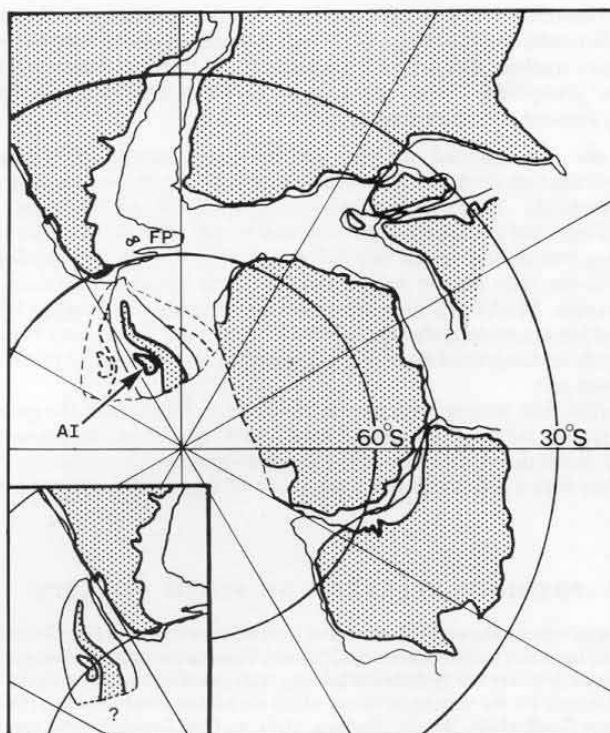
TEXT-FIG. 2. 110 ma reconstruction of the southern continents showing possible positions of the Antarctic Peninsula plate. Computer map by A. G. Smith (using program as in Smith *et al.* 1981). Shape of Antarctic Peninsula plate after Dewit (1977). Inset shows a possible position of the Antarctic Peninsula plate adjacent to southern South America (see text).

during the Early Cretaceous are, therefore, unlikely. Reconstructions using the expanding earth model (Owen 1976) also reposition south-east Alexander Island within the Cretaceous polar circle at a latitude of 67° S.

WOOD TAXONOMY

The taxonomy of the fossil wood presented considerable problems and a full discussion is beyond the scope of this paper. However, some of the problems involved are summarized below:

1. The classification of fossil wood is at present unresolved. Comprehensive keys (e.g. Krausel 1949) are effective only when crucial details of fine structure are preserved. Some diagnostic structures have been obscured or modified by decay and mineralization in the Alexander Island fossil woods.

2. Structural variability of wood from different parts of individual trees leads to complications in classification of fossil material which require more careful consideration than has usually been given.

3. Although the Alexander Island fossil woods are clearly gymnospermous, composed mainly of tracheids (vertical elements) and medullary rays (radial elements) and are devoid of resin ducts, they show characteristics of tracheid and ray pitting which are intermediate between the 'Araucaria type' and 'Cupressus type' groupings. Therefore the two taxa which were recognized cannot be referred satisfactorily to any existing genera or species.

The two taxa are distinguished on the presence or absence of parenchyma cells, the parenchymous wood bearing distinct, ?resin-filled parenchyma cells distinct from and smaller than the surrounding tracheids. These cells occur throughout the growth ring. Both woods are characterized by well-marked growth rings of variable size; transition from early- to late-wood cells is gradual over the ring but abrupt in the last 5-7 cells terminating in 3-5 small thick-walled cells. Bordered pits are borne only on the radial walls of tracheids and are predominantly circular, uniseriate, and separate. Medullary rays are uniseriate, variable in height (1-33 cells), and are composed of cells which are rectangular in tangential section but which may be round or oval. The ray cells are pitted only on tangential walls (walls adjacent to tracheid walls) and the cross-field bears one oval or two round pits.

In terms of the cross-field pitting both woods agree most closely with the genus *Circoporoxylon* Krausel but some species within *Phylocladoxylon* Gothan and *Protocupressinoxylon* Eckhold are equally comparable. Some proposed solutions to the problems encountered in the classification of the fossil woods, together with a full systematic description of them, will be presented in a forthcoming paper.

PREVIOUS RESEARCH ON FOSSIL FORESTS

Although much has been written about fossil wood and isolated standing trees (see Chaloner and Creber 1973, and references therein), far less is known about fossil forests. There are a number of accounts of Carboniferous standing tree fossil forests, but very few of these contain any truly petrified trees. The *Sigillaria* trunks of Joggins, Nova Scotia, studied mainly for the vertebrate fauna which the hollow trunks contain (Carroll *et al.* 1972), the lycopods of the Francis Creek Shale, Illinois (Shabica 1979), and the *Lepidodendron* trunks of Victoria Park, Glasgow (Seward 1919) all decayed and were subsequently filled by sediment. One exception is the calcified forest floor on the north coast of the Isle of Arran (Tyrrell 1928), but most of the stumps have now either been removed or eroded by the sea and provide little opportunity for further study. Krasilov (1975, p. 34) mentioned six horizons of forest development in the Middle Jurassic of the Yagnob river valley (Siberia), where burial was by mud-flows. He also described a Cretaceous conifer forest in the Ana Darya area of northern USSR, where trees are coated in ferruginous sheaths. Calcified fossil conifer stumps make up the Cretaceous 'Purbeck Forest' of the Great Dirt Bed of Dorset and are preserved in supratidal algal burrs (Jane Francis, pers. comm.). Francis found that growth rings were highly variable (though less so than in the Alexander Island fossil woods) and attributed this to an arid climate.

Calder (1953) described a Tertiary *Araucaria*-dominated forest preserved in rhyolitic ash in the Desearo river valley, Patagonia. As this is highly silicified, and little organic material remains, few growth rings are preserved. This forest, like the other Tertiary Argentinian forests and the famous petrified forest of Arizona (Ash 1970), is made up almost entirely of fallen trees. The silicified forest near Sarmiento, northern Patagonia, consists of fallen *Araucaria* logs in red sandstones and siltstones (pers. obs. 1979). Preservation of rings and cell structure is excellent, with fine details like the tori (the membranes in the centre of bordered pits) preserved in silica. The best documented fossil forests are those of Yellowstone National Park, north-west USA. Although these are all Tertiary in age (Dorf 1964), the sedimentary and diagenetic environments leading to mineralization appear to be similar to those in Alexander Island. Dorf (1964) regarded many of the Yellowstone Park forest beds as volcanic debris flows, but recent work by Fritz (1980a) suggests that most of the trees were buried by alluvial sandstones and conglomerates. These are 80-90% water-transported air-fall ash and 10-20% reworked detrital volcaniclastic material. The preservation of growth rings and cell structure in Yellowstone Park is comparable with, but rather more consistent than, the Alexander Island material, probably because of the higher percentage of volcanic material in the sediment (see Jefferson 1981).

THE ALEXANDER ISLAND FOSSIL FORESTS

Distribution

Most of the fossil wood found in the Fossil Bluff Formation occurred in the form of standing trees and stumps and the term 'fossil forest' is used in this study for any group of trees or stumps which are clearly in position of growth at a distinct stratigraphical level. The number of trees constituting a fossil forest depends on the area of its exposure, rather than on the original area of tree cover; whenever a bed contained *in situ* stumps at one outcrop, stumps were also found in all nearby but separate exposures, suggesting continuous tree cover over areas of at least 1 km². *In situ* fossil forests were found at seven of the localities shown in text-fig. 1*b* (KG.2812, KG.2813-16, KG.2820, and KG.2821) and it is mainly with these that this paper is concerned.

Some of the fossil wood, however, occurred as isolated branches and trunks which were transported from the site of growth and deposited at a low angle to bedding within fluvial sandstones. Transport and break-up of the trunks and branches probably took place during flooding. Trunks transported by mud-flows and deposited in an upright position as described by Fritz (1980*b*) were not seen. Drifted wood was often found in sandstone units at the same stratigraphical level as fossil forests and most of this material was probably derived locally from these forests. At other stratigraphical levels, however, some of the wood is likely to have been derived from more varied or more distant sources and represent true 'drifted assemblages'. The recognition of these on the basis of growth patterns is discussed below.

Modes of preservation

The form of each fossil forest is determined by the type and extent of mineralization, and this, in turn, is related to the way in which the trees were buried. The processes of decay and mineralization are discussed in detail in Jefferson (1981). The characteristics of the sediment which control silicification are 1, grain size; 2, mineralogy; and 3, porosity. Substantial quantities of mineral-rich fluid (in this case the mineral is free silica) must be available before decay takes place, and this fluid must be highly mobile within the sediment. Secondary wood buried in sediment with a low primary porosity is not permineralized because of low availability and mobility of free silica, but decomposes and becomes carbonized as sediment compaction takes place. Thin coalified lenses and sheets of coaly material, commonly found within the finer-grained rocks, are the only remnants of trunks and branches. Burial by sediment with a low volcaniclastic component also led to preservation failure, irrespective of porosity, because early generation of free silica depends on the diagenetic breakdown of meta-stable volcanic material (Sigleo 1979). Coarse volcaniclastic sediment with a high porosity provides the optimum conditions for petrifaction. Point-counting of thin sections of sandstones from the east Titan Nunatak fossil forest indicates that 70-85% is detrital volcaniclastic material. Trees may be buried in this type of sediment in two ways:

1. By a single influx of sediment: because the coarse volcaniclastic sandstone units are usually only 25 cm thick and rarely more than 1 m thick, only the stumps and basal portions of the trunk are enclosed in sediment favourable for mineralization (Pl. 66, figs. 1-2). Where burial of the rest of the tree was by fine non-volcaniclastic sediment, the upper trunk was not preserved. Forests buried in this manner are preserved as fossil forest floors (best seen at the top of nunataks where large expanses of near horizontal bedding planes are exposed). Forest floors are also exposed in cliff sections, but it is likely that many were not recognized in the field due to indifferent preservation, lateral discontinuity of tree cover, and/or the possibility that a short cliff section through a forest floor might not intersect a tree.

2. By repeated influxes of sediment: provided that the intervals between these influxes were not sufficient for death and decay of the trees to occur, trunks were preserved as standing trees. Standing-tree fossil forests are exposed only in cliff sections, where trees up to 6 m high are found (Pl. 66, figs. 3-5).

There are gradations between those sediments most favourable for mineralization and those in which mineralization is impossible. Wood preserved in medium-grained sandstones with a low to moderate volcanic component is highly carbonized and sparsely distributed. Partial mineralization of trees is common, and no tree has been completely or uniformly preserved.

GENERAL FEATURES OF THE FOSSIL FORESTS

Forest floors

Petrified tree stumps were found at all seven localities which are studied in detail. In several cases these were poorly preserved and apparently isolated (either because of preservation failure or as a function of the original distribution). Stumps can be recognized as the remains of trees within a
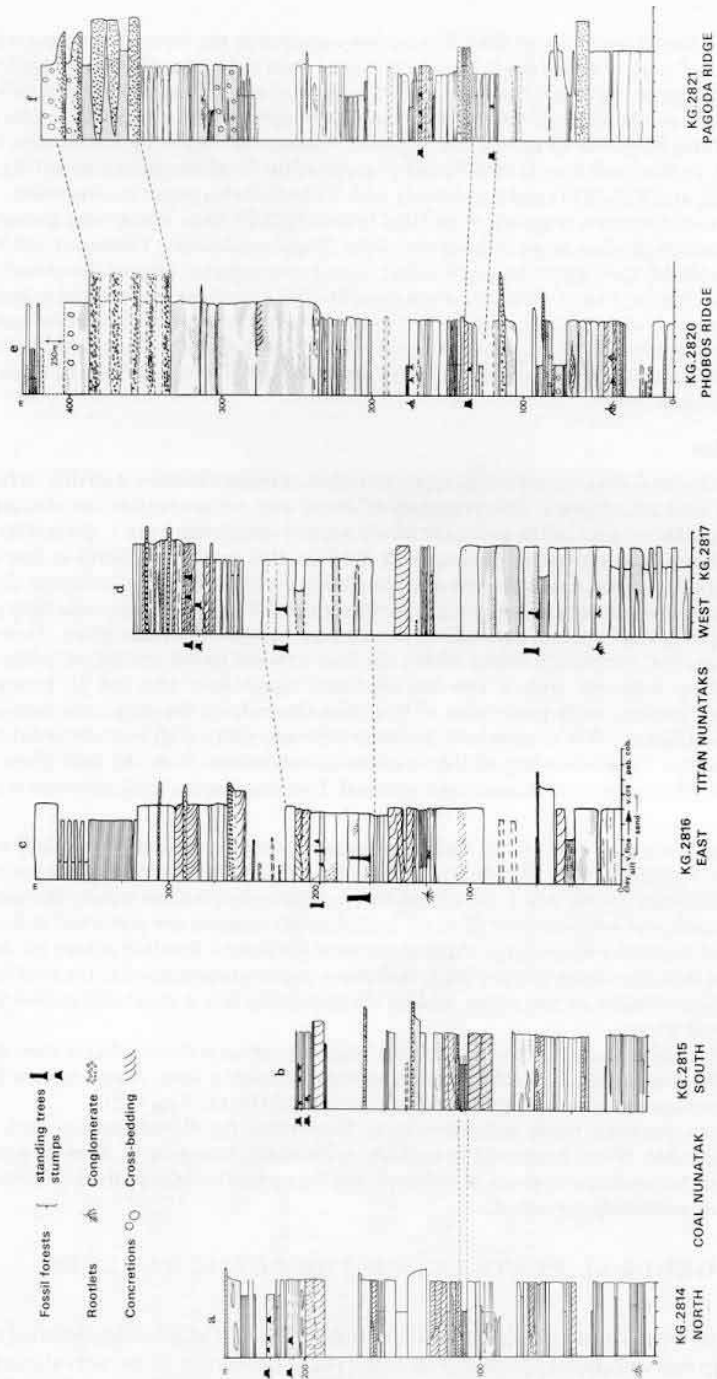
TEXT-FIG. 3. Stratigraphic logs of localities studied in detail. Lithological correlation by eye.

forest rather than of isolated trees in four cases. The location of these is shown in text-fig. 1*b* and the stratigraphical position in text-fig. 3. The two most extensive floors will be described in more detail.

