

Palaeoclimate analysis of Late Cretaceous angiosperm leaf floras, James Ross Island, Antarctica

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Abstract: The fossilized remains of Cretaceous angiosperm leaves are preserved within sandstones and siltstones of the Coniacian Hidden Lake Formation (Gustav Group) and the Santonian–early Campanian Santa Marta Formation (Marambio Group) in the James Ross Basin, Antarctic Peninsula region. The leaves represent the remains of vegetation that grew at approximately 65°S on an emergent volcanic arc, now represented by the Antarctic Peninsula, and were subsequently transported and buried in marine sediments in the adjacent back-arc basin. Some of the angiosperm leaf morphotypes show similarities to leaves of living families such as Sterculiaceae, Lauraceae, Winteraceae, Cunoniaceae and Myrtaceae. Palaeoclimate analysis based on physiognomic aspects of the leaves, such as leaf-margin analysis, indicates that the mean annual temperatures for the Hidden Lake and Santa Marta formations were 13–21 °C (mean 17 °C) and 15–23 °C (mean 19 °C), respectively. The fossil plants are indicative of warm climates without extended periods of winter temperatures below freezing and with adequate moisture for growth. This period of Cretaceous warmth in Antarctica corresponds with the Cretaceous thermal maximum, an interval of peak global warmth from the Turonian to the early Campanian.

Vegetation was able to thrive on the Antarctic continent during the Cretaceous, even though it was situated at palaeolatitudes above 60°S, because the Cretaceous greenhouse climate system provided the polar regions with annual warmth (Skelton *et al.* 2003). Studies of the fossilized remains of this vegetation, preserved as leaves, petrified wood, pollen and spores, and reproductive organs (e.g. Askin 1989; Césari *et al.* 2001; Cantrill & Poole 2002; Eklund *et al.* 2004; Poole & Cantrill 2006), are now providing details of the composition and biodiversity of these floras. In addition, the plant fossils contain a record of past climatic conditions that provide clues to the nature of high-latitude Cretaceous climates in the southern polar regions (e.g. Francis & Poole 2002; Howe & Francis 2005; Poole *et al.* 2005). Angiosperm leaf fossils are an important part of the Antarctic fossil record from the mid-Cretaceous onwards. They are particularly valuable because they can provide an indication of past

climate, both through Nearest Living Relative (NLR) comparisons and through statistical analyses that are based on the relationship of climate to physiognomic characters of the leaves.

The earliest occurrence of dicotyledonous angiosperm leaf fossils in Antarctica is of late Albian leaves from Alexander Island on the western side of the Antarctic Peninsula (Cantrill & Nichols 1996). From the James Ross Basin, to the east of the Antarctic Peninsula, the oldest known angiosperm leaf fossils are of Coniacian and Santonian age. This particular interval appears to be within a period of peak warming in high latitudes (Huber 1998), so these plant fossils may provide clues about the warmest climates and potentially the most diverse high-latitude floras in the Cretaceous greenhouse. The aim of this paper is to present new information about Late Cretaceous palaeoclimates at high latitudes deduced from two new angiosperm leaf floras.

Geological setting

The fossil leaves are preserved within proximal marine sediments in the James Ross Basin, part of the larger Larsen Basin (Macdonald & Butterworth 1990; del Valle *et al.* 1992; Hathway 2000). This basin contains more than 6 km of sediments that were deposited in a back-arc setting during Late Jurassic–Cenozoic times. The basin formed on the eastern side of an emergent volcanic arc that was constructed during subduction of the Pacific Ocean crust beneath Gondwana. This emergent arc (the eroded roots of which now form the Antarctic Peninsula, Fig. 1) is the likely location of the forests that yielded the fossil plant material (Francis 1986; Hathway 2000).

The basin infill consists of siltstones, sandstones and conglomerates that were deposited in progressively shallowing conditions in proximal submarine-fan and slope-apron settings, shelf settings and deltaic environments (Elliot 1988; Ineson 1989). The succession is divided into three main units: the Gustav Group (Aptian–Coniacian); the Marambio Group (late Coniacian–Palaeocene); and the Seymour Island Group (Palaeocene–latest Eocene/earliest Oligocene) (Pirrie *et al.* 1991; Riding *et al.* 1998; McArthur *et al.* 2000). The palaeolatitude of this region was approximately 65°S during the Cretaceous (Lawver *et al.* 1992).

The oldest flora in this study, the Hidden Lake flora, is preserved within the Hidden Lake

