

100 Million Years of Antarctic Climate Evolution: Evidence from Fossil Plants

J. E. Francis,¹ A. Ashworth,² D. J. Cantrill,³ J. A. Crame,⁴ J. Howe,¹ R. Stephens,¹ A.-M. Tosolini,¹ V. Thorn¹

ABSTRACT

The evolution of Antarctic climate from a Cretaceous greenhouse into the Neogene icehouse is captured within a rich record of fossil leaves, wood, pollen, and flowers from the Antarctic Peninsula and the Transantarctic Mountains. About 85 million years ago, during the mid-Late Cretaceous, flowering plants thrived in subtropical climates in Antarctica. Analysis of their leaves and flowers, many of which were ancestors of plants that live in the tropics today, indicates that summer temperatures averaged 20°C during this global thermal maximum. After the Paleocene (~60 Ma) warmth-loving plants gradually lost their place in the vegetation and were replaced by floras dominated by araucarian conifers (monkey puzzles) and the southern beech *Nothofagus*, which tolerated freezing winters. Plants hung on tenaciously in high latitudes, even after ice sheets covered the land, and during periods of interglacial warmth in the Neogene small dwarf plants survived in tundra-like conditions within 500 km of the South Pole.

INTRODUCTION

The Antarctic Paradox is that, despite the continent being the most inhospitable continent on Earth with its freezing

climate and 4-km-thick ice cap, some of the most common fossils preserved in its rock record are those of ancient plants. These fossils testify to a different world of globally warm and ice-free climates, where dense vegetation was able to survive very close to the poles. The fossil plants are an important source of information about terrestrial climates in high latitudes, the regions on Earth most sensitive to climate change.

Although plants of Permian and Triassic age provide a signal of terrestrial climates for the Transantarctic region for times beyond 100 million years (Taylor and Taylor, 1990), it is during the Cretaceous that the Antarctic continent reached the approximate position that it is in today over the South Pole (Lawver et al., 1992). Without the cover of ice Cretaceous vegetation flourished at high latitudes. Even when ice built up on the continent during the Cenozoic, fossil plants indicate that vegetation was still able to grow in relatively inhospitable conditions. The plant record thus provides us with a window into past climates of Antarctica, particularly during the critical transition from greenhouse to icehouse (Francis et al., forthcoming).

Reviews of the paleobotany that focus on floral evolution, rather than paleoclimate, can be found in the work of Askin (1992) and Cantrill and Poole (2002, 2005) and references therein. This paper is not intended to be an exhaustive review of all paleoclimate or paleobotanical studies but presents new information about Antarctic climate evolution deduced from some new and some selected published studies of fossil plants.

WARMTH IN THE CRETACEOUS GREENHOUSE

The most detailed record of Cretaceous terrestrial climates from plants comes from Alexander Island on the Antarctic

¹School of Earth and Environment, University of Leeds, UK.

²Department of Geosciences, North Dakota State University, Fargo, ND 58105-5517, USA.

³National Herbarium of Victoria, Royal Botanic Gardens Melbourne, Private Bag 2000, South Yarra, Victoria 3141, Australia.

⁴British Antarctic Survey, High Cross, Madingley Road, Cambridge, UK.