At Triton Point (KG.2813) fossil forest floors are exposed at two levels, 5 m apart, at the top of the cliffs. There are two exposures of the upper forest floor horizon, one with eight exposed stumps and one with six, and one of the lower with six stumps. Although the relationship between the two is not clear, they are regarded as a single forest and it is likely that the first forest survived, at least in part, and gave rise to the second. The stumps are preserved in a medium-grained white tuffaceous sandstone which is devoid of sedimentary structures. Roots which penetrated the underlying coarse brown sandstone, decayed, were filled by sediment during compaction and are now preserved only as casts with a carbonized coating. The original soil has been compacted to an irregular carbonaceous palaeosol less than 2 cm thick. The margins of all stumps are carbonized and poorly defined due to pre-petrifaction decay.

At the South Coal Nunatak (KG.2815) an extensive fossil forest floor is exposed on a single bedding plane at the summit of this flat-topped nunatak. The floor occurs 1·45 m from the top of the section (text-fig. 3*b*) with a total exposure of 25 × 38 m and a total of fifty-four *in situ* stumps: thirty-one of these occur in an unbroken exposure 22 × 25 m. Stumps vary in diameter from 22 to 8 cm and have weathered out from a coarse brown sandstone with a high volcanic content (Pl. 66, figs. 1–2). The stumps are between 3 and 5 m apart, with an average density of 1 per 17 m² and an average spacing of 4·2 m. Where a thin layer of the overlying fine white tuffaceous sandstone covers the forest floor, parts of the trunks are totally carbonized.

Many of the stumps are asymmetrical with a consistent north–south trend (text-fig. 4*a*). Jointing, and subsequent frost shattering and weathering, however, are thought to have produced these shapes. Close examination of the growth rings indicates that the original cross-sectional shape of the trees was very different from the stump shapes produced by these secondary effects. The marked asymmetry of growth rings in many stumps has a wide range of orientations (text-fig. 4*b*). These are as likely to have been produced by local effects of competition (shading, etc.), as they are to have been a product of preferential growth towards low incident light (Kossovich 1935; Smirnoff and Connelly 1980), strong prevailing winds (Schwarzbach 1963), or angle of slope (Dorf 1933).
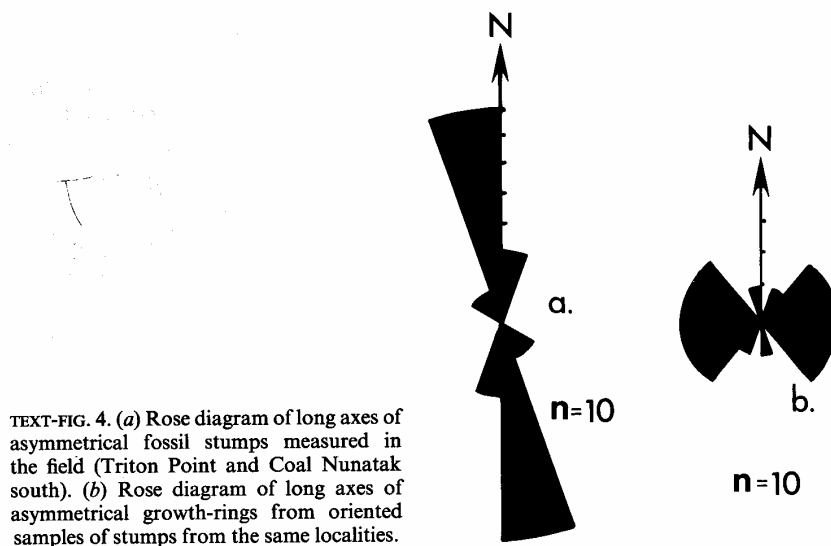
TEXT-FIG. 4. (*a*) Rose diagram of long axes of asymmetrical fossil stumps measured in the field (Triton Point and Coal Nunatak south). (*b*) Rose diagram of long axes of asymmetrical growth-rings from oriented samples of stumps from the same localities.

Standing tree fossil forests

Standing tree forests were found at three distinct stratigraphic levels at four localities (KG.2815, 16, 17, and 21; see text-figs. 1b and 3), and in varying states of preservation. At least one other has been reported from Corner Cliffs (Pl. 66, fig. 3) (L. E. Willey, unpublished field notes), a locality not studied in the course of this work. A few isolated standing trees also occur in poorly exposed or inaccessible beds.

The trees in two of the forests were preserved to a height of only 1 m and much of the wood collected was found to be poorly preserved. The fossil forest exposed in a cliff 1·5 km long at east Titan Nunatak is, however, well exposed and is also seen at west Titan Nunatak. At east Titan Nunatak the standing trees are preserved in a coarse volcaniclastic sandstone unit 17·3 m thick. Text-fig. 5 shows the detailed stratigraphy of this unit, in which at least four of the bedding surfaces exposed in cross-section were forest covered. The flask-like shape of the basal portion of several of the trees suggests that they survived the influx of sediment (Pl. 66, fig. 4). This shape is common in modern conifers when roots and basal parts of trunks have been covered for long periods by standing water or sediment. Stone and Vasey (1968) found this form of retardation in radial growth of redwoods from western Canada. This was because of reduced root aeration when they were inundated by flood water and buried by silt up to 120 cm thick. The trees also developed new roots in the top layers of the newly deposited sediments. Krasilov (1975), who described this type of broad tree base as 'hygrophytic', also noted the development of adventitious roots, but there is no evidence of the latter in any Alexander Island fossil trees. Land surfaces formed by newly deposited sediment were apparently rapidly colonized by trees. These often grew within 1 m of other trees which had probably survived inundation (Pl. 66, fig. 5).

The suggestion that at least some of the trees survived sediment influx is supported by the fact that most of their height is above the surface formed by the first sediment influx. The height of the tallest tree remains found is 7 m, and of this at least 5 m protrudes above the first bedding plane. However, modern trees killed by the influx of sediment, or by standing water, sometimes withstand decay for several decades. For example, trees at the margins of Lago Argentino (Argentina) are periodically submerged (pers. obs. 1979). The Perito Moreno glacier forms an ice dam at five- to twenty-year intervals, and the water level rises until the dam collapses. Although all the trees are killed by the submergence, many remain in an upright position for many years. In this case water-logged fallen trees are common below the water line.

Fallen trees and branches are rare in Alexander Island fossil forests, suggesting that loose woody material drifted off and was carried away before it became waterlogged. In the Yellowstone Park fossil forests more than 60% of trees are in a horizontal position (Fritz 1980a, b). Transported trees commonly became wedged against standing trees when flooding of the Potomac river in 1961 buried

---

EXPLANATION OF PLATE 66

Fig. 1. Silicified stump in the fossil forest floor at Coal Nunatak south. Specimen KG.2815.254 taken from upper left to stump.

Fig. 2. Silicified stump in cliff section at same level as fig. 1.

Fig. 3. Silicified standing tree 3·05 m high from corner cliffs. Note curved form of trunk. Photograph by L. E. Willey.

Fig. 4. Silicified standing tree at east Titan Nunatak (see text-fig. 5). Trunk shown is 1·65 m high but continues for a further 1·05 m. Note impressions of roots and bulbous base. Specimen KG.2816.39 taken from 1 m height on left side of outer trunk.

Fig. 5. Three trees (a, b, c) in standing-tree fossil forest as in fig. 4. Tree on left (a) has fallen from cliff leaving silicified material only at base. Central tree (b) as in fig. 4.

Fig. 6. Carbonized rootlets in coarse tuffaceous sandstone 130 m from the base of section KG.2816 (see text-fig. 3c).

PLATE 66
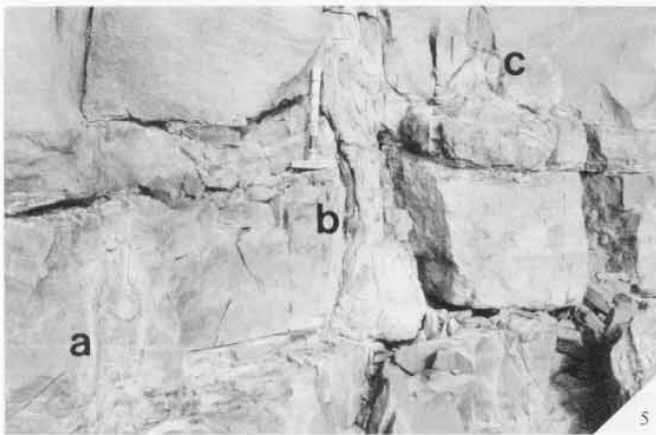
JEFFERSON, fossil forests
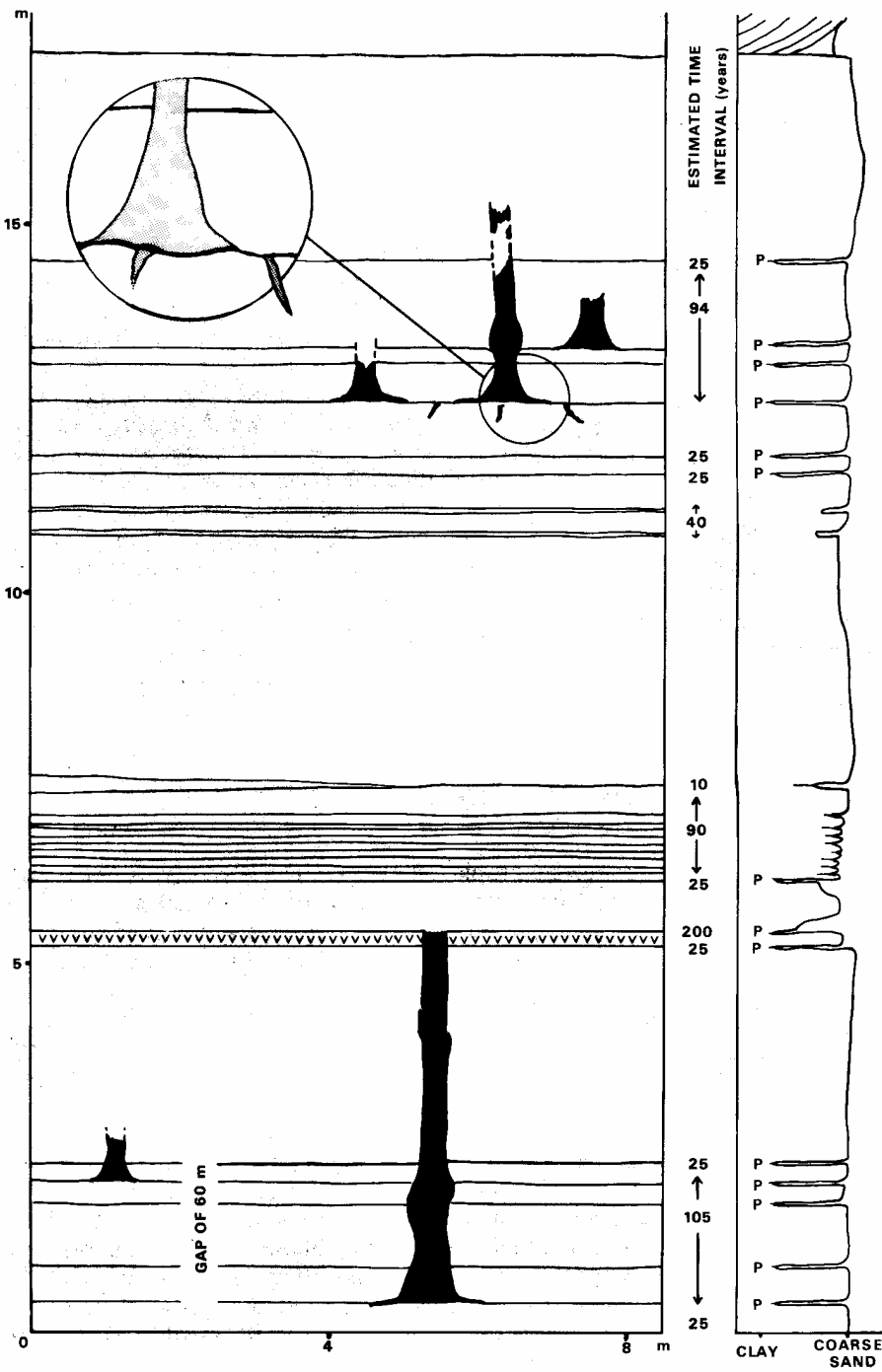
TEXT-FIG. 5. Detailed section through part of the unit containing the standing-tree fossil forest at east Titan Nunatak (see text-fig. 3c). vvvv = tuff bed. P = palaeosol.