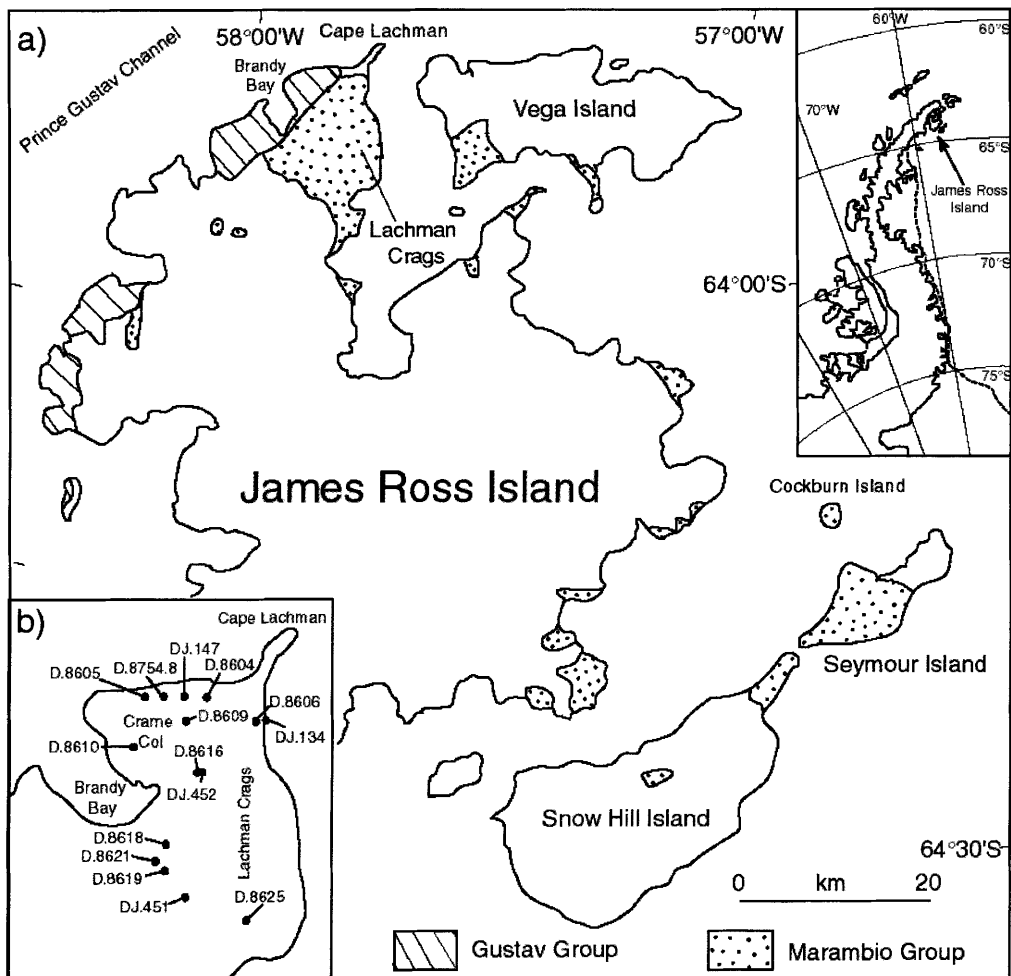


Fig. 1. (a) Location map showing the position of the James Ross Island to the east of the Antarctic Peninsula and location of the main geological groups from which the fossil leaves were recovered. (b) The leaves come from various localities in the NW part of James Ross Island; numbers indicate location of samples.

Formation of the Gustav Group. This formation consists of 300–400 m of coarse-grained volcanoclastic conglomerates, sandstones and mudstones, representing base-of-slope, fan-delta and basin-floor environments of deposition in a relatively deep marine environment below wave base (Ineson *et al.* 1986; Pirrie *et al.* 1991; Whitham *et al.* 2006). Macrofaunal and palynological studies suggested a probable age range of Coniacian–Santonian, but Sr isotope data confirm an entirely Coniacian age (88.7–86.4 Ma) for this formation (McArthur *et al.* 2000; Riding & Crame 2002). Petrographical studies have shown that the primarily volcanoclastic sediment source was nearby (Pirrie 1991). The fossil leaves in this formation therefore most probably originated on the volcanic arc and were washed only a short distance into the marine basin.

The younger flora in this study is the Santa Marta flora from the Santa Marta Formation of the Marambio Group. This formation conformably overlies the Hidden Lake Formation and is exposed on NW James Ross Island (Fig. 1). Silty and muddy sandstones and marls with concretionary beds were deposited in shallow-marine shelf environments (Pirrie 1989; Crame *et al.* 1991). Petrographical and mineralogical studies indicate that the sediment was sourced from erosion of volcanic and plutonic elements of the Antarctic Peninsula (Browne & Pirrie 1995; Dingle & Lavelle 1998). The flora is found within the Lachman Crags Member, a sequence of sandstones and bioturbated silty sandstones and mudstones, from a mid- to outer-shelf setting (Pirrie 1989; Crame *et al.* 1991). This member has been dated using molluscan faunas and dinoflagellate cysts, which provided an early Santonian–early Campanian age (Crame *et al.* 1991; Keating 1992). However, more recent studies suggest that the Coniacian–Santonian boundary is within the lower 150 m of the Lachman Crags Member (McArthur *et al.* 2000); hence, a late Coniacian–early Campanian age is likely.

Preservation of the floras

Over 200 dicotyledonous angiosperm leaf specimens were included in a study by Hayes (1999). The fossils examined were collected by several Antarctic geologists from 1985 to 1990 from various localities within NW James Ross Island (Fig. 1). All specimens are held at the British Antarctic Survey (BAS), Cambridge, and are numbered with BAS locality and specimen numbers.

