

Fossils and Fossil Climate: The Case for Equable Continental Interiors in the Eocene



Scott L. Wing; David R. Greenwood

Philosophical Transactions: Biological Sciences, Vol. 341, No. 1297, Palaeoclimates and their Modelling with Special Reference to the Mesozoic Era (Aug. 28, 1993), 243-252.

Stable URL:

<http://links.jstor.org/sici?sici=0962-8436%2819930828%29341%3A1297%3C243%3AFACCTC%3E2.0.CO%3B2-N>

Philosophical Transactions: Biological Sciences is currently published by The Royal Society.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/rsl.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Fossils and fossil climate: the case for equable continental interiors in the Eocene

SCOTT L. WING AND DAVID R. GREENWOOD

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A.

SUMMARY

There are many methods for inferring terrestrial palaeoclimates from palaeontological data, including the size and species diversity of ectothermic vertebrates, the locomotor and dental adaptations of mammals, characteristics of leaf shape, size, and epidermis, wood anatomy, and the climatic preferences of nearest living relatives of fossil taxa. Estimates of palaeotemperature have also been based on stable oxygen isotope ratios in shells and bones. Interpretation of any of these data relies in some way on uniformitarian assumptions, although at different levels depending on the method.

Most of these methods can be applied to a palaeoclimatic reconstruction for the interior of North America during the early Eocene, which is thought to be the warmest interval of global climate in the Cenozoic. Most of the data indicate warm equable climates with little frost. Rainfall was variable, but strong aridity was local or absent. The inferred palaeoclimate is very different from the present climate of the region and from model simulations for the Eocene. This suggests that models fail to incorporate forcing factors that were present at that time, that they treat the heat régime of continents unrealistically, and/or that model inputs such as sea surface temperature gradients or palaeotopography are incorrect.

1. PALAEOLOGICAL METHODS OF CLIMATE INFERENCE

The distributions of plant and animal species, as well as community characteristics, are strongly influenced by climate. It is not surprising then, that fossils have been used as indicators of palaeoclimate for more than a century, and that the presence of warm-climate animals, and of forests, at high latitudes was the first indication that Mesozoic and early Cenozoic climates were much warmer than those of the present. Most methods of palaeontological inference can be considered under one of two categories depending on the uniformitarian assumption they make: those based on taxonomic analogy, and those based on morphological analogy. Taxonomic methods assume that the climatic preferences of an extinct animal or plant were similar to those of its nearest living relatives (NLR). Morphological (physiognomic) methods assume that characteristics of species or communities bore the same relation to climate in the past that they do now.

The main advantage of taxonomy-based approaches is that the raw data are densely distributed in space and time. The disadvantages of taxonomy-based methods are that they depend critically on correct identification, and that climatic preferences of NLRs may not accurately reflect those of extinct forms because of evolutionary change, extinction, or geographic range restriction related to non-climatic factors. All these problems become

more serious as older time periods and fossils are considered.

The chief advantage of morphology based palaeoclimatic inference is that correlations between climate and the morphology or anatomy of organisms reflect underlying physiological, mechanical, and physical processes that are less affected by evolution, extinction, and range restriction than are the climatic preferences of taxonomic groups. Even so, correlations between climate and morphology are very poorly understood for many groups of Mesozoic animals and plants. The chief disadvantage of morphological approaches is that they require data on a particular feature, thus limiting the number of fossil assemblages that can be used in an analysis.

(a) *Foliar physiognomy*

The rate at which leaves can photosynthesize is strongly related to their temperature, and to the availability of water. Leaf temperature and rate of evapotranspiration are determined in part by the shape and size of the leaf, and so these characters can be expected to correlate with climatic variables. Initial work by Bailey & Sinnott (1916) demonstrated that the percent of dicot species with entire margined leaves in local vegetation increased with increasing mean annual temperature (MAT). Later authors (Chaney & Sanborn 1933; Dilcher 1973) noted that leaf size and apex shape were also related to climate.

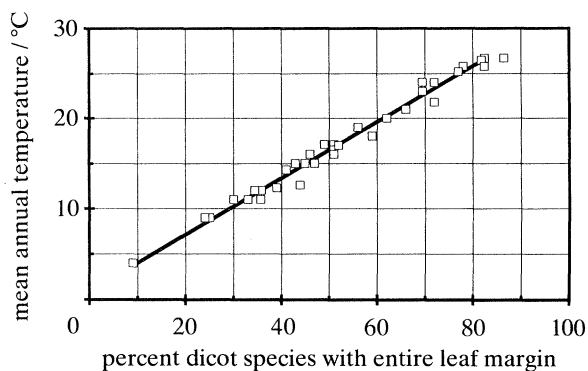


Figure 1. Percentage of entire margined species against MAT. Data from Wolfe (1979). $\text{MAT} = 1.141 + (0.306 \times \text{percent of entire margined species})$. $R^2 = 0.983$, $p < 0.001$, standard error of the estimate = 0.788°C .

Floral and climatic data supporting the correlation of margin type with temperature were greatly increased by Wolfe (1979), who derived a quantitative relationship of 3% change in percent of entire margined species for every 1°C change in mean annual temperature (figure 1).

The relationship between percent entire margined species and MAT observed by Wolfe (1979) is subject to significant limitations. It was based on mesic vegetation of East Asia, and different correlations have been observed in Southern Hemisphere vegetation (Wolfe 1985; Greenwood 1992), and in vegetation under seasonal or low rainfall. Soil types or other non-climatic variables also modify the relationship between MAT and percent of entire margined species, potentially decreasing the precision of temperature estimates (Dolph & Dilcher 1979). Differential production, transport, and preservation of canopy versus non-canopy leaves and stream-side versus 'climax' vegetation can influence the leaf forms present in a fossil assemblage (MacGinitie 1974; Burnham 1989; Greenwood 1992) and degrade the precision of palaeotemperature estimates derived from leaf margin analysis (LMA). To counteract these problems, Wolfe (1985) has recommended that LMA only be done on floras with greater than 30 species; multiple samples from the same area and time can also increase the confidence of the MAT estimate.

