Aust. Met. Mag. 30 (1982) 169-173 551.583.7(99)

Antarctica: the vegetation of the past and its climatic implications*

Elizabeth M. Truswell, Bureau of Mineral Resources, Canberra

(Manuscript received August 1981)

On the geological time scale, it was normal for Antarctica to carry a vegetation cover of vascular plants: the present cold desert is an exception to that norm. For much of its history, the Antarctic vegetation differed little from that of contemporary lower latitudes, indicating less steep temperature gradients between equator and pole. The Late Palaeozoic glaciation (about 280 million years ago) profoundly modified but did not eliminate the vegetation, probably as a result of the accessibility of refuge sites. Mesozoic vegetation, dominated by ferns, conifers and cycads, suggests warm temperatures and high equability throughout. The cool-temperate beech forests which replaced this in the late Mesozoic and Tertiary persisted in moist coastal regions until at least 37 million years ago; chilling events at that time must have adversely affected their growth, but the timing of their final demise remains unclear.

Introduction

The idea that Antarctica supported a fairly luxuriant vegetation until quite recently has been current for more than a century. Charles Darwin, in *The Origin of Species,* wrote of 'a former warmer period, . . . when the Antarctic lands now covered by ice, supported a highly peculiar and isolated flora'. Darwin's assertion was then pure speculation, based only on the disjunct distributions of plant taxa which now live in South America, southern Africa, Australia and New Zealand. At the time he wrote there was no firm evidence for the ancient Antarctic flora.

These speculations long ago gave way to a more factual base of knowledge concerning the ancient Antarctic vegetation. Plant fossils were found as long ago as 1901 during the Swedish South Polar Expedition, when wood and leaves were found in strata on the Antarctic Peninsula; and there were extensive collections made during the expeditions of Scott and Mawson between 1910 and 1914. Since these early finds, knowledge of the past vegetation has increased enormously, but because of very limited rock outcrop, understanding of vegetation history remains hazy in comparison with other continents. Enough is known, however, to establish that, on a geologic time-scale, it was the normal situation for Antarctica to be vegetated; the present cold desert, from which vascular plants are virtually absent, is an exception to that norm. Further, the past vegetation of Antarctica was neither peculiar nor isolated as Darwin thought it must have been; in fact it closely resembled that of the other continents (Australia, Africa, South America, India) which, formerly united, made up the Gondwanaland landmass.

What conclusions can be drawn from these fossil plants relating to past climates? Palaeobotanists use divergent approaches when evaluating palaeoclimates. One approach involves the identification of the nearest living relatives of fossil plant taxa, the determination of the climatic tolerances of these in terms of moisture, mean annual temperature and range of temperatures, and the assignment of these parameters to the fossil locality (Dolph and Dilcher 1979). Contrasted with the 'nearest living relative' approach is one using the physical characters of plants to assign palaeoclimates. Leaf characters, i.e. size and the nature of the leaf margin (foliar physiognomy), are believed to be temperature dependent. Today, the highest proportion of large, smooth-edged leaves occurs in tropical rainforests; leaf size and the proportion of smooth-edged leaves decrease with decreasing temperature (Wolfe 1979). Both approaches have limitations. The 'nearest living relative' method becomes less dependable with increasing age of fossil floras; the foliar physiognomy method suffers uncertainties in the leaf form and climate correlation, and from the fact that fossil leaf accumulations may be sorted by sedimentary processes during deposition, and thus they present an incomplete or biased record of a contemporary flora.

Here, fossil floras of Antarctica, since the advent of land plants, are reviewed in chronological sequence beginning with the oldest. The nature of the fossil material whether it is leaves, wood, or dispersed pollen, is discussed. Using the methods outlined above, an attempt is made to assess the

*This paper is based on material presented to the Royal Meteorological Society (Australian Branch) Symposium on Antarctica: Weather and Climate, Melbourne, May 1981.

climates that supported these Antarctic floras. These discussions have been set, as far as possible, in the context of palaeolatitudes, since these have been the ultimate determinants of climate throughout geological time. It is notable, from the palaeogeographic maps presented in Figs 1 and 2, that Antarctica appears to have occupied a near-polar position throughout, a factor which in itself must have imposed certain stresses on plant growth in terms of temperature and available light.

