

OXYGEN ISOTOPE AND PALEOBOTANICAL ESTIMATES OF TEMPERATURE AND $\delta^{18}\text{O}$ -LATITUDE GRADIENTS OVER NORTH AMERICA DURING THE EARLY EOCENE

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ABSTRACT. Empirical estimates of climate parameters such as mean annual temperature (MAT) are essential to describe both ancient climate and to ground truth climate model simulations of past climates. In terrestrial settings, no single proxy record is able to provide detailed temporal yet geographically widespread information, and it thus becomes essential that paleoclimatic information obtained from different proxies be comparable. As an example of how to compare estimates, and to illustrate what can be learned by doing so, we measured oxygen isotope ratios of phosphate in the tooth enamel of fossil mammals and the body scales of freshwater fish in order to estimate the mean annual temperature (MAT) in which they lived. The samples were collected from Paleogene rocks of the Bighorn, Green River, and Powder River basins of Wyoming. Earliest Eocene samples provide MAT estimates that are similar to MAT estimates for the same times and areas obtained from leaf margin analysis. Furthermore, isotopic data from the Paleocene Eocene Thermal Maximum (PETM), which has not yet yielded fossil floras, indicate a significantly higher MAT of 26°C. We also used temperature estimates obtained by both methods to investigate paleoelevation and to reconstruct geographic patterns of MAT over North America for the early Eocene. Larger Laramide basins have higher temperatures and lower inferred elevations compared to associated volcanic highlands where cooler temperatures are consistent with substantial elevations. In turn, latitudinal gradients in temperature indicate that warming centered on polar regions played an important role during the Eocene “hothouse”. Lastly, we show that the reconstructed Eocene relation between oxygen isotope ratios of precipitation and MAT is significantly different from the modern relation between these two variables. Because the relation has changed over time, the modern correlation should not be used to estimate paleo-MAT from measurements of oxygen isotope ratios in fossil material.

INTRODUCTION

Terrestrial climate plays a critical role in mineral weathering, in biogeochemical cycling, and in the evolution of plants and animals, and it is therefore essential that geoscientists be able to both describe and understand the nature of terrestrial climate change over time. Such studies of terrestrial climate change fall generally into two categories. One centers on the use of proxy records to provide quantitative descriptions of past climatic conditions. These empirical records can be obtained by many means, including the statistical analyses of large samples of well-preserved fossil leaves (for example, Wolfe, 1979; Wolfe and Upchurch, 1987; Wing and others, 1991), animal remains (for example, Markwick, 1995), and sedimentary features (for example, Ziegler and others, 1985), and by the chemical analysis of authigenic and biogenic minerals found in sedimentary rocks. The applicability of each method, however, is limited by the occurrence of each material over geologic time and geographic area.

In contrast to empirical proxy records, general circulation models (GCMs) provide spatially complete estimates for a wide range of terrestrial climate parameters, including temperature, precipitation, humidity, and wind direction for almost any

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time period of interest. Equally important, climate models can help identify the geochemical and physical processes that cause climate change, and can thus lead to a better understanding of the how and why climate changes over time. Predictions of GCMs, however, are very sensitive to input parameters such as greenhouse gas concentrations, orbital variations, the distribution of land/ocean/vegetation, and the coupling between ocean and atmospheric circulation, and these variables are not known precisely for much of the geologic past. Therefore model predictions of past climate have to be tested against empirical data from the geologic record, and as a result empirical and modeling approaches to describing and understanding terrestrial climates of the past are complementary.

While the wide geographic distribution of mineralogically uniform sediments on ocean floors makes it possible to collect internally consistent sets of sedimentological, paleontological, and geochemical data that can be compared over time and space (for example, Huber and others, 1995, 2002; Barrera and Savin, 1999; Zachos and others, 2001), it is much more difficult to create such a framework for terrestrial settings. One primary reason is that many of the materials available for studying terrestrial environments require specific depositional settings or geochemical conditions in order to form and be preserved, and are thus not widespread. The inherently patchy distribution and preservation of depositional basins in terrestrial settings, and variations in sedimentology and geochemistry within and between basins, also make it difficult to compile a continuous and regionally extensive climate record using any single paleoclimate proxy. Integrating paleoclimate estimates obtained from different methods is the most effective way to develop a geographically widespread and temporally dense proxy data set. In turn, this makes it important to determine if paleoclimate information obtained using different methods is both reliable and comparable.

In this paper we focus on two very different methods of estimating mean annual temperature (MAT) of the past, leaf margin analysis and oxygen isotope analysis of fossil remains. The former uses the proportion of fossil plant species with untoothed, leaves to estimate MAT, while the latter takes advantage of the temperature-dependent fractionation of oxygen isotopes during biogenic mineral formation. Estimates of MAT from each method are demonstrated to be comparable for the early Eocene of North America, and we thus conclude that they can be used in tandem to compile a more complete record of terrestrial climate. This record implies high temperatures and shallow temperature gradients in polar regions, and captures a temperature increase in continental environments during the Paleocene-Eocene Thermal Maximum. Lastly, oxygen isotope ratios of authigenic and biogenic minerals can be used to infer oxygen isotope ratios of precipitation, which at the present time correlate with MAT, and may thus provide an additional means of indirectly estimating MAT in the past. We demonstrate here that the oxygen isotope–MAT correlation during the early Eocene was significantly different than at present, and that care must be taken if this approach is used in studying terrestrial paleoclimate.

PALEOBOTANY AND PALEOTEMPERATURE

A variety of techniques have been developed that allow quantitative estimates of paleotemperature and paleoprecipitation to be made from the size and shape of fossil leaves (for example, Wolfe, 1993; Wilf, 1997; Wilf, and others, 1998; Jacobs, 1999, 2002; Gregory-Wodzicki, 2000; Kennedy and others, 2002). The most widely applied of these is leaf margin analysis (LMA), which is based on the observation made on living vegetation that the proportion of dicotyledonous species with entire-margined, or untoothed, leaves (P) is directly correlated with MAT (Wolfe, 1979). The use of leaf margin proportion, or any other morphological feature of leaves, to estimate the MAT of fossil assemblages makes the uniformitarian assumption that plants in the early Cenozoic evolved morphological responses to climate in the same way that they do

today, and therefore that the relationship between P and MAT has remained constant. In general, this assumption is thought to be valid because most Cenozoic floras contain a substantial proportion of extant genera and families.