Leaf physiognomic analyses that combine leaf size, shape and margin configuration have been explored by several workers (e.g. Davis & Taylor 1980; Christophel & Greenwood 1988; Greenwood 1992). The most comprehensive multi-character study of the relationship between dicot leaf physiognomy and climate has been carried out by Wolfe (1990, 1993), who examined a set of 106 samples from North America, Japan, and the Caribbean region. This analysis is called climate-leaf analysis multivariate program, or CLAMP. Each sample of leaves was taken from a local area of vegetation near a climate station. Wolfe scored leaves for a series of semi-quantitative descriptors of leaf size (seven states), shape (eight states), base shape (three states), apex shape (four states), and marginal configuration (seven states), and

recorded the percent of species possessing each character state. These percentages were ordinated using correspondence analysis. Theoretically, a multivariate data set should describe leaf physiognomy more fully, and thus reveal more precisely the relationships between physiognomy and climate. Wolfe (1993) has noted correlations within the CLAMP data set between physiognomy and precipitation, as well as temperature. Below we compare palaeotemperature estimates based on the CLAMP data set with those based on LMA.

Relationships between leaf physiognomy and temperature may have been different in the Mesozoic than the Cenozoic as Cretaceous dicots generally had less efficient vascular tissue than Tertiary dicots (Wheeler & Baas 1991). This suggests that at a given temperature Cretaceous dicot leaves would have had features associated with lower evapotranspiration rates than Tertiary dicots (e.g. smaller size and more lobation). 'Modern' relationships between dicot leaf physiognomy and climate probably were established during the latest Cretaceous or early Tertiary, and it has been suggested that palaeoclimate estimates based on physiognomy should not be attempted for floras older than Late Cretaceous (Wolfe & Upchurch 1987).

Future improvements in inferring palaeoclimate from leaf physiognomy may involve tallying physiognomic characters by specimen rather than by taxon (e.g. Greenwood 1992); this approach avoids the need to segregate fossil floras into morphotypes or species, which is one step where errors can occur. Leaf physiognomy might also be extended to more of the Mesozoic by applying multivariate physiognomic techniques to the foliage of cycads, conifers, and ferns.

(b) *Other morphological features*

Leaf surfaces are the primary area for water loss in most vascular plants, so features of the epidermis and cuticle are influenced by temperature, humidity, and water availability. Generally, few, small or sunken stomata, the absence of stomata on the upper leaf surface, and the presence of protective hairs, papillae, or thickened cuticle indicate water stress (Wolfe & Upchurch 1987), but there presently is no system for deriving quantitative estimates of palaeoclimate from cuticular features. In some cases the taxonomic composition and morphology of epiphyllous fungi can also provide palaeoclimatic information (Lange 1976).

The vascular tissue of plants displays a variety of features that correlate with climate, especially with seasonality. At a broad taxonomic scale, manoxylic wood (the kind of soft wood seen in cycads and palms) is frost sensitive, whereas denser pycnoxylic wood (seen in conifers and many dicots) is less frost sensitive. Wood rings in pycnoxylic wood indicate discontinuous growth, generally the result of seasonal fluctuation in temperature or water availability (Creber & Chaloner 1985). The degree of irregularity in growth ring thickness is expressed as mean sensitivity. Other features of wood anatomy of potential value for inferring palaeoclimate include vulnerability, and conductance (Carlquist 1975; Gartner *et al.* 1990). Conductance is a measure of the rate at which fluids

can pass through the vascular tissue, whereas vulnerability is a measure of the redundancy of the vascular system. Conductance is known to correlate with evergreen habit in some regions (Gartner *et al.* 1990). High vulnerability, that is having few vessels each of very large diameter, is correlated with warmer more mesic climate (Carlquist 1975).

Most wood features correlate strongly with plant habit and size as well as with climate, which complicates palaeoclimatic inference from small wood fragments. The strong anatomical differences between Cretaceous and Tertiary dicot woods, suggest that climatic correlates of wood features may be different between the two periods (Wheeler & Baas 1991).

(c) *Nearest living relatives in plants*

Palaeoclimate reconstruction based on nearest living relatives has been the most commonly used method for much of the 20th century (e.g. MacGinitie 1941; Hickey 1977). Generally, confidence in an NLR analysis is increased by: (i) close relationships between fossil species and their nearest living relatives; (ii) a large number of fossil–NLR pairs; (iii) living relatives that belong to a diverse and widespread higher taxon, rather than a relictual or monotypic one; and (iv) use of plant groups that uniformly have anatomical or physiological features that constrain their climatic tolerances.

As taxonomic understanding of late Mesozoic and early Cenozoic angiosperms has improved, it has become clear that many of them belong to extinct genera, especially in Palaeocene and older floras. In spite of this most Eocene and younger floras have extant genera that can be used in NLR analysis. Recent greenhouse studies of the climatic tolerances of NLRs of key Australian Tertiary taxa, such as *Nothofagus* show how NLR inferences about threshold temperatures can be refined (Read & Hill 1989).

A few higher taxa are particularly important in constraining minimum palaeotemperature estimates: palms, gingers, cycads, and tree ferns. These groups are today moderately to very diverse, but are without exception restricted to mild climates with rare frost. Frost intolerance in these groups is intrinsic to their basic structure and physiology: manoxylic wood; large, unprotected buds; soft, water-rich tissues; and a near absence of frost ‘hardening’ mechanisms such as increasing solute concentrations and reduction in intercellular water (Sakai & Larcher 1987). Leaves of the most frost tolerant palm species (e.g. *Trachycarpus fortunei*) are extensively damaged by temperatures of -14°C , and the roots and seedlings of the same species are killed by temperatures of -2 to -8°C . The susceptibility of seedlings and roots prevents palms from establishing populations wherever the ground freezes (Sakai & Larcher 1987), and their natural limits correspond to climates with average minimum temperatures warmer than -10°C , and cold month means (CMM) greater than $5-7^{\circ}\text{C}$ (Sakai & Larcher 1987). Experimental work on the ginger *Alpinia* shows it is killed by temperatures between -2 and -4°C . Because palms, gingers, and tree ferns are

diverse today (thousands of species of palms and gingers, hundreds of species of tree ferns), it is very unlikely that extinct species possessed greater tolerance to cold than living species. To the contrary, the cooler climates of the late Cenozoic are likely to have weeded out the most frost-sensitive lineages even among warm-climate groups, as appears to have happened under equable climates in Australia (Read & Hill 1989). Thus the past distribution of palms, etc. provide very strong evidence for CMMs above 5°C and average minimum temperatures above -10 to -4°C , even though they do not permit quantitative estimates of MAT.