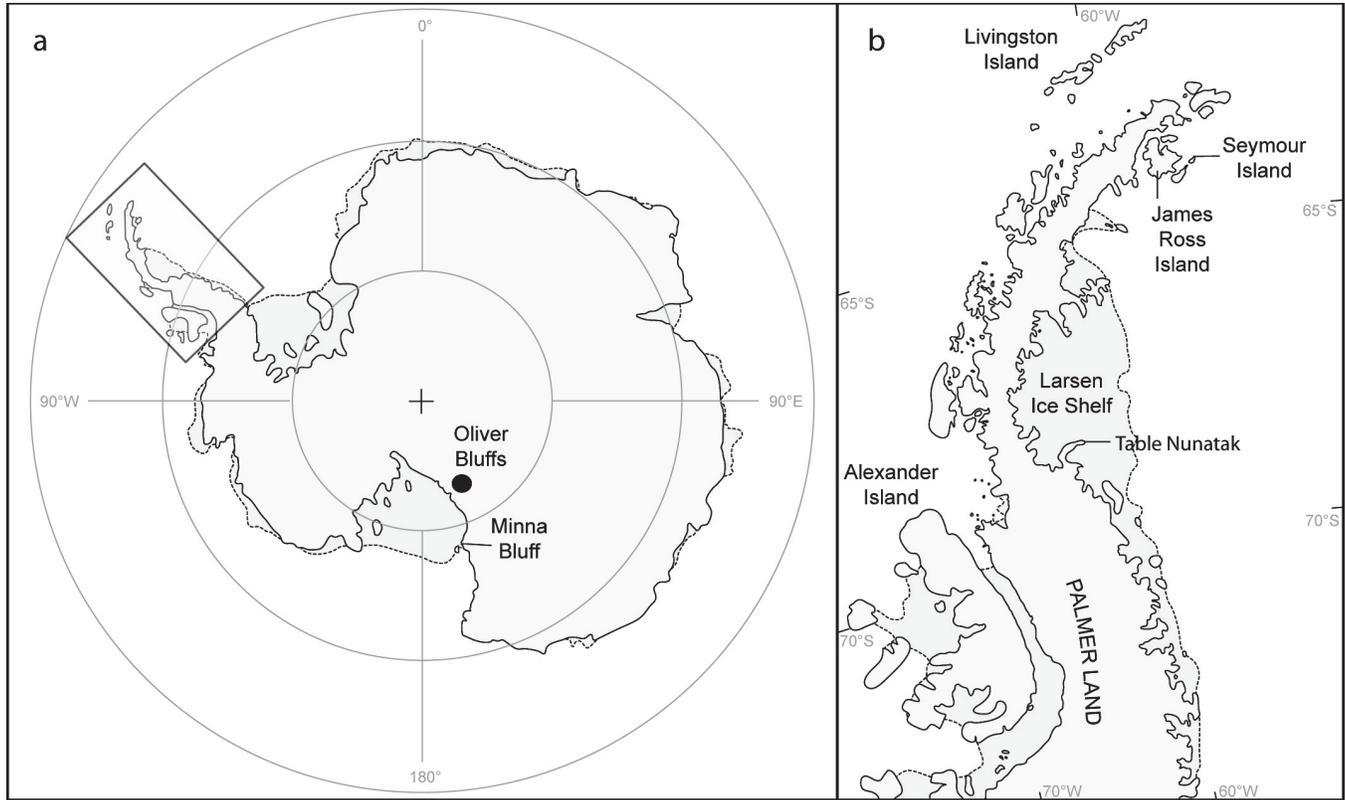


FIGURE 1 Map of Antarctica showing locations mentioned in the text.

Peninsula (Figure 1). Here the mid-Cretaceous (Albian) Fossil Bluff Group sediments include a series of marine, submarine fan, fluvial, and deltaic sediments formed as the infill of a subsiding fore-arc basin. Floodplains and midchannel bars of braided and meandering river systems (Triton Point Formation, Nichols and Cantrill, 2002) were extensively forested by large trees with a rich undergrowth.

Many of the plants are preserved in their original positions, having been encased by sheet flood and crevasse splay deposits during catastrophic flooding events. In addition, finely laminated flood deposits draped small plants, preserving them in place.

The *in situ* preservation of the plants has allowed detailed reconstructions of the forest environments by Howe (2003). Three vegetation assemblages were identified through statistical analysis of field data: (1) a conifer and fern assemblage with mature conifers of mainly araucarian type and an understory of *Sphenopteris* ferns; (2) a mixed conifer, fern, and cycad assemblage with araucarian conifers and ginkgo trees; and (3) a disturbance flora of liverworts, *Taeniopteris* shrubs, ferns, and angiosperms. Reconstructions of these assemblages and their depositional setting are presented in Figure 2.

An artist's reconstruction is presented in Figure 3. This

reconstruction portrays spacing of the large trees, such as ginkgos, podocarps, and araucarian conifers, as accurately as possible from field data. The undergrowth consists of ferns, cycadophytes, liverworts, mosses, and small shrubby angiosperms. The extinct plant *Taeniopteris* formed thickets in the disturbed clearings in the forest (Cantrill and Howe, 2001). The picture also shows the volcanoes on the adjacent arc that were the source of volcanoclastic sediment, much of which was deposited as catastrophic deposits that engulfed standing trees (in the distance in this picture).

Paleoclimatic interpretation using fossil plants on Alexander Island is based mainly on comparison with the ecological tolerances of similar living Southern Hemisphere taxa (Falcon-Lang et al., 2001). This indicates that the climate was generally warm and humid to allow the growth of large conifers, with mosses and ferns in the undergrowth. According to Nichols and Cantrill (2002), river flow is considered to have been perennial, based on sedimentary evidence, but with periodic floods indicative of high rainfall.

Evidence from fossil soils, however, provides a somewhat different climate story. The paleosols, in which trees are rooted, have structures such as blocky peds, clay cutans, and mottling that are typical of modern soils that form under seasonally dry climates (Howe and Francis, 2005). Although