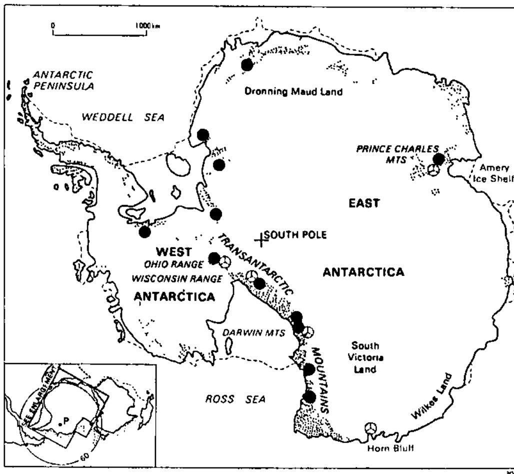
Palaeozoic vegetation: the impact of an early glaciation

The Devonian period (405-350 million years ago), on a global scale, saw the first widespread colonisation of land areas by vascular plants. Several sites in Antarctica have yielded plant remains of this age, from the Transantarctic Mountains to the coast of Marie Byrd Land. There are both megafossils — mainly stems of lycopods, the giant club mosses — and microfossils — assemblages of highly resistant reproductive spores. Lycopod trunks of late Devonian age in the Transantarctic Mountains show that the growth of woody trees had been achieved in these early phases of plant history in Antarctica, as elsewhere. The spore accumulations suggest that the floras were almost as diverse as those from contemporary low latitudes (McGregor 1979) and contain some species in common with those from palaeotropical regions; this seems to indicate that temperature gradients between equator and pole were then considerably less steep.

The next time interval represented in the record is the late Carboniferous through Permian (310-230 million years ago), an interval that encompassed the late Palaeozoic glaciation of Antarctica. Information on the composition of Antarctic floras through this time interval is available from a wide scatter of sites; in Fig. 1, sites yielding megafossils (leaves and wood) and microfossils (spores and pollen) are indicated. The oldest plant fossils of this age occur in moraine deposits in the Transantarctic Mountains where spores and pollen probably reflect a periglacial flora growing in the initial stages of glacial retreat (Kemp 1975). Apparently contemporaneous pollen suites occur in glacial rocks on other Gondwanaland continents. There is some evidence that this late Palaeozoic glaciation was not of sufficient magnitude to entirely destroy the pre-existing flora; according to the pollen record in Australia and South America a number of plant taxa persisted through the cold phase, probably in ice-free refugia, and expanded again in post-glacial habitats.

Pollen in the glacial rocks probably represent the earliest beginnings of the *Glossopteris* flora; the oldest megafossil remains occur in coal measures a short distance above. There, tongue-shaped leaves of

Fig. 1 Localities in Antarctica yielding Permo-Carboniferous plant fossils. Plant megafossil sites shown by solid circles; microfossil sites by Y marked circles. Inset shows Antarctica's relation to the rest of Gondwanaland in the Permian, and the approximate position of the south pole.