The most common method of quantifying palaeoclimate estimates based on NLR methods is through the use of ‘transfer functions’ (Imbrie & Kipp 1971). Transfer functions are created in a two-step process. First, the relative abundances of species are recorded at a number of sites across a climatic gradient, and the samples are subjected to factor analysis. In the second step, the scores of the sites from the factor analysis are used as independent (predictor) variables in a multiple regression analysis in which temperature or other environmental variables are dependent. The multiple regression analysis produces coefficients that can be applied to lists of fossil species to predict palaeoenvironmental variables.

(d) *Nearest living relatives in animals*

Living crocodylians and large, terrestrial turtles are restricted to areas of warm climate (Hutchison 1982). Because of the high thermal inertia of water, small aquatic reptiles can survive cold winters by hibernating below the surface. For larger aquatic and terrestrial reptiles this is not an option. The northern limit of the most cold-hardy crocodylians (*Alligator* sp.), approximately coincides with the 4.4°C CMM; there is no evidence that crocodylians can survive extended periods of subfreezing temperatures (Hutchison 1982). Terrestrial and semi-terrestrial turtles exist in cold-winter regions, but do not attain shell lengths more than 30 cm except in climates where the CMM is greater than 13°C (Hutchison 1982).

The presence of dinosaurs has little use as a palaeoclimatic indicator because a range of thermal physiologies were present in this group (Spotila *et al.* 1991). It is also possible that some dinosaurs migrated long distances to take advantage of seasonally available resources in high latitudes (Brouwers *et al.* 1987), thus giving no information on year-round conditions.

(e) *Ecological diversity spectra and cenograms*

Although mammals are homeothermic, and thus less affected by ambient temperature than reptiles, several aspects of mammalian community composition are correlated with vegetation type, and hence indirectly with climate. Ecological diversity spectra (EDS) is a technique pioneered by Andrews & Lord (1979) where each species in a local mammalian fauna is assigned to a body size category, a feeding-type (e.g. frugivore, insectivore), and a locomotor category (e.g.

arboreal, terrestrial). Histograms illustrating the distribution of species from a fossil fauna can be compared with living faunas from known habitat and vegetation types (Collinson & Hooker 1987). Faunas with high proportions of arboreal frugivores and insectivores live in forested habitats with warm climates where food resources are available year-round. Although the EDS approach is informative about local vegetation and seasonality, the relationship between the EDS histograms and climatic parameters has not been quantified. Vegetational and climatic reconstructions have also been based on tooth crown height and the degree of sexual dimorphism among ungulates (Janis 1984).

Cenograms are another method for extracting vegetational-climatic information from mammalian faunas (Legendre & Hartenberger 1992). The cenogram simply orders the herbivore species in a local mammalian fauna according to their body weight. Among living faunas there is greater diversity of small herbivores in warm, forested environments than in more open and cooler habitats (Legendre *et al.* 1991; Gingerich 1989).

(f) *Stable isotopes from shell and bone*

Recent research attempts to use the ratio of $^{18}\text{O}/^{16}\text{O}$ in the shells of freshwater molluscs to determine the water temperature at which the shell was precipitated (Dettmann & Lohman 1993). Ratios for Palaeocene unionid clams in the Powder River Basin of Wyoming and Montana are extremely negative; comparable to those found in the northern U.S. and Canada today. Several factors prevent these ratios from being interpreted strictly in terms of water temperature. Chief among these are that the isotopic balance of freshwater is sensitive to rain-out effects (i.e. the first precipitation to drop from a cloud is preferentially composed of heavy oxygen, so that continental interiors receive the last, and isotopically lightest, precipitation), and that isotopic ratios of lakes and streams may be highly influenced by the ratio in higher altitude, and therefore cooler, headwaters (Dettmann & Lohmann 1993). Strong annual fluctuations in $^{18}\text{O}/^{16}\text{O}$ values imply seasonal snowmelt, presumably from high altitudes in the Bighorn Mountains, or seasonally alternating sources of isotopically 'heavy' and 'light' rainfall (Dettmann & Lohmann 1993).

$^{18}\text{O}/^{16}\text{O}$ ratios in mammalian teeth are also thought to reflect the isotopic ratios of surface waters (Koch *et al.* 1991). Values from the lower part of the early Eocene sequence in the Bighorn Basin, Wyoming, are consistent with an MAT of 9.5°C (Koch *et al.* 1991), about 4°C cooler than estimates based on LMA.

2. CONTINENTAL CLIMATE DURING THE EARLY EOCENE

Virtually all sources of palaeoclimate proxy data, oxygen isotopes in foraminifera (Miller *et al.* 1987), terrestrial plants and animals (Wolfe 1985; Collinson & Hooker 1987), and sedimentology (Robert & Chamley 1991) agree the acme of Cenozoic warmth

was during the early Eocene. With the exception of mountain glaciers in Antarctica (Birkenmajer 1990), the world appears to have been essentially ice free. The early Eocene is the most recent 'hothouse' interval, and because all methods of palaeoclimate inference are more reliable and accurate for more recent times, it will eventually become the best characterized period of globally warm climate. This makes the early Eocene a good test case for global climate models.

Recent model simulations of Eocene climate have suggested that continental interiors should have high thermal seasonality, in spite of global warmth (Sloan & Barron 1990, 1992). In North America these model predictions are directly contradicted by palaeontological data (Wing 1991; Archibald 1991). Here we use most of the methods outlined above to generate palaeoclimate estimates for the interior of North America based on the broadest possible set of palaeontological data.

(a) *Methods and data*

The peak of Cenozoic warmth appears to have been 50–52 Ma (timescale of Cande & Kent 1992). The floras used in this study range from 46–53 Ma on the basis of radiometric dates or faunal correlation (table 1). Analyses of the Green River, Kisinger Lakes, Chalk Bluffs, and Camels Butte floras are based on figured specimens, analyses of the Wind River, Bear Paw, and Sepulcher (Yellowstone) floras are based on specimens at the U.S. National Museum of Natural History. With the exception of the Green River assemblage, the floras were derived from fluvial environments.

