

Eocene continental climates and latitudinal temperature gradients

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ABSTRACT

Global climate during the Mesozoic and early Cenozoic is thought to have been warmer than at present, but there is debate about winter temperatures. Paleontological data indicate mild temperatures even at high latitudes and in mid-latitude continental interiors, whereas computer simulations of continental paleoclimates produce winter temperatures closer to modern levels. Foliar physiognomy and floristic composition of 23 Eocene floras from the interior of North America and Australia indicate cold month means generally $>2^{\circ}\text{C}$, even where the mean annual temperature (MAT) was $<15^{\circ}\text{C}$. Reconstructed Eocene latitudinal gradients of MAT are curvilinear but are about 0.4°C per 1° of latitude in continental interiors at mid-latitudes, much less than the $0.8\text{--}1.0^{\circ}\text{C}$ per 1° of latitude observed in eastern and central North America today, but similar to modern gradients in the Southern Hemisphere mid-latitudes and on the west coast of North America. Latitudinal temperature gradients reconstructed here are broadly representative of Eocene climates, showing that the discrepancy between proxy data and simulations will not be resolved by regional adjustments to paleogeography or reinterpretation of individual fossil assemblages. Similar discrepancies between proxy data and general circulation model simulations for other time periods suggest that there is a basic flaw with the way climate models simulate heat transport to, or loss from, continental surfaces.

INTRODUCTION

Isotopic marine records and paleontological evidence indicate that the early Eocene was the warmest part of the Cenozoic (Miller et al., 1987) and that latitudinal sea-surface temperature (SST) gradients were shallower than at present (Zachos et al., 1994). Early general circulation models (GCMs) of Eocene continental climates predicted lower mean annual temperatures (MAT) and greater thermal seasonality for continental interiors than inferred from fossil evidence, cold month means (CMM) being substantially below freezing (Sloan and Barron, 1990, 1992).

More recent modeling studies have given MAT estimates close to paleontologically inferred values and support shallow Eocene latitudinal temperature gradients, but there is still broad disagreement between proxy data and simulations of CMM values (modeling—Sloan and Barron, 1992; Sloan, 1994; proxy data—Hutchison, 1982; Wing and Greenwood, 1993; Markwick, 1994). Similar differences between simulations and proxy data for Permian Gondwana have been in part attributed to the effect of lakes and uncertainty about paleocoastlines and paleoelevations of interior regions (Yemani, 1993). Recent simulations show that the Eocene Green River Lake system would have raised minimum winter temperatures in a small downwind area (Sloan, 1994). In this paper we summarize the geographic extent of equable climates (i.e., those with little seasonal variation in temperature) during the Eocene to see if regional paleogeography can account for equable continental interiors.

North America and Australia were large land areas with well-defined continental interiors during the Paleogene. The latitude of North America has changed little since the Eocene, but Australia has drifted from high to middle southern latitudes since the early Paleogene (Fig. 1). Topography in Australia was subdued during Paleogene time (Quilty, 1994), removing paleoaltitude as a potential source of confusion in reconstructing climate.

METHODS OF PALEOCLIMATIC INFERENCE

Plant populations persist only if all stages of the life cycle can tolerate the local climate; therefore, the distribution of plants is influenced strongly by climate. Plant megafossils, especially leaves, are generally deposited locally and reflect local vegetation and climate (Greenwood, 1992). Paleoclimate has been inferred from fossil plants on the basis of the climatic preferences of nearest living relatives of taxa found in the fossil assemblage and correlations between dicot leaf physiognomy and climate parameters. We apply both approaches here.

Temperature Limits of Palms

Palms cannot withstand sustained freezes and are today limited to areas that are largely free of frost (Fig. 2). This frost intolerance is due to their soft, water-rich tissue, their exposed growth point(s), and their lack of physiological mechanisms for frost tolerance. Only a few degrees of cold hardening can be induced, and no species shows much seasonal fluctuation in frost sensitivity (Sakai and Larcher, 1987). The most cold-tolerant palm species (e.g., *Trachycarpus for-*

tunei) show differential freezing tolerance at different stages of life and between different organs: adult palms can survive at -10 to -12°C for a few hours but are killed by sustained freezes; roots and seedlings are killed at -1.5 to -8°C , and all palms are killed by ground frost (Sakai and Larcher, 1987). Frost sensitivity of palms restricts them to climates with MAT $>10^{\circ}\text{C}$, CMM $>5^{\circ}\text{C}$, and yearly minimum temperature $> -10^{\circ}\text{C}$ (Fig. 2).

Nearest living relative-based paleoclimatic inference can be unreliable because lineages evolve and because the nearest living relatives of some Tertiary taxa (e.g., *Metasequoia*) no longer occupy the range of climatic conditions they can tolerate (Wolfe, 1979). This is likely not a problem with palms, which are morphologically and taxonomically diverse and yet uniformly limited in their cold hardiness. Furthermore, Eocene palms represent modern tribes (e.g., Corypheae, Nypoideae), and have leaf, stem, and root anatomy indistinguishable from that of modern palms (Daghlian, 1978; Schaal and Ziegler, 1992), indicating that the climatic tolerances of Paleogene palms are well represented by living species. Fossil palms are reliable “threshold” measures of paleo-MAT and CMM. Global climatic cooling in the Cenozoic may have favored evolution of palms with greater cold tolerance, so palm-based estimates of minimum temperature are more likely to be too cool than too warm.