several forested areas. The current velocities recorded during this flooding (Sigafoos 1964) were in excess of 20 ft/sec (6·1 m s⁻¹), which was sufficient to transport not only large fallen trees, but also several tons of concrete bridgework. Most mature trees survived the Potomac floods, but many young trees and saplings were killed by persistent standing water. The basal parts of trees were in some areas buried in 3 ft (0·9 m) of sediment, a thickness comparable with the beds of east Titan Nunatak. An absence of fallen trees in the Alexander Island fossil forests suggests that few trees were uprooted by flooding and that standing water, capable of floating fallen trees and branches free, was more persistent. The immature volcanic component is likely to have been weathered into clay minerals before colonization could take place but there are no well-developed palaeosol profiles. The forests developed in an immature soil, probably consisting of leaf litter and the layers rich in decomposed organic material. Lack of a well-developed podzolic soil profile may have been due to excessive waterlogging, or, more likely in view of the successful growth of conifers, to insufficient time between depositional events. Present-day mature soils may take over 5000 years to develop (Fitzpatrick 1971).

Roots were confined to this fine-grained, organic-rich soil and were therefore in a position of low preservation potential. They were also subject to compaction, which reduced soil thicknesses considerably. Calculation of original soil thickness was attempted using roots from east Titan Nunatak (Pl. 66, fig. 3, text-fig. 5). Casts of roots with a carbonaceous coating extend from the tree through the thin remnant palaeosol layer, and into the underlying sandstone. Extrapolating the position at which the roots would join the base of the trunk, were it raised to its pre-compactional position, gives an estimation of the amount of material lost by compaction. In this case an original soil approximately 35 cm deep is now represented by a layer 3·6 cm thick, a reduction of 90%. This depth of organic material is common in modern podzolic soil profiles (Fitzpatrick 1971). These residual palaeosols are packed with poorly preserved leaf litter, but no leaf material can be precisely identified. Rootlets, on a much smaller scale, are occasionally preserved within the coarse volcaniclastic beds. Although no cellular detail is preserved, the general pattern of rooting is clear (Pl. 66, fig. 6).

GROWTH RING MORPHOLOGY

Reaction-wood

Examination of the growth patterns reveals a rapidly developed asymmetry in some trees (Pl. 67, figs. 3-4). Growth rings which are very small or even absent on one side of the trunk are up to 5 mm across on the other. This is interpreted as reaction-wood and is found both in specimens from standing trees and from those not found in growth position, many of which probably represent branch material. This sort of growth pattern is typical in the trunks and branches of modern trees which have been tilted from the vertical. Ewart and Mason-Jones (1906) first pointed out that the formation of this asymmetric wood is a response to a gravitational stimulus. Sinnot (1952) recognized the development of 'reaction-wood' as a regulatory mechanism to restore or maintain the geometric relationships among parts of a tree and to maintain vertical growth in the trunk.

In the case of branches, which are permanently non-vertical, reaction-wood develops throughout the life of the tree as a regular asymmetry. Spurr and Hyvarinen (1954) reported that reaction-wood develops as a response to temporary bending of trunks, even if they revert to the vertical, as on the lee side of trunks after high winds, and explained the 'negative geotropism' as being instigated by increased concentrations of auxins on the underside of tilted branches and stems. Nečesaný (1958) suggested that the auxin responsible, for reaction-wood growth was β-indole-acetic acid. Robards (1969) confirmed that, in both angiosperms and gymnosperms, the response to a gravitational stimulus is triggered off by the 'redistribution of endogenous growth substances', and stated that 'reaction-wood allows aerial organs which are displaced from the vertical in woody plants to maintain or resume their predetermined growth positions'. Robards (1965) also stated that a tilt of only five degrees is capable of stimulating the production of reaction-wood. The response in angiosperms is to lay down tension-wood on the upper side of tilted stems, while the response in

gymnosperms is to produce compression-wood on the underside. Angiosperm reaction-wood is not considered here. Published descriptions of reaction-wood in fossil trees appear to be confined to a single specimen of a late Jurassic gymnosperm from Norfolk, and to several specimens in the Carboniferous lycopod genus *Lepidodendron* (Creber 1972).

Marked reaction-wood development is common in the Alexander Island trees (Pl. 67, figs. 3–4). Of the thirty-three sufficiently large and well-preserved cross sections examined in detail, fourteen had at least one area of marked asymmetry developed during a single year's growth, and accentuated by further asymmetric growth over a period of 2–6 years (KG.1703.24; KG.1704.10, 11; KG.2813.1, 15; KG.2814.252–254, 256; KG.2815.71, 77; KG.2816.39; KG.2817.15, 16). The interpretation of all such asymmetries as responses to a gravitational stimulus, however, must be treated with some caution. Slash pine trees in Florida develop discontinuous growth rings when growing in high-density stands (Larson 1956). Suppression of the crown on one side of the tree through shading by other trees is thought to lead to reduced auxin production just below expanding buds. Delayed arrival or absence of these hormones on one side of the tree suppresses cambial activity and growth is reduced. Growth rings are often absent on one side of the tree or represented only by a few late wood cells. However, both Robards (1965) and Creber (1975) pointed out that the characteristics of cells of true reaction-wood in most trees are different to those of 'normal wood'. Many of the anatomical features, and all the chemical features such as the high concentration of lignin in cell walls, are unlikely to survive mineralization. In many of the asymmetric rings, preservation is not good enough to recognize any subtle morphological differences. Nevertheless, in several specimens, cells in the reaction-wood are markedly rounded and have thicker cell walls than their normal counterparts (Pl. 67, fig. 5). Intercellular spaces are also larger and more common. The much more gradual transition in cell size from early to late wood in reaction-wood (Carrara 1979) is also seen in these specimens. Unfortunately, the markedly helical striations on tracheid walls (Pl. 67, fig. 6), described as indicative of reaction-wood (Côté and Day 1965), are not distinguishable from those resulting from pre-mineralization decay, or splitting at the time of mineralization. It is probable that at least some of the rapidly developed asymmetries represent reaction-wood induced by a gravitational stimulus.

Reaction-wood production after tilting of trees by various natural causes is documented. Trees bent by avalanches produce reaction-wood on trunk and branch undersides (Burrows and Burrows 1976; Carrara 1979). In some cases, growth rates are abruptly increased, due to reduction in competition, whereas in others they decrease because of loss of foliage. The 1958 movement of the Fairweather fault, south-east Alaska, tilted many conifers (Page 1970) and reaction-wood developed the following year, the maintenance of the geometric relationships between trunk and branches being effected by particularly marked reaction-wood development in the branches. Movement of the San Andreas fault in California caused similar tilting of trees and production of reaction-wood (LaMarche and Wallace 1972). In Colorado, erosion of roots has been shown to cause slight tilting of trees and the development of reaction-wood growth on the uneroded side (Carrara and Carroll 1979). In this case the destruction of cambial cells by erosion, and consequent retardation of growth on that side, is an important additional factor. On the west coast of Canada living redwood's are often tilted by flood waters (Stone and Vasey 1968). Trees respond by intensifying wood production on the under-side (i.e. producing reaction-wood) to form buttress-like supports. Angiosperms in the

EXPLANATION OF PLATE 67

Figs. 1–2. Acetate peels of silicified wood showing general asymmetry of growth. 1, KG.2817.16, × 0·75. 2, KG.2814.252, × 2.
Figs. 3–4. Acetate peels of silicified wood showing reaction-wood. 3, KG.2816.39, × 3. 4, KG.1704.11, × 3.
Fig. 5. Detail from fig. 3, showing rounded cells and intercellular spaces. × 200.
Fig. 6. SEM photograph of helical thickening on the radial wall of a tracheid, KG.2817.15, × 500.
Figs. 7–8. Acetate peels of KG.1704.10. 7, × 0.4. 8, detail × 1.

PLATE 67
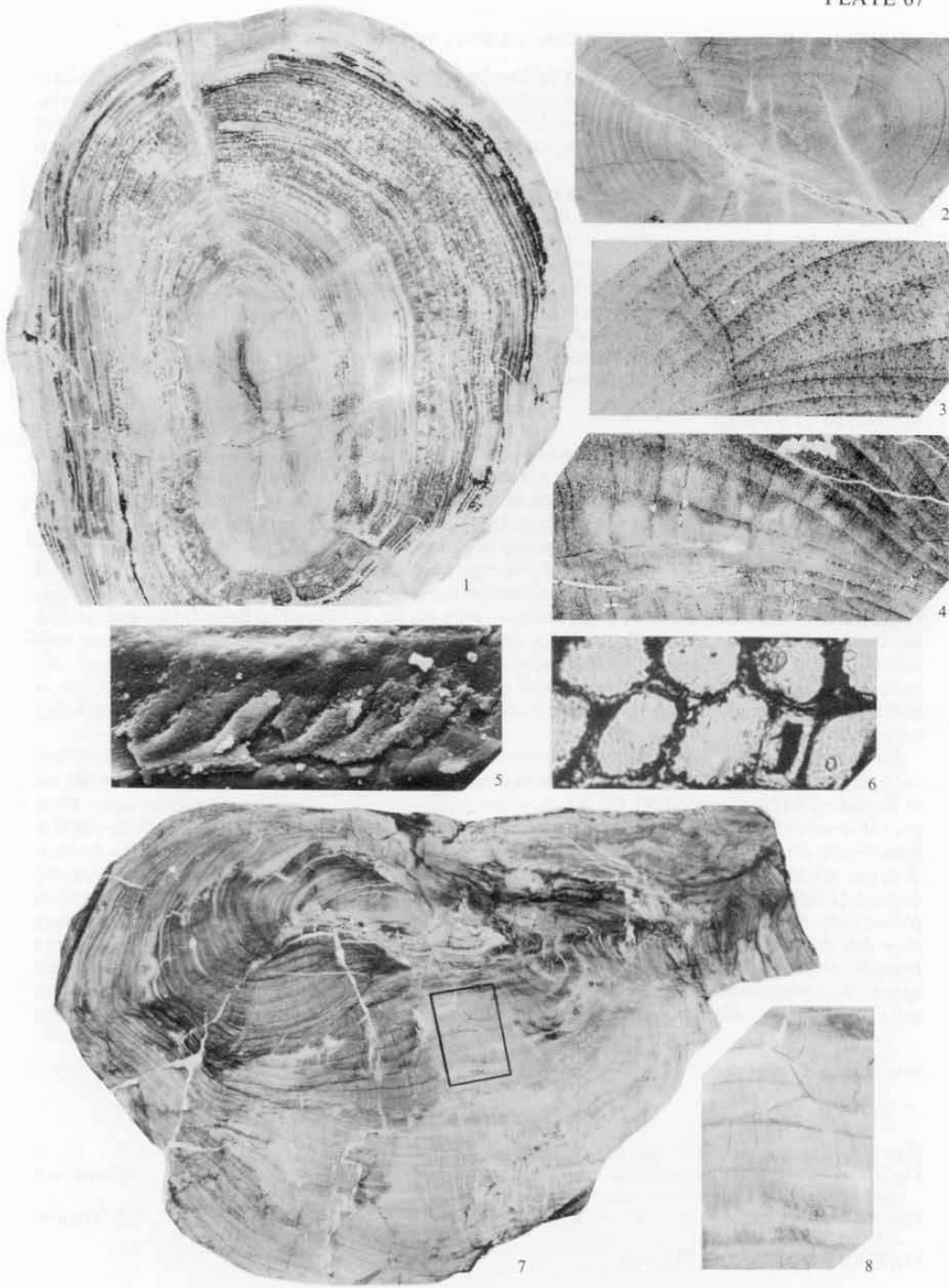
JEFFERSON, fossil forests

Potomac valley are also frequently bent by flooding (Sigafoos 1964). Growth from inclined trees is generally in the form of vertical shoots regardless of trunk angle. Few gymnosperms exist in this area, so that their behaviour under these conditions is unknown. It is also likely that changes in the intensity and effective direction of light, due to removal of competitors, influence the response to tilting.