We used both LMA (Wolfe 1979) and a multiple regression approach based on the CLAMP data set (Wolfe 1993) to derive palaeoclimate estimates. Multiple regression estimates of MAT have been generated from an earlier version of the CLAMP data (Gregory & Chase 1992). Before carrying out the multiple regression analysis we transformed the raw data by taking the arcsin of the squareroot, as is recommended in comparing bounded (i.e. percentages) with unbounded variables (Sokal & Rohlf 1969). Our initial multiple regression of the full set of 29 physiognomic (predictor) variables against MAT (dependent variable) revealed a high degree of multicollinearity, so we reduced the number of predictor variables by applying three criteria: (i) not more than one variable for each aspect of leaf form to avoid intercorrelation (e.g. one size variable, one base shape variable); (ii) low correlation with variables already selected for the model; and (iii) reasonably high correlation with the dependent climate variable in bivariate plots. Separate multiple regression models were developed for each dependent variable (table 2). All statistical procedures were carried out using SYSTAT 4.0 (Wilkinson 1988).

The multiple regression models presented here are derived from a subset of 74 CLAMP sites at which the cmm was greater than -2.0°C . This is justified on two grounds. First, there is overwhelming evidence from

Table 1. Age, sedimentary facies, physiognomic characteristics, and floristic notes for Eocene floras in this study (Facies codes: FVC = fluvial volcaniclastic; F = Fluvial; L = Lacustrine.)

flora	age	facies	# spp.	specimens	% entire	teeth comp.	emarg. apex	atten. apex	acute base	L:W < 1:1	L:W 2-3:1	meso 2	source	NLRs
Bear Paw	49-51	FVC	32	153	33	8	0	50	69	10	33	12	Brown & Pecora (1949) ^a	palms, conifers, dicots
Sepulcher	50-51	FVC	25	69	30	4	0	26	65	4	56	6	Smedes & Prostka (1972) ^a	treeferns, cycads, conifers
Camels Butte	53-55	F	19	46	26	15	0	0	46	0	37	15	Hickey (1977)	palms, dicots
Chalk Bluffs	50-52	F	67	158	49	6	1	18	55	5	34	16	MacGinitie (1941)	palms, dicots
Green River	45-48	L	53	154	46	0	6	15	67	5	23	1	MacGinitie (1969)	palms, dicots
Kisinger Lakes	49-50	FVC	36	76	57	0	0	6	63	4	30	4	MacGinitie (1974)	palms, dicots
Wind River	50-51	FVC	39	218	57	4	4	23	43	3	28	2	MacGinitie (1974) ^a	palms, cycads, dicots

^a Age only.

NLR analysis of Eocene North American floras and faunas that there were no prolonged periods of severe frost at that time in the Rocky Mountain region, therefore it is most appropriate to develop correlations between physiognomy and climate based on similar modern sites. Second, correlations between climate and leaf physiognomy are known to be different in areas with prolonged winter freezes than in warmer climates (Wolfe 1979, 1993). This shift is most pronounced at about the -2.0°C CMM (Wolfe 1979). The exclusion of these floras from the CLAMP data set leads to palaeo-MAT estimates that are approximately $1-2^{\circ}\text{C}$ warmer than those obtained with the full data set, and with slightly smaller standard errors.

We note that the standard errors of our palaeoclimate estimates (table 2) reflect only the error in the models resulting from the imprecision of physiognomy-climate correlations in the CLAMP data set. Error is also introduced by taphonomic alteration of fossil leaf assemblages and by sampling problems (Christophel & Greenwood 1988; Burnham 1989; Greenwood 1992) so the true errors of our palaeoclimate estimates are greater than the standard errors of our models.

(b) Palaeobotanical results

Figure 2 illustrates the distribution of frost intolerant plants in North America at about 50 Ma. Results of our physiognomic analyses are in table 3. The general agreement between the palaeotemperature estimates based on LMA and the multivariate method is not surprising because margin configuration is the most important character in the multiple regression models (table 2). The trends in our MAT and CMM estimates generally are consistent with expectations. By both methods, the Bear Paw, Sepulcher, and Camels Butte sites are the three coolest. Bear Paw is the most northern, Sepulcher had the highest elevation (Fritz & Harrison 1985; table 3), and Camels Butte is the oldest and therefore predates the peak of early Eocene warmth. Bear Paw and Sepulcher are floristically different from the other sites in having abundant *Pinus*, which is typically more abundant in temperate than in tropical climates. The Wind River and Kisinger Lakes floras give the warmest temperature estimates and also have the greatest number of paratropical and subtropical taxa. The Green River flora is cooler than the Wind River and Kisinger Lakes floras, perhaps because it is younger and postdates the peak Eocene temperatures. There is no evidence of any 'lake effect' in which the Green River flora would be expected to yield warmer temperature estimates than floras from fluvial settings. The only anomalous result is that the coastal and more southerly Chalk Bluffs flora yields a lower MAT estimate than do Kisinger Lakes and Wind River. This may be influenced by inaccurate taxonomic sorting in the published flora.

The MAT estimates we have derived (figure 3 and table 3) are similar to those in living broad-leaved evergreen, and mixed broad-leaved evergreen and deciduous forest (Wolfe 1979), which is consistent

Table 2. Multiple regression models used to predict climate parameters in table 3

(Raw data (present of species in a local vegetation showing the physiognomic characteristic) must be transformed by taking the arcsin of the square-root before applying constants and coefficients.)

dependent variable	R^2	standard error	constant	multiple regression models coefficients (p values in parentheses)						
				no. teeth (entire)	teeth compound	apex emarg.	apex attenuate	L:W < 1:1	L:W 2-3:1	mesophyll 2
MAT	.863	1.988	2.536	17.372 (< 0.000)		2.896 (0.081)		-8.592 (0.006)		
MART	.451	5.051	22.048			-10.221 (0.01)		12.057 (0.045)		-34.840 (< 0.000)
CMM	.759	3.551	-5.278	17.627 (< 0.000)		6.741 (0.024)		-15.301 (0.006)		
WMM	.661	2.923	30.892		-20.886 (< 0.000)					
MAP	.497	57.967	11.489				167.948 (0.002)			377.735 (< 0.000)
TDM	.550	8.910	-24.489				45.54 (< 0.000)	38.186 (0.005)		
TGSP	.583	47.226	-172.859				110.841 (0.024)	320.457 (< 0.000)		179.775 (0.012)

with taxonomic composition, leaf textures, and leaf length:width ratios. However, the presence of frost intolerant palms, gingers, and cycads, and frost sensitive cyatheaceous tree ferns, is difficult to reconcile with CMM estimates below about 5°C. Yet at least one of these groups is present at the three coldest sites: Bear Paw (CMM 0.6°C), Sepulcher (CMM 1.9°C), and Camels Butte (CMM 3.5°C). Our CMM estimates can only be reconciled with frost intolerant plants if temperature fluctuations during the cold month were less than a few degrees: a climate *more* equable than that of southern New Zealand or other mid-latitude