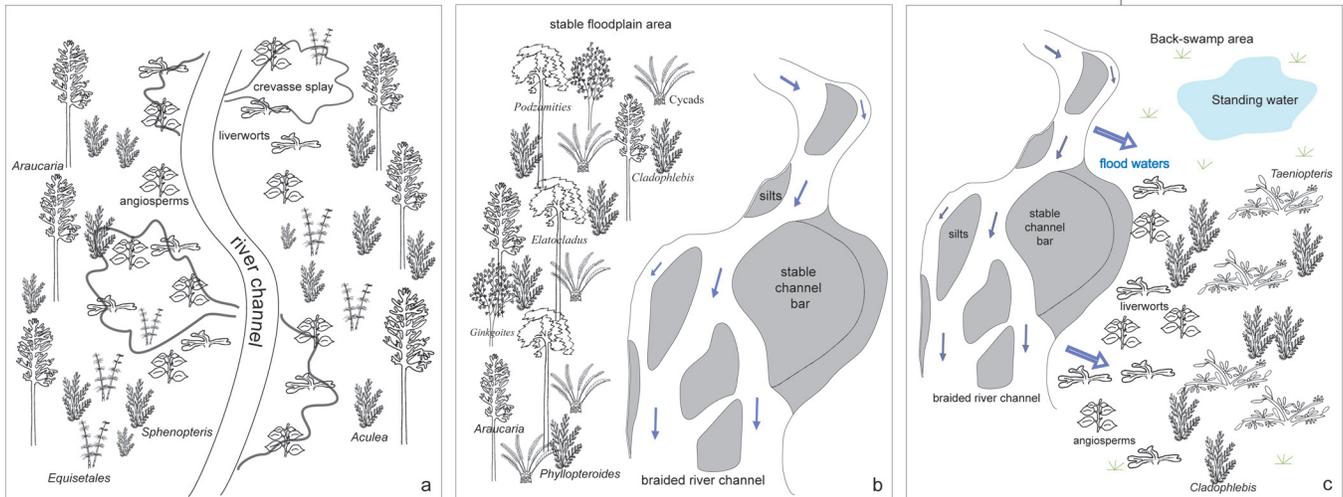


FIGURE 2 Reconstruction of paleoenvironment and community structure of (a) an open woodland community that grew on areas of the floodplain distal to a meandering river channel but subjected to frequent, low-energy floods; (b) a patch forest community of mature conifers and ferns, growing on floodplain areas affected by catastrophic floods; and (c) disturbance vegetation growing in back-swamp areas of a braided river floodplain, subjected to frequent low-energy flood events and ponding (Howe, 2003).

evidence of intermittent flooding is apparent from the fluvial sandstones and mudstones that volumetrically dominate the rock sequence, the paleosols indicate that this high-latitude mid-Cretaceous environment was predominantly seasonally dry. Whereas the flood sediments are likely to have been deposited relatively rapidly (days or weeks), the paleosols likely represent hundreds to thousands of years for soil development and forest growth, suggesting a predominantly dry climate for this high-latitude site.

Climate models for the mid-Cretaceous predicted warm, humid climates for this region. Valdes et al. (1996) predicted high summer temperatures of 20–24°C and low winter temperatures just above freezing. There is no evidence of freezing in the paleosols. However, it is likely that the more significant climate parameter that influenced the soils was rainfall and soil moisture. The models of Valdes et al. (1996) of seasonal mean surface soil moisture distribution (the balance between precipitation and evaporation) predict a seasonal moisture regime with dry conditions in summer but wet in winter, supporting the seasonal signature seen in the paleosols.

Younger Cretaceous strata preserved within the James Ross Island back-arc basin, and which crop out on James Ross, Seymour, and adjacent islands, contain a series of fossil floras that are providing new information about biodiversity and climate. During the Late Cretaceous angiosperms (flowering plants) became an important component of the vegetation. The Coniacian Hidden Lake Formation (Gustav Group) and the Santonian-early Campanian Santa Marta Formation (Marambio Group) in particular contain fossil angiosperm leaves that have yielded information about

paleoclimate. The leaves represent the remains of vegetation that grew at approximately 65°S on the emergent volcanic arc that is now represented by the Antarctic Peninsula. They were subsequently transported and buried in marine sediments in the adjacent back-arc basin, and are now preserved as impressions and compressions in volcanoclastic siltstones and carbonate concretions (Hayes et al., 2006).

The angiosperm leaf morphotypes have been tentatively compared with those of living families such as Sterculiaceae, Lauraceae, Winteraceae, Cunoniaceae, and Myrtaceae (Hayes et al., 2006) (Figure 4). Most of these families today can be found in warm temperate or subtropical zones of the Southern Hemisphere. Sterculiaceae is a tropical and subtropical family found in Australia, South Asia, Africa, and northern South and Central America. The Laurales today live in tropical or warm temperate regions with a moist equable climate. Both the Cunoniaceae and Elaeocarpaceae are tropical and subtropical trees and shrubs found in equatorial tropical regions, and the Winteraceae are concentrated in wet tropical montane to cool temperate rainforests of the southwest Pacific and South America.