Sedimentological evidence from Alexander Island, together with the survival and retardation in growth of trees, strongly suggests that the forests were buried by rapid influxes of fluvial sediment during flooding. Consequent tilting of trees is the most likely cause of the abundant reaction-wood. Several of the trees found in growth position are obviously tilted. The tree in Plate 66, fig. 2 is curved, with its base inclined to the bedding at an angle of 80–85 degrees, and the upper trunk approximately perpendicular. This suggests a recovery from tilting by reaction-wood growth. The tree shown in Plate 66, fig. 3 also tilts slightly and reaction-wood associated with the under-side has been found. Calculation of short-term sedimentation rates using flood-induced reaction-wood, together with palaeosol development, may be possible after further rigorous sampling.

Recognition of tree-rings

Ring-widths were measured directly from acetate peels of specimens cut at 90 degrees to the axis of tracheids. These transverse surfaces were polished and etched in 10% hydrofluoric acid for 165–250 seconds, depending on the amount of carbon remaining in the cell wall. Densitometer and other automatic techniques (see Polge 1969; Fritts 1976) proved unsatisfactory for the measurement of tree-rings because of variations in the quality of preservation (Pl. 68, fig. 3) and because of the occurrence of false rings and crush zones. False rings are easily recognized under the microscope and are discussed below. Pre-petrifactional compaction leads to the development of crush zones within rings, which could be mistaken for ring boundaries (Pl. 68, fig. 1). Microbial degradation and relative cell thickness are important in determining the form and extent of crushing. Since they have very small wall:lumen ratios, early-wood cells are often deformed preferentially, whereas late-wood cells have much thicker walls and therefore greater strength (Pl. 68, fig. 2). In many cases, the reduction in width caused by crushing can be estimated accurately and the ring can be used to build up a ring sequence.

Growth rings in the Alexander Island wood are extremely well defined (Pl. 68, figs. 3–6) and indicate marked seasonality. The cells at the beginning of each ring are invariably large (up to 100 μm in diameter) and thin-walled (Pl. 68, fig. 6). These represent cells which have developed under good growth conditions. Ford, Robards, and Piney (1978) explained the formation of cells in conifers (specifically *Picea sitchensis*) as a progressional development involving 1, cell production by division of active cambial cells; 2, cell expansion; 3, wall thickening; 4, maturation of cells. At a time when cell division is rapid cells join the development 'queue' more quickly and spend longer in the expansion phase. Cells at the end of the rings are small and very thick-walled. These are the products of very slow cell division. Ford *et al.* (1978) considered that the transition to late-wood production was brought about by conditions of low light- or water-availability leading to a low photosynthate supply. Experimental evidence reviewed by Fritts (1976) and Creber (1977), however, indicates that cell division is controlled by the concentration of endogenous growth substances. Gibberelic acid has
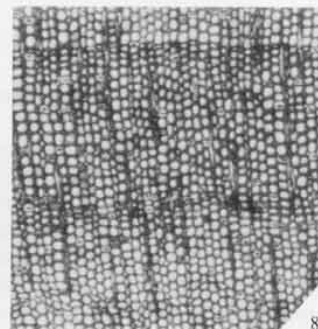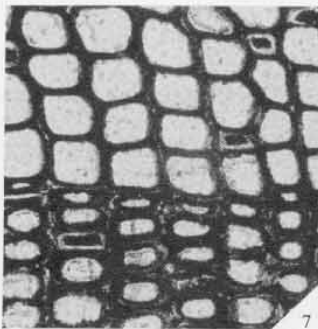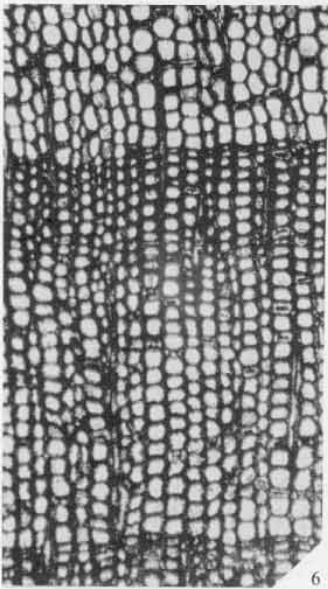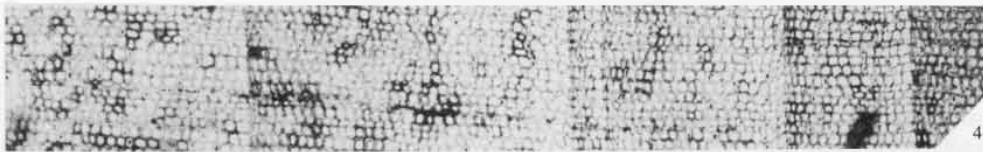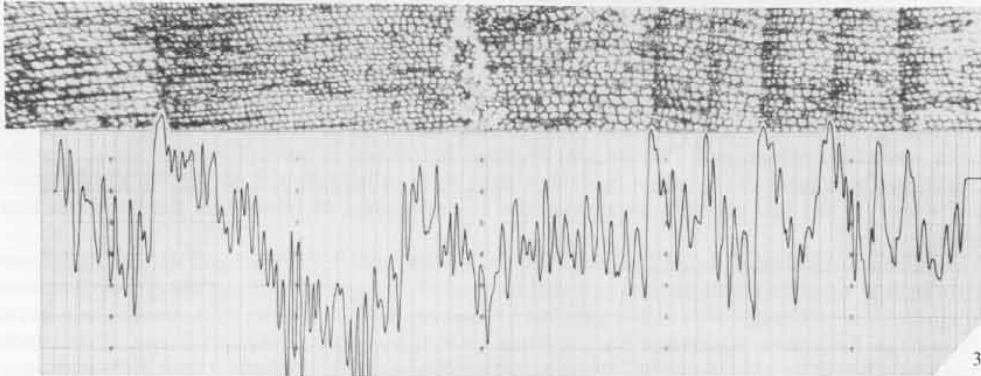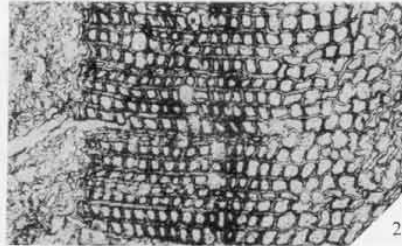
EXPLANATION OF PLATE 68

Figs. 1–2. Acetate peels of deformed cells. 1, KG.1702.2, × 20. 2, KG.2817.16, × 40.
Fig. 3. Growth-rings and densitometer trace showing anomalous density fluctuations in the poorly preserved central part of the large growth-ring, KG.2814.70, × 20.
Figs. 4–7. Growth-rings. 4, KG.2821.98, × 30. 5, KG.2814.254, × 40. 6, KG.1702.2, × 200. 7, KG.2814.254, × 100.
Fig. 8. False ring, KG.2814.252, × 20.

PLATE 68
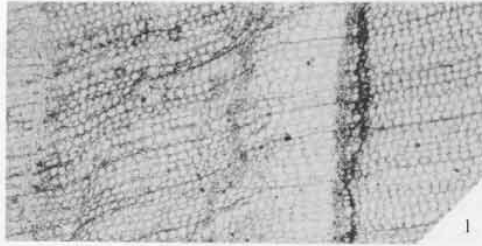
JEFFERSON, fossil forests

been shown to stimulate cambial division, while indoleacetic acid promotes differentiation of cells into xylem. It is the concentrations of these, plus several other auxins, which control the change from early- to late-wood production, and the small size of the late-wood cells. It has been demonstrated that the concentration of these auxins is very closely linked to environmental factors, particularly photoperiod (Chaloner and Creber 1973, and references cited). In the Alexander Island fossil woods, decrease in cell size and cell wall:lumen ratio is very gradual throughout each growth ring until both parameters decrease rapidly in the last 3–5 cells (Pl. 68, figs. 2–4). This late-wood zone of small, thick-walled cells is confined to 3–5 cells regardless of the overall size of the growth ring. The boundary between the late wood of one ring and the early wood of the succeeding ring is very well marked (Pl. 68, figs. 5–6). Once the level of auxins present within the tree fell below the threshold which controlled cell division and expansion, a maximum of 3–5 late-wood cells were produced.

False rings

Growth rings, which represent pauses in growth independent of, or in addition to, the main growth pattern, are easily recognized. The gradual decrease in cell size is not followed by an abrupt size increase, but by a gradual transition back into large thin-walled cells (Pl. 68, fig. 7). Furthermore, 'false' rings are far less continuous around the circumference of trees than the 'true' seasonal rings.

The palaeoclimatological significance of false rings is unclear. In different species, and in different environments, adverse environmental conditions can retard growth during the growing season. Drought and frost (Glock 1951) and insect attack (Koerber and Wickman 1970), are the main causes of false rings. Sedimentological and floral evidence strongly suggests that the climate of Alexander Island was not arid (see Jefferson 1981). Almost all the deposits were water-lain, and there is evidence of widespread flooding. Shallow lake deposits bear no evidence of desiccation such as mud-cracks, evaporite minerals, or pseudomorphs. The flora is abundant and diverse and none of the species displays any xeromorphic characteristics (e.g. fleshy leaves with thick cuticle, prickly stems, etc.). Pteridophytes are dominant in many assemblages and common in all. These, particularly the broad net-veined *Hausmannia*-like leaves, are unlikely to have been able to survive periodic drought (Kobayashi 1942). The preservation potential of evidence of insect attack is very low. There is one very well preserved case of fungal attack, which may have exploited insect damage. No insect remains silicified within tracheids, or partially eaten leaves, were found, but this sort of external control cannot be entirely ruled out. In view of the probable palaeolatitude of the fossil forests (65–70° S.) frost during the growing season is a possibility. The implications and difficulties raised by this deduction are discussed below.

False rings can also be produced by stimulating growth at the end of a growing season. This happens when nearby competitors are removed, thus raising the amount of effective available light back above the threshold at which growth is stimulated. Page (1970) described an example of this phenomenon brought about by fault movements. Large-scale flooding may have had the same effect on trees in Alexander Island. Several of the false rings do occur at the end of seasonal rings (Pl. 68, fig. 7).

Significance of tree-rings

In almost all modern trees from temperate latitudes, each ring represents an annual increment of growth (Chaloner and Creber 1973). V. C. LaMarche (pers. comm.) regarded rings which are as clearly defined as those in the Alexander Island woods as annual, regardless of the dominant environmental control. Non-annual growth rings are usually drought-controlled and are much less well defined, with diffuse boundaries (LaMarche *et al.* 1979; Cook and Jacoby 1979). Drought control on growth in Alexander Island is extremely unlikely (see above). Defoliation of trees by insects, which has been discussed, can be a secondary environmental control, but this would shorten the annual ring, or produce a recognizable false ring. Plate 68, figs. 2–6 compare very closely with the undoubtedly annual growth rings of larch trees (Schweingruber 1979, figs. 2 and 6), which have very similar cell patterns, densitometer traces, and false rings.