There are, however, three major sources of potential error in paleotemperature estimates based on leaf margin percentage. First, there are geographic variations in the relationship between P and MAT in extant floras (for example, Wolfe, 1993; Wilf, 1997; Jacobs, 1999; Gregory-Wodzicki, 2000; Kennedy and others, 2002; Kowalski, 2002; Greenwood and others, 2004). Geographic variation in the correlation of P and MAT is poorly understood. It could reflect variation in the taxonomic composition of floras in different regions, differences in soils, differences in the way climate variables interact with one another, or all of the above. In practice this problem is dealt with by using a P:MAT correlation that is derived from modern sites that are taxonomically similar to the fossil assemblage. A second source of error is simple binomial sampling error that results from having a limited sample of the species that were present in the regional flora (Wilf, 1997). Wilf calculated the size of the sampling error based on the assumption that there was an equal probability of sampling species with the two different margin types, and recommended using more than 30 species in each analysis in order to reduce the error of the estimated MAT below $\pm 2^\circ\text{C}$. Tests with data from extant forests have shown that species of a given margin type may not be equally abundant, thus violating the assumption that there is an equal probability of sampling different margin types, and increasing the proportion of the local flora that needs to be sampled in order to derive an accurate MAT estimate (Wilf, 1997; Burnham and others, 2001). Furthermore, early successional, riparian, swamp, and lake-side forests have a higher proportion of non-entire species than adjacent terra-firma forest, making it likely that fossil assemblages recovered from fluvial and lacustrine sediments will lead to underestimates of MAT (Burnham, 1989; Burnham and others, 2001; Kowalski and Dilcher, 2003). The third source of error in using leaf morphology to reconstruct paleoclimate is possible taphonomic bias against preservation of some types of leaves. Greenwood (1992) observed a bias against occurrence of large leaves in fluvial systems compared with their source forests, presumably due to preferential transport of small leaves by the wind and preferential destruction of larger leaves. This taphonomic bias would have an effect on estimation of paleoprecipitation, for which leaf size is an important character (Wilf and others, 1998), but is not known to be important for leaf margin.

$\delta^{18}\text{O}$ AND PALEOTEMPERATURE

A complementary, yet very different, approach to estimating mean annual temperature relies on the oxygen isotope analysis of phosphate in skeletal apatite [$\text{Ca}_5(\text{PO}_4, \text{CO}_3)_3(\text{OH}, \text{CO}_3)$]. This biogenic phosphate is well suited for studying older geologic time periods because it is resistant to oxygen isotope exchange during diagenesis, particularly when it occurs as part of the large and tightly-packed apatite crystals in tooth enamel and some fish body scales (Lee-Thorpe and Van der Merwe, 1991; Ayliffe and others, 1994; Zazzo and others, 2004). In fact, several recent studies have indicated that primary isotopic information can be preserved as far back as the late Mesozoic (Fricke and others, 1998a; Barrick and others, 1999; Fricke and Rogers, 2000). Equally important, the vertebrate fossil material necessary for isotopic analysis is common over a broad range of time and space.

The utility of the oxygen isotope ratio of phosphate from biogenic apatite ($\delta^{18}\text{O}_{\text{bp}}$) in estimating paleotemperature lies (1) in its relation to $\delta^{18}\text{O}$ values of local precipitation ($\delta^{18}\text{O}_{\text{pr}}$), and (2) in the temperature-dependent nature of oxygen isotope fractionation during apatite formation. The former relation exists because the water ingested by animals from surface reservoirs of precipitation, such as streams, ponds, or plants, plays a major role in determining the $\delta^{18}\text{O}$ of their body water, and

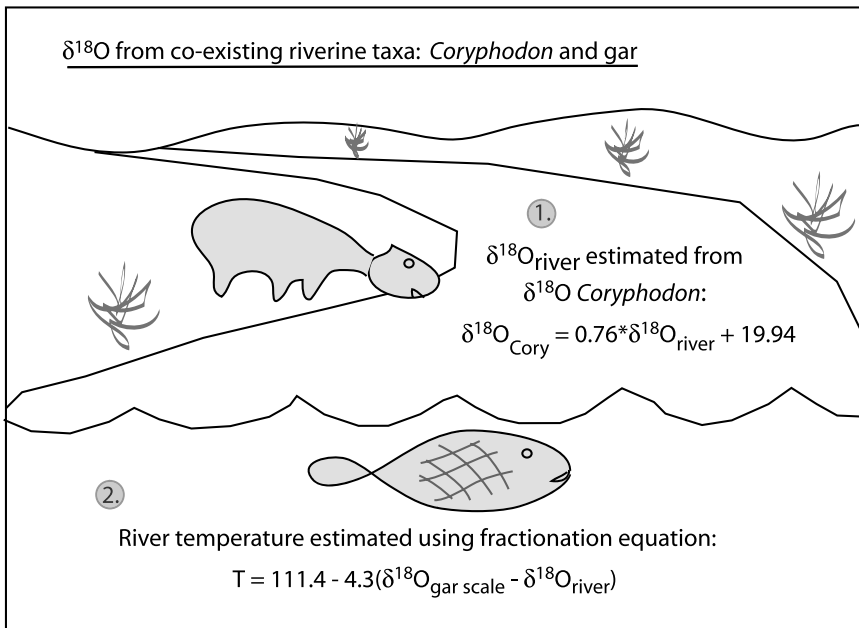


Fig. 1. Illustration of how oxygen isotope ratios from two taxa living in a single riverine environment can be used to estimate local atmospheric temperature. (1) Biogenic phosphate in mammals is formed at a constant temperature and is used along with a physiological model to estimate $\delta^{18}\text{O}$ of river water. (2) This value is substituted along with measured $\delta^{18}\text{O}_{\text{bp}}$ values from fish into this phosphate-water fractionation equation to estimate river water temperature, which is assumed to be similar to that of the overlying atmosphere (fig. 2).