Foliar Physiognomy

Leaf margin analysis is based on the positive correlation between MAT and the proportion of entire-margined woody dicot species in 34 extant East Asian mesic forests (Wolfe, 1979). Leaf margin analysis has been criticized for being based on floral lists, not vegetation samples, and for ignoring the role of soil and moisture in controlling physiognomy (Dolph and Dilcher, 1979). However, data from North American and Australian forests have shown similar though less-precise correlations between leaf margin type and MAT (Dolph and Dilcher, 1979; Greenwood, 1992).

The CLAMP (climate analysis multivariate program) method developed by Wolfe (1993) improves on leaf margin analysis by describing foliar physiognomy with multiple size, shape, and margin states. The CLAMP data set is derived largely from modern vegetation in North America and Central

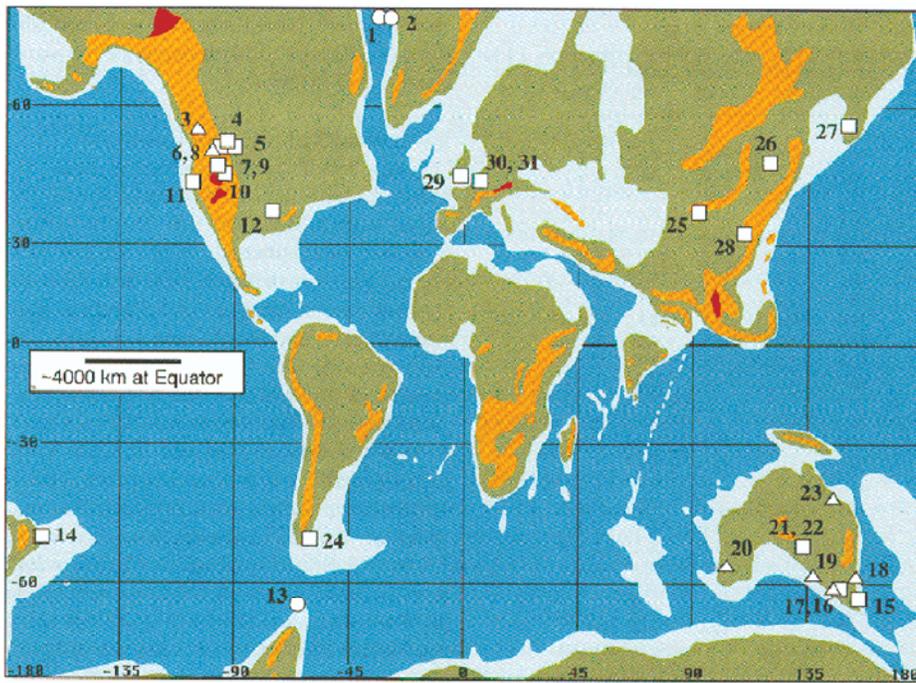


Figure 1. Eocene reconstruction (from PGIS/Mac™) showing distribution of megafloras providing quantitative paleoclimate estimates, and frost intolerant plants. Squares = palms, triangles = cycads, gingers, or tree ferns, and circles = no frost intolerant plants; green = lowlands, yellow = uplands, red = higher upland areas. Numbers 1–23 are keyed to Table 1; 24—Tierra del Fuego, 25—Zhangye, 26—Yilan, 27—Kamchatka, 28—Sorachi, 29—London Clay, 30—Messel, 31—Geiseltal.

America. Wolfe used reciprocal averaging ordination to study the relation of 29 leaf characters to seven climatic parameters, including MAT, CMM, and mean annual range of temperature (MART). We have analyzed the CLAMP data set using multiple regression to develop a set of equations to predict MAT, CMM, and MART on the basis of a subset of the physiognomic variables (Wing and Greenwood, 1993). A similar analysis by Gregory and Chase (1992) was based on an earlier version of the CLAMP data set.

EOCENE CLIMATE ESTIMATES

North America

Multiple regression analyses of North American Eocene floras estimated MATs in the range 9–24 °C (Table 1). Inferred thermal seasonality was moderate for all sites (MART 8–19 °C), and winter temperatures were above freezing (CMM >0 °C except for Arctic sites), even where MAT estimates were 10–15 °C. CMM estimates for the Bears Paw, upper Willwood, Camels Butte, Wind River, and Kisinger Lakes assemblages are particularly important for understanding the influence of a possible Green River Lake effect. These sites are 120–650 km north of the lake, and the first three pre-date major lake development in the Green River basin. CMM at these sites is constrained by palms and crocodilians to have been >5 °C, although the multiple regres-

sion estimates of CMM at Bears Paw and Camels Butte are lower. The Arctic floras give CMM estimates from –2.0 to –0.8 °C, but the presence of crocodilians in the Arctic implies a minimum CMM of 5–7 °C (Markwick, 1994). The discrepancy between nearest living relative and multiple regression model estimates of CMM for floras north of about 50°N paleolatitude probably results from deciduousness induced by low winter light; floras that were deciduous in response to light rather than winter cold may produce physiognomy-based temperature estimates that are too low (Basinger et al., 1994).