TREE-RING ANALYSIS

Methods

Twenty-seven ring sequences were built up from twenty-one well-preserved trees. The selected specimens all have a continuous sequence of consecutive rings which are not interrupted by areas of poor preservation, or pre-mineralization crushing (e.g. Pl. 67, figs. 7–8). In some cases building up such a sequence involved traversing around the circumference of a ring boundary, for up to 10 degrees, in order to find an area of better preservation.

The data for sequences with more than forty rings are reproduced graphically in text-fig. 6. Table 1 sets out the results of statistical analysis to find the 'mean sensitivity'. This is a statistical measure of variation in annual increments of growth used by dendroclimatologists (e.g. Glock 1955; Fritts and Shatz 1975; Fritts 1976; LaMarche *et al.* 1979). It was devised by Douglass (1928) in order to assess accurately whether a ring sequence was 'complacent' or 'sensitive'.

TABLE 1. Results of statistical analyses of tree-ring data showing mean sensitivity and mean and maximum ring-widths.

Locality	Specimen number	Number of Rings	Mean Sensitivity	Standard Deviation	Mean ring-width	Standard Deviation	Maximum ring-width
Georgian	KG.18.25a	18	0·739	0·474	1·144	1·048	3·80
Cliffs	KG.18.25b	23	0·535	0·405	1·269	1·114	4·24
	KG.18.30	130	0·338	0·351	0·401	0·342	2·27
Hyperion	KG.1702.2	29	0·029	0·050	0·980	0·083	1·12
Nunataks	KG.1702.3	53	0·528	0·410	1·340	0·665	2·77
	KG.1702.6	43	0·621	0·378	1·503	0·684	3·00
Triton	KG.2813.1	52	0·422	0·331	1·496	0·784	3·02
Point	KG.2813.15	33	0·415	0·367	1·262	0·826	3·90
Coal	KG.1703.23	49	0·404	0·269	0·993	0·928	4·52
Nunatak	KG.2814.2	141	0·393	0·310	1·510	0·613	4·24
(north)	KG.2814.254	43	0·404	0·361	0·959	0·733	4·70
Coal	KG.2815.71	34	0·326	0·278	1·161	0·736	4·24
Nunatak	KG.2815.256a	77	0·373	0·376	0·751	0·379	1·81
(south)	KG.2815.256b	38	0·434	0·333	1·309	0·794	3·33*
Titan	KG.1704.10	58	0·468	0·383	2·517	1·595	6·85
Nunatak	KG.1704.11	45	0·421	0·401	2·941	1·500	5·85
(east)	KG.2816.39a	44	0·408	0·318	0·582	0·360	1·83
	KG.2816.39b	14	0·430	0·290	1·094	1·016	4·23*
	KG.2816.39c	37	0·339	0·236	0·557	0·315	1·49
	KG.2816.40	38	0·418	0·352	1·594	0·921	3·93
Titan	KG.2817.15	96	0·443	0·315	1·080	0·874	3·12
Nunatak	KG.2817.16a	68	0·492	0·478	0·849	0·597	2·21
(west)	KG.2817.16b	88	0·423	0·330	0·980	0·487	2·91
Pagoda	KG.1719.3a	19	0·420	0·311	3·581	1·785	7·78
Ridge	KG.1719.3b	20	0·442	0·391	2·309	1·560	7·42
	KG.2821.97	13	0·393	0·314	1·620	0·633	2·73
	KG.2821.98	21	0·403	0·292	1·934	0·963	3·96

* = Reaction-wood
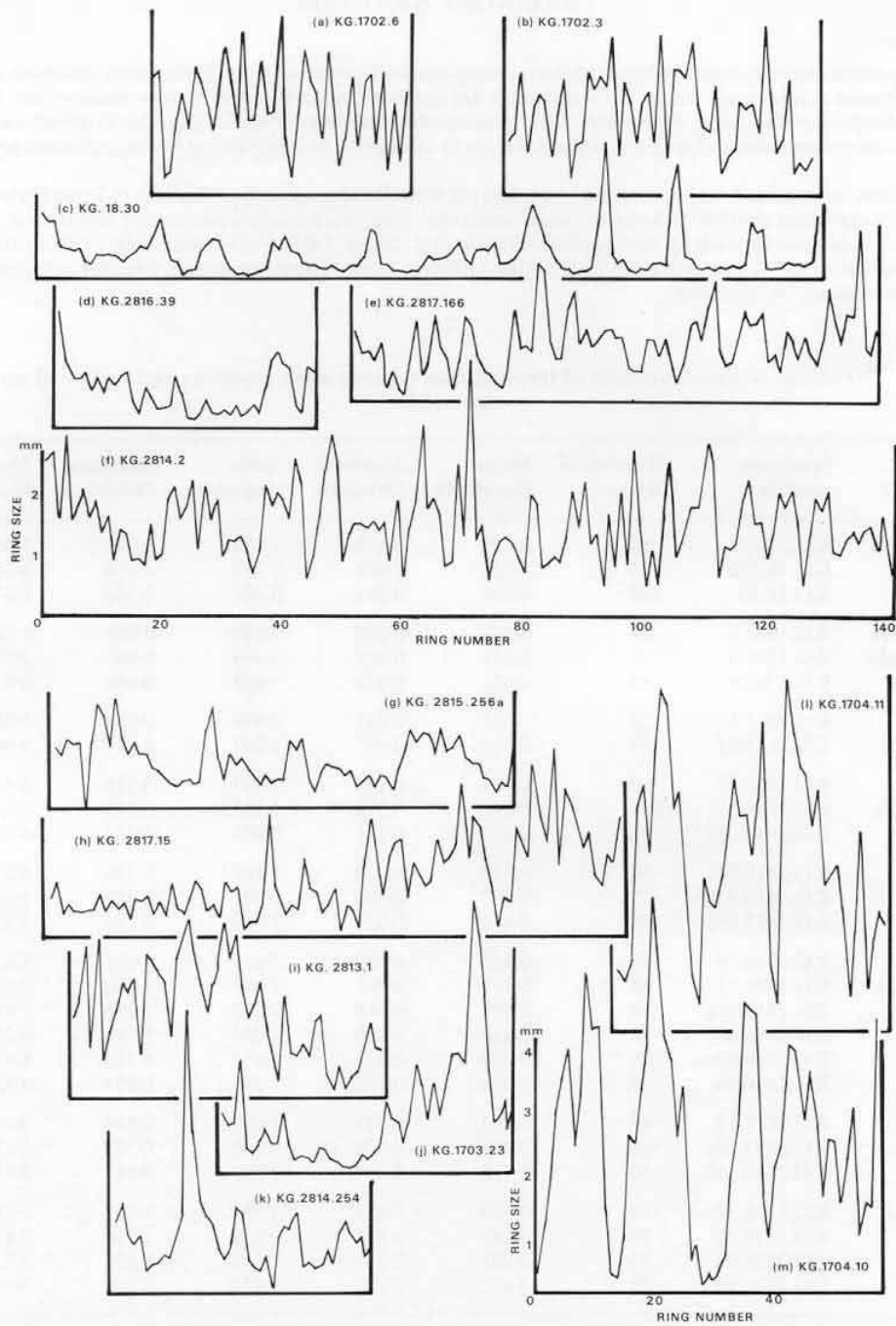
TEXT-FIG. 6. Plots of growth-ring sequences used in statistical analyses.

The 'annual sensitivity' is the difference in width of each pair of consecutive rings divided by their mean width:

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

$$\text{and Mean sensitivity} = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_t + x_{t+1}} \right|,$$

where x is the ring-width, t is the year number of the ring, and n is the number of rings in the sequence. A modification of the formula (Schulman 1956; Furst 1963) which simplifies calculation was rejected by Creber (1977) and by other workers in the field as it is necessary to discard data from the first fifty rings. Trees with mean sensitivities above 0·3 are by convention sensitive, and those with values below 0·3 are complacent.

Results

The results set out in Table 1 show 1, consistently high mean sensitivities of most of the trees; 2, high mean ring-widths; and 3, very high maximum ring-widths.

The data fall into two groups based on mean sensitivity, one with very variable (mean 0·463, standard deviation 0·249), and the other with consistent (mean 0·411, standard deviation 0·039), mean sensitivities. The first group consists of wood from Georgian Cliffs (KG.18) and Hyperion Nunataks (KG.1702) (text-fig. 1). At both localities the wood is clearly drifted. At Georgian Cliffs the wood occurs in marine rocks and much is heavily bored by marine bivalves. At Hyperion Nunataks the facies is uncertain, but no standing trees or stumps have been found and rare and fragmentary leaf fossils indicate a drifted flora. The assemblages from these localities appear to be mixed, with wood from both very sensitive and complacent trees. All the wood at the second group comes either from beds containing *in situ* forests or from beds close to these forests, and the tree-rings indicate no environmental changes throughout the time period, or over the geographical area represented by the southern part of the Fossil Bluff Formation. The distribution of annual sensitivities also shows a distinction between the two groups (text-fig. 7). The annual sensitivities of the wood in the 'drifted' assemblages are dominated by low values ($< 0·1$) but have a number of very high values, whereas the mode of the '*in situ*' sensitivities is 0·2–0·3 and the distribution is much less skewed.

The mean ring-widths and maximum ring-widths are far less consistent because samples inevitably come from different parts of trees. Some of the sequences probably come from branch material (e.g. KG.2815.256). Others were taken from the suppressed parts of reaction-wood (e.g. KG.2816.39). However, many of the trees show very high mean ring-widths, often well above 2 mm (Table 1). The largest ring recorded is 9·55 mm across (Pl. 67, fig. 7) and 50% of the *in situ* group bear rings in excess of 3·9 mm (Table 1).

Comparisons with living trees

Modern sensitive trees are almost entirely confined to marginal environments. When a tree is growing close to the limits of its ecological range any fluctuation in the climatic limiting factor will be reflected in the growth ring laid down that year. The only conifers which consistently show mean sensitivities near to, or above, 0·4 are those growing in a semi-arid environment, where it is variation in water availability which is reflected in the growth rings (Fritts and Schatz 1975). In such environments in western North America mean sensitivities of 0·6 have been recorded (Schulmann 1956 and data in Schulmann processed by Creber, pers. comm.). As stated above, however, all the sedimentological and floral evidence points to a humid climate during the deposition of the Fossil Bluff Formation.

In other marginal environments for conifer growth (high altitude and high latitude) growth is controlled by temperature or day length. LaMarche and Stockton (1974) found that bristle-cone pines at the upper tree-line were not sensitive. Mean sensitivities of trees from the nine sites in the Great Basin and Colorado–New Mexico areas range from 0·12 to 0·26 with a mean of 0·19. In contrast, bristle-cones from the lower forest border give a mean sensitivity of 0·43.