A more quantitative analysis of the leaves based on physiognomic aspects of the leaves, using leaf margin analysis and simple and multiple linear regression models, provided data on paleotemperatures and precipitation. Estimates of mean annual temperatures (MATs) range from 15.2 (±2) to 18.6 (±1.9)°C for the Coniacian, and 17.1 (±2)°C to 21.2 (±1.9)°C for the late Coniacian-early Santonian. Averaging all data from all methods gives a MAT for the Coniacian of 16.9°C and 19.1°C for the late Coniacian-early Santonian (Hayes et al., 2006). Estimates of annual precipitation range

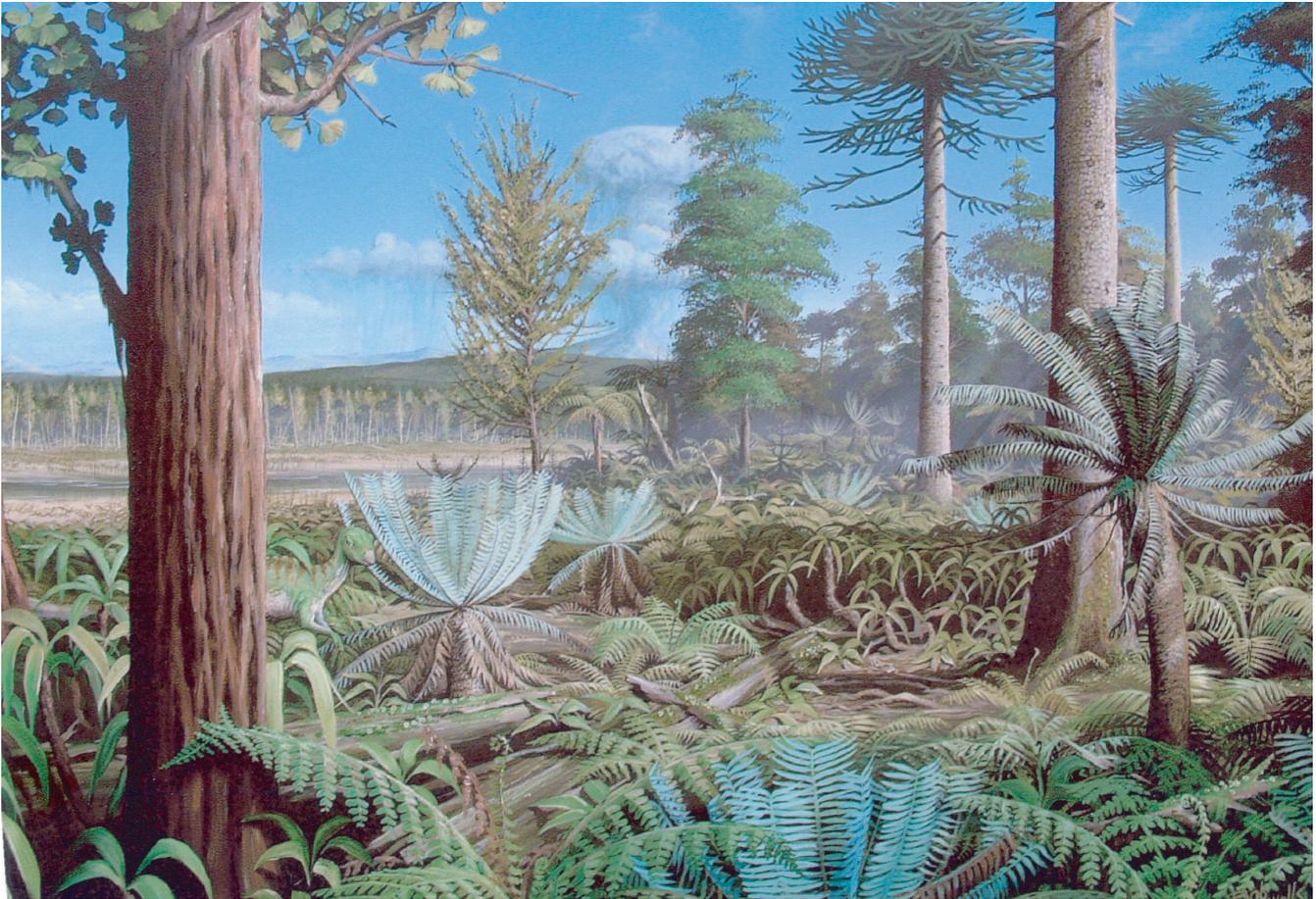


FIGURE 3 Reconstruction of the forest environment on Alexander Island during the Cretaceous, based on the work of Howe (2003) and British Antarctic Survey geologists (see text and references).

SOURCE: Image is a painting by Robert Nicholls of Paleocreations.com, and is housed at the British Antarctic Survey.

from 594 to 2142 (± 580) mm for the Coniacian and 673 to 1991 (± 580) mm, for the late Coniacian-early Santonian, with very high rainfalls of 2630 (± 482) and 2450 (± 482) mm for the growing seasons, respectively, comparable with those of equatorial tropical rainforests today. However, these data must be considered with caution as some important aspects of leaf morphology related to rainfall are not preserved in the fossil assemblage.

These fossil plants are thus indicative of tropical and subtropical climates at high paleolatitudes during the mid-Late Cretaceous, without extended periods of winter temperatures below freezing and with adequate moisture for growth. In other Antarctic paleoclimate studies evidence for strong warmth at this time was found by Dingle and Lavelle (1998) in their analyses of clay minerals and from analysis of fossil woods (Poole et al., 2005). This warm peak may have also been the trigger for the expansion of the angiosperms in the Antarctic, represented by a marked increased abundance of angiosperm pollen in Turonian sediments (Keating et al., 1992). On a global scale this corresponds to the Cretaceous thermal maximum, from about 100-80 Ma, reported from

many sites (e.g., Clark and Jenkyns, 1999; Huber et al., 2002), and possibly attributed to rising atmospheric CO_2 levels due to a tectonically driven oceanographic event in the opening of the equatorial Atlantic gateway (Poulsen et al., 2003).