Most of the leaf fossils are preserved scat-

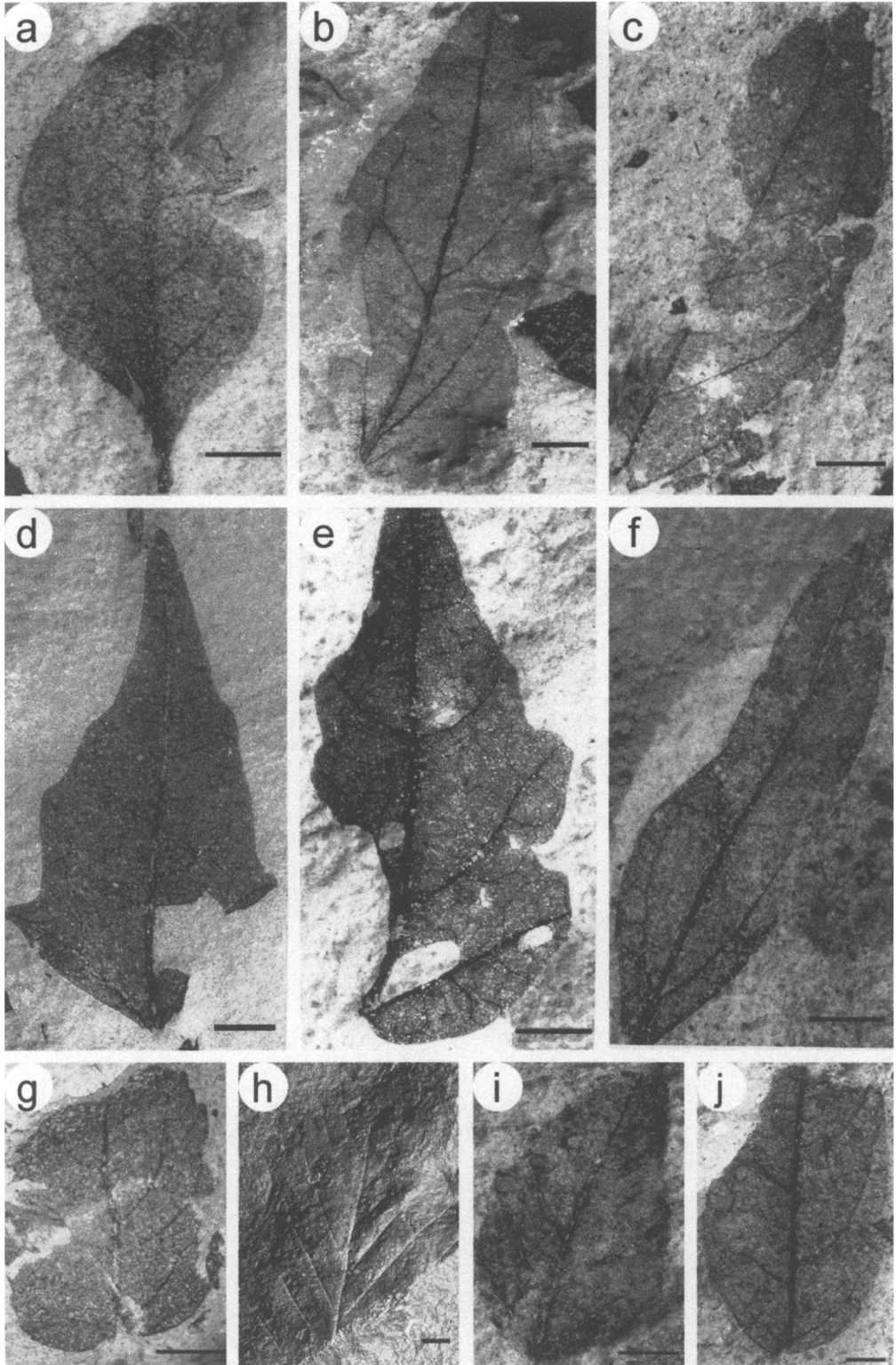
tered on uneven bedding planes as impressions, frequently with brown carbonaceous residues retained on the surfaces (Fig. 2). Some of the Santa Marta Formation fossils are also found within fine-grained carbonate concretions and many of these leaf impressions are preserved with a mineral coating of calcite. Approximately 25% of the leaves of both floras are almost whole, some with both part and counterpart preserved, but the majority are fragmentary. Although there is no cuticle present, architectural features of the leaves, such as leaf form, margins and venation patterns of the primary, secondary, tertiary and occasionally higher orders, are clearly visible in most specimens, allowing the isolation of taxonomic groups and palaeoclimatic analysis.

Angiosperms dominate the floras, with some ferns, and rare conifer and bennettitalean remains. Only the angiosperms are considered in this paper as at present the palaeoclimate significance of these other plants is less well constrained. This is the first published palaeoclimate analysis of these Cretaceous angiosperm floras. Further collecting and larger sample size is likely to provide more robust palaeoclimate data in the future.

Floral composition

Each of the leaf fossils was drawn and described in detail by Hayes (1999), including features such as leaf form, apical and basal styles, the nature of the leaf margin and venation characteristics. A multivariate statistical approach was developed to utilize many characters simultaneously in the definition of morphotypes (taxa delineated according to morphological similarities: Hayes 1999). A total of 41 morphotypes were described. Of these, 30 are present within the Hidden Lake flora and 31 within the Santa Marta flora, with 20 common to both floras. Detailed descriptions of each morphotype and the analytical technique used to define the morphotype groups can be found in Hayes (1999). Figure 3 illustrates a typical leaf of each morphotype.

Several of the morphotypes, clearly defined by their distinguishing characters, possess features common to disparate angiospermous groups, but many of the leaf forms show similarities to modern angiosperm orders and even families. The dominant morphotype of both floras is considered to show similarity to the Magnoliales and both floras share a strong component of lauralean-like leaf forms. Morphotypes sharing diagnostic features with leaves of the Sterculiaceae, Lauraceae,



Elaeocarpaceae and Winteraceae are common to both floras. A leaf form showing similarities to the Atherospermataceae is present within the Hidden Lake flora only and a morphotype showing similarities to the Myrtaceae is restricted to the Santa Marta flora. Morphotypes with architectural characteristics typical of the Cunoniaceae and Nothofagaceae occur within the Hidden Lake flora but are more abundant within the Santa Marta flora (Hayes 1999).