The North American paleotemperature estimates show expected trends; MAT and

CMM decrease with increasing latitude, and interior sites have greater MART than coastal sites (Figs. 1 and 3). The coolest estimates are derived from floras (Yellowstone and Bears Paw) that are inferred to be upland on the basis of geological evidence (Fritz and Harrison, 1985; Fig. 1). Our estimates at lower latitudes (e.g., Puryear) are also consistent with nearest living relative estimates from a mangrove biota found at a similar latitude in Texas (Westgate and Gee [1990] estimated SST of 24 °C and CMM of 19 °C).

Although our paleoclimate estimates show the expected trends, leaf margin analysis and nearest living relative analyses of some of the floras used in this study have given MAT and CMM estimates 2–3 °C higher than ours (MacGinitie, 1974; Hickey, 1977). The multiple regression approach yields cooler estimates because it is sensitive to the low proportions of species in Eocene floras with emarginate apices, and because of deciduousness induced by light rather than temperature seasonality. Particularly at high latitudes, nearest living relative-based minimums of the CMM are probably more reliable than those based on physiognomy.

Australia

Estimates of MART (12–22 °C) and CMM (5–15 °C) suggest that no area of Australia (at sea level) had significant freezing temperatures (Table 1). The MAT and CMM multiple regression estimates from Australian floras are consistent with previous physiognomic and nearest living relative analyses, including the presence of palms, particularly the thermophilic mangrove palm *Nypa* (Greenwood, 1994). The dominance of Lauraceae at many of these sites and the presence of crocodiles throughout the Eocene (Willis and Molnar, 1991) are also consistent with our MAT and CMM estimates. Eocene palynofloras in southwestern Australia, and eastward along the coast, indicate widespread development of man-

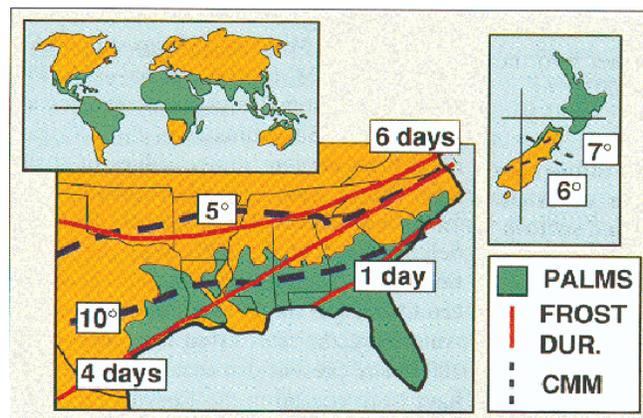


Figure 2. Modern distribution of palms worldwide and detail for eastern United States (*Sabal* spp.) and New Zealand (*Rhopalostylis sapida*) showing climatic limits to palm distribution. Solid red lines = average duration (DUR.) of longest annual frost; dashed blue lines = cold month mean (CMM) temperature in °C. Data on palm distribution from Moore (1973), Little (1977), and Wardle (1991); climatic data from Gentilli (1971) and Bryson and Hare (1974).