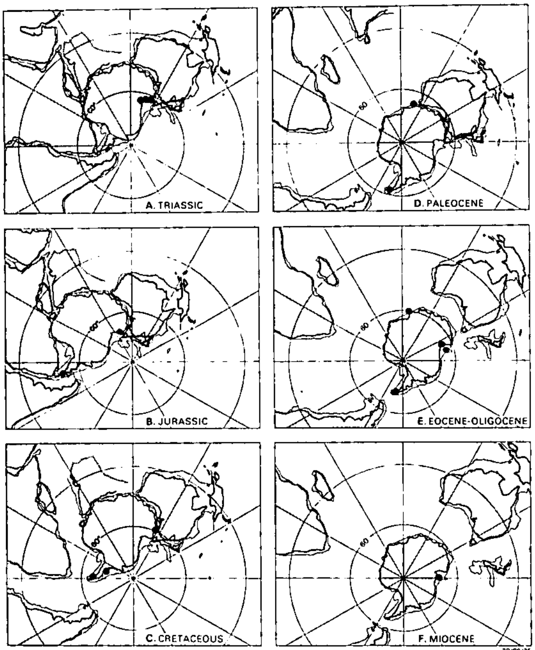


the seed-fern *Glossopteris* are most common, and woody roots of the same plant are also abundant. Fossil wood is abundant, and is of particular climatic interest in that all fragments display pronounced annual rings. This dendrological evidence for strongly seasonal growth is compatible with a high latitude position, but some aspects remain puzzling. Trees such as the Arctic Willow, which grow today just within the Arctic circle, produce very thin annual rings — usually of the order of a few millimetres — but those in the Permian Antarctic wood are up to a centimetre thick, from growth sites considerably closer to the contemporary pole. This anomaly so impressed the American palaeobotanist J. M. Schopf, who described these Antarctic floras, that he experienced great difficulty in believing Antarctica to be polar at the times the trees were growing (Schopf 1973). Further support for a strongly seasonal post-glacial Permian climate is provided by the apparent deciduousness of *Glossopteris*, evidenced by the accumulation of leaves in autumnal bank deposits. In Australia *Glossopteris* leaves have recently been found in the autumn and winter layers of varved sediments (Retallack 1980).

Mesozoic vegetation: plant growth in a prolonged phase of equability

Whether Antarctic floras of the Mesozoic Era (230-65 million years ago) had the same mechanisms for dormancy as *Glossopteris* is unclear. Information is scarce for this interval, and what exists has not been clearly correlated with climate; there are however sufficient data to suggest that the vegetation of Antarctica throughout this globally warm phase differed little from that of low latitudes.

Fig. 2 Palaeogeographic maps showing Antarctica's relation to other Gondwanaland continents and to palaeolatitudes through the Mesozoic and Tertiary. Palaeobotanical localities shown for each epoch include both plant megafossil and microfossil sites. The time intervals for which these reconstructions are drawn are, A, Triassic, 220 million years; B, Jurassic, 160 m.y.; C, Cretaceous, 100 m.y.; D, Paleocene, 60 m.y.; E, Eocene-Oligocene, drawn for the Late Eocene, 40 m.y.; F, Miocene, 20 m.y.



The *Glossopteris* flora was succeeded in the Triassic by assemblages dominated by leaves of the seed-fern *Dicroidium*; numerous sites in the Transantarctic Mountains record this transition (Fig. 2A). In the Jurassic, ferns, cycads and conifers predominate; the flora at Hope Bay on the Antarctic Peninsula is the best known example, but there are also floras from higher palaeolatitudes in Transantarctic Mountain sites (Fig. 2B). Cretaceous floras are poorly known — those from Alexander Island are currently being studied, and show the same fern-cycad-conifer composition as the Jurassic ones (Fig. 2C). Conifer wood from this locality shows pronounced rings, indicating substantial annual growth under seasonal conditions (T. H. Jefferson quoted in Hickey (1981)).

Little effort has yet been directed towards a palaeoclimatic analysis of the Mesozoic floras, but the ferns in them provide some data relevant to contemporary conditions, based on a broadly applied 'nearest living relative' approach. The fossil fern *Dictyophyllum*, for instance, which occurs at Hope Bay, grew in Jurassic times across a span of 50°-60° latitude on both sides of the equator (Barnard 1973): modern genera of the family Dipteridaceae, to which it belongs, grow today in highland Malaya under mean annual temperatures of 18°C and conditions of high equability. Direct application of these conditions to the Antarctic localities involves the assumption that plant tolerances have changed little in the past 170 million years, which is open to challenge.

Tertiary vegetation: the temperate beech forests and their demise

In the latest Mesozoic (90-80 million years ago), the flowering plants reached their present dominant position in the world vegetation. Interpretations of palaeoclimates for the essentially 'modern' floristic interval of the last 90 million years or so are therefore somewhat sounder than for earlier periods, although still only the broadest of figures can be obtained. In Antarctica, there is clear evidence of vegetation cover in coastal regions in the Paleocene and Eocene Epochs (65-37 million years ago; Figs 2D, E). After that, the record is confused by the nature of the fossil materials available, and there is no clear indication as to precisely when this vegetation disappeared. Isotopic and sedimentological records suggest that the icecap was fully fledged by about 12 million years ago; by how much the demise of the vegetation preceded that remains uncertain.