Palaeoclimate analysis

Techniques

Although fossil leaves from the Hidden Lake and Santa Marta formations are rare and fragmentary, they are a valuable source of information about Late Cretaceous climates in Antarctica. Angiosperm leaf floras can be used to provide qualitative and quantitative assessments of palaeoclimate using a variety of techniques. These include Nearest Living Relative (NLR) approach and analyses of leaf physiognomy, which do not rely on accurate identification of fossil leaf taxa and are thus particularly useful (Spicer 1990).

Nearest Living Relative (NLR) analysis. This approach involves assigning a fossil morphotype to a modern group and extrapolating back the climatic tolerances of the extant taxon (Spicer 1990; Chaloner & McElwain 1997). Qualitative assessments of palaeoclimates can be derived that will provide a first indication of palaeoclimate and the nature of the boundary conditions (e.g. warm, cool, lack of freezing) (Mosbrugger 1999). There are, however, limits to this approach, especially for these Antarctic leaves, as many of the morphotypes possess architectural features that occur across several living families. Application to families or higher groupings rather than genera is problematic because of the breadth of ecological tolerances. In addition, the ecological tolerances of fossil taxa that lived under greenhouse climates not present on Earth today may have been different from those that have suffered geographical

restrictions during the Quaternary. Most significantly, angiosperms were rapidly diversifying during the Cretaceous and were not as dominant in global vegetation as they are today (Lidgard & Crane 1990).

Leaf margin analysis (LMA). The analysis of the relationship of non-entire (toothed) leaf margins to mean annual temperature (MAT) is considered one of the most useful and robust techniques in palaeoclimate reconstruction (Wolfe & Upchurch 1987; Burnham 1989). Early work on extant dicotyledonous angiosperm floras from around the world by Bailey & Sinnott (1915, 1916) showed that species with entire margined leaves are dominant in warm tropical environments, while leaves with non-entire margins predominate in cooler temperate regions. Based on extensive studies of living humid to mesic eastern Asian forests, Wolfe (1971, 1979) established a linear relationship between MAT and the proportion of entire-margined species. This relationship only breaks down in areas of low moisture availability and in very cold or arid regions where there is an increased proportion of entire margined species (Gregory & McIntosh 1996). The relationship established for the Northern Hemisphere is an increase of 1 °C for every 3% increase in entire margined species, with 60% corresponding to a MAT of 20 °C. In the Southern Hemisphere there is thought to be a higher proportion of evergreen plants reflected in a higher percentage of entire margined species, and so Wolfe (1979) adjusted the relationship so that a 1 °C increase in MAT corresponds to a 4% increase in entire-margined species, with 68–70% entire-margined species corresponding to a MAT of 20 °C.

The use of this relationship for Southern Hemisphere floras has caused some debate because it was thought that the correlation between LMA and MAT was poor in this region, and that MATs for Australian and New Zealand vegetation were overestimated (Jordan 1997). Greenwood *et al.* (2004) showed, however, that there is a statistically significant relationship between leaf margin and MAT for Australian rainforest vegetation. The slope of

Fig. 2. A selection of angiosperm leaf fossils from the Hidden Lake and Santa Marta formations. (a) D.8754.8.45a. Hidden Lake flora. Morphotype 3. (b) D.8754.8.54a. Hidden Lake flora. Morphotype 11 (Laurales). (c) D.8754.8.4a. Hidden Lake flora. Morphotype 17. (d) D.8754.8.3a. Hidden Lake flora. Morphotype 2 (Sterculiaceae). (e) D.8754.8.1a Hidden Lake Flora. Morphotype 2 (Sterculiaceae). (f) D.8754.8.57a. Hidden Lake flora. Morphotype 11 (Laurales). (g) D.8754.8.30a. Hidden Lake flora. Morphotype 20 (Elaeocarpaceae). (h) D.8621.27a. Santa Marta flora. Morphotype 7 (Nothofagaceae). (i) D.8754.8.8a. Hidden Lake flora. Morphotype 25. (j) D.8754.8.42a Hidden Lake flora. Morphotype 10. Scale bar 5 mm for all leaves. Names in brackets indicate possible similar living orders or families.



Fig. 3. Line drawings showing the venation features of the morphotypes identified in the floras discussed here. For detailed descriptions of each morphotype see Hayes (1999).

the regression is similar to that of East Asia, North America and Bolivia, but with a different intercept so that fewer toothed species are present at a given temperature. They proposed that palaeotemperature estimates would be a minimum estimate if the Southern Hemisphere regression line was used and a maximum estimate if the Northern Hemisphere regression relationship of Wolfe (1979) was used. This dual approach was used, for example, by Kennedy *et al.* (2002) in a palaeoclimate analysis of Late Cretaceous and Paleocene floras from South Island, New Zealand and by Hunt & Poole (2003) in palaeoclimate analysis of Tertiary floras from King George Island, West Antarctica.