Southern Hemisphere sites today. Other sources of data indicate that CMMs were significantly higher than our estimates. CMMs closer to 10°C are supported by fossil wood from Yellowstone, which varies in expression of growth rings from very indistinct to distinct (Wheeler *et al.* 1978), and by NLR-based palaeotemperature estimates for the Camels Butte flora (MAT 17.8°C, CMM 11.7°C; Hickey 1977). Our cold physiognomy-based estimates of CMM for Bear Paw, Sepulcher, and Camels Butte may in part result from having relatively few dicot species at these sites, but our multiple regression based estimates for all the floras

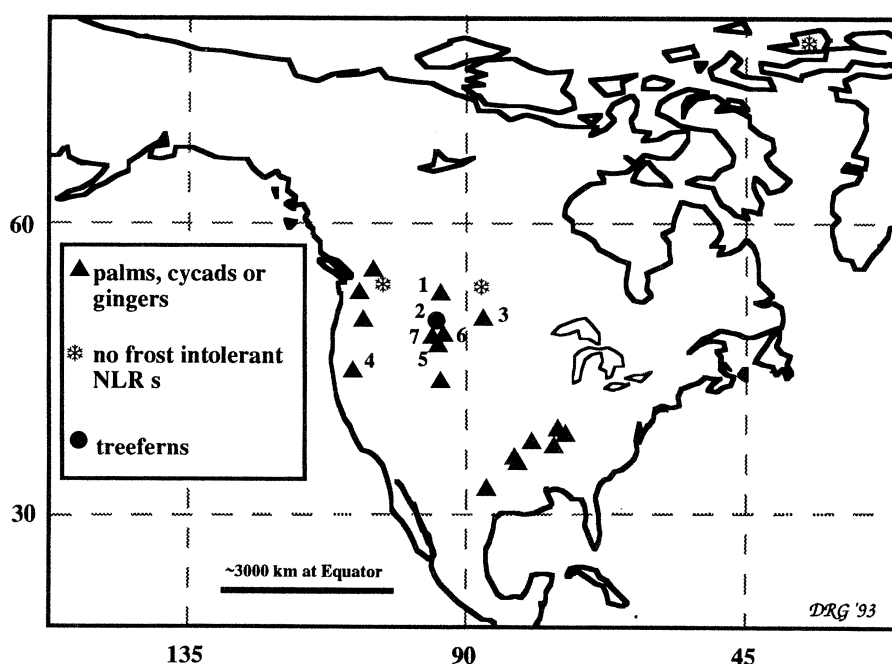


Figure 2. Map of North America at about 50 Ma, palaeogeography from PGIS-MAC. Data symbols indicate floras with palms (triangles), with cycads or zingiberaleans (circles), and lacking all three (snowflakes). Sites: 1, Bear Paw; 2, Sepulcher; 3, Camels Butte; 4, Chalk Bluffs; 5, Green River; 6, Kisinger Lake; 7, Wind River.

Table 3. *Palaeoclimate estimates of Eocene floras in this study*

(Latitudes are contemporary. Palaeoaltitude estimates are rough approximations based on proximity to coastline, volcanic centres and Eocene uplifts. MAT 1, mean annual temperature from LMA; MAT 2, mean annual temperature from multiple regression model; MART, mean annual range temperature from multiple regression model; CMM, cold month mean temperature; WMM, warm month mean temperature; MAP, mean annual precipitation; TDM, three driest months precipitation; TGSP, three month growing season precipitation.)

flora	MAT 1 °C	MAT 2 °C	MART °C	CMM °C	WMM °C	MAP mm	TDM mm	TGSP mm	paleoaltitude	latitude (modern)
Bear Paw	11.2	10.4	13.6	0.6	25.0	2770	340	1740	500–1000	48.5
Sepulcher	10.5	10.9	15.9	1.9	28.0	1950	320	2020	~1000	44.9
Camels Butte	9.1	11.2	8.2	3.5	23.4	1620	0	1080	< 200	46.8
Chalk Bluffs	17.1	14.4	9.4	5.6	26.7	2410	190	1500	< 200	39.17
Green River	15.2	14.3	18.7	6.1	31.9	1160	120	500	500–1000	39.8
Kisinger Lakes	18.6	15.7	17.5	6.7	31.7	1290	90	770	500–1000	43.8
Wind River	18.6	16.5	17.1	8.5	27.0	1490	190	870	500–1000	43.7

are at least 2–3°C cooler than have been obtained by others (MacGinitie 1969, 1974; Hickey 1977; Wolfe 1985; Wing *et al.* 1991).

The physiognomy of all six continental interior floras implies seasonal variation in precipitation, although the estimates are of low precision. Precipitation during the three driest months (TDM) is estimated to have been under 120 mm for the Camels Butte, Kisinger Lakes, and Green River floras, and 190 mm for the Wind River Flora. The Bear Paw is inferred to have been the wettest, with a TDM estimate of 350 mm. The existence of seasonally dry climates in the western interior during the early Eocene is

supported by evidence from palaeosols (Bown & Kraus 1981) and local evaporite deposits (Smoot 1983).