hence $\delta^{18}\text{O}$ of biogenic phosphate in skeletal apatite that forms from body water (Longinelli, 1984; Luz and Kolodny, 1985; Bryant and Froelich, 1995; Kohn, 1996). This relation between $\delta^{18}\text{O}_{\text{bp}}$ and $\delta^{18}\text{O}$ of ingested waters is not one-to-one for land-dwelling animals because ~25 to 30 percent of oxygen input to the body is from the atmosphere which has a uniform $\delta^{18}\text{O}$ value (Kohn, 1996). Despite these complexities, however, relations between $\delta^{18}\text{O}$ of ingested water and $\delta^{18}\text{O}_{\text{bp}}$ can be quantified using physiological models that account for the fluxes and fractionations of oxygen during the formation of biogenic phosphate from ingested waters, the atmosphere, and plants (Bryant and Froelich, 1995; Kohn, 1996). Biogenic phosphate from mammalian skeletal material is particularly well suited as a proxy for $\delta^{18}\text{O}$ of ingested water because it is precipitated in equilibrium with body water at a constant temperature. Therefore, any change in $\delta^{18}\text{O}_{\text{bp}}$ over time or space should reflect only a change in $\delta^{18}\text{O}$ of water ingested from surface reservoirs of precipitation.

One way of estimating MAT using oxygen isotope ratios of biogenic phosphate relies on the temperature-sensitive fractionation of oxygen isotopes between phosphate and water at the scale of the local environment (fig. 1). In this approach, two coexisting taxa, a terrestrial mammal with a constant body temperature and a freshwater fish, are both assumed to be ingesting river water that has a source in precipitation. Because biogenic phosphate in mammals is formed at a constant and known temperature of ~37°C, $\delta^{18}\text{O}_{\text{bp}}$ from mammals can be used along with a physiological model to estimate $\delta^{18}\text{O}$ of river water ($\delta^{18}\text{O}_r$). In contrast, freshwater fish do not regulate their body temperatures, so isotopic fractionation between $\delta^{18}\text{O}_{\text{river}}$ and $\delta^{18}\text{O}$ of fish skeletal material also depends on water temperature (for example, Kolodny and others, 1983;

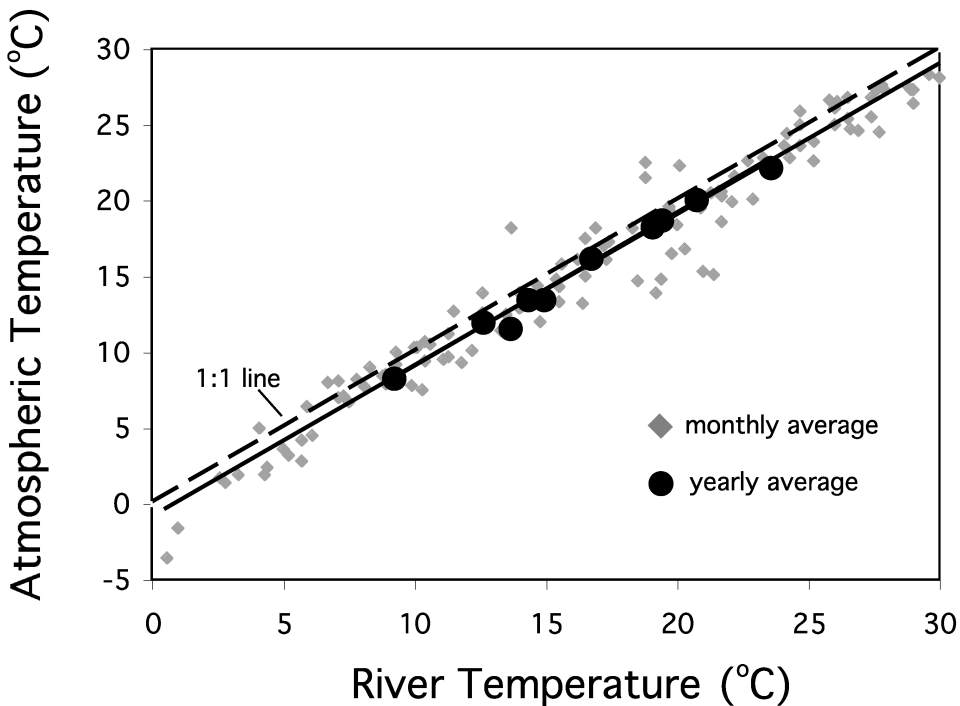


Fig. 2. Relation between river water temperatures (Alexander and others, 1996) and atmospheric temperatures (Worldclimate.com, 1996–2004) for ten United States localities. The 1:1 relation is illustrated by the dashed line, while the solid line is a linear regression through yearly averages from the ten localities ($y = 1.01x - 1.13$; $R^2 = 0.99$). Not shown is a linear regression through monthly average data from each locality ($y = 0.99x - 0.93$; $R^2 = 0.95$). River water temperatures are $\sim 1^\circ\text{C}$ higher than atmospheric temperatures for all localities investigated, which include Yellowstone River, Billings, MT; Alabama River, Montgomery, AL; Apalachicola River, Chattahoochee, FL; Rappahannock River, Fredericksburg, VA; Klamath River, Klamath, CA; Peace River, Arcadia, FL; Schuylkill River, Philadelphia, PA; Red River, Shreveport, LA; Tar River, Tarboro, NC; Willamette River, Portland, OR.

Patterson and others, 1993). Thus $\delta^{18}\text{O}_{\text{bp}}$ values of fish are influenced by both the isotopic composition *and* temperature of river water, and these relations can be illustrated using the phosphate-water fractionation equation of Longinelli and Nuti (1973): $T_{\text{river}} = 111.4 - 4.3 [\delta^{18}\text{O}_{\text{r}} - \delta^{18}\text{O}_{\text{bp}}]$.

This equation is used to estimate temperature by substituting $\delta^{18}\text{O}_{\text{r}}$ values estimated from mammalian phosphate along with measured $\delta^{18}\text{O}_{\text{bp}}$ values from fish scales to estimate river water temperature (Kolodny and others, 1983; Fricke and others, 1998a; Barrick and others, 1999; fig. 1). In turn, mean annual river water temperatures provide an excellent approximation of mean annual temperatures of the overlying atmosphere at any given location (fig. 2). The greatest advantage of this approach is that it provides an independent temperature estimate that does *not* rely on present-day spatial relations between $\delta^{18}\text{O}_{\text{pt}}$ and MAT (see below) *or* on the absolute $\delta^{18}\text{O}$ value of river water. For this reason, we favor the use of this oxygen isotope paleothermometer over other stable isotope approaches.