Simple linear regression (SLR) models. Simple linear regression equations have also been derived for the relationship between MAT and leaf-margin character based on the LMA relationship documented by Wolfe (1979). Several SLR equations have been derived by palaeobotanists who have quantified the relationship of percentage of taxa with entire (untoothed) margins in living floras with climate for specific regions. SLR equations have, for example, been derived by Wing & Greenwood (1993), Wiemann *et al.* (1998) and Wilf (1997) for data from East Asian forests, Australian forests, temperate and tropical floras of North and South America, and from the CLAMP data set of Wolfe (1993) (see below).

Some SLR models are used to estimate precipitation, rather than temperature, based on leaf size (e.g. Wilf *et al.* 1998). Studies by Wiemann *et al.* (1998) concluded that leaf size is one of the most important predictors of precipitation. In these fossil floras only about 25% of the specimens are almost whole leaves, the majority being fragments. However, the likely original size of a leaf was reconstructed by Hayes (1999) by first identifying the morphotype from venation characteristics in the fragment, if well enough preserved, and then reconstructing the whole leaf based on comparable whole specimens of that morphotype. In this way estimates of leaf sizes were successfully obtained for many fragmentary specimens. Maximum estimated leaf areas per fossil morphotype, obtained as described above, were then used to predict mean annual precipitation (MAP). Estimates of MAP using this method (see Table 1) have to be treated with some caution because the fossil leaf assemblages must have been subject to considerable taphonomic bias (Greenwood 1992), especially as it is likely that the larger leaves were eradi-

cated during transport (Ferguson 1985; Gastaldo *et al.* 1996). Estimates of MAP are therefore likely to be minimum estimates.

Multivariate analyses. These models use a selection of leaf attributes, rather than just one as in SLR, to interpret climates. Two techniques are presented below.

Climate–Leaf Analysis Multivariate Programme (CLAMP) (Wolfe 1993; Kovack & Spicer 1996; Wolfe & Spicer 1999). This is a multivariate statistical technique that relates the climatic signal preserved in the physiognomy of leaves of woody dicotyledonous angiosperms to meteorological characteristics of the region in which the plants grow. CLAMP uses Canonical Correspondence Analysis (CANOCO) (Ter Braak 1986), a direct ordination method used widely in plant ecology, to analyse the relationship between leaf attributes and climate. CLAMP datasets of leaf attributes and climate parameters have been compiled for 173 predominantly Northern Hemisphere modern vegetation sites, although subsets of data are often used if more relevant to the likely palaeoclimate (e.g. cold climate sites are often removed). For analysis of fossil floras, the fossil leaf data are positioned within the modern data set and the corresponding palaeoclimate determined from the analysis.

Reliable CLAMP analysis requires sample sizes of greater than 20 species for MAT (25 for precipitation analysis), with the majority of leaf characters preserved. The incomplete preservation of the Antarctic leaves and preponderance of missing characters means that full CLAMP analysis was not suitable in this study. However, simplified CLAMP data sets of modern vegetation and climate characters have been used to derive multiple linear regression models that can be applied to these Antarctic floras, as discussed below.

Multiple linear regression (MLR) models. Several MLR models (regression equations) have been derived from characters in the CLAMP data set, but using only a reduced number of characters that are more frequently preserved in fossil floras, more consistently scored by researchers and more useful for palaeoclimate prediction. For example, Wing & Greenwood (1993) obtained regression equations using a subset of the CLAMP data set with sites experiencing extreme cold removed, thus creating a data set more representative of environments in past greenhouse climates. Wiemann *et al.* (1998) derived their own MLR

models from the CLAMP data set for specific sites that included temperate and tropical America and Japan. Their study of correlation coefficients between the CLAMP leaf characters and climate parameters demonstrated that leaf morphology has a stronger relationship with temperature than precipitation. MAT was most highly correlated with leaf-margin character, and growing season precipitation (GSP) with length/width ratio, leaf shape, the presence of an attenuate apex and leaf size. The MLR methods used are shown in Table 1.

Results

Palaeoclimate from NLR analysis

Although the Antarctic fossil leaves cannot be confidently assigned to modern orders or families, comparable modern plant groups that share similar architectural characteristics can provide some indication of the climate window in which the fossils lived. Most living types comparable to the fossil leaves can be found in warm temperate or subtropical zones of the Southern Hemisphere today. For example, the Winteraceae are characteristic of wet tropical montane to cool temperate rainforests of Tasmania and New Zealand. Sterculiaceae is a tropical to subtropical family extending throughout Australia, south Asia, Africa and northern South and Central America. Laurales are trees, shrubs and woody vines that live today in tropical or warm temperate regions with a

moist equable climate. Elaeocarpaceae is a widespread family of tropical and subtropical trees and shrubs present in eastern Asia, Australasia, Indomalaysia, the Pacific area, South America and the West Indies. The Cunoniaceae occur as trees, shrubs and woody climbers in tropical and warm temperate Australia, New Guinea and New Caledonia. From the list above it is apparent that examples of plant groups with which the fossil leaves share characteristics are typical of tropical, subtropical or warm temperate regions today. There is little evidence for cool and cold climates from the fossil plants or their possible modern equivalents.

Palaeoclimate analyses of leaf physiognomy

Palaeoclimate data for the Coniacian and late Coniacian–early Santonian, obtained from the Hidden Lake and Santa Marta floras, are shown in Table 1. Leaf margin, SLR and MLR analyses give estimates of mean annual palaeotemperatures that range from 15.2 (± 2) to 18.6 (± 1.9) °C for the Coniacian, and 17.1 (± 2) to 21.2 (± 1.9) °C for the late Coniacian–early Santonian. The mean values of MAT, averaging all methods, are 16.9 °C for the Coniacian and 19.1 °C for the late Coniacian–early Santonian.