The high levels of Cretaceous climate warmth are also recorded in an unusual assemblage of late Santonian fossil plants from Table Nunatak on the east side of the Antarctic Peninsula. A small isolated outcrop has yielded layers of charcoal, produced by wildfires, within a sequence of sandstones, siltstones, and mudstones, deposited in shallow marine conditions at the mouth of an estuary or in a delta distributary channel. The charcoal layer contains the remains of burnt plants, including megaspores; fern rachids; conifer leaves, wood, shoots, seeds and pollen cones; angiosperms leaves, fruits and seeds (Eklund et al., 2004).

The most unusual of these fossils are tiny fossil flowers, the oldest recorded from Antarctica. Eklund (2003) identified several types of angiosperm flowers, some of which are most likely related to the living families Siparunaceae, Wintera-

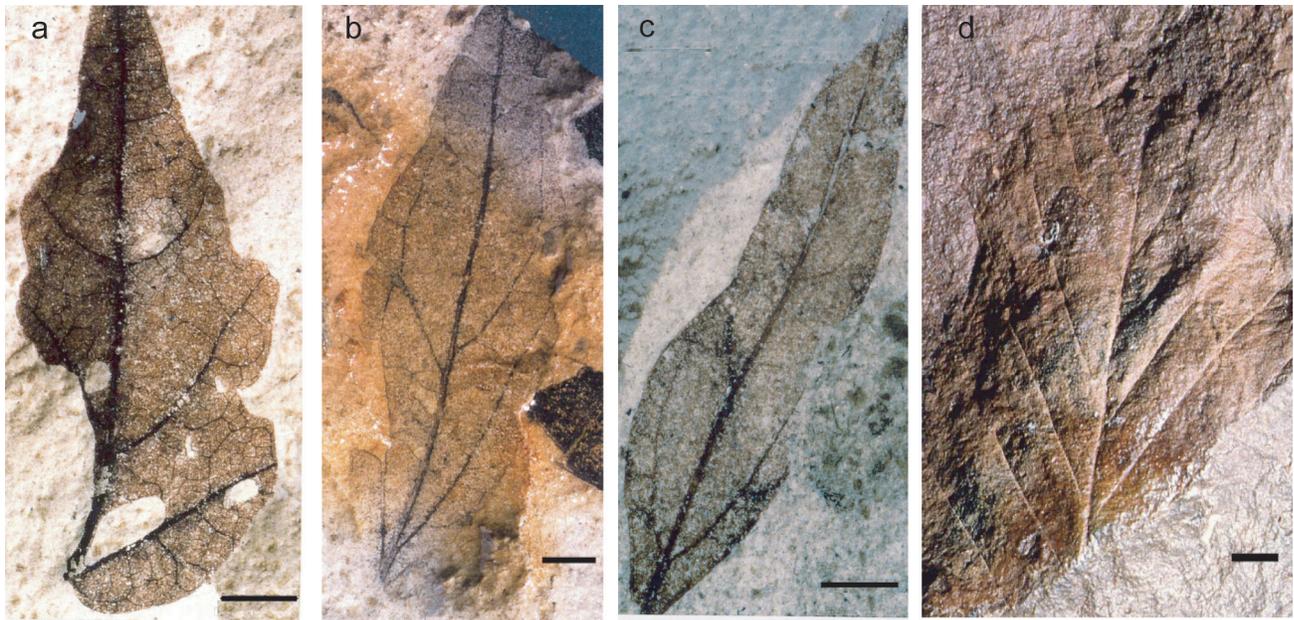


FIGURE 4 A selection of fossil leaves from the Hidden Lake Formation: (a) D.8754.1a, Morphotype 2 (Sterculiaceae); (b) D.8754.8.54a, Morphotype 11 (Laurales); (c) D.8754.8.57a, Morphotype 11 (Laurales); (d) D.8621.27a, Morphotype 10 (unknown affinity). Botanical names in parentheses refer to most similar modern family (Hayes et al., 2006). Scale bar 5 mm for all leaves. Numbers refer to the British Antarctic Survey numbering system.

ceae, and Myrtaceae, as well as several unidentified types. The Siparunaceae family is now confined to the tropics, and the Winteraceae (e.g., mountain pepper tree) and Myrtaceae (e.g., eucalypts) are warm-cool temperate types from the Southern Hemisphere. Interestingly, the *Siparuna*-like fossil flowers have a flat-roofed structure with a central pore, which in the living plants acts as a landing platform for gall midges that lay their eggs inside the flower head. Since the developing gall midge larvae usually destroy the flowers as they grow (Eklund, 2003), the preservation of such flowers as fossils would normally be extremely unlikely. The fortuitous occurrence of wildfires during the Cretaceous has thus helped preserve such flowers as rare fossils.