TABLE 1. CLIMATE ESTIMATES FOR EARLY AND MIDDLE EOCENE FLORAS

Site	Latitude	Paleoaltitude (m)	No. of species	MAT1 (°C)	MAT2 (°C)	MART (°C)	CMM (°C)	NLR s*
North America								
1 Axel Heiberg-188	79°55'N	200	12	9.3	--	13.8	-0.8	3, 4
2 Ellesmere-111	79°44'N	<500	15	8.2	--	14.0	-2.0	3, 4
3 McAbee	50°47'N	500	22	10.7	--	13.3	1.7	2, 3, 4
4 Bears Paw	48°30'N	500-1000	32	10.4	11.2	13.6	0.6	1, 2, 3, 4
5 Camels Butte	46°48'N	<200	15	11.2	9.1	8.2	3.5	1, 2, 3
6 Yellowstone-Sepulcher	44°54'N	1000	25	10.9	10.5	15.9	1.9	2, 3, 4
7 Kisinger Lakes	43°48'N	500-1000	36	15.7	18.6	17.5	6.7	1, 2, 3, 6
8 Upper Willwood	43°48'N	500-1000	30	15.3	17.0	10.0	6.3	1, 2, 6
9 Wind River	43°42'N	500-1000	39	16.5	18.6	17.1	8.5	1, 2, 6
10 Green River	43°33'N	500-1000	53	14.3	15.2	18.7	6.1	1, 2, 6
11 Chalk Bluffs	39°10'N	<200	67	14.4	17.1	9.4	5.6	1, 2
12 Puryear-Buchanan	36°26'N	<200	47	23.9	--	10.2	16.1	1, 2, 6
Australia and other Southern Hemisphere sites								
13 Seymour Island	64°15'S	<200	10	10.0	--	--	--	3, 4
14 Livingstone, NZ	44°58'S	<200	13	13.0	--	15.5	3.5	1, 4
15 Hastings	41°01'S	500	7	16.2	--	22.1	8.6	1, 2, 4
16 Anglesea	38°25'S	<200	28	17.1	--	13.9	8.2	1, 2, 4, 6
17 Deans Marsh	38°24'S	500	18	12.2	--	13.4	4.6	2, 6
18 Nerriga	35°07'S	500	24	19.4	--	16.4	10.2	2, 6
19 Golden Grove	34°47'S	200	21	18.7	--	17.7	10.2	2, 4, 6
20 West Dale†	32°14'S	<200	29	17.9	--	18.3	10.4	2, 4, 5
21 Poole Creek	29°30'S	SL	11	21.1	--	13.1	14.7	1, 2, 5
22 Nelly Creek	29°19'S	SL	14	18.9	--	12.1	12.5	1, 2, 4, 5
23 Moranbah-Goonnyella	22°20'S	500	18	20.7	--	13.4	13.2	2, 4

Note: Climate parameters estimated from multiple regression models (Wing and Greenwood, 1993), except for MAT2, which is based on leaf margin analysis. Standard errors: MAT1 ± 2.0 °C; MAT2 ± 1.0 °C; CMM ± 3.6 °C; MART ± 5.1 °C. MAT is mean annual temperature, CMM is cold month mean temperature, MART is mean annual range of temperature (difference between warm month mean and cold month mean), and NLR is nearest living relative.

*1 - Palms (MAT >10 °C, CMM >5 °C); 2 - large monocots, cycads, or treeferns (CMM >0 °C); 3 - deciduous dicots (seasonality of light, temperature, or precipitation); 4 - conifers with moderate frost tolerance (e.g., CMM >-10 °C); 5 - scleromorphs; 6 - diverse Lauraceae (MAT >15 °C).

†Age may be early Eocene to Oligocene.

cene, but only North America and Australia have produced abundant evidence for warm continental interiors.

Latitudinal Temperature Gradients

Using modern meteorological data, we reconstructed latitudinal gradients of the MAT and CMM for the Northern and Southern hemispheres, along east and west coasts, and north-south transects through the continental interiors of Antarctica, Australia, Africa, and North America and South America (Fig. 3). Modern data have been plotted as an envelope, the combined interior and coastal data trends being expressed as a polynomial regression. The MAT decreases poleward in the Southern Hemisphere in an almost linear manner at a gradient of 0.4 °C/1° latitude (west coasts) to 0.6 °C/1° latitude (interior and east coasts), to high-middle to high latitudes, where the gradient steepens. The MAT gradient along the North American west coast is mostly linear at about 0.4 °C/1° latitude from the equator to about 50°–60°N, where a significant steepening of the gradient to 1.2 °C/1° latitude occurs. The North American interior and east coast gradients of the MAT and CMM are almost linear, with gradients of 1.0 °C/1° latitude and 0.8 °C/1° latitude. The principal reason for nonlinear gradients in both hemispheres is a significant decrease in CMM (but not warm month mean) at the points of deflection.

Our estimates of Eocene temperatures have gaps along the latitudinal transects, but trends can be examined. The most dramatic observation is the low latitudinal temperature gradient in the Eocene, caused by high values of both MAT and CMM at middle to high latitudes (Fig. 3). If, as we have argued, the North American foliar physiognomic estimates of MAT and CMM are 2–3 °C too cool, then Eocene thermal gradients for the Northern Hemisphere at middle latitudes (polynomial regression) would have been about 0.4 °C/1° latitude. There is little difference between the latitudinal gradient of MAT estimated from continental floras and the gradient estimated from $\delta^{18}\text{O}$ data (Fig. 3; Zachos et al., 1994). These are similar to the “low-gradient” GCM simulations of Eocene climate (Sloan and Barron, 1992). The gradient estimated for Eocene continents is similar to the gradient seen along the coasts of Southern Hemisphere continents today at low to middle latitudes, and less than half of current gradients in the interior of North America. Paleobotanical evidence for tropical temperatures in the Eocene suggests warm rather than cool tropics, with MAT and CMM at 9°N paleolatitude being within 2–3 °C of present values (Graham, 1994). Paleobotanical data confirm

groves, including *Nypa* (Truswell, 1993). These floras imply SST >20 °C adjacent to much of southern Australia at paleolatitude 50°S.