The most comprehensive data for trees at the sub-Arctic tree-line come from Alaska, northern Canada, and northern Norway, though tree-ring data from other sub-Arctic zones are closely comparable (Adamenko 1963). In Alaska, Giddings (1943), Andersen (1955), and Garfinkle and
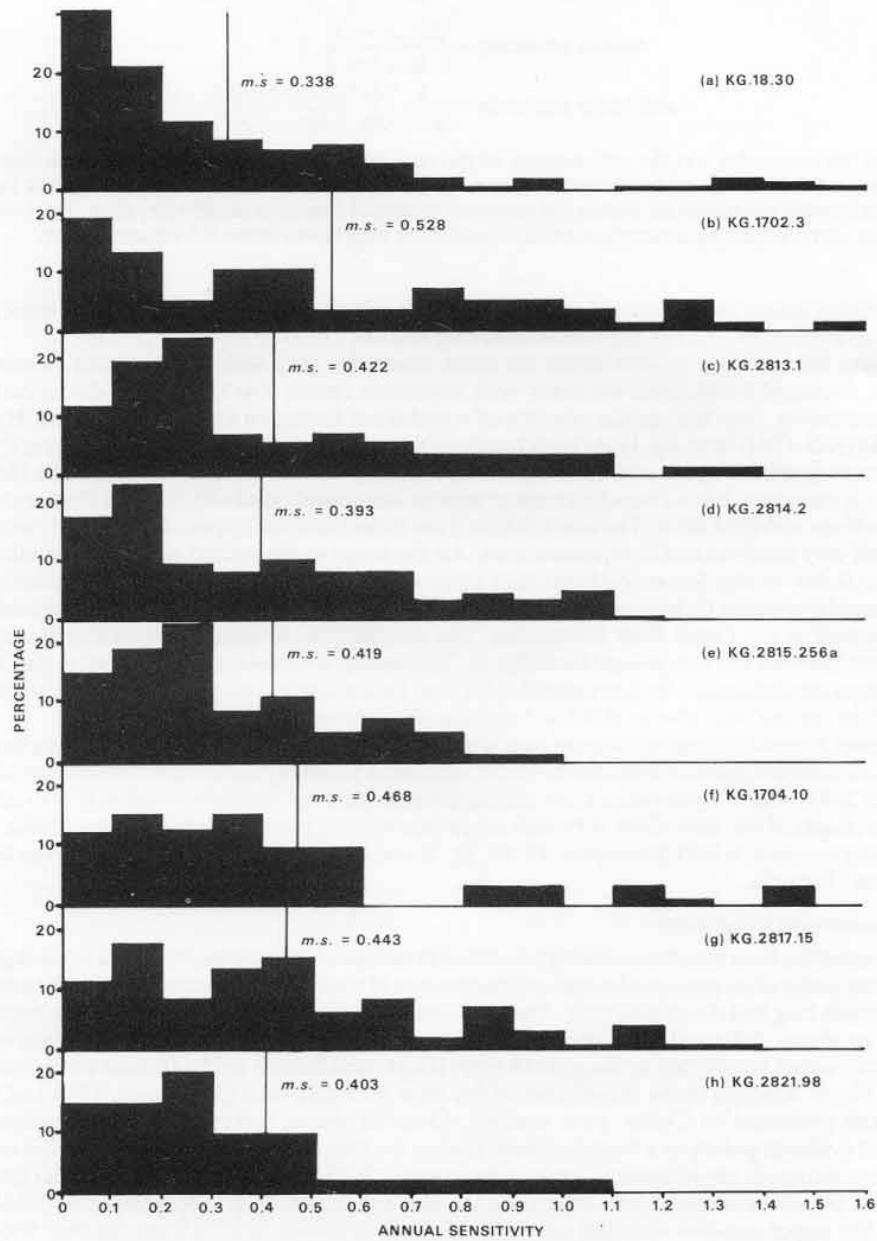
TEXT-FIG. 7. Histograms allowing comparison of variation in the annual sensitivities from eight of the fossil trees. E.g., in (a) 31% of the annual sensitivities have values less than 0·1, 20% have values between 0·1 and 0·2, etc.

Brubaker (1980) emphasized the dominance of growing-season temperatures in the control of growth in sub-Arctic trees. Important features of the trees from Gidding's (1943) spruce tree-line sites (69° N) are the low mean and maximum ring-widths, which at the site giving the highest values are only 0·9 mm and 2·2 mm, respectively. Ording (1941) found that late May temperatures were the major control on growth at the northern Norwegian tree-line and that even in this marginal environment the trees were complacent. An analysis, in 100-year blocks, of Ording's (1941) 530-year ring-sequence from fifteen trees in lat. 58° N gives an overall mean sensitivity of 0·1489 and a maximum of 0·1795. Mean ring-widths are again small, 0·54 mm at the tree-line, and less than 1 mm at 60° N. The largest ring for any tree north of 60° is 2·05 mm.

Data from northern Canada (Drew 1975) also indicate low sensitivity at the northern tree-line. The highest mean sensitivity for any sub-Arctic site is 0·1999 at lat. 68° N and the average for nine such sites north of 60° is 0·163. Mean and maximum ring-widths are again low, approximately 1 mm and 1·87 mm, respectively. Dimensions given by Riley and Young (1974) indicate that in Labrador Sitka spruces commonly have mean ring-widths as low as 0·35 mm.

Conclusions

Any analogy between high latitude climatic regimes today and those operating in similar latitudes during the early Cretaceous is clearly untenable. In interpreting the climatic type which is most likely to have produced the tree-growth patterns observed in the Alexander Island fossils, there is a further complication. Work by LaMarche (in press) suggested that, to a certain extent, growth patterns may be genetically controlled. Even in a marginal environment, where climate strongly influences growth, only sensitive species of trees will give high mean sensitivities. This is highlighted by the work of Dunwiddie and LaMarche (1980) on *Widdringtonia cedarbergensis*, from a marginal site in the Cedarberg Mountains of South Africa. Despite a very close correlation between growth and climate (75% of variation in growth-ring size is accounted for by variation in temperature and rainfall), the mean sensitivities of the trees is only 0·15 (LaMarche *et al.* 1979). In contrast, data on the genus *Phyllocladus* (celery top pine) from southern New Zealand and Tasmania show that these very sensitive trees reacted strongly to environmental fluctuations in a less marginal environment. These primitive podocarps grow between latitudes 35° and 44° S in temperate rain forests on humic soils. LaMarche *et al.* (1979) analysed trees in the genus *Phyllocladus* at fifteen sites and found that the mean sensitivities were consistently high. Although the average was 0·32, three sites gave values in excess of 0·4 and one in excess of 0·5. Mean ring-widths were up to 1·47 mm and the largest ring index was 2·32 mm. Since the ring indices for each site are compiled from four to twenty-three trees, many individual trees will have considerably higher maximum ring-widths. The similarity of the growing patterns of the Alexander Island fossil trees to those of living *Phyllocladus* indicates that they grew under conditions much closer to those found in present-day warm–temperate rain forests than to those found in high latitude regions.

The rapid growth rates indicated by the mean and maximum ring-widths would be very high for modern conifers even at low latitudes. However, the environmental range of the conifers is influenced to a large extent by the distribution of the angiosperms, and climatic controls in operation today are unlikely to be an accurate reflection of those during the Cretaceous. One factor which is widely believed to have remained constant during this period is the solar constant (see Foukal 1980 and references therein). Bearing this in mind, the amount of solar energy received at a latitude equivalent to south-east Alexander Island in the lower Cretaceous would be sufficient to sustain tree-growth. Twenty-four-hour daylight during at least part of the growing season might be expected to stimulate production of growth-promoting hormones. Photoperiod has been proved experimentally as the major control on these auxins (Larson 1956; Fritts 1976; Creber 1977). Ford *et al.* (1978) found that cell division could take place only if trees received more than 15 mJ m^{-2} d^{-1}. Data on solar energy received at sites close to the Antarctic circle today (Farman and Hamilton 1978) suggest that a growing season of five months could be sustained at these sites, but substantial growth would be limited to two months. The harshness of the winter and high frequency of frost during the growing season preclude the colonization of polar regions by modern trees capable of rapid growth. Although

these may not have been in operation during the Early Cretaceous, the low availability of light would restrict tree-growth. Furthermore, the low angle of incidence of the sun's rays would lead to extreme problems of shading in dense forests. Even at midday of the summer solstice the sun is at an elevation of only 48·5°, and two months either side of this the elevation is 27°. Text-fig. 8 shows the arrangement of the fossil forest floor at Coal Nunatak south (KG.2815). Although the trees are spaced widely enough to survive, the length of the growing season would be reduced, together with the number of hours per day with effective sunlight. Ground-dwelling vegetation, of which there is considerable evidence, would also be shaded out by this tree cover.
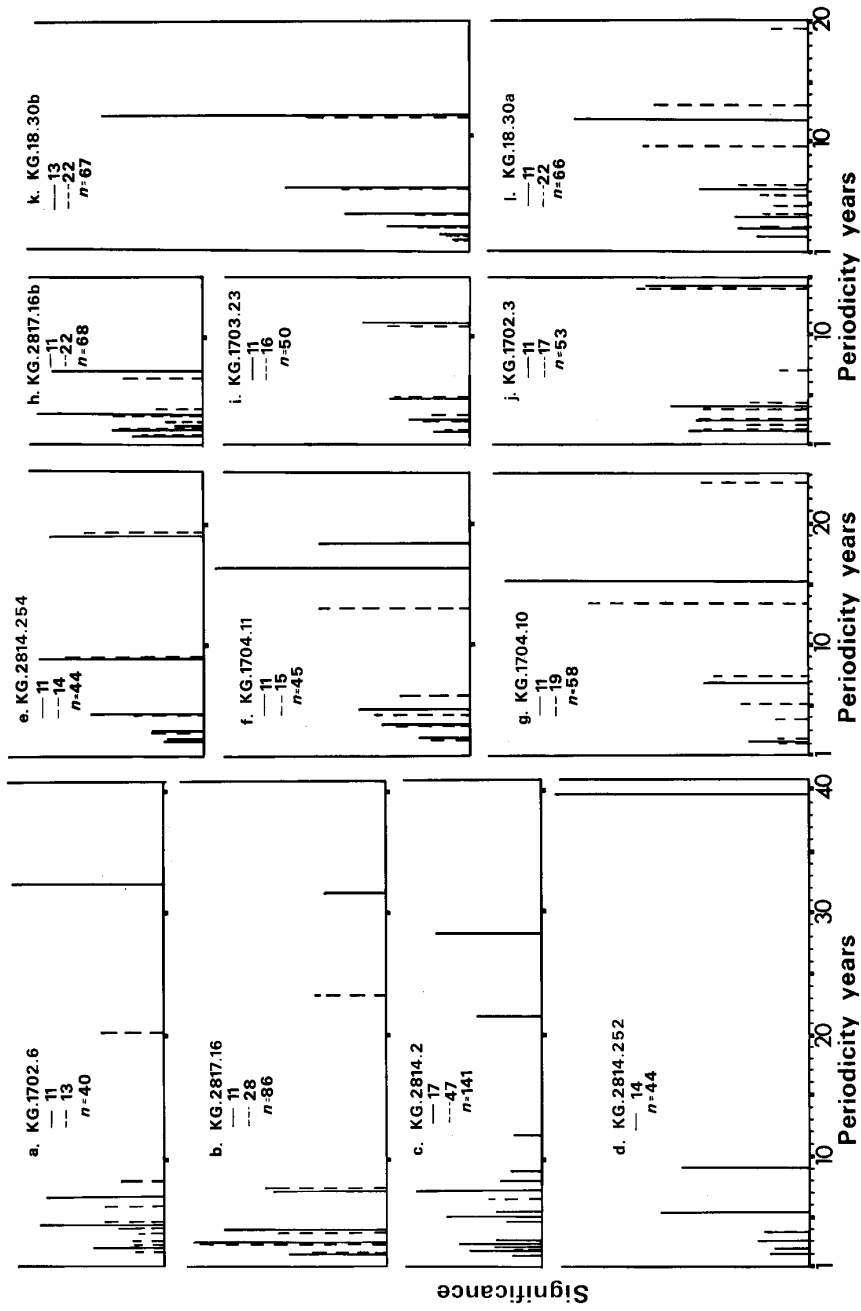
PERIODICITY OF TREE GROWTH

Methods

All tree-ring sequences with over forty rings were analysed for significant periodicities in their growth patterns. Strongly periodic growth can be picked up visually from graphical representation of the data. The regular repetition of peaks in text-fig. 6c suggests a periodicity of between ten and twelve years in specimen KG.18.30. However, in most cases periodicities are smaller and are masked by interaction with other periodicities (text-fig. 6f), and can only be discovered by mathematical analysis. The computer program used was Maximum Entropy Spectral Analysis (MESA) (Ross 1975), which for short lengths of data has a resolution superior to other methods

The effect of any stimulus on tree-growth in a given year will affect growth in subsequent years. Thus a particularly short, cold, growing season will produce a small growth-ring, but its effects will be seen in the next few rings. As a result, the growth-ring for year n will correlate very closely with that for year $n+1$ and progressively less well with years $n+2$, $n+3$, $n+4$, etc. This is likely to mask the effect of periodic growth. The first part of the program analyses this autocorrelation due to the lag effect of climatic stimuli, and removes it from the raw data. Such autocorrelation in the Alexander Island fossil trees is very low and rarely significant beyond $n+1$. The data are then processed by searching for periodicities within sections of the series using a 'window' through which a fixed number of data poits are analysed. The window then moves on one point, repeats the analysis, and so on until the end of the series. The program uses a range of window-widths from one data point to one-third of the number of data points, selects the one which reveals the clearest periodicities, and gives the results of this analysis together with that using the highest window-width. The results for each ring-sequence are reproduced graphically in text-fig. 9.
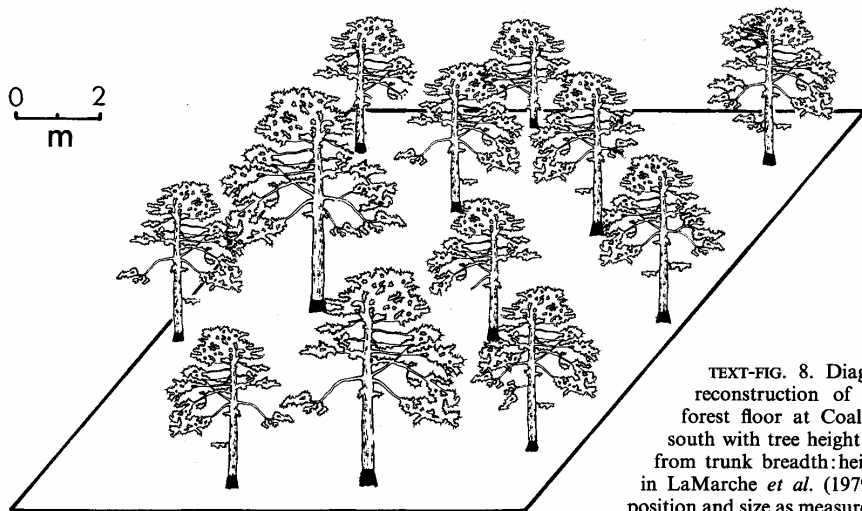
TEXT-FIG. 8. Diagrammatic reconstruction of the fossil forest floor at Coal Nunatak south with tree height estimated from trunk breadth:height ratios in LaMarche et al. (1979). Stump position and size as measured.