Knowledge of the early Tertiary vegetation is based on leaf and other megafossil remains from several relatively low-latitude sites in the Antarctic Peninsula, and from pollen accumulations in the Ross Sea and elsewhere. The leaves, from Seymour Island, Alexander Island and the South Shetland Islands, are dominated by *Nothofagus*, the southern beech, which grows today in southern South America, New Zealand, in isolated pockets in eastern Australia, and in the New Guinea and New Caledonian highlands. Leaf physiognomic analysis of fossils from the South Shetland Islands showed some 70 per cent of leaves to have non-entire margins (Barton 1964), which accords with a cool temperate forest, although the sample was too small to be definitive. As well as *Nothofagus*, the assemblages contain leaves of Proteaceae — the family that includes *Grevilleas* and *Banksias* — and of Winteraceae, a primitive family with a southern distribution. There are fruits of *Araucaria* and an abundance of ferns. The closest modern vegetation analogue is probably the lowland rainforest of southern Chile, between 37°S and 49°S which contains conifers of the families Araucariaceae and Podocarpaceae, as well as *Nothofagus*; the analogy between fossil and living vegetation, however, is not precise.

Modern *Nothofagus* comprises three species groups, identified by characters of the pollen. The *N. brassii* group is confined to the tropical parts of the geographic range; the *N. menziesii* and *N. fusca* types grow in the southern, cool temperate areas. Fossil pollen suites from Antarctica contain a mixture of all three forms, although the *fusca* group predominates. Most modern species require high and uniformly distributed rainfall; figures between 1500 and 1800 mm are necessary for *N. brassii*; some *N. fusca* species require much less, as typified by species in southern Chile and Patagonia, which survive on some 400 mm per year. These South American beech forests grow, albeit in stunted fashion, under mean summer temperatures of 8–10°C, and mean annual temperatures of about 5°C (McQueen 1976). Such temperatures could reasonably be extrapolated back to the early Tertiary of moist coastal Antarctica, before the last major cooling began.

In the Ross Sea area, at palaeolatitudes of around 70°S, the floral record is based on pollen evidence only. Boulders near McMurdo contain pollen again suggestive of a *Nothofagus*-dominated cool temperate forest (McIntyre and Wilson 1966), with subsidiary Podocarpaceae (southern conifers, including Huon Pine), Myrtaceae and Proteaceae. Nothing is known of the structure of this vegetation, whether it was closed forest with large trees, or merely stunted scrub. The boulders represent pre-glacial deposits, and are about 40–45 million years old. Further records of the same vegetation have been obtained from drill sites offshore in the Ross Sea. One site drilled north of the Ross Ice Shelf yielded pollen in sediments about 26 million years old (Oligocene); at this site pollen was recovered from sediments of glacial origin, that is, sediments deposited by melting out of debris from calving glaciers or floating bergs. The vegetation thus appears to have survived into the early stages of ice-sheet development (Kemp and Barrett 1975). At a second Ross Sea site, a hole drilled through the Ross Ice Shelf enabled the recovery of pollen from seafloor sediments thought at first to be 15 million years old — this dating has suggested persistence of the Antarctic land vegetation into the Miocene (Brady and Martin 1979). However, it has recently been established, using diatoms, that these pollen-bearing muds are in fact less than a million years old (Kellogg and Kellogg 1981). This type of glacial marine sediment is notorious for its content of recycled fossils, and the pollen recovered has apparently been eroded out from much older deposits by processes of glacial erosion and then redeposited into the younger sediments. This recycling process presents a major obstacle in interpreting Antarctic vegetation history, and makes it particularly difficult to determine precisely just when the final demise of this cool-temperate vegetation occurred.

Theoretical considerations reinforce the possibility that forest cover — or beech tundra, as it may have been — did not persist in Greater Antarctica much beyond the end of the Eocene, some 37 million years ago. The end of the Eocene was marked, globally, by a chilling event that was most evident in high latitudes. Oxygen isotopic data suggest that surface waters close to Antarctica fell to around 0°C at this time (Shackleton and Kennett 1975), a figure which probably represents an annual maximum. If this is accurate, then temperatures on the continent would have been even lower, and it would have been difficult to sustain forest growth for many generations beyond that point, although modern *Nothofagus* can withstand temperatures as low as −15°C (Sakai et al. in press).