FROM GREENHOUSE TO ICEHOUSE

After the peak warmth of the mid-Late Cretaceous, climate appears to have cooled globally during the latest part of the Cretaceous, as seen also in the Antarctic fossil wood record (Francis and Poole, 2002; Poole et al., 2005). However, warm climates returned to the high latitudes during the Paleocene and early Eocene, as is reflected in fossil plants.

The Paleogene sedimentary sequence on Seymour Island (Figure 1) contains plant-rich horizons that hold signals to ancient climates. An unusual new flora from La Meseta Formation has been studied by Stephens (2008). The flora is dominated by permineralized branches of conifers and compressions of angiosperm leaves, and found within car-

bonate concretions within the shallow marine Campamento allomember of Marensi et al. (1998) (equivalent to Telm 3 of Sadler [1988]). This unit has been dated as 51.5–49.5 Ma through links with global eustatic lowstands (Marensi, 2006) and by Sr dating by Stephens, which yielded a latest early Eocene (late Ypresian) age.

The flora is unusual in that it is dominated by leaves, cone scales, and leafy branches of araucarian conifers, very similar in all respects to living *Araucaria araucana* (monkey puzzle) from Chile. Study of three-dimensional arrangement of leaves using the technique of neutron tomography illustrates that leaf and branch arrangement is characteristic of living *Araucaria araucana* (Figure 5). A limited array of angiosperm leaves are preserved in the nodules and include morphotypes that are similar to leaves of living Lauraceae, Myricaceae, Myrtaceae, and Proteaceae. It is notable that many of the fossil leaves appear to have particularly thick carbonaceous compressions and, indeed, the living equivalents are evergreen Southern Hemisphere trees that have thick waxy cuticles. This may signal taphonomic sorting of some kind rather than a climate signal, as the more fragile leaves, including *Nothofagus*, are unusually absent from this flora. Climate interpretation of this flora, based on the nearest living types, especially the araucarian conifers, suggests that the latest Eocene climate was cool and moist. Oxygen isotope analyses of marine molluscs in the same concretions yielded cool marine paleotemperatures of 8.3–12.5°C, comparable to other estimates for Telm 3 from marine oxygen isotopes