Many of the plant taxa in the Australian megaforas are today restricted to, or most speciose in, high-rainfall equable climates with a MAT of 18–22 °C (Kershaw and Nix, 1988). Greenhouse experiments with nearest living relatives of key Australian Eocene genera indicate that the modern tolerances of these taxa have a strong physiological basis (Read and Hill, 1989), and are therefore likely to reflect Eocene tolerances. Most of the Australian megaforas analyzed were near Eocene coasts, but the Nelly Creek and Poole Creek floras are indicators of paleoclimate in the interior. Leaf cuticles and pollen from these sites are similar to those in coeval sites in basins even farther into the Australian interior (Truswell, 1993).

Other Areas

At middle to high latitudes throughout the world there is evidence for warm climates in the Eocene. Tropical and subtropical elements are common in the early Eocene London Clay flora, including *Nypa* and other palms, mangroves, and zingiberaleans (Collinson, 1983). Thermophilic fauna and flora in Germany indicate MAT >20 °C and CMM >10 °C during the early and middle Eocene (Schaal and Ziegler, 1992). Eocene

palms have been reported from Kamchatka (Budantsev, 1992), inland north China (Guo, 1990), northern Japan (Tanai, 1992), and Tierra del Fuego (Romero, 1993). In China vegetation as far as 50°N paleolatitude was dominantly broad-leaved evergreen, implying a CMM >1 °C (Guo, 1990; Tanai, 1992). The paleogeographic positions of these points are plotted in Figure 1.

Foliar physiognomy and presence of *Nypa* indicate MAT of 15–20 °C, and CMM >10 °C for New Zealand middle Eocene floras at paleolatitudes of 45°–55°S (Pocknall, 1990; Pole, 1994). Eocene floras from the Antarctic peninsular (Birkenmajer and Zastawniak, 1986; Case, 1988) and Transantarctic Mountains (Stilwell et al., 1993; M. Pole, 1994, personal commun.) contain *Araucaria* and *Nothofagus*, suggesting MAT >6 °C, and CMM >0 °C, at 65°–75°S. Paleobotanical estimates for Antarctica are consistent with SST estimates of 8–12 °C, derived from oxygen isotope values of shells from James Ross Island (Ditchfield et al., 1994), and winter SSTs of 9 °C for the Weddell Sea (Stott et al., 1990). With the exception of the Zhangye and Yilan sites in northern China and the Mount Discovery site in Antarctica, the sites listed here are within 100 km of present-day coastlines, and may have been coastal in the Eocene. High-latitude warmth was clearly global in the Eo-

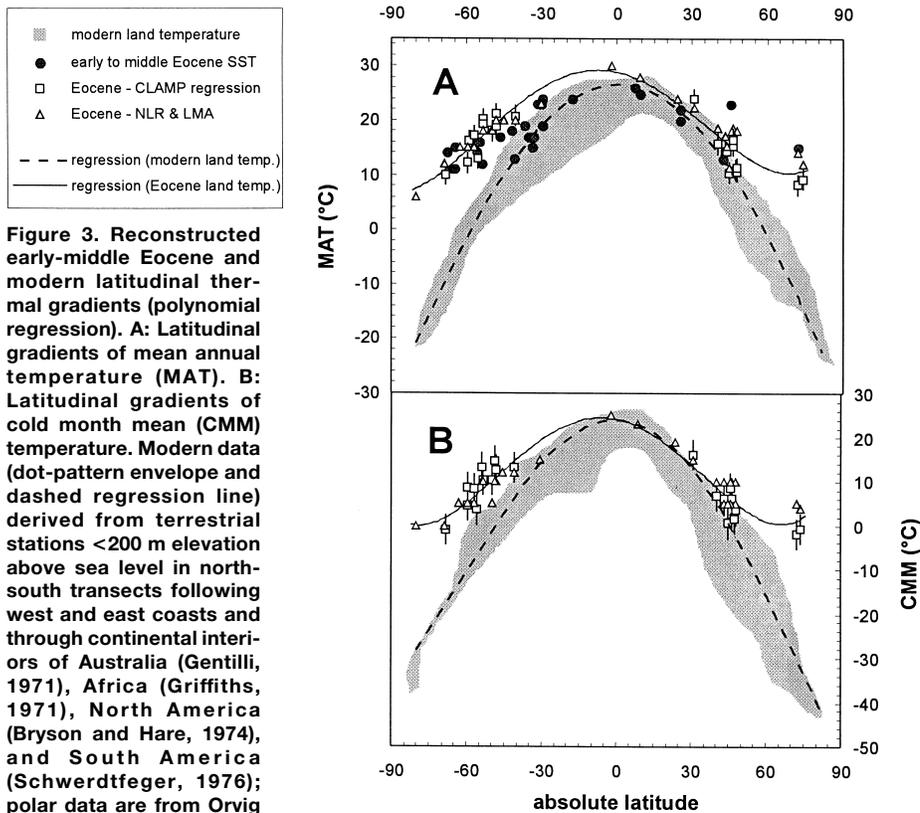


Figure 3. Reconstructed early-middle Eocene and modern latitudinal thermal gradients (polynomial regression). A: Latitudinal gradients of mean annual temperature (MAT). B: Latitudinal gradients of cold month mean (CMM) temperature. Modern data (dot-pattern envelope and dashed regression line) derived from terrestrial stations <200 m elevation above sea level in north-south transects following west and east coasts and through continental interiors of Australia (Gentili, 1971), Africa (Griffiths, 1971), North America (Bryson and Hare, 1974), and South America (Schwerdtfeger, 1976); polar data are from Orvig (1970). Dot-pattern circles = inferred early-middle Eocene sea-surface temperature (SST) values (Zachos et al., 1994). CLAMP = Climate Analysis Multivariate Program; NLR = nearest living relative; LMA = leaf margin analysis.