(c) Palaeozoological evidence

Fossil reptiles and amphibians have been collected from many early to middle Eocene sites in the northern Rocky Mountain region (Hutchison 1982; Archibald 1991). Based on the occurrence of tortoises with carapaces up to 60 cm long (Hutchison 1982), CMMs would have been above 13°C during the early Eocene as far north as northern Wyoming (palaeolati-

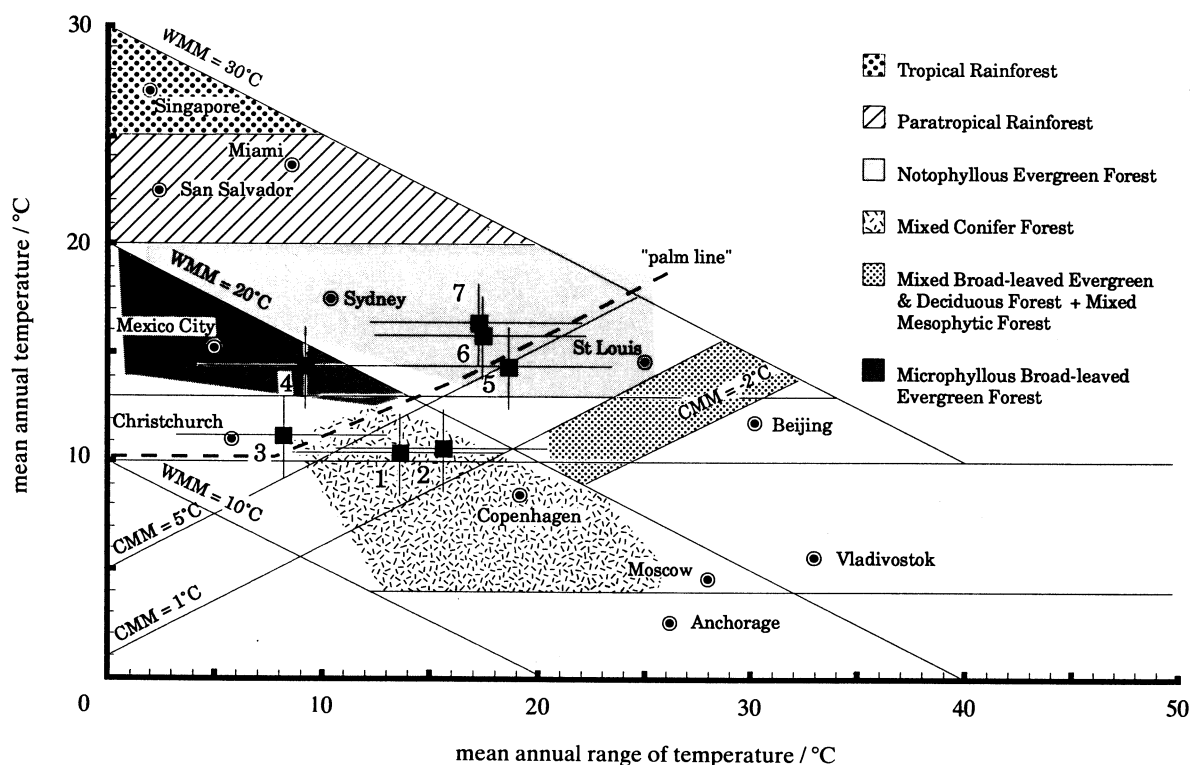


Figure 3. Nomogram showing MAT and MART for major vegetation types and fossil floras in this study. Note that localities 1, 2, and 5 fall below the 'palm line' even though they have palms or cycads. Locality codes as given in figure 2. MAT and MART estimates for fossil sites were derived from the multiple regression models in table 2.

tude 47°N). Large crocodylians are also known from late Palaeocene and early Eocene sites in Wyoming (Bartels 1980; Grande 1984); living crocodylians do not hibernate, nor do they live in areas of hard frosts. The diversity of small lizards in the Palaeocene and Eocene of the northern Rockies is another indicator of relatively mild winter temperatures (Bartels 1980).

Mammalian faunas from the Bighorn and Wind River Basins in Wyoming are noted for being highly diverse and have a large component of arboreal frugivores and insectivores (Rose 1981; Stucky 1992). Early Eocene faunas of the northern Rocky Mountains are similar to coeval faunas of Europe, both taxonomically and in the distribution of species among major ecological types. Based on the diversity of small-bodied insectivores and frugivores that require appropriate food resources year-round, Hooker & Collinson (1987) concluded the European assemblages were most similar to those living in tropical forests. Cenograms of early Eocene mammalian faunas from northern Wyoming also confirm that early Eocene faunas existed in a forested environment (Gingerich 1989).

The palaeoclimatic implications of terrestrial invertebrates in the Eocene are not well understood. However, latest Palaeocene rocks of the Bighorn Basin preserve a diverse gastropod fauna in which most taxa are allied to living groups that occupy tropical forest (E. Evanoff, personal communication 1991). A preserved nest of subterranean termites from the early Eocene of the Bighorn Basin also belongs to an exclusively tropical extant group (T. Bown, personal communication 1993).

3. CONCLUSIONS

There is unequivocal and highly reliable palaeontological evidence from the interior of North America that demonstrates equable climate during the early Eocene. Sea-level CMMs were greater than 5°C between 45 and 50°N palaeolatitude, and these regions experienced no sustained periods (longer than a day) below freezing, nor minimum temperatures ever below -10°C. Typical CMMs between 45° and 50°N would most likely have been 8–10°C, and MATs would have been no lower than 12–18°C. The palaeontological evidence for these temperature conditions extends over a large area including much of the states of Wyoming, Montana, and adjacent North Dakota. Floristic and faunal similarity can be used to extend these palaeoclimatic inferences to much of the North American continent (Tiffney 1985). Evidence for the relatively sluggish atmospheric circulation that would attend such an equable climate is seen in the small grain size of wind-blown dust found in ocean bottom cores of early Eocene age (Rea *et al.* 1985).

Climate simulations for the Eocene yield continental interiors with temperature seasonality similar to what is seen today (Sloan & Barron 1990, 1992). The palaeontological data that contradict these simulations cannot reasonably be dismissed as 'ambiguous' nor as limited to a small area (Sloan & Barron 1992). Several factors may contribute to overestimates of

seasonality in climate simulations: higher levels of CO₂ or water vapor in the Eocene atmosphere, inaccurate estimates of palaeotopography or coastlines, or incorrect estimates of sea-surface temperatures (Adams *et al.* 1990). Individually, none of these factors accounts for the large differences between the simulations and the data (Sloan & Barron 1992). The failure of model simulations to concur with the proxy data may relate to unrealistic simplifications in the models, such as their failure to account adequately for the effect of vegetation on albedo and water balance, rather than incorrect boundary conditions. This might also explain the hyper-seasonal climate simulations that have been produced for other places and periods in earth history (e.g. Crowley *et al.* 1989; Yemani 1993).