Some unsolved problems

Problems in interpreting the palaeoclimates that supported the past floras of Antarctica arise from two factors: first, much fewer data are available than for any other continent; second, and more fundamental, is the problem that all interpretations of plant/climate relationships are based of necessity on the modern earth, and this provides a very inadequate model for deciphering the past. Understanding of plant physiology at high latitudes is based on modern temperature and day length interactions; growth there is restrained by rigorous winters and short cool summers. Physiologists have no concept of what growth forms or patterns might pertain if the winter months were relatively warm, as they must have been through much of the geological past when heat transfer from equatorial to polar regions was greater; hence interpretation of fossil growth forms lacks an accurate scale of reference. Problems in applying the modern plant/climate model to interpret high-latitude floras of the past have given rise to some radical explanations, such as the suggestion that the earth's spin axis was near-vertical prior to the late Eocene chilling event (Wolfe 1979). This explanation was invoked to explain leaves of apparent evergreen character in Tertiary deposits at 65°N. The difficulties of interpreting climates under which plants once grew are exacerbated by the inadequacies of the fossil record; dormancy, for instance, which is a 'behavioural' trait for survival in long periods of cold or darkness, rarely leaves a clear fossil imprint.

For the future, further drilling in near-shore areas of Antarctica may provide a clearer pollen record, one which details the decline of the last forest cover, if sequences which pass from pollen-rich pre-glacial rocks up into glacially deposited sediments can be found. And, there is an urgent need for re-examination of known collections of leaf and wood fossils from a physiognomic point of view — some collections made at the turn of this century have not been looked at since. But interpretation of climate-dependent characters in these fossils must be reinforced by experimental physiological work involving plant growth under conditions more closely resembling the now extinct climates that pertained in near-polar regions in non-glacial times.

Acknowledgments

Publication is by permission of the Director, Bureau of Mineral Resources.

References

Barnard, P. W. D. 1973. Mesozoic floras. In Hughes, N. F. ed., *Organisms and continents through time. Special papers in palaeontology, 12.* Palaeontological Association London, 175–87.

Barton, C. M. 1964. Significance of the Tertiary fossil floras of King George Island, South Shetland Islands. In Adie, R. J. ed., *Antarctic Geology.* North Holland, Amsterdam, 603–8.

Brady, H. T. and Martin, H. A. 1979. Ross Sea region in the Middle Miocene: a glimpse into the past. *Science 203, 4379,* 437–8.

Dolph, G. E. and Dilcher, D. L. 1979. Foliar physiognomy as an aid in determining paleoclimate. *Palaeontographica Abt. B, 170,* 151–72.

Hickey, L. J. 1981. Paleobotany. *Geotimes 26, (2),* 45–6.

Kellogg, T. B. and Kellogg, D. E. 1981. Pleistocene sediments beneath the Ross Ice Shelf. *Nature 293,* 130–3.

Kemp, E. M. 1975. The palynology of Late Palaeozoic glacial deposits of Gondwanaland. In Campbell, K. S. W. ed., *Gondwana Geology.* Australian National University Press, Canberra, 397–413.

Kemp, E. M. and Barrett, P. J. 1975. Antarctic glaciation and early Tertiary vegetation. *Nature, 258,* 507–8.

McGregor, D. C. 1979. Spores in Devonian stratigraphical correlation. *Special papers in palaeontology, 23,* 163–84.

McIntyre, D. J. and Wilson, G. J. 1966. Preliminary palynology of some Antarctic Tertiary erratics. *N.Z. Jl Bot., 4,* 315–21.

McQueen, D. R. 1976. The ecology of *Nothofagus* and associated vegetation in South America. *Tuatara 22,* 38–68.

Retallack, G. 1980. Late Carboniferous to Middle Triassic megafossil floras from the Sydney Basin. In Herbert, C. and Helby, R. eds, *A Guide to the Sydney Basin, Geological Survey of N.S.W., Bull. 26,* 384–430.

Sakai, A., Paton, D. M. and Wardle, P. (in press). Freezing resistance of trees of the south temperate zone, especially subalpine species of Australasia.

Schopf, J. M. 1973. Coal, climate and global tectonics. In Tarling, D. H. and Runcorn, S. K. eds, *Implications of continental drift to the earth sciences.* Academic Press, London and New York, 605–22.

Shackleton, N. J. and Kennett, J. P. 1975. Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analyses in DSDP sites 277, 279, 281. *Initial Reports of the Deep Sea Drilling Project 29,* U.S. Govt. Printing Office, Washington, 743–55.

Wolfe, J. A. 1979. A paleobotanical interpretation of Tertiary climates in the northern hemisphere. *Amer. Sci., 66,* 692–703.