that the Eocene world had a much more even distribution of heat across latitude than at present.

Proxy Data-Model Discrepancies

A key area of dispute between earlier GCM simulations of Eocene climate and the terrestrial paleontological proxy record is the latitudinal and geographic extent of sub-freezing temperatures in continental interiors (Sloan and Barron, 1990, 1992; Wing, 1991; Wing and Greenwood, 1993). The latest GCM simulations for Eocene North America (Sloan, 1994) in which a CO_2 value twice that of present was used (Green River Formation Eocene Lake [LAKE] case) predicted a zone of winter freezing (CMM $< 0^\circ\text{C}$) covering most of the interior of the continent north of 40°N , except in areas close to the lake. The freezing zone was displaced to about 50°N in the simulation using a CO_2 value six times that of present. Only the warmest of these scenarios begins to be consistent with proxy data, because floras north of the Green River Lake to about 50°N contain palms, indicating CMM $> 5^\circ\text{C}$. The regression line for CMM by latitude (Fig. 3) implies that in North America CMM $< 0^\circ\text{C}$ would have occurred only north of about 60°N and south of the Arctic Ocean coast. In this region, CMM would

have been between 2°C and -2°C , and MAT would be $8\text{--}15^\circ\text{C}$. This result demonstrates continuing disagreement between the proxy record and model prediction, the extent and degree of freezing within North America being much less severe (i.e., CMM 2 to -2°C vs. 0 to -10°C) than predicted by the model.

All lines of paleontological proxy evidence indicate that in the early to middle Eocene North America and Australia had equable climates lacking severe frost in both interior and coastal regions. Discrepancies between the different lines of paleontological proxy evidence are small. MAT is estimated by all methods to be greater in the Eocene at middle to high palaeolatitudes than in comparable areas today ($15\text{--}23^\circ\text{C}$ at middle latitudes, about 10°C at sea level in high latitudes). CMMs are estimated to have been $> 5^\circ\text{C}$ and perhaps $> 10^\circ\text{C}$ throughout all of Australia in the Eocene, and in most of North America.

CONCLUSIONS

For at least the first 10 m.y. of the Eocene, a large part of Earth's surface, including continental interiors, had climates with much higher than modern winter temperatures. Latitudinal gradients of MAT and CMM in Eocene continental interiors were

similar to Eocene SST gradients, and to present-day Southern Hemisphere mid-latitude values. Some recent simulations (Sloan, 1994) have produced predictions close to the estimates given here, but these "warm" simulations have been achieved either by modeling very high partial pressures of CO_2 (six times present), which are not supported by proxy data or carbon cycle modeling (Cerling, 1991; Berner, 1991), or by including lakes, or both. There is geologic evidence for large lakes in the Green River basin from the late-early through middle Eocene, but the "lake effect" does not explain warm proxy data points from far north of the Green River basin or the global extent of warm climate proxies at high latitudes (Sloan, 1994; Sloan et al., 1995).

Given the widespread and long-lasting evidence for equable climates in continental interiors and coastal regions alike, the discrepancy between Eocene models and data is likely to represent a major flaw in the models (Walker and Sloan, 1992). This flaw may relate to simulated heat flow to and from continental surfaces, and/or to overly simplified modeling of paleovegetation feedbacks, as has been demonstrated in studies of the Holocene boreal forest (Foley et al., 1994). The world of the models is still too much like the present.

ACKNOWLEDGMENTS

We thank James Basinger, David Dilcher, Kirk Johnson, Neville Pledge, Mike Pole, Lisa Sloan, Paul Willis, and Jack Wolfe for advice. Cathy Greenwood and Jim McRea provided technical assistance. This work was completed during a Smithsonian postdoctoral fellowship at the National Museum of Natural History (Greenwood), and is Evolution of Terrestrial Ecosystems contribution 28.