An alternative oxygen isotope-based approach to estimating MAT of the past relies on spatial relations between $\delta^{18}\text{O}$ of precipitation and mean annual temperature. Such a relation between $\delta^{18}\text{O}_{\text{pt}}$ and MAT occurs at the present time because ^{18}O is preferentially incorporated into condensate as water is precipitated and removed from

cooling air masses as they move from warm tropical sources to cooler polar sinks (for example, Dansgaard, 1964; Rozanski and others, 1993). As more precipitation is removed from an air mass, $\delta^{18}\text{O}$ of the remaining vapor becomes progressively lower. It has been suggested that this spatial $\delta^{18}\text{O}$ -MAT relation could be used along with estimates of $\delta^{18}\text{O}$ in the past to estimate terrestrial paleotemperatures, and that the 0°C intercept of the modern relation can be used to infer the presence of ice and snow in the geologic past (for example, Norris and others, 1996, 2000; Ferguson and others, 1999; Dettman and Lohmann, 2000; Nordt and others, 2003). In order for this approach to produce reliable results, spatial relations between $\delta^{18}\text{O}_{\text{pt}}$ and MAT must not change over *time*. The validity of this assumption for the early Eocene, and its impact on the study of ancient terrestrial environments using $\delta^{18}\text{O}_{\text{pt}}$ -MAT relations, is discussed in more detail below.

MATERIAL

Plants

Fossil floras of early to middle Eocene age in North America are known from the Gulf Coastal plain to Arctic Canada, a range of almost 45 degrees of latitude (table 1). Most of these fossil leaf assemblages are drawn from lowland, wetland depositional environments, typically fluvial backswamps or small lakes or ponds formed in abandoned channels (Greenwood and Wing, 1995; Davies-Vollum and Wing, 1998; Wilf, 2000). The exception is the Little Mountain flora from the Green River Basin, which was deposited in a lake of moderate-size (Wilf, 2000).

Each of the floras listed in table 1 is comprised of several to many sampling quarries from which fossil leaves were collected. Individual quarry samples in fluvial environments typically contain leaves from a small area of the original vegetation, and therefore multiple samples are required to reflect the local diversity of the forest (Wing and DiMichele, 1995). In order to increase the diversity of the floral samples, and hence the reliability of the MAT estimates, in most cases it was necessary to lump quarry samples from a stratigraphic interval representing hundreds of thousands of years. As a result, the floral estimates of MAT average a geologically significant amount of time, possibly including orbital-time-scale fluctuations in climate.

Vertebrates

For our method of estimating paleoMAT, it is necessary to estimate $\delta^{18}\text{O}$ of ancient river water using $\delta^{18}\text{O}$ of mammalian tooth enamel, and we do so here by using oxygen isotope ratios of *Coryphodon* tooth enamel. Paleontological evidence suggests that *Coryphodon* was an herbivorous mammal and most likely lived near, or perhaps in, rivers that flowed through Paleogene basins. In addition, as large mammals they were likely obligate drinkers that satisfied most of their water needs by drinking from rivers they inhabited as opposed to obtaining a large percentage of water from non-aquatic plants and leaves.

Although their exact behavior is unknown, there is isotopic evidence to suggest that *Coryphodon* did ingest more river water than plant/leaf water. It has been observed that leaf water can often have $\delta^{18}\text{O}$ values much higher than local surface waters due to evaporation at the surface of leaves (Sternberg, 1989). As a result, non-aquatic browsers and grazers may have higher average $\delta^{18}\text{O}$ values of tooth enamel compared to semi-aquatic taxa living in the same area. In fact, such a difference has been observed between modern and fossil hippopotamuses and other associated taxa from Africa, with hippos having lower $\delta^{18}\text{O}$ values of tooth enamel than animals such as zebras, elephants, gazelles and rhinoceros (Bocherens and others, 1996; Clementz and others, 2003; Palmqvist and others, 2003). Similarly in the case of the Eocene, $\delta^{18}\text{O}$ ratios of *Coryphodon* tooth enamel are on average lower than $\delta^{18}\text{O}$ ratios of three other

TABLE 1
Estimates of MAT with associated uncertainties based on early- or early-middle Eocene leaf fossil assemblages from North America.

Locality	Latitude (decimal degrees)	Epoch/Age	Method	# species	percent entire	MAT1 ¹	binomial error ²	MAT2 ³	SE regression ³
Axel Heiberg-188	79.9	M. Eoc	MR	12		9.3			
Ellesmere-111	79.7	E. Eoc	MR	15		8.2			
McAbee	50.8	E. Eoc	LMA	22	29	10	2.9°C	12.8	3.6°C
Bear's Paw	48.5	E. Eoc	LMA	32	33	11.2	2.6°C	14.2	3.6°C
Camel's Butte	46.8	E. Eoc	LMA	15	26	9.1	3.5°C	11.7	3.6°C
Yellowstone-Sepulcher	44.9	E. Eoc	LMA	25	30	10.5	2.9°C	13.1	3.6°C
Kisinger Lakes	43.8	M. Eoc	LMA	36	57	18.6	2.5°C	22.9	3.6°C
Upper Willwood (621 m level)	43.8	E. Eoc	LMA	48	69	22.2	2.0°C	27.3	3.6°C
Lower Willwood (57.5 m level)	43.8	E. Eoc	LMA	43	56	18.2	2.3°C	22.6	3.6°C
Wind River	43.7	E. Eoc	LMA	39	57	18.6	2.4°C	22.9	3.6°C
Green River (Sourdough)	41.8	E. Eoc	LMA	44	66	21.3	2.3°C	26.1	3.6°C
Green River (Niland)	41.5	E. Eoc	LMA	14	71	23	3.7°C	28.1	3.6°C
Green River (Little Mtn.)	41.2	E. Eoc	LMA	49	60	19.6	2.1°C	24.1	3.6°C
Green River (Latham)	41.7	E. Eoc	LMA	17	50	16.4	4.4°C	20.4	3.6°C
Chalk Bluffs	39.2	E. Eoc	LMA	67	49	17.1	1.9°C	20.0	3.6°C
Puryear-Buchanan	36.4	M. Eoc	LMA	47	91	29.1	1.2°C	35.3	3.6°C

Notes

1—from regression of Wolfe (1979)

2—from Wilf (1997)

3—from regression of Kowalski and Dilcher (2003)

Calculations made using multiple regression (MR) and leaf margin analysis (LMA). For the latter, MAT is estimated using the percent of entire-margined species in a fossil population and linear regressions from modern east Asian plants (Wolfe, 1979) and North American wetland plants (Kowalski and Dilcher, 2003).

mammal taxa also living in the same area (Koch and others, 1995). Thus both paleontological and isotopic evidence indicates that $\delta^{18}\text{O}_{\text{bp}}$ of *Coryphodon* tooth enamel should be a very reasonable proxy for $\delta^{18}\text{O}$ of river water.