We thank Jack Wolfe for sharing his in press manuscript and the CLAMP data set, Cathy Greenwood for help with scoring fossil floras, and M. Buzas, L. Hayek, C. W. Wing, and S. B. Wing for help with statistics.

REFERENCES

- Adams, C.G., Lec, D.E. & Rosen, B.R. 1990 Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary. *Palaeogeogr. Palaeoclim. Palaeoecol.* **77**, 289–313.
- Andrews, P. & Lord, J.M. 1979 Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol. J. Linn. Soc.* **11**, 177–205.
- Archibald, J.D. 1991 Comments and reply on "‘Equable’ climates during Earth history?" *Geology* **19**, 539.
- Bailey, I.W. & Sinnott, E.W. 1916 The climatic distribution of certain types of angiosperm leaves. *Am. J. Bot.* **3**, 24–39.
- Bartels, W.S. 1980 Early Cenozoic reptiles and birds from the Bighorn Basin, Wyoming. In *Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming* (ed. P. D. Gingerich) (*Univ. Michigan Pap. Paleont.* **24**), pp. 73–79. Ann Arbor.
- Birkenmajer, J. 1990 Geochronology and climatostratigraphy of Tertiary glacial and interglacial successions on King George Island, South Shetland Islands (West Antarctica). In *Zentralblatt für Geologie und Paläontologie Teil I Workshop on Antarctic Geochronology* (ed. H. Miller), pp. 141–151. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.
- Bown, T.M. & Kraus, M.J. 1981 Lower Eocene alluvial paleosols (Willwood Formation, Northwest Wyoming, U.S.A.) and their significance for paleoecology, paleoclimatology and basin analysis. *Palaeogeogr. Palaeoclim. Palaeoecol.* **34**, 1–30.
- Brouwers, E.M., Clemens, W.A., Spicer, R.A., Ager, T.A., Carter, L.D. & Sliter, W.V. 1987 Dinosaurs on the North Slope, Alaska: high latitude, Latest Cretaceous environments. *Science, Wash.* **237**, 1608–1610.
- Brown, R.W. & Pecora, W.T. 1949 Paleocene and Eocene strata in the Bearpaw Mountains, Montana. *Science, Wash.* **109**, 487–489.
- Burnham, R.J. 1989 Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. *Rev. Palaeobot. Palyn.* **58**, 5–32.
- Cande, S.C. & Kent, D.V. 1992 A new geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. *J. geophys. Res.* **97**, 13917–13952.
- Carlquist, S. 1975 *Ecological strategies of xylem evolution*. (257 pages.) Berkeley, California: University of California Press.