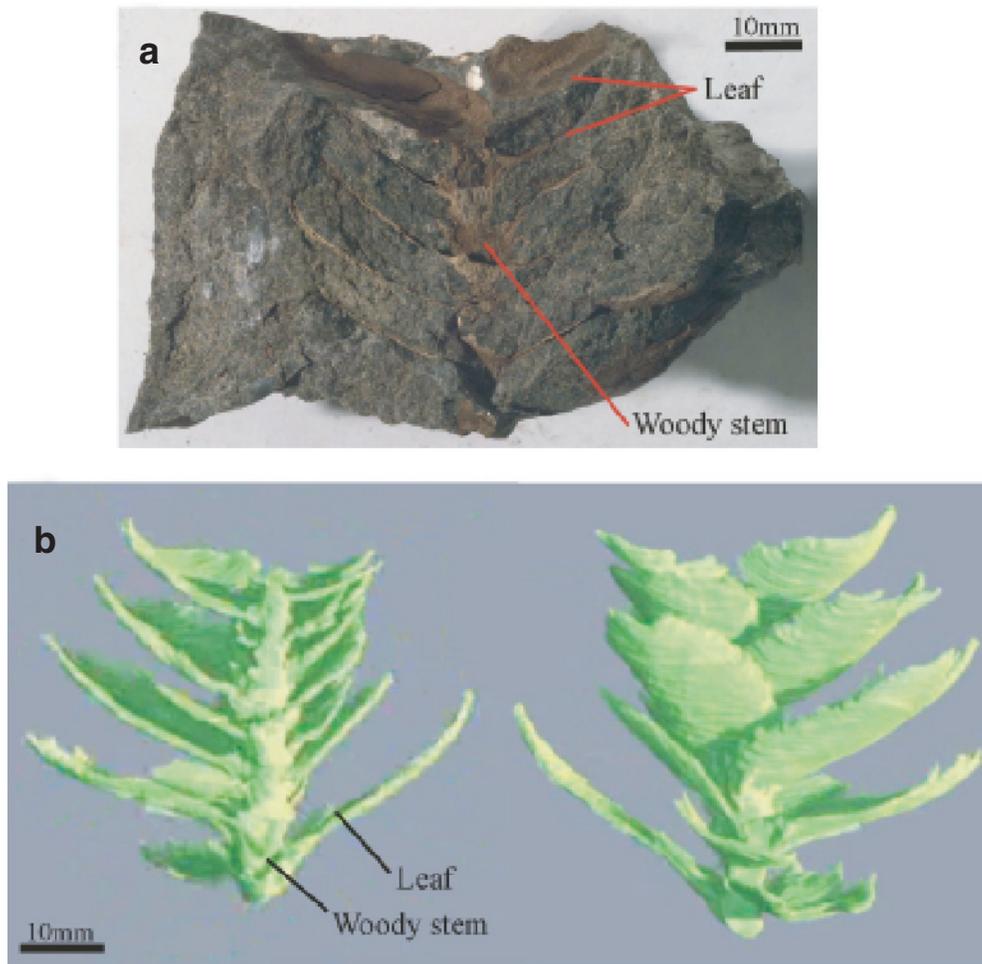


FIGURE 5 Image of three-dimensional leafy branch of fossil araucarian conifer from La Meseta Formation, Seymour Island (sample DJ.1103.189). (a) The branch as it appears in hand specimen. (b) Reconstruction from tomographic image showing the leafy branch in three dimensions. Neutron tomography to create the figure was undertaken at the Institut Laue Langevin facility, Grenoble, France.

of 8-13.2°C (Pirrie et al., 1998) and 10.5-19.6°C (Dutton et al., 2002).

New paleoclimate data have also been derived from new collections of fossil angiosperm leaves from the Nordenskjöld flora in the Cross Valley Formation of Late Paleocene age (Elliot and Trautman, 1982) and from the Middle Eocene Cucullaea 1 flora (Telm 5 of Sadler [1988], Cucullaea 1 allomember of Marenssi et al. [1998], dated as 47-44 Ma by Dutton et al. [2002]). In the Late Paleocene flora 36 angiosperm leaf morphotypes were identified, along with two pteridophytes (ferns), and podocarp and araucarian conifers. The angiosperm leaf component is dominated by types with possibly modern affinities to the Nothofagaceae, Lauraceae, and Proteaceae, along with other types, such as Myrtaceae, Elaeocarpaceae, Winteraceae, Moraceae, Cunoniaceae, and Monimiaceae, some of which have no identifiable modern affinities as yet. The fossil assemblage contains a mix of

families of subtropical and cool-temperate nature and represents cool-warm temperate mixed conifer-broad-leaved evergreen and deciduous forest, dominated by large trees of *Nothofagus* (southern beech) and araucarian and podocarp conifers, with other angiosperms as mid-canopy trees and understory shrubs. In comparison the Middle Eocene flora shows a 47 percent decrease in diversity with only 19 leaf morphotypes. The flora is dominated by *Nothofagus*, most similar to modern cool-temperate types, and has much rarer subtropical and warm-temperate types, such as Proteaceae. The decline in diversity indicates a substantial cooling of climate over this interval.

Paleoclimate data were derived using CLAMP (Climate Leaf Analysis Multivariate Program) (Wolfe and Spicer, 1999) and several leaf margin analysis techniques based on physiognomic properties of the leaves. CLAMP results are given below. A MAT of $13.5 \pm 0.7^\circ\text{C}$ was determined for the

Late Paleocene. A strongly seasonal climate was implied, with a warm month mean of $25.7 \pm 2.7^\circ\text{C}$ and a cold month mean of $2.2 \pm 2.7^\circ\text{C}$, with 2110 mm annual rainfall. By the Middle Eocene the climate had cooled considerably; the MAT was $10.8 \pm 1.1^\circ\text{C}$ with a warm month mean of $24 \pm 2.7^\circ\text{C}$, and a cold month mean of $-1.17 \pm 2.7^\circ\text{C}$, with 1534 mm annual rainfall. This suggests that the climate was still markedly seasonal but that winter temperatures were often below freezing.

The Late Paleocene floras thus represent warm Antarctic climates probably without ice, even in winter. However, Seymour Island floras suggest that by the Middle Eocene (47-44 Ma) climates had cooled considerably and ice may have been present on the Antarctic continent, at least during winter months. Several Eocene macrofloras dominated by *Nothofagus* from King George Island, South Shetland Islands, suggest mean annual temperatures of about 10-11°C (seasonality unknown) (e.g., Birkenmajer and Zastawniak, 1989; Hunt and Poole, 2003), and the highest latitude Eocene floras, from Minna Bluff in the McMurdo Sound region, are suggestive of cool temperate climates (Francis, 2000). Other geological evidence also points to significant cooling by the latter part of the Eocene; fluctuating volumes of ice on Antarctica from about 42 Ma have been implied by Tripathi et al. (2005) from isotope measurements of marine sediments and, from the Antarctic region, Birkenmajer et al. (2005) proposed a glacial period from 45-41 Ma, based on valley-type tillites of Eocene-Oligocene age from King

George Island. Ivany et al. (2006) have also reported the glacial deposits of possible latest Eocene or earliest Oligocene age from Seymour Island.

PLANTS IN THE FREEZER

Despite the onset of glaciation and the growth of ice sheets on Antarctica during the latest Eocene or earliest Oligocene, vegetation was not instantly wiped out but clung on tenaciously in hostile environments. Even though many warmth-loving plant taxa disappeared during the mid-Eocene, floras dominated by *Nothofagus* remained for many millions of years. Single leaves of *Nothofagus* of Oligocene and Miocene age have been found in CRP-3 and CIROS-1 drill cores, respectively (Hill, 1989; Cantrill, 2001), but one of the most remarkable Antarctic floras is preserved within glacial diamictites of the Meyer Desert Formation, Sirius Group, at Oliver Bluffs (85°S) in the Transantarctic Mountains.