Because mammalian tooth enamel forms incrementally over time scales of months, seasonal variations in $\delta^{18}\text{O}$ of ingested water can be recorded (for example, Koch and others, 1989; Fricke and O'Neil, 1996; Fricke and others, 1998b). Indeed, $\delta^{18}\text{O}_{\text{bp}}$ varies from 1 to 4 permil along the length of single *Coryphodon* teeth from the Bighorn Basin, and these intra-tooth variations have been attributed to such seasonal variations in the isotopic ratio of ingested waters (Fricke and others, 1998a). Fortunately, it is possible to capture much of this seasonal variability in $\delta^{18}\text{O}$ of ingested water by taking a number of bulk tooth enamel samples from a population of animals found at a single locality (Clementz and Koch, 2001). Therefore, the average $\delta^{18}\text{O}_{\text{bp}}$ of multiple samples are used when comparing data from different localities.

River-dwelling fish provide the necessary complement to the mammal *Coryphodon*, and analyses were made on body scales of *Lepisosteus* (Pisces, *Lepisosteiformes*), a freshwater fish commonly known as gar. The outer surfaces of gar scales are covered by an enamel-like aggregate of apatite crystals known as ganoine, and they are commonly found as isolated but well preserved elements in terrestrial sediments.

Coryphodon and gar samples included as part of this study have been collected from a large latitudinal range of early Eocene localities in North America, including Big Bend, Texas, the San Juan Basin of New Mexico, the Green River, Big Horn, and Powder River Basins of Wyoming, and Ellesmere Island in Arctic Canada (fig. 3; table 2). All localities date from the Wasatchian (Wa) North American Land Mammal Age (~55.5 to 50.1 Ma). Bighorn basin samples can be given more precise age estimates within mammalian faunal zone Wa-6 (~53.35 to 52.9 Ma, Wing and others, 2000), while fossil assemblages from the Powder River basin are restricted in age to mammalian faunal zone Wa-2 (~54.6 to 54.2 Ma, Wing and others, 2000) and Green River basin samples are thought to be from mammalian faunal zones Wa-3 or Wa-4 (Savage and Russell, 1983; ~54.2 to 53.5 Ma, Wing and others, 2000). By restricting our analysis to *Coryphodon* and gar regardless of location, we avoid any systematic offsets in $\delta^{18}\text{O}$ that may exist between taxa due to differences in physiology and/or behavior.

It is very important to note that although both plant and vertebrate fossils are deposited in the same fluvial and fluvio-lacustrine settings, they are not often found together. Fossil leaves are characteristically found in organic shales and interlaminated silt/sand deposits, while *Coryphodon* tooth fragments and gar scales occur in oxidized, pedogenically modified mudstones or coarser channel deposits that generally do not include plant remains. As a result it is difficult to compare directly paleobotanical and stable isotope estimates of MAT for a single fossil-bearing locality even if both types of remains are found in the same sequence of strata.

RESULTS

Leaf Margin Analysis

Estimates of MAT based on fossil leaves are presented in table 1. All but three of the estimates are based on leaf margin analysis using the modern correlation observed in east Asian floras (Wolfe, 1979), which are taxonomically similar to Eocene floras from western North America. The estimates from Axel Heiberg and Ellesmere Islands (Greenwood and Wing, 1995) are based on the application of a multiple regression model derived by Wing and Greenwood (1993) from the CLAMP database of Wolfe (1993). Leaf margin percentage data for these floras were not available to us. Estimated MAT for the Mississippi Embayment locality in Texas was published by Wolfe and Dilcher (2000) using CLAMP methods and the database described by (Wolfe, 1993).

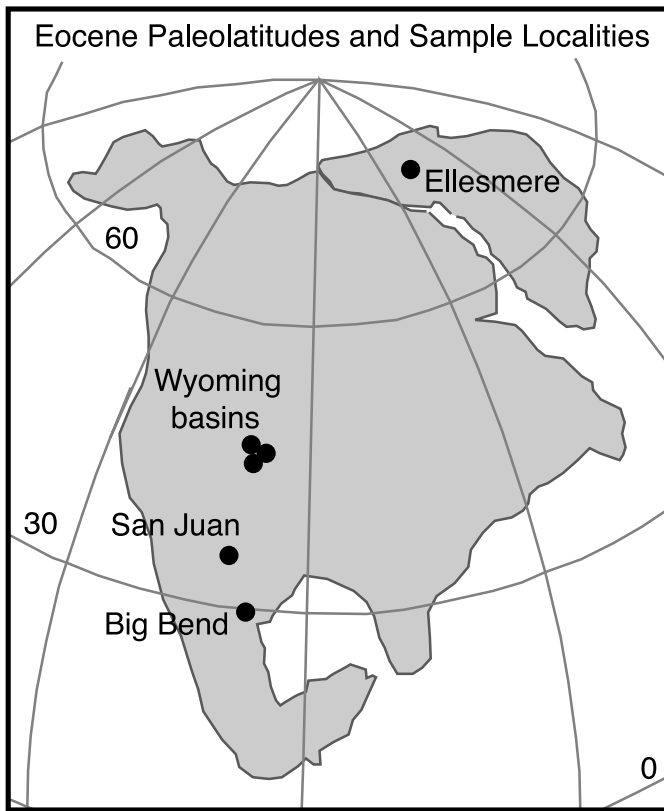


Fig. 3. Paleogeographic map of North America during the early Eocene. Sample localities are shown by circles, and approximate paleolatitudes are from Scotese (1999). The Mississippi Embayment extends ~5 degrees latitude farther north during the Eocene relative to the present day.