REFERENCES CITED

- Basinger, J. F., Greenwood, D. R., and Sweda, T., 1994, Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation, in Boulter, M. C., ed., Arctic plants and climates: 65 million years of change: Berlin, Springer-Verlag.
- Berner, R. A., 1991, A model for atmospheric CO_2 over Phanerozoic time: American Journal of Science, v. 291, p. 339-376.
- Birkenmajer, K., and Zastawniak, E., 1986, Plant remains of the Dufayel Island Group (early Tertiary?), King George Island, South Shetland Islands (West Antarctica): Acta Palaeobotanica, v. 26, p. 33-54.
- Bryson, R. A., and Hare, F. K., 1974, Climates of North America (World Survey of Climatology, Volume 11): Amsterdam, Elsevier, 420 p.
- Budantsev, L. Y., 1992, Early stages of formation and dispersal of the temperate flora in the boreal region: Botanical Reviews, v. 58, p. 1-48.
- Case, J. A., 1988, Paleogene floras from Seymour Island, Antarctic Peninsula, in Feldmann, R. M., and Woodburne, M. O., eds., Geology and paleontology of Seymour Island, Antarctic Peninsula: Geological Society of America Memoir 169, p. 523-530.

- Cerling, T. E., 1991, Carbon dioxide in the atmosphere: Evidence from Cenozoic and Mesozoic paleosols: *American Journal of Science*, v. 291, p. 377–400.
- Collinson, M. E., 1983, Fossil plants of the London Clay: *Palaeontological Association Field Guides to Fossils*, No. 1, 121 p.
- Daghlian, C. P., 1978, Coryphoid palms from the Lower and Middle Eocene of southeastern North America: *Palaeontographica*, Abt. B, v. 166, p. 44–82.
- Ditchfield, P. W., Marshall, J. D., and Pirrie, D., 1994, High latitude palaeotemperature variation: New data from the Tithonian to Eocene of James Ross Island, Antarctica: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 107, p. 79–101.
- Dolph, G. E., and Dilcher, D. L., 1979, Foliar physiognomy as an aid in determining palaeoclimate: *Palaeontographica*, Abt. B, v. 170, p. 151–172.
- Foley, J. A., Kutzbach, J. E., Coe, M. T., and Levis, S., 1994, Feedbacks between climate and boreal forests during the Holocene epoch: *Nature*, v. 371, p. 52–54.
- Fritz, W. J., and Harrison, S., 1985, Early Tertiary volcanoclastic deposits of the northern Rocky Mountains, in Flores, R. M., and Kaplan, S. S., eds., *Cenozoic paleogeography of the west-central United States*: Denver, Colorado, Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists, p. 383–402.
- Gentilli, J., 1971, Climates of Australia and New Zealand (*World Survey of Climatology*, Volume 13): Amsterdam, Elsevier, 405 p.
- Graham, A., 1994, Neotropical Eocene coastal floras and $^{18}\text{O}/^{16}\text{O}$ -estimated warmer vs. cooler equatorial waters: *American Journal of Botany*, v. 81, p. 301–306.
- Greenwood, D. R., 1992, Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates: *Review of Palaeobotany and Palynology*, v. 71, p. 149–190.
- Greenwood, D. R., 1994, Palaeobotanical evidence for Tertiary climates, in Hill, R. S., ed., *History of the Australian vegetation, Cretaceous to Recent*: Cambridge, United Kingdom, Cambridge University Press, p. 44–59.
- Gregory, K. M., and Chase, C. G., 1992, Tectonic significance of paleobotanically estimated climate and altitude of the late Eocene erosion surface, Colorado: *Geology*, v. 20, p. 581–585.
- Griffiths, J. F., 1971, Climates of Africa (*World Survey of Climatology*, Volume 10): Amsterdam, Elsevier, 604 p.
- Guo, S.-X., 1990, A brief review on megafossil successions and climatic changes of the Cretaceous and early Tertiary in China, in Knobloch, E., and Kvaček, Z., eds., *Paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary*: Prague, Geological Survey, p. 23–38.
- Hickey, L. J., 1977, Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota: *Geological Society of America Memoir* 150, 181 p.
- Hutchison, J. H., 1982, Turtle, crocodylian, and champsosaur diversity changes in the Cenozoic of the north-central region of western United States: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 37, p. 149–164.
- Kershaw, A. P., and Nix, H. A., 1988, Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant taxa: *Journal of Biogeography*, v. 15, p. 589–602.
- Little, E. L., 1977, Atlas of United States trees, Volume 4. Minor eastern hardwoods: U.S. Department of Agriculture Forest Service Miscellaneous Publication 1342, 230 p.
- MacGinitie, H. D., 1974, An early middle Eocene flora from the Yellowstone-Absaroka volcanic province, northwestern Wind River Basin, Wyoming: *University of California Publications in Geological Sciences*, v. 108, 103 p.
- Markwick, P., 1994, “Equability,” continentality, and Tertiary “climate”: The crocodylian perspective: *Geology*, v. 22, p. 613–616.
- Miller, K. G., Fairbanks, R. G., and Mountain, G. S., 1987, Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion: *Paleoceanography*, v. 2, p. 1–19.