TEXT-FIG. 9. Periodicity of growth from individual trees against amplitude as measured by MESA (see text, p. 702, for explanation). Solid lines = periodicity found using lower filter coefficient. Broken lines = periodicity found using coefficient N/3.

In most cases use of the greatest window-width picks out the same periodicity as use of the optimum width (e.g. text-fig. 9e, i–k); in others it replaces some periodicities recognized by the optimum window with two less significant periodicities with similar frequencies (text-fig. 9f, l). In most cases it emphasizes the lower frequency periodicities (e.g. text-fig. 9g, j, l). The ring-sequence for KG.18.30 was run in two halves. The use of the optimum window-width on the first half of the sequence produced an eleven-year periodicity which was 'split' by the use of the greatest window-width. This periodicity was much more prominent in the second half of the data (the second half of the tree's life) and was not 'split' when a larger window was used.

Results and discussion

A histogram combining periodicities shown by all the trees analysed is shown in text-fig. 10. Two-, three-, and four-year periodicities are shown by most of the trees analysed. These may be purely biological in origin or may be related to the biennial or triennial solar cycles (Schove 1978). LaMarche and Stockton (1974) and Schove (1978) found 2·2- and 3·3-year cycles in ring-sequences from living trees. A very strong eleven- to twelve-year cycle is present in four of the trees (KG.18.30; KG.1704.10, 11; KG.2814.2) and is probably externally controlled. Although the interpretation of such a small data base from a localized area must be treated with caution the well-documented sunspot cycle (eleven and twenty-two years) is one possible cause of tree-growth periodicity which could be considered. Eddy (1976) showed that greatly reduced sunspot activity (the 'Maunder minimum') coincided with a 'little ice age' between 1645 and 1715. Stuiver and Quay (1980) found that the proportion of ^{14}C in tree-rings corresponded closely to sunspot cycles and demonstrated that three other cold periods since AD 1000 coincided with low sunspot activity. Few living trees show any eleven- or twenty-two-year periodicity (Monin and Vulis 1971; LaMarche and Fritts 1972), though Erlandsson (1936) found an eleven-year periodicity (amongst others) in pines from northern Sweden, and Bitvinskas (1971) reported a strong correlation between tree-growth and the twenty-two-year
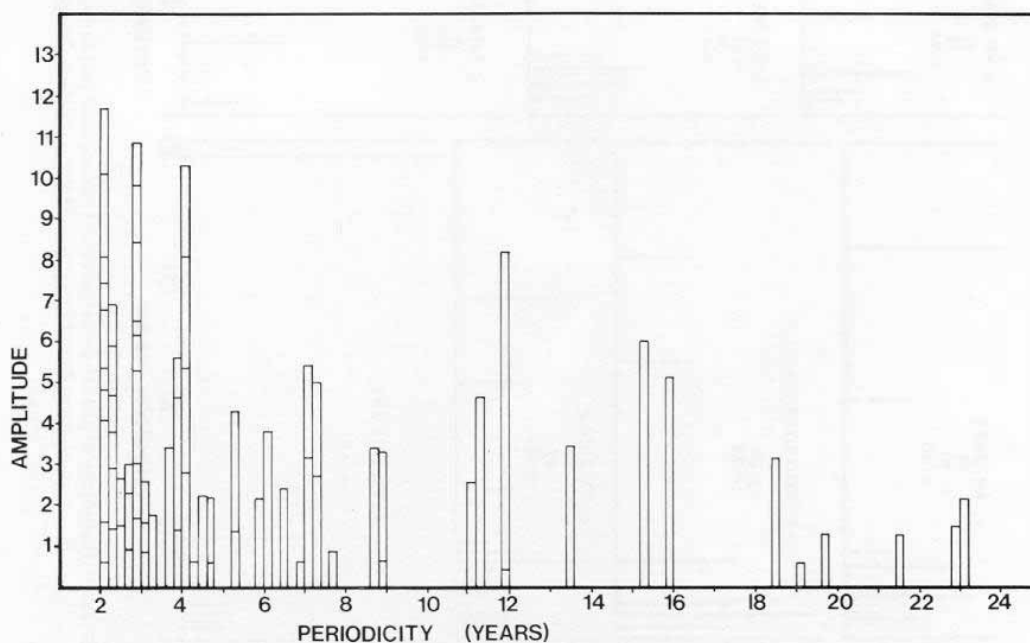
TEXT-FIG. 10. Compilation of periodicities and amplitudes for all trees. Each 'block' represents data from one tree.

solar cycle in Lithuanian pines. The effect of sunspots on climate probably relates to the increased short-wave radiation at sunspot maxima. This radiation causes reactions producing nitrogen oxide and ozone which increase the albedo of the atmosphere (Foukal 1980) but Kondratyev and Nikolsky (1970, 1979) suggested that the mechanisms are more complex.

In climatically sensitive trees like those growing on Alexander Island during the Early Cretaceous, an eleven-year periodicity of growth may be induced by sunspot-related climatic fluctuation. More data from a wide range of areas and time periods will be necessary in order to fully test this hypothesis.

A strong seven-year periodicity is present in at least five of the fossil trees (KG.1704.10, KG.1702.3 and 6, KG.2814.2, and KG.2817.16). This may relate to volcanic dust in the atmosphere after a major volcanic eruption (Chance and Kelly 1979). Volcanic activity in the nearby volcanic arc may have had an effect on climatically sensitive vegetation in the Alexander Island area. Although the destructive effects of ash clouds on forests immediately surrounding a volcano have been dramatically demonstrated by the recent eruption of Mount St. Helens (Fritz 1980b), the long-term effect on trees outside the area of destruction is not fully understood.

CONCLUSIONS

1. In the Early Cretaceous, conifer forests grew in Alexander Island. The characteristics of these forests (see 2–5) are apparently inconsistent with the approximate palaeolatitude (70° S) in most palaeogeographical reconstructions.

2. Silicification depended on rapid burial of trees in coarse volcaniclastic sediment and early release of silica during diagenesis. Flask-shaped bases and reaction-wood developed as a result of inundation by water and sediment influx.

3. Analysis of tree-rings indicates rapid growth rates, high climatic sensitivity, and seasonality of growth. These are characteristics of some trees growing in warm–temperate climatic regimes with long growing seasons.

4. The trees were closely spaced. If the angle of incidence of the sun's rays was the same as at similar latitudes today, this would further reduce the amount of available light (and therefore the length of the growing season) by shading.

5. Growth patterns show strong two-, three-, four-, seven-, and eleven-year periodicities. This suggests that the biologically induced high-frequency growth cycles found in living trees operated during the Early Cretaceous. It also implies the existence of external periodic controls on growth, such as sunspot activity and volcanic dust in the atmosphere.

6. The apparent inconsistencies between geophysical and palaeobotanical evidence are supported by the evidence from leaf floras from the same area (Jefferson 1981). There are four possible explanations for these inconsistences:

(a) It is possible that reconstructions of the local palaeogeography of Lesser Antarctica are incorrect. The Antarctic Peninsula may have been displaced to the north and situated west of South America (e.g. Harrison, Barrow, and Hay 1979), or its eastern margin may have been situated parallel to the Falkland Plateau (text-fig. 2). However, even in these unlikely cases the 110 ma palaeolatitudes are 60° and 66° S respectively.

(b) Today, no polar land areas are maintained at high temperatures during the polar night by the influence of globally high sea temperatures. Any sort of uniformitarian approach to palaeobotanical interpretation may, therefore, be incorrect; no vegetation adapted to such an environment exists today. The remarkable similarity of wood structure between the fossil trees and living trees, and considerations of functional morphology, suggest that this is unlikely.

(c) One or more of the basic assumptions inherent in any palaeogeographic reconstruction may be incorrect. Palaeomagnetic data fix continental positions relative to the magnetic pole and it is possible that over long periods of time this may not relate as perfectly to the geographic pole as present geomagnetic theory suggests.

(*d*) The earth's geographic poles are assumed to have been orientated at the same angle to its axis of rotation around the sun (23·5°) throughout geological time. Recent theories (e.g. Williams 1974) suggest that this may not be the case and that, during the Early Cretaceous, the angle was between ten and fifteen degrees. This would move the polar circles and all other climatic belts approximately ten degrees poleward in terms of photoperiod.

REFERENCES

ADAMENKO, V. N. 1963. On the similarity in the growth of trees in northern Scandinavia and in the polar Ural Mountains. *Jl Glaciol.* **4**, 449–451.

ANDERSEN, H. E. 1955. Climate in southeast Alaska in relation to tree growth. *Alaska Forest Research Center Station Paper*, No. 3. U.S. Forest Service, Juneau, Alaska.

ASH, S. R. 1970. *Pagiophyllum simpsoni*, a new conifer from the Chinle Formation (Upper Triassic) of Arizona. *Jl Paleont.* **44**, 945–952.

BARKER, P. F. and BURRELL, J. 1977. The opening of Drake Passage. *Mar. Geol.* **25**, 15–34.

——and GRIFFITHS, D. H. 1977. Towards a more certain reconstruction of Gondwanaland. *Phil. Trans. R. Soc. Lond.* **B**, **279**, 143–159.

BITVINSKAS, T. T. 1971. The relationship between solar activity, climate and the growth of tree stands. *In* GNEVYSHEV, M. M. and OL', A. I. (eds.). *Effects of Solar Activity on the Earth's Atmosphere and Biosphere*, 53–57. [Translated 1977. NTIS, Springfield, VA.]

BURROWS, C. J. and BURROWS, U. L. 1976. Procedures for the study of snow avalanche chronology using growth layers of woody plants. *INSTAAR Occas. Papers*, No. 243. University of Colorado.

CALDER, M. G. 1953. A coniferous petrified forest in Patagonia. *Bull Br. Mus. nat. Hist. (Geol.)*, **2**, 99–158.

CARRARA, P. E. 1979. The determination of snow avalanche frequency through tree ring analysis and historical records at Ophir Colorado. *Bull. geol. Soc. Am.* **90**, 773–780.

——and CARROLL, T. R. 1979. The determination of erosion rates from exposed tree roots in the Piceane basin, Colorado. *Earth Surf. Process.* **4**, 307–317.

CARROLL, R. L., BELT, E. S., DINELEY, D. L., BAIRD, D. and MCGREGOR, D. C. 1972. Vertebrate palaeontology of Eastern Canada. *Guidebook Excursion A59, 24th Int. Geol. Congr.* 1–113. Montreal.

CHALONER, W. G. and CREBER, G. T. 1973. Growth rings in fossil woods and evidence of past climates. *In* TARLING, D. H. and RUNCORN, S. K. (eds.). *Implications of continental drift to the earth sciences*, 425–437. Academic Press, London.

CHANCE, A. and KELLY, P. M. 1979. An apparent periodicity in an index of volcanic activity. *Nature, Lond.* **280**, 671–672.