Column eight in table 1 gives estimates of MAT derived from the regression of leaf margin percent against MAT published by Kowalski and Dilcher (2003). This regression is based on 10 modern wetland sites in eastern North America. Although the strength of the statistical relationship between leaf margin percentage and MAT is lower than for the Wolfe (1979) dataset, it may produce more accurate paleo-MATs. Kowalski and Dilcher showed that living wetland floras have higher proportions of toothed species at a given MAT than surrounding terra firme vegetation, and given the lowland, wetland, depositional environments that typically preserve fossil leaves, it is likely that Eocene paleofloras are also enriched in toothed species. We have plotted the MAT estimates generated with the Wolfe (1979) regression so that our estimates can be more easily compared with previous MAT estimates, and because they are less friendly to our hypothesis that paleo-MAT estimates from LMA and isotopic analyses are congruent.

Oxygen Isotope Analysis

Oxygen isotope ratios of biogenic phosphate from tooth enamel and from gar scales were measured using two different methods (table 2). One is the technique of O'Neil and others (1994) that involves the isolation of the phosphate radical as Ag_3PO_4 , the reaction of this material with graphite at 1400°C in a sealed quartz tube to

form CO_2 , and the introduction of this gas to the inlet system of a mass spectrometer. A second method involved the reduction of Ag_3PO_4 in a graphite furnace at 1400°C to produce CO that is then introduced by means of continuous flow techniques into a mass spectrometer (Kornhexl and others, 1999; Venneman and others, 2002). A rigorous comparison of these methods (Venneman and others, 2002) reveals that the O'Neil and others (1994) method is characterized by a scale compression, and necessary data corrections have been applied to results presented here that were first reported in Fricke and others (1998a).

In order to use oxygen isotope data from *Coryphodon* and gar to study Cenozoic environments, it is necessary to know if primary isotopic information has been preserved by biogenic phosphate. Although notoriously difficult to determine definitively, the occurrence of isotopic offsets between ecologically and physiologically distinct taxa such as *Coryphodon* and gar (table 2) is a reasonable test of whether $\delta^{18}\text{O}_{\text{bp}}$ values have been altered during diagenesis (Fricke and others, 1998a; Barrick and others, 1999; Fricke and Rogers, 2000). Such isotopic offsets between taxa would not occur if isotopic alteration was extensive, as isotopic exchange with ground waters or secondary precipitation of apatite during diagenesis would result in uniform $\delta^{18}\text{O}$ values of phosphate.

Oxygen isotope ratios for *Coryphodon* have been published previously (Fricke, 2003) and average ratios for each locality are also included in table 2. Because these animals are extinct, it is not possible to construct an exact relation between $\delta^{18}\text{O}$ of ingested water and $\delta^{18}\text{O}_{\text{bp}}$. However, all empirical relations of this type determined for modern mammals are similar to each other and to results of physiological models (Kohn, 1996). For this reason, we rely on the model of Kohn (1996) to estimate $\delta^{18}\text{O}$ of river water ingested by *Coryphodon*: $\delta^{18}\text{O}_{\text{bp}} = 0.76 * \delta^{18}\text{O}_{\text{river}} + 19.94$, assuming a relative humidity of 75 percent. This model takes into account the fluxes of oxygen into and out of the body of an animal (Kohn, 1996), and has an uncertainty of ± 1.39 permil that is due to small taxonomic differences in physiology, diet, and behavior. Most error introduced is related to absolute estimates of $\delta^{18}\text{O}$ using data from a singular mammalian taxon. For any given taxon, however, physiology, diet, and behavior are not likely to vary significantly, and differences in estimated $\delta^{18}\text{O}$ of river water between localities (that is $\delta^{18}\text{O}$ - latitude gradients), are likely to have much smaller errors associated with them.

Substituting $\delta^{18}\text{O}_r$ values estimated from *Coryphodon* tooth enamel phosphate along with $\delta^{18}\text{O}_{\text{bp}}$ values from gar scales into the phosphate - water fractionation equation of Longinelli and Nuti (1973), average river water temperatures at each locality are estimated (table 2). There is a strong relation between water and air temperatures for a number of North American rivers at the present time, although rivers are on average 1°C warmer than atmosphere (fig. 2). This temperature difference probably reflects differences in heat capacity and cooling rates of water and air. We assume both the slope and intercept of this were the same during the Eocene, and therefore that atmospheric temperatures were 1°C lower than river water (table 2). These lower, atmospheric, temperatures are used in the following discussion. Because of the uncertainty of ± 1.39 permil associated with using *Coryphodon* $\delta^{18}\text{O}_{\text{bp}}$ and the physiological model of Kohn (1996) to estimate $\delta^{18}\text{O}_r$, MAT, estimates have an uncertainty of at least $\pm 5.5^\circ\text{C}$ (1σ).

DISCUSSION

Comparing Estimates of MAT for Wyoming

A major goal of this research is to make as direct a comparison as possible between paleobotanical and oxygen isotope estimates of MAT. The Wyoming localities are best suited for this comparison because of excellent stratigraphic and temporal control.

TABLE 2
Sample location, paleolatitude, age $\delta^{18}O_{bp}$, average $\delta^{18}O_r$, and estimated MAT of river and atmosphere.