The lowest temperature estimates were obtained from the SLR analyses using the complete CLAMP data set derived by Wilf (1997); this produced MATs of 15.5 (± 3.4) °C for the Hidden Lake flora and 17.8 (± 3.4) °C for the Santa Marta flora with large standard errors.

Table 1. Predicted palaeoclimate data for the Coniacian and late Coniacian–early Campanian, based on LMA, SLR and MLR analyses of the Hidden Lake and Santa Marta floras. (MAT, mean annual temperature; MAP, mean annual precipitation; GSP, growing season precipitation.) Refer to source for details of specific models

Model	Hidden Lake flora			Santa Marta flora		
	MAT (°C)	MAP (mm)	GSP (mm)	MAT (°C)	MAP (mm)	GSP (mm)
LMA – Northern Hemisphere (Wolfe 1979)	18.0 \pm 1.8			20.7 \pm 2.1		
LMA – Southern Hemisphere (Wolfe 1979)	16.3 \pm 1.6			18.3 \pm 1.8		
SLR (Wolfe 1979; Wing & Greenwood 1993)	17.7 \pm 0.8			20.1 \pm 0.8		
SLR (Wiemann <i>et al.</i> 1998)	16.3			18.0		
SLR (Wilf 1997)	17.7 \pm 2.0			20.0 \pm 2.0		
SLR–CLAMP (Wilf 1997)	15.5 \pm 3.4			17.8 \pm 3.4		
SLR–CLAMP with cold sites excluded (Wilf 1997)	16.4 \pm 2.1			18.4 \pm 2.1		
SLR–CLAMP large leaves (Wilf <i>et al.</i> 1998)		1093			673	
SLR–leaf-area analysis (Wilf <i>et al.</i> 1998)		772 (–233, +333)			956 (–288, +413)	
SLR – large leaves (Wilf <i>et al.</i> 1998)		594			591	
MLR – Wing & Greenwood (1993)	15.2 \pm 2	2142 \pm 580		17.1 \pm 2	1991 \pm 580	
MLR – Wiemann <i>et al.</i> (1998)	18.6 \pm 1.9		2630 \pm 482	21.2 \pm 1.9		2450 \pm 482

The inclusion of extremely cold sites with winter freezing in the CLAMP data set is likely to have produced these cooler temperature estimates. However, Wing & Greenwood (1993) and Wilf (1997) derived MLR and SLR models from the CLAMP data set with the cold sites removed, as the exclusion of cold sites has been shown to produce significantly better correlation between leaves and climate in studies of modern floras (Gregory & McIntosh 1996). These produced MATs of 15.2 (± 0.2) and 16.4 (± 2.1) °C for the Hidden Lake flora, and 17.1 (± 0.2) and 18.4 (± 2.1) °C for the Santa Marta flora, using the methods of Wing & Greenwood (1993) and Wilf (1997), respectively.

The warmest estimates of MAT for these floras were produced by the Wiemann *et al.* (1998) MLR equation; in testing various SLR and MLR methods on modern vegetation in Florida, Wiemann *et al.* (1998) ground this model to be the closest match to the actual MAT. This method produced MATs of 18.6 ± 1.9 °C for the Hidden Lake flora and 21.2 ± 1.9 °C for the Santa Marta flora.

It is apparent from these analyses that, although there is some overlap in temperature estimates when the potential errors are taken into account, there is a clear signal of an increase in temperature, of about 2 °C, from the Coniacian to the early Santonian.

Estimates of annual precipitation (Table 1) range from 594 to 2142 (± 580) mm for the Hidden Lake flora and 673 to 1991 (± 580) mm for the Santa Marta flora. The Wiemann *et al.* (1998) model predicts growing season precipitation of 2630 (± 482) mm for the Hidden Lake flora and 2450 (± 482) mm for the Santa Marta flora. These estimates, especially those above about 2000 mm year⁻¹, are indicative of high rainfall, comparable to rainfall today of tropical regions such as the Amazon Basin and Indonesia tropical rainforest zones (FAO 2003). However, the MLR and SLR models may produce precipitation estimates that are not reliable for this study because they require information on leaf apex character, a feature that is not well preserved in these fossil assemblages, and on whole leaf size. The methods that produce the lowest estimates of rainfall use only leaf size to predict precipitation; however, leaf size amongst the fossils may have been strongly influenced by taphonomic sorting. The estimates for Cretaceous rainfall must therefore be considered with some caution.

Discussion

Analysis of the fossil leaves from James Ross Island using a range of methods indicate warm

climates at high latitudes of about 65°S in the mid-Late Cretaceous. Mean annual temperatures are predicted of about 17 °C in the Coniacian (range of all methods 12–21 °C) and 19 °C (range 14–23 °C) in the late Coniacian–early Campanian.

Comparison with other Antarctic palaeotemperature estimates

Estimates of terrestrial palaeoclimates for this interval and this location have been obtained from various sources. For example, Dingle & Lavelle (1998) produced climate curves for the Late Cretaceous and Cenozoic in the James Ross Basin based on the Chemical Index of Alteration that reflects alteration of clay minerals. By assuming that the climate was relatively humid (based on the belief that forests grew on Antarctica through this period), they derived a temperature history for the Antarctic Peninsula. They found evidence of strong chemical weathering during the Santonian–Campanian interval that was interpreted as representing a warm climate, peaking in the mid-Campanian, the warmest part of the Late Cretaceous.