COOK, E. R. and JACOBY, G. C. 1979. Evidence for quasi-periodic July drought in the Hudson Valley. *Ibid.* **282**, 390–392.

CÔTÉ, W. A., Jr. and DAY, A. C. 1965. Anatomy and ultrastructure of reaction wood. *In* CÔTÉ, W. A., Jr. (ed.). *Cellular Ultrastructure of Woody Plants*, 391–418. Syracuse University Press.

CREBER, G. T. 1972. Gymnospermous wood from the Kimmeridgian of East Sutherland and from the Sandringham Sands of Norfolk. *Palaeontology*, **15**, 655–661.

——1975. The effects of gravity and the earth's rotation on the growth of wood. *In* ROSENBURGH, G. D. and RUNCORN, S. K. (eds.). *Growth rhythms and history of the earth's rotation*, 75–87. Wiley, New York and London.

——1977. Tree-rings: a natural data storage system. *Biol. Rev.* **52**, 349–383.

DALZIEL, I. W. D. and ELLIOT, D. H. 1973. The Scotia Arc and Antarctic margin. *In* NAIRN, A. E. M. and STEHLI, F. G. (eds.). *The ocean basins and their margins*, 1. *The South Atlantic*, 171–245. Plenum Press, New York.

DeWITT, M. J. 1977. The evolution of the Scotia Arc as a key to the reconstruction of southwestern Gondwanaland. *Tectonophysics*, **37**, 53-81.

DORF, E. 1933. Pliocene floras of California. *Publs. Carnegie Instn*. No. 412. Washington.

——1964. The petrified forests of Yellowstone Park. *Scient. Am.* **210**, 107-114.

DOUGLASS, A. E. 1928. Climatic cycles and tree growth. *Publs. Carnegie Instn*. No. 289, vol. iii. Washington.

DREW, L. G. 1975. Tree-ring chronologies of Western America, VI. Western Canada and Mexico. *Chronology series I, Laboratory of Tree-Ring Studies*, University of Arizona, Tucson, Arizona.

DUNWIDDIE, P. W. and LaMARCHE, V. C., Jr. 1980. A climatically responsive tree-ring record from *Widdringtonia cedarbergensis*, Cape Province, South Africa. *Nature, Lond.* **286**, 796-797.

EDDY, B. J. 1976. The sun since the Bronze age: Physics of solar planetary environments. *In* WILLIAMS, D. J. (ed.). *Proc. Internat. Symp. on Solar Terr. Phys., Am. Geophys. Union*, 958-972.

ERLANDSSON, S. 1936. Dendrochronological studies. *Data. 23 fran Stockholms Hogsk. Geochron. Inst.* Stockholm.

EWART, A. J. and MASON-JONES, A. J. 1906. The formation of red wood in conifers. *Ann. Bot.* **20**, 201-203.

FARMAN, J. A. and HAMILTON, R. A. 1978. Measurements of radiation at the Argentine Islands and Halley Bay, 1963-72. *Scient. Rep. Br. Antarct. Surv.* No. 99.

FITZPATRICK, E. A. 1971. *Pedology*. Oliver & Boyd, Edinburgh.

FORD, E. D., ROBARDS, A. W. and PINEY, M. D. 1978. Influence of environmental factors on cell production and differentiation in the early wood of *Picea sitchensis*. *Ann. Bot.* **42**, 683-692.

FOUKAL, P. 1980. Does the Sun's luminosity vary? *Sky and Telescope*, **59**, 111-114.

FRITTS, H. C. 1976. *Tree-rings and climate*. Academic Press, London.

——and SCHATZ, D. J. 1975. Selecting and characterizing tree-ring chronologies for dendroclimatic analysis. *Tree-Ring Bull.* **35**, 31-40.

FRITZ, W. J. 1980a. Reinterpretation of the depositional environments of Yellowstone 'fossil forests'. *Geology*, **8**, 309-313.

——1980b. Stumps transported and deposited upright by the Mount St. Helens mudflows. Ibid. **8**, 586-588.

FURST, V. O. 1963. Vergleichende Untersuchungen über räumlich und zeitliche Unterschiede interannueller Jahrringbreitenschwankungen und ihre klimatologische Auswertung. *Flora*, **153**, 469-508.

GARFINKLE, H. L. and BRUBAKER, L. B. 1980. Modern climate-tree growth relationships and climate reconstruction in sub-arctic Alaska. *Nature, Lond.* **287**, 872-874.

GIDDINGS, J. L. 1943. Some climatic aspects of tree growth in Alaska. *Tree-Ring Bull.* **9**, 25-32.

GLOCK, W. S. 1951. Cambial frost injuries and multiple growth layers at Lubbuck, Texas. *Ecology*, **32**, 28-36.

——1955. Growth rings and climate. *Bot. Rev.* **21**, 73-188.

HARRISON, G. G. A., BARRON, E. J. and HAY, W. W. 1979. Mesozoic evolution of the Antarctic Peninsula and the southern Andes. *Geology*, **7**, 374-378.

JEFFERSON, T. H. 1981. Palaeobotanical contributions to the geology of Alexander Island, Antarctica. Unpublished Ph.D. thesis, University of Cambridge.

KELLOGG, K. S. 1980. Palaeomagnetic evidence for oroclinal bending of the southern Antarctic Peninsula. *Bull. geol. Soc. Am.* **91**, 414-420.

KOBAYASHI, T. 1942. On the climatic bearing of the Mesozoic floras of East Asia. *Jap. Jl Geol. Geogr.* **18**, 157-196.

KOERBER, T. W. and WICKMAN, B. E. 1970. Use of tree-ring measurements to evaluate impact of insect defoliation. *In* SMITH, J. G. H. and WORRAL, J. (eds.). *Tree-Ring Analysis with Special Reference to Northwest America. Univ. British Columbia Faculty of Forestry Bull.* No. 7, 101-106.

KONDRATYEV, K. YA. and NIKOLSKY, G. A. 1970. Solar radiation and solar activity. *Q. Jl R. Met. Soc.* **96**, 509.

——————1979. The stratospheric mechanics of solar and anthropogenic influences on climate. *In* MCCORMACK, B. M. and SELIGA, T. A. (eds.). *Solar-Terrestrial influences on climate*, 317-323. Reidel, Dordrecht.

KOSSOVICH, N. L. 1935. On the difference in structure of the north and south of conifer trunks. *Bot. Zh. SSSR*, **20**. [Russian with English summary.]

KRASILOV, V. A. (1972) 1975. *The Palaeoecology of Terrestrial Plants*. Vladivostok. [*In* Russian. Translation, 1975, Wiley, New York.]

KRAUSEL, R. 1949. Die Fossilen Koniferenhölzer, Teil II. *Palaeontographica*, **89 B**, 89-203.

LaMARCHE, V. C., Jr. In press. Sampling strategies in dendroclimatology. In *Climate from tree-rings*. Cambridge University Press, Cambridge.

——and FRITTS, H. C. 1972. Tree-rings and sunspot numbers. *Tree-ring Bull.* **32**, 19-33.

——HOLMES, R. L., DUNWIDDIE, P. W. and DREW, L. G. 1979. Tree ring chronologies of the southern hemisphere. 1. Argentina. 2. Chile. 3. New Zealand. 4. Australia. 5. South Africa. *Chronology series V, Laboratory of Tree-Ring Research*, University of Arizona. Tucson, Arizona.

LAMARCHE, V. C., Jr., and STOCKTON, C. W. 1974. Chronologies from temperature sensitive Bristlecone pines at the upper tree line in western U.S.A. *Tree-Ring Bull.* **34,** 21–45.
——and WALLACE, R. C. 1972. Evaluation of effects on trees of past movements on the San Andreas fault, Northern California. *Bull. geol. Soc. Am.* **82,** 2665–2676.

LARSON, P. R. 1956. Discontinuous growth rings in suppressed slash pine. *Trop. Woods,* **104,** 80–99.

MONIN, A. S. and VULIS, I. L. 1971. On the spectra of long period oscillation of geophysical parameters. *Tellus,* **23,** 337–345.

NEČESANÝ, V. 1958. Effect of β-indoleacetic acid on the formation of reaction wood. *Phyton,* **11,** 117–127.

ORDING, A. 1941. Årringanalyser på grøn og furu. *Meddr norske Skogforsøksves.,* No. 25.

OWEN, H. G. 1976. Continental displacement and expansion of the Earth during the Mesozoic and Cenozoic. *Phil. Trans. R. Soc. Lond.* A, **281,** 223–291.

PAGE, R. 1970. Dating episodes of faulting from tree-rings: Effect of the 1958 rupture of the Fairweather fault on tree-rings. *Bull. geol. Soc. Am.* **81,** 3085–3094.

POLGE, H. 1969. Further considerations about the X-ray and beta-ray methods for the determining wood density. *Jl Inst. Wood Science,* **4,** 39–44.

RILEY, D. and YOUNG, A. 1974. *World Vegetation.* Cambridge University Press, Cambridge.

ROBARDS, A. W. 1965. Tension wood and eccentric growth in crack willow (*Salix fragilis* L.). *Ann. Bot.* **29,** 419–431.

——1969. The effect of gravity on the formation of wood. *Sci. Prog. Oxf.* **57,** 513–532.

ROSS, G. H. 1975. Maximum Entropy Spectral Analysis. *Occas. Note Meteorol. Office,* No. 21, 75/2.

SCHOVE, D. J. 1978. Tree-ring and varve scales combined, c. 13500 B.C. to A.D. 1977. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **25,** 209–233.

SCHULMAN, E. 1956. *Dendroclimatic changes in semi-arid America.* University of Arizona Press, Tucson, Arizona.

SCHWARZBACH, M. 1963. *Climates of the Past.* Van Nostrand, New York.

SCHWEINGRUBER, V. F. H. 1979. Auswirkungen des Larchenwicklerbefalls auf die Jahrringstruktur der Larch. *Schweiz. Z. Forstwes.* **130,** 1071–1093.

SEWARD, A. C. 1919. *Fossil Plants,* vol. 4. Cambridge University Press, Cambridge.

SHABICA, L. W. 1979. Pennsylvanian sedimentation in Northern Illinois. *In* NITECKI, M. H. (ed.). *Mazon Creek Fossils,* 13–40. Academic Press, New York.

SIGAFOOS, R. S. 1964. Botanical evidence of floods and flood plain deposition. *Prof. Pap. U.S. geol. Surv.* **485A,** 1–35.

SIGLEO, A. C. 1979. Geochemistry of silicified wood and associated sediments, Petrified Forest National Park, Arizona. *Chem. Geol.* **26,** 151–163.

SINNOTT, E. W. 1952. Reaction wood and the regulation of tree form. *Am. Jl Bot.* **39,** 69–78.

SMIRNOFF, L. and CONNELLY, W. 1980. Axes of petrified tree stumps in growth position as possible indicators of paleosouth, Alaska Peninsula. *Geology,* **11,** 587–588.

SMITH, A. G., HURLEY, A. M. and BRIDEN, J. C. 1981. *Phanerozoic palaeocontinental world maps.* Cambridge University Press, Cambridge.

SPURR, S. H. and HYVARINEN, M. J. 1954. Compression wood in conifers as a morphogenetic phenomenon. *Bot. Rev.* **20,** 551–560.

STONE, E. C. and VASEY, R. B. 1968. Preservation of Coast Redwood on alluvial flats. *Science, N.Y.* **159,** 157–161.

STUIVER, M. and QUAY, D. D. 1980. Changes in atmospheric C14 attributed to a variable sun. Ibid. **207,** 11–181.

SUÁREZ, M. 1976. Plate tectonic model for the southern Antarctic peninsula and its relation to the southern Andes. *Geology,* **4,** 211–214.

TAYLOR, B. J., THOMSON, M. R. A. and WILLEY, L. E. 1979. The geology of the Ablation Point to Keystone Cliffs area, Alexander Island. *Br. Antarct. Surv. Scient. Rep.* No. 82.

TYRRELL, G. W. 1928. *The geology of Arran.* Mem. Geol. Surv., Edinburgh.

WILLIAMS, G. E. 1974. Discussion of late Precambrian glacial climate and the Earth's obliquity. *Q. Jl geol. Soc. Lond.* **130,** 599–601.

TIMOTHY H. JEFFERSON

The Ohio State University Institute of Polar Studies
103 Mendenhall
125 South Oval Mall
Columbus, Ohio 43210
USA