Locality	Paleolat. (° N)	Age (Wa-biozone)	$\delta^{18}O_{bp}$ (‰)	avg. $\delta^{18}O_r$ (‰)	MAT _r	MAT _{atm}
Big Bend	29	Wa-6			32.5	31.5
Gar 1			17.8			
Gar 2			17.7			
Coryphodon (n=5)			19.6±0.86	-0.5		
San Juan Basin	36	Wa-6			28.8	27.8
Gar 1			16.2			
Gar 2			16.6			
Gar 3			16.4			
Gar 4			16.0			
Coryphodon (n=7)			17.8±0.43	-2.8		
Green River Basin	44	Wa-6			16.5	15.5
Gar 1*			17.2			
Gar 2*			18.5			
Gar 3*			18.9			
Gar 4*			17.9			
Gar 5*			18.3			
Cory 4			18.2			
Coryphodon (n=3)			17.0±0.35	-3.9		
Bighorn Basin	45	Wa-6 (53.01)			19.3	18.3
91513 gar†			12.1			
92116 gar†			11.1			
96510 gar†			11.8			
BHWA6gar1*			15.6			
BHWA6gar2*			15.6			
BHWA6gar3*			12.9			
Coryphodon (n=6)			13.7±0.81	-8.2		
		Wa-0 (55.50)			26.3	25.3
98427-gar1†			14.2			
98427-gar2†			15.8			
98427-gar3†			14.8			
86137-gar1†			12.6			
86137-gar2†			13.2			
79893-gar†			14.2			
83478-gar1†			13.8			
83478-gar1†			14.3			
83569-gar1†			14.6			
83613 Cory†			15.7	-5.6		

TABLE 2
(Continued)

Locality	Paleolat. (° N)	Age (Wa-biozone)	$\delta^{18}\text{O}_{\text{bp}}$ (‰)	avg. $\delta^{18}\text{O}_{\text{r}}$ (‰)	MAT _r	MAT _{atm}
Powder River Basin	45	Wa-2			19.7	18.7
Gar 1*			13.5			
Gar 2*			13.5			
Gar 4*			15.9			
Coryphodon (n=3)			14.6±0.72	-7.0		
Ellesmere Island	73	Wasatchian			5.0	4.0
Fish 1*	vertebrae		5.9			
Fish 2*	vertebrae		5.4			
Coryphodon (n=6)			5.4±0.134	-19.1		

Approximate paleolatitudes of each locality are from Scotese (1999). Ages are given in mammalian biozones of the Wasatchian North American Land Mammal Age, and in millions of years when possible. Average $\delta^{18}\text{O}_{\text{bp}}$ and standard deviation (1 σ) for *Coryphodon* are from Fricke (2003). These average values were used along with a physiological model (Kohn, 1996; see text) to estimate average $\delta^{18}\text{O}_{\text{r}}$. $\delta^{18}\text{O}_{\text{r}}$ was in turn used along with $\delta^{18}\text{O}_{\text{bp}}$ and data from gar fish to estimate MAT of river waters (see text for details). Atmospheric temperatures during the Eocene are assumed to have been 1°C lower than river temperatures (see fig. 2). †corrected gar $\delta^{18}\text{O}_{\text{bp}}$ values first reported in Fricke and others (1998a) obtained using high temperature reduction.

†denotes corrected gar $\delta^{18}\text{O}_{\text{bp}}$ values first reported in Fricke and others (1988a).

*denotes $\delta^{18}\text{O}_{\text{bp}}$ values obtained using high temperature reduction.

Even there, however, it is difficult to make a direct statistical comparison because MAT changes significantly over time, fossil floras and vertebrate remains are very rarely found together in sediments of the exact same age, and there are uncertainties in ages of fossil localities.

We have compared MAT estimates from the two different sources by fitting a series of second-order polynomial curves to the time series of LMA estimates, then comparing isotopic estimates of MAT to the interpolated values based on LMA (fig. 4). With the exception of the Paleocene-Eocene boundary, estimates of MAT made using oxygen isotope ratios of fossil remains are 0.2 to 2.1°C higher than estimates made using leaf margin analysis. Given the limited dataset it is not clear whether higher isotopic estimates of MAT represent a systematic difference in temperature estimates between methods, though we note that in studies that attempt to account for the wetland bias of paleofloras, estimates of MAT are several degrees higher than those we provide here (Kowalski and Dilcher, 2003; table 1). Even without taking into account systematic biases in the LMA estimates, three of the four oxygen isotope MAT estimates have error bars that overlap the MAT curve derived from LMA. These similarities in MAT estimates are the first to indicate that oxygen isotope and leaf margin methods produce comparable estimates of MAT for the Eocene, even in the face of changing MAT and uncertainties in age of plant and animal fossils.

The one isotopic estimate of MAT that falls far from the LMA curve is within the short interval of elevated temperatures (the Paleocene-Eocene Thermal Maximum or PETM) that is well-documented to occur in the earliest Eocene (for example, Zachos and others, 1994, 2001). The ~10°C difference in MAT between the LMA curve and MAT estimated using oxygen isotope data for this interval is a result of a short-term temperature fluctuation that can not be detected in the temporally coarse LMA record. The discordance in estimates at the PETM highlights the difficulty in comparing MAT estimates when MAT changes significantly over time. However, the PETM estimate also highlights the importance of a multi-proxy approach in providing a more

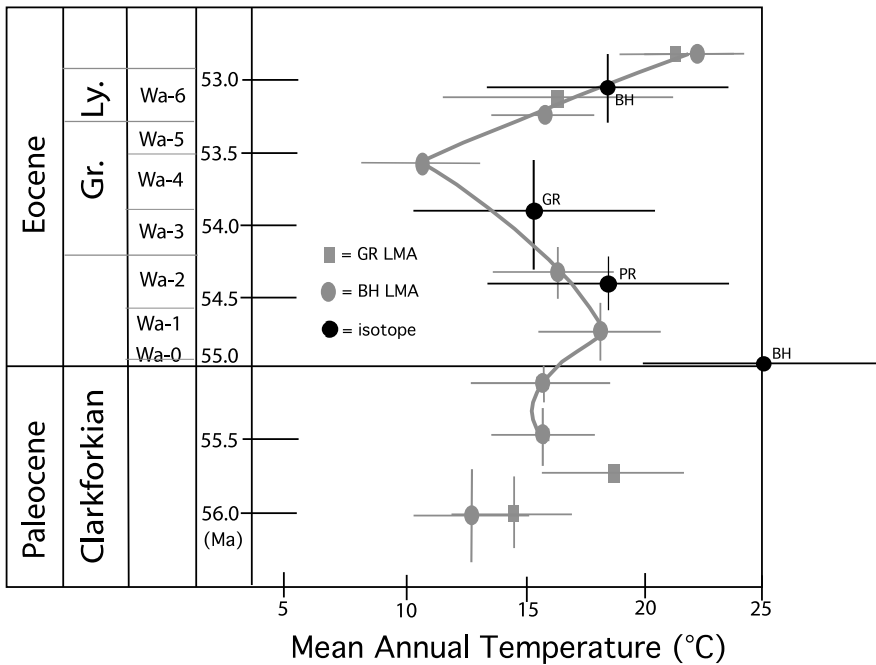


Fig. 4. Stratigraphic comparison of atmospheric MAT estimates made using leaf margin and oxygen isotope methods. Epoch and land mammal boundaries are after Wing and others, 2000. LMA estimates are from the Bighorn basin (Wing and others, 2000; gray ovals) and the green River basin (Wilf, 2000; gray rectangles). Black circles represent isotope estimates of MAT from the Bighorn basin (BH), Green River basin (GR) and Powder River basin (PR). In all cases, horizontal lines represent uncertainties in MAT estimates (1σ) and vertical lines represent uncertainties in age estimates. Three separate second order polynomial functions were fit through LMA data in order to estimate MAT for time periods when no fossil samples were available.