- Chaney, R.W. & Sanborn, E.I. 1933 The Goshen flora of west central Oregon. *Carnegie Inst. Washington Publ.* **439**, 1–103.
- Christophel, D.C. & Greenwood D.R. 1988 A comparison of Australian tropical rainforest and Tertiary fossil leafbeds. *Proc. ecol. Soc. Aust.* **15**, 139–148.
- Collinson, M.E. & Hooker, J.J. 1987 Vegetational and mammalian faunal changes in the Early Tertiary of southern England. In *The origins of angiosperms and their biological consequences* (ed. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 259–304. Cambridge University Press.
- Creber, G.T. & Chaloner, W.G. 1985 Tree growth in the Mesozoic and early Tertiary and the reconstruction of palaeoclimates. *Palaeogeogr. Palaeoclim. Palaeoecol.* **52**, 35–60.
- Crowley, T.J., Hyde, W. T. & Short, D.A. 1989 Seasonal cycle variations on the supercontinent of Pangaea. *Geology* **17**, 457–460.
- Davis, J.M. & Taylor, S.E. 1980 Leaf physiognomy and climate: a multivariate analysis. *Quat. Res.* **14**, 337–350.
- Dettman, D.L. & Lohmann, K.C. 1993 Seasonal changes in Paleogene surface water delta ¹⁸O: fresh-water bivalves of western North America. *J. geophys. Res.* (In the press.)
- Dilcher, D.L. 1973 A paleoclimatic interpretation of the Eocene floras of southeastern North America. In *Vegetation and vegetational history of northern Latin America* (ed. A. Graham), pp. 39–59. Amsterdam: Elsevier Press.
- Dolph, G.E. & Dilcher, D.L. 1979 Foliar physiognomy as an aid in determining paleoclimate. *Palaeontographica Abt. B* **170**, 151–172.
- Fritz, W.J. & Harrison, S. 1985 Early Tertiary volcanoclastic deposits of the northern Rocky Mountains. In *Cenozoic paleogeography of the west-central United States* (ed. R. M. Flores & S. S. Kaplan), pp. 383–402. Denver, Colorado: Rocky Mountain Section Society of Economic Paleontologists and Mineralogists.
- Gartner, B.L., Bullock, S.H., Mooney, H.A., Brown, V.B. & Whitbeck, J.L. 1990 Water transport properties of vine and tree stems in a tropical deciduous forest. *Am. J. Bot.* **77**, 742–749.
- Gingerich, P.D. 1989 New earliest Wastachian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. *Univ. Michigan Pap. Paleont.* **28**, 1–97.
- Grande, L. 1984 Paleontology of the Green River Formation, with a review of the fish fauna. *Geol. Surv. Wyoming Bull.* **63**, 1–333.
- Greenwood, D.R. 1992 Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates. *Rev. Palaeobot. Palyn.* **71**, 149–190.
- Gregory, K.M. & Chase, C.G. 1992 Tectonic significance of paleobotanically estimated climate and altitude of the Late Eocene erosion surface, Colorado. *Geology* **20**, 581–585.
- Hickey, L.J. 1977 Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. *Geol. Soc. Am. Mem.* **150**, 1–181.
- Hutchison, J.H. 1982 Turtle, Crocodylian, and Champsosaur diversity changes in the Cenozoic of the north-central region of western United States. *Palaeogeogr. Palaeoclim. Palaeoecol.* **37**, 149–164.
- Imbrie, J. & Kipp, N.G. 1971 A new micropaleontological method for quantitative paleoclimatology: application to a late Pleistocene Caribbean core. In *The late Cenozoic glacial ages* (ed. K. K. Turekian), pp. 213–220. New Haven: Yale University Press.
- Janis, C.M. 1984 The use of fossil ungulate communities as indicators of climate and environment. In *Fossils and climate* (ed. P. Brenchley), pp. 85–104. London: John Wiley & Sons Ltd.
- Koch, P.L., Zachos, J.C. & Gingerich, P.D. 1991 Paleocene-Eocene climates in western North America: inferences from oxygen isotope analysis of mammal teeth and soil carbonates. *Geol. Soc. Am. Abstr. Prog.* **23**, 301.
- Lange, R.T. 1976 Fossil epiphyllous ‘germling’, their living equivalents and their palaeohabitat indicator value. *N. Jahrbuch f. Geologie u. Paläont. Abhand.* **151**, 142–165.
- Legendre, S. & Hartenberger, J.L. 1992 The evolution of mammalian faunas in Europe during the Eocene and Oligocene. In *Eocene-Oligocene climatic and biotic evolution* (ed. D. R. Prothero & W. A. Berggren), pp. 516–528. Princeton University Press.
- Legendre, S., Badgley, C. & Gingerich, P.D. 1991 Cenograms and environmental parameters for mammalian faunas. *J. Vert. Paleont.* **11** (3: suppl.), 42.
- MacGinitie, H.D. 1941 A Middle Eocene flora from the central Sierra Nevada. *Carnegie Inst. Washington Publ.* **534**, 1–94.
- MacGinitie, H.D. 1969 The Eocene Green River flora of northwestern Colorado and northeastern Utah. *Univ. Calif. Publ. Geol. Sci.* **83**, 1–202.
- MacGinitie, H.D. 1974 An early middle Eocene flora from the Yellowstone-Absaroka volcanic province, northwestern Wind River Basin, Wyoming. *Univ. Calif. Publ. Geol. Sci.* **108**, 1–103.
- Miller, K.G., Fairbanks, R.G. & Mountain, G.S. 1987 Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. *Paleoceanography* **2**, 1–19.
- Rea, D.K., Leinen, M. & Janecek, T.R. 1985 Geologic approach to the long-term history of atmospheric circulation. *Science, Wash.* **227**, 721–725.
- Read, J. & Hill, R.S. 1989 The response of some Australian temperate rain forest tree species to freezing temperatures and its biogeographical significance. *J. Biogeogr.* **16**, 21–27.
- Robert, C. & Chamley, H. 1991 Development of Early Eocene warm climates, as inferred from clay mineral variations in oceanic sediments. *Palaeogeogr. Palaeoclim. Palaeoecol.* **89**, 315–331.
- Rose, K.D. 1981 Composition and species diversity in Paleocene and Eocene mammal assemblages: an empirical study. *J. Vert. Paleont.* **1**, 367–388.
- Sakai, A. & Larcher, W. 1987 *Frost survival of plants: responses and adaptation to freezing stress*. (321 pages.) Berlin: Springer-Verlag.
- Sloan, L.C. & Barron, E.J. 1990 ‘Equable’ climates during Earth history? *Geology* **18**, 489–492.
- Sloan, L.C. & Barron, E.J. 1992 A comparison of Eocene climate model results to quantified paleoclimatic interpretations. *Palaeogeogr. Palaeoclim. Palaeoecol.* **93**, 183–202.
- Smedes, H.W. & Prostka, H.J. 1972 Stratigraphic framework of the Absaroka volcanic supergroup in the Yellowstone National Park region. *U.S. Geol. Surv. Prof. Pap.* **729-C**, 1–33.
- Smoot, J.P. 1983 Depositional subenvironments in an arid closed basin, the Wilkins Peak Member of the Green River Formation (Eocene), Wyoming, U.S.A. *Sedimentology* **30**, 801–827.
- Sokal, R.R. & Rohlf, F.J. 1969 *Biometry*. (869 pages.) San Francisco: W. H. Freeman & Co.
- Spotila, J.R., O’Connor, M.P., Dodson, P. & Paladino, F.V. 1991 Hot and cold running dinosaurs: body size, metabolism and migration. *Modern Geol.* **16**, 203–227.
- Stucky, R.K. 1992 Mammalian faunas in North America of Bridgerian to early Arikarean ‘Ages’ (Eocene and Oligocene). In *Eocene-Oligocene climatic and biotic evolution*

- (ed. D. R. Prothero & W. A. Berggren), pp. 464–493. Princeton University Press.
- Tiffney, B.H. 1985 The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the northern hemisphere. *J. Arnold Arb.* **66**, 243–273.
- Wheeler, E.A. & Baas, P. 1991 A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. *IAWA Bull.* **12**, 275–332.
- Wheeler, E.F., Scott, R.A. & Barghoorn, E.S. 1978 Fossil dicotyledonous woods from Yellowstone National Park, II. *J. Arnold Arb.* **59**, 1–26.
- Wilkinson, L. 1988 *SYSTAT: The system for statistics*. (687 pages.) SYSTAT, Inc. Evanston.
- Wing, S.L. 1991. Comment and reply on “‘Equable’ climates during Earth history?” *Geology* **19**, 539–540.
- Wing, S.L., Bown, T.M. & Obradovich, J.D. 1991 Early Eocene biotic and climatic change in interior western North America. *Geology* **19**, 1189–1192.
- Wolfe, J.A. 1979 Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the northern hemisphere and Australasia. *U.S. Geol. Surv. Prof. Pap.* **1106**, 1–37.
- Wolfe, J.A. 1985 Distribution of major vegetational types during the Tertiary. *Geophys. Mon.* **32**, 357–375.
- Wolfe, J.A. 1990 Paleobotanical evidence for a marked temperature increase following the Cretaceous/Tertiary boundary. *Nature, Lond.* **343**, 153–156.
- Wolfe, J.A. 1993 A method of obtaining climatic parameters from leaf assemblages. *U.S. Geol. Surv. Bull.* **2040**, 1–73.
- Wolfe, J.A. & Upchurch, G.R. Jr 1987 Leaf assemblages across the Cretaceous-Tertiary boundary in the Raton Basin, New Mexico and Colorado. *Proc. natn. Acad. Sci. U.S.A.* **84**, 5096–5100.
- Yemani, K. 1993 Contribution of Late Permian palaeogeography in maintaining a temperate climate in Gondwana. *Nature, Lond.* **361**, 51–54.