- Moore, M. E., 1973, Major groups of palms and their distribution: *Gentes Herbarium*, v. 11, p. 27–141.
- Orvig, S., 1970, Climates of polar regions (*World Survey of Climatology*, Volume 14): Amsterdam, Elsevier, 370 p.
- Pocknall, D. T., 1990, Palynological evidence for the early to middle Eocene vegetation and climate history of New Zealand: *Review of Palaeobotany and Palynology*, v. 65, p. 57–69.
- Pole, M., 1994, An Eocene macroflora from the Taratu Formation at Livingstone, North Otago, New Zealand: *Australian Journal of Botany*, v. 42, p. 341–367.
- Quilty, P. G., 1994, The background: 144 million years of Australian palaeoclimate and palaeogeography, in Hill, R. S., ed., *History of the Australian vegetation, Cretaceous to recent*: Cambridge, United Kingdom, Cambridge University Press, p. 14–43.
- Read, J., and Hill, R. S., 1989, The response of some Australian temperate rain forest tree species to freezing temperatures and its biogeographical significance: *Journal of Biogeography*, v. 16, p. 21–27.
- Romero, E. J., 1993, South American paleofloras, in Goldblatt, P., ed., *Biological relationships between Africa and South America*: New Haven, Connecticut, Yale University Press, p. 62–85.
- Sakai, A., and Larcher, W., 1987, Frost survival of plants: Responses and adaptation to freezing stress: Berlin, Springer-Verlag, p. 1–321.
- Schaal, S., and Ziegler, W., eds., 1992, *Messel. An insight into the history of life and of the Earth*: Oxford, United Kingdom, Clarendon Press, 322 p.
- Schwerdtfeger, F., 1976, Climates of South America (*World Survey of Climatology*, Volume 12): Amsterdam, Elsevier, 367 p.
- Sloan, L. C., 1994, Equable climates during the early Eocene: Significance of regional paleogeography for North American climate: *Geology*, v. 22, p. 881–884.
- Sloan, L. C., and Barron, E. J., 1990, “Equable” climates during Earth history?: *Geology*, v. 18, p. 489–492.
- Sloan, L. C., and Barron, E. J., 1992, A comparison of Eocene climate model results to quantified paleoclimatic interpretations: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 93, p. 183–202.
- Sloan, L. C., Walker, J. C. G., and Moore, T. C., Jr., 1995, Possible role of oceanic heat transport in early Eocene climate: *Paleoceanography*, v. 10, p. 347–356.
- Stilwell, J. D., Levy, R. H., and Harwood, D. M., 1993, Preliminary paleontological investigation of Tertiary glacial erratics from the McMurdo Sound region, East Antarctica: *Antarctic Journal of the United States*, v. 28, p. 16–19.
- Stott, L. D., Kennett, J. P., Shackleton, N. J., and Corfield, R. M., 1990, The evolution of Antarctic surface waters during the Paleogene: Inferences from the stable isotopic composition of planktonic foraminifers, ODP Leg 113, in Barker, P. F., Kennett, J. P., et al., *Proceedings of the Ocean Drilling Program, Scientific results, Volume 113: College Station, Texas, Ocean Drilling Program*, p. 849–863.
- Tanai, T., 1992, Tertiary vegetational history of East Asia: *Mizunami Fossil Museum Bulletin*, v. 19, p. 125–163.
- Truswell, E. M., 1993, Vegetation changes in the Australian Tertiary in response to climatic and phytogeographic forcing factors: *Australian Systematic Botany*, v. 6, p. 533–558.
- Walker, J. C. G., and Sloan, L. C., 1992, Something is wrong with climate theory: *Geotimes*, v. 37, no. 6, p. 16–18.
- Wardle, P., 1991, *Vegetation of New Zealand*: New York, Cambridge University Press, 672 p.
- Westgate, J. W., and Gee, C. T., 1990, Paleoeecology of a middle Eocene mangrove biota (vertebrates, plants, and invertebrates) from southwest Texas: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 78, p. 163–177.
- Willis, P. M. A., and Molnar, R. E., 1991, A new middle Tertiary crocodile from Lake Palankarina, South Australia: *South Australian Museum Records*, v. 2, p. 39–55.
- Wing, S. L., 1991, “Equable” climates during Earth history?: *Comment: Geology*, v. 19, p. 539–540.
- Wing, S. L., and Greenwood, D. R., 1993, Fossils and fossil climates: The case for equable continental interiors in the Eocene: *Royal Society of London Philosophical Transactions*, ser. B, v. 341, p. 243–252.
- 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. Geological Survey Professional Paper 1106, 37 p.
- Wolfe, J. A., 1993, A method of obtaining climatic parameters from leaf assemblages: *U.S. Geological Survey Bulletin* 2040, p. 1–71.
- Yemane, K., 1993, Contribution of Late Permian palaeogeography in maintaining a temperate climate in Gondwana: *Nature*, v. 361, p. 51–54.
- Zachos, J. C., Stott, L. D., and Lohmann, K. C., 1994, Evolution of early Cenozoic marine temperatures: *Paleoceanography*, v. 9, p. 353–387.

Manuscript received April 6, 1995
 Revised manuscript received July 19, 1995
 Manuscript accepted July 28, 1995