Climatic signals from fossil plants also point to warm terrestrial climates. Rees & Smellie (1989) derived MATs of 13–20 °C for the Cenomanian–Campanian from leaf-margin and leaf-size analyses of angiosperm fossils (although only from six taxa) from Livingston Island, South Shetland Islands. A range of palaeoclimatic data were also derived by Poole *et al.* (2005) from analyses of fossil wood and other plant fossils. They deduced that the Coniacian–Campanian interval was the warmest part of a trend that involved warm wet Late-Cretaceous climates, cooler and drier climates towards the end Cretaceous and into the Palaeocene, a warm wet phase in the latest Palaeocene, followed by a cooler and drier phase through the Middle–Late Eocene. Their study, however, considered the Coniacian–Campanian as one data point, rather than as separate stage intervals, so direct comparison with the two leaf assemblages here is not possible. Their analyses produced a rather broad range of palaeoclimate estimates for this Cretaceous interval, partly due to lack of samples and also due to problems associated with the application of the coexistence approach to Cretaceous floras. Like NLR the Coexistence Approach relies on the extrapolation of the climate tolerances of nearest living relatives, which is considered as less reliable for floras of Cretaceous age due to the evolutionary state of floras at this time, and the unknown response of

floras to a greenhouse climate with atmospheric CO₂ levels much higher than present.

An average mean annual temperature for this interval of 15.3 °C was determined by Poole *et al.* (2005), the average of MATs of 13.5 °C derived from physiognomic analyses of angiosperm wood and 17.1 ± 4.2 °C from Coexistence Approach. Despite concerns with the Coexistence Approach outlined above, this temperature of 17.1 °C corresponds well with the MAT derived here for the Coniacian. A mean annual temperature range (MART) of 3.4 °C was derived from physiognomical analysis of wood, and cold month mean temperatures (CMMT) of 29 and 7.6 °C from wood analysis and Coexistence Analysis, respectively; however, Poole *et al.* (2005) conclude that these data are too imprecise to warrant consideration. An average warm month mean of 24.7 °C was derived from Coexistence Analysis. A mean annual precipitation value of 5620 mm was derived from wood analysis (an exceptionally high value found today only in small areas of equatorial Amazonian Andes and Indonesia; FAO 2003) but only 947 ± 60 mm from Coexistence Approach. Wood analysis predicted seasonal variation in rainfall (Poole *et al.* 2005).

The fossil plant analyses above provide palaeoclimate information for terrestrial climates under which the plants grew. It is important to compare the results with marine palaeotemperatures for the same region; however, marine palaeotemperature data may have been influenced by, for example, ocean currents and depth of water, and so comparisons must be made with care. In the adjacent oceans temperatures were also very high, according to oxygen isotope analyses of Ditchfield *et al.* (1994). They found peak warmth in the Coniacian and Santonian, within cooler climates during the Aptian–Cenomanian and from Campanian to Maastrichtian. Isotopic analysis of oysters gave palaeotemperatures of 18.5 °C for the Hidden Lake Formation and higher temperatures of 19.2 °C from ammonites, but 13 °C from belemnites (Pirrie & Marshall 1990; Marshall *et al.* 1993; Ditchfield *et al.* 1994).

Comparison with Arctic Cretaceous climates

This warm peak in the southern high latitudes is also reflected in the northern polar region. In the Arctic region Parrish & Spicer (1988) derived a MAT of about 13 °C at 80°N for the Alaskan North Slope region during the Coniacian, based on leaf-margin analysis and vegetation physiognomy of fossil floras. Using an

estimated Cretaceous latitudinal temperature gradient of 0.3 °C per degree latitude (Wolfe & Upchurch 1987), this suggests MATs of approximately 17.5–19 °C at palaeolatitudes of 65°N, comparable to those of the James Ross region. These temperatures for the Arctic are remarkably similar to those from Antarctica. Parrish & Spicer (1988) also found that climate cooled after the Santonian, a trend similar to that seen in the south. From the Russian Arctic Spicer *et al.* (2002) obtained palaeoclimate data for the uppermost Albian–lower Cenomanian from analysis of the Grebenka flora at a palaeolatitude of about 76°N. CLAMP analysis of angiosperms yielded a MAT of 13 ± 1.8 °C moderately high rainfall and no apparent dry season or winter freezing. Herman & Spicer (1996) derived similar MATs of 12.5 ± 1.8 and 9.0 ± 1.8 °C for the North Slope Alaska and Kamchatka, respectively, for Coniacian angiosperm leaves.

Three floras from NE Russia, studied by Craggs (2005), produced much lower MAT estimates of 8.1 ± 1.2, 7.3 ± 1.2 and 9.4 ± 1.2 °C for the early Coniacian. She found cold month mean temperatures around freezing (−1.5 ± 1.9, −2.7 ± 1.9 and 0.9 ± 1.9 °C) for the Russian region. This region was situated at 78°N palaeolatitude, about 13° poleward of the equivalent for the James Ross floras. The low winter temperatures suggest freezing conditions in these northern high latitudes, at odds with other data for peak Cretaceous warmth.