In a meter-thick layer of sandstone, siltstone, and mudstone sandwiched between tillites, small twigs of fossil *Nothofagus* wood are preserved entwined around cobbles (Figure 6). The twigs are the branches and rootlets of small dwarf shrubs preserved within their positions of growth. Fossil leaf mats of *Nothofagus* leaves (*Nothofagus beardmorensis*) (Hill et al., 1996) are also preserved in the same horizon. Several other fossil plants have also been recovered, including moss cushions, liverworts, and fruits, stems, and seeds of several

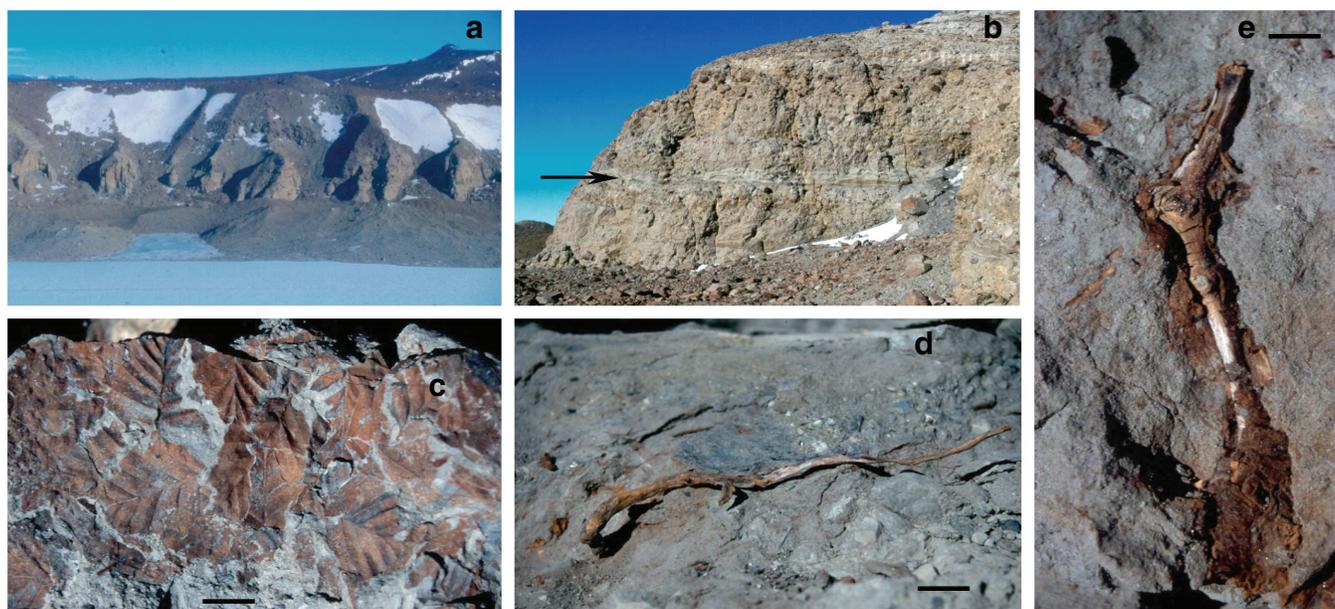


FIGURE 6 Sirius Group sediments and fossil plants, Oliver Bluffs, Transantarctic Mountains. (a) General view of Oliver Bluffs. (b) View of bluff composed of glacial diamictites. Arrow points to meter-thick horizon of glacial sandstone, equivalent to plant-bearing horizon. (c) *Nothofagus* leaves from upper part of plant-bearing horizon. (d) Small branch of fossil wood in growth position within paleosol horizon. (e) Small branch in situ in paleosol horizon, with delicate bark still attached. Scale bars represent 1 cm.

vascular plants, as well as remains of beetles, a gastropod, bivalves, a fish, and a fly (Ashworth and Cantrill, 2004).

All the evidence for paleoclimate from these remarkable fossils (Ashworth and Cantrill, 2004), from growth rings in the twigs (Francis and Hill, 1996), and from paleosols (Retallack et al., 2001) points toward a tundra environment with a mean annual temperature of about -12°C , with short summers up to $+5^{\circ}\text{C}$ but with long cold winters below freezing. Dated as Pliocene in age but disputed (see Ashworth and Cantrill, 2004), this periglacial or interglacial environment existed at a time when glaciers retreated briefly from the Oliver Buffs region, allowing dwarf shrubs to colonize the exposed tundra surface only about 500 km from the South Pole.

As Antarctica's climate cooled further into the Pleistocene deep-freeze, vascular plants were lost from the continent. However, its rich fossil plant record retains its legacy of past warmth.

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