Global climate warmth

Not only is this interval of warm climates apparent at high latitudes but it has been reported from many sites globally. The Cretaceous ‘thermal maximum’, about 100–80 Ma, has been identified in many reports as a peak of global warmth. The warmest climates occurred at some point between the Cenomanian–Turonian transition and the Early Campanian (Huber *et al.* 1995, 2002; Clarke & Jenkyns 1999; Wilson *et al.* 2002). Poulsen *et al.* (2003) suggested that the Cretaceous thermal maximum attributed to high atmospheric CO₂ levels was at least partly the climatic expression of a tectonically driven oceanographic event (formation of the Equatorial Atlantic gateway). Unfortunately, Turonian leaf floras have not been discovered in Antarctica, but the palaeoclimate data derived from the James Ross floras suggest that the very warm phase is reflected in the Coniacian and Santonian vegetation record.

This warm peak during the Late-Cretaceous may have also been the trigger for expansion of the angiosperm floras in Antarctica. Angiosperm

pollen, which first appears in the early Albian Kotick Point Formation (Dettman & Thomson 1987; Riding & Crame 2002) on James Ross Island, increases in abundance in Turonian strata (Keating *et al.* 1992) and maintains high levels throughout the Marambio Group strata (Coniacian–Danian) (Dettmann & Thomson 1987; Dolding 1992; Keating 1992; Dutra & Batten 2000). The timing of this expansion matches well with a marked Turonian–Campanian diversification of angiosperm taxa in the northern high latitudes (Lupia *et al.* 1999), suggesting that angiosperm radiation occurred in both polar regions at the same time. Although this may well have been driven by this interval of global warmth, Lupia *et al.* (1999) state that the sparse sampling of pre-Turonina sediments produced a spurious jump in trend curves for angiosperm abundance.

Comparison with outputs from climate models

The Cretaceous has been a focus for several computer climate models (General Circulation Models, GCMs) (e.g. Valdes *et al.* 1996; Price *et al.* 1998; DeConto *et al.* 2002). Early models predicted seasonally extreme temperatures with mid continental freezing (e.g. Barron *et al.* 1993, 1995), even if atmospheric CO₂ levels were increased. These climate simulations were at odds with geological data that implied equable climates, at least for the mid-Cretaceous (Barron 1983; Francis & Frakes 1993 suggest winter freezing conditions at high latitudes for the Early Cretaceous).

The most detailed climate simulations relevant to the geological age of the floras described here were produced by Valdes *et al.* (1996) for the late Albian–early Cenomanian, using a GCM model with prescribed ocean conditions. For the Antarctica Peninsula region (at that time still joined to South America, Lawver *et al.* 1992) the model predicted summer surface air temperatures of over 20 °C, and winter temperatures of between 4–8 °C. The winter temperatures were above freezing (probably because the adjacent ocean was prescribed as warm), although further south on the main Antarctic continental freezing conditions were predicted. Soil moisture predictions (that indicate the balance between precipitation and evaporation) indicate dry soils in summer but saturated in winter, implying a seasonal precipitation regime. This agrees with palaeobotanical analyses of Poole *et al.* (2005) for the James Ross Basin region and with evidence from palaeosols for seasonally dry

climates in the Alexander Island region on the west side of the peninsula (Howe & Francis 2005).

The climate models (NCAR GENESIS GCM with a mixed layer ocean and prescribed ocean heat transport) of Otto-Bliesner & Upchurch (1997) examined the effect of forest vegetation in high latitudes on climate. Although they worked with Maastrichtian boundary conditions and palaeogeography, considered to be a time of cooler climates compared to the early Late Cretaceous, they discovered that the polar forests had a warming effect on climate of about 2.2 °C. They suggested that the low albedo of the polar vegetation led to warmer land surfaces that then warmed adjacent oceans, preventing sea ice formation and causing higher winter temperatures. In addition, DeConto *et al.* (1999) used Campanian palaeogeography and a GCM that was interactively coupled with a predictive vegetation model (EVE) to assess the conditions required to sustain polar forests. Their results indicated that CO₂ levels of 1500 ppm (over four times present-day levels) and greater poleward oceanic heat transport was required to maintain forests at the poles. They found that high-latitude forests reduced surface albedo and also added more water vapour to the atmosphere through evapotranspiration, which both induced greater warming.

The presence of forest vegetation on the Antarctic Peninsula, such as that now preserved as the Hidden Lake and Santa Marta floras, thus provided a positive feedback effect and created warmer climates that favoured the growth of forest vegetation in southern high latitudes.

Summary

Two fossil leaf floras have been recovered from the Coniacian Hidden Lake and late Coniacian–early Campanian Santa Marta formations in the James Ross Basin, Antarctic Peninsula. The floras represent vegetation that once grew on the adjacent emergent volcanic arc, which now forms the Antarctic Peninsula itself, but were subsequently deposited within sediments of the back-arc basin.

Palaeoclimate analysis of the angiosperm leaf floras, using leaf-margin analysis, and simple and multiple linear analysis methods, suggest that the mean annual temperatures for the Hidden Lake and Santa Marta formations were 13–21 °C (mean 17 °C) and 15–23 °C (mean 19 °C), respectively. Rainfall was high but was probably seasonal (although estimates of precipitation must be considered with care). This geological evidence supports climate simulations from computer climate and

vegetation models that suggest warm summer temperatures over 20 °C and winter temperatures above freezing. The presence of these floras at high latitudes probably positively contributed to the past polar warmth through their effect of decreasing albedo and increasing atmospheric water vapour (the most powerful greenhouse gas). These warm climates may also have been part of the Cretaceous thermal maximum, an interval of warm global climates, related to a phase of enhanced tectonic activity and CO₂ outgassing.

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