complete high-resolution record of MAT change, a record that can capture short intervals of temperature change that might be missed using a single proxy alone.

In addition to increasing temporal (and spatial) resolution of MAT records, a comparison of datasets also provides a means of checking results and testing assumptions associated with each method. Although limited, the similarity of results presented here from non-PETM time increases our confidence in both oxygen isotope and leaf margin methods for generating Eocene MAT estimates, and is particularly impressive because the methods are based on different assumptions and measurements, and come from different strata. In case of the oxygen isotope method, which has not been used extensively and has never been compared to other techniques, it provides the first evidence that isotope data from coexisting taxa to estimate river water temperatures is a legitimate approach to reconstructing atmospheric temperatures. For LMA estimates, the comparison with isotopic data reinforces the thought that there could be a wetland bias toward toothed leaves (Kowalski and Dilcher, 2003) that makes our Eocene estimates of MAT too cool.

It should be stressed that while leaf margin and oxygen isotope estimates of MAT between the Bighorn, Green River, and Powder River basins are similar, *absolute* $\delta^{18}\text{O}_{\text{bp}}$ and hence $\delta^{18}\text{O}_{\text{r}}$ values between basins are not. This isotopic offset between basins crosses taxonomic lines (table 2), and implies that hydrological differences existed between river basins during the Eocene and that these rivers had different $\delta^{18}\text{O}$ values. One possible reason for such isotopic offsets is orographic cooling of air masses as they

are forced over intervening mountains and the preferential removal of ^{18}O into the resulting precipitation and river water (Fricke, 2003). It is also possible that the Green River basin was characterized by intensive evaporation (Smoot, 1983), which would have caused a shift to higher $\delta^{18}\text{O}$ values (Fricke, 2003). These examples of how $\delta^{18}\text{O}_r$ and hence $\delta^{18}\text{O}_{bp}$ can vary for reasons other than a change in MAT are excellent illustrations of why present-day spatial relations between $\delta^{18}\text{O}$ and MAT must be used with care when applied to the geologic past, as is discussed in more detail below.

Latitudinal Temperature Gradients and Paleoelevation

Latitudinal gradients of MAT during the Eocene have been estimated for North America by applying several approaches to fossil floras: multiple regression, leaf margin analysis, and nearest living relative techniques (Greenwood and Wing, 1995). The results indicated that latitudinal (aka "meridional") temperature gradients were shallower than at present ($0.4^\circ\text{C}/1^\circ$ latitude versus $0.6^\circ\text{C}/1^\circ$ latitude in the Northern Hemisphere). Here we reconstruct a latitudinal temperature gradient for the early Eocene of North America using LMA and oxygen isotope estimates (fig. 5A). Because of uncertainties in dating, particularly outside of the Bighorn, Powder River, and Green River basins, samples included in this analysis may range in age from early to middle Eocene. Over this time period it is possible that MAT changed significantly in one area (fig. 4), and thus some error may be introduced when constructing these latitudinal gradients. Three paleobotanical temperature estimates made using multiple regression techniques rather than leaf margin analysis are included in the combined dataset, but they have little effect on the calculated latitudinal gradients.

Plotting all Eocene MAT estimates against paleolatitude shows the expected decline in MAT with increasing latitude (fig. 5). Most Eocene temperature estimates are $\sim 10^\circ\text{C}$ higher than those at the present time with the notable exception of temperatures from a group of middle latitude sites from California, Wyoming, Montana, and British Columbia (circled in fig. 5A). If a polynomial regression is fit through all Eocene MAT estimates, the result is an MAT-latitude relation characterized by an inflection point that divides two domains with different slopes (short dash, fig. 5A). Between 30° and 50°N the Eocene gradient is steeper than at present, ~ 1.1 degrees C per degree of latitude, while from 50° to 80°N the gradients is almost flat at ~ 0.01 degrees C per degree of latitude. In contrast, if only the coastal localities of Ellesmere Island, Texas, and Puryear-Buchanan, are used in calculating a regression, there is no inflection point, and the Eocene MAT-latitude gradient is a constant 0.45 degrees C per degree of latitude (long dash line, fig. 5A).

One likely explanation for the cluster of low Eocene MAT estimates at middle latitudes is that these sites were above sea level in the Eocene, and thus had lower MATs because of adiabatic cooling. Previous studies have compared paleobotanical estimates of MAT from Laramide basins with estimates from coastal localities at approximately the same latitude in the Pacific Northwest, and concluded that lower Wyoming temperatures reflect higher elevations (for example, Gregory and Chase, 1992; Gregory-Wodzicki, 1997; Chase and others, 1998). By applying modern temperature/elevation lapse rates ranging from $6^\circ\text{C}/1000$ m to $3^\circ\text{C}/1000$ m, to the difference in temperature between coastal and Wyoming localities, these authors estimate that intermontane basins may have been at elevations of 2 to 4 km (for example, Gregory and Chase, 1992; Gregory-Wodzicki, 1997; Chase and others, 1998).

Although elevated areas in the Rocky Mountains were no doubt present during the Eocene, determining paleoelevation in the manner described above can be problematic. One concern is that MAT from any one 'coastal' Eocene site may be overestimated, and in turn the temperature difference between low and high-elevation localities is too large. At the present time, shallow water embayments and large valleys in coastal areas often have higher temperatures than are found at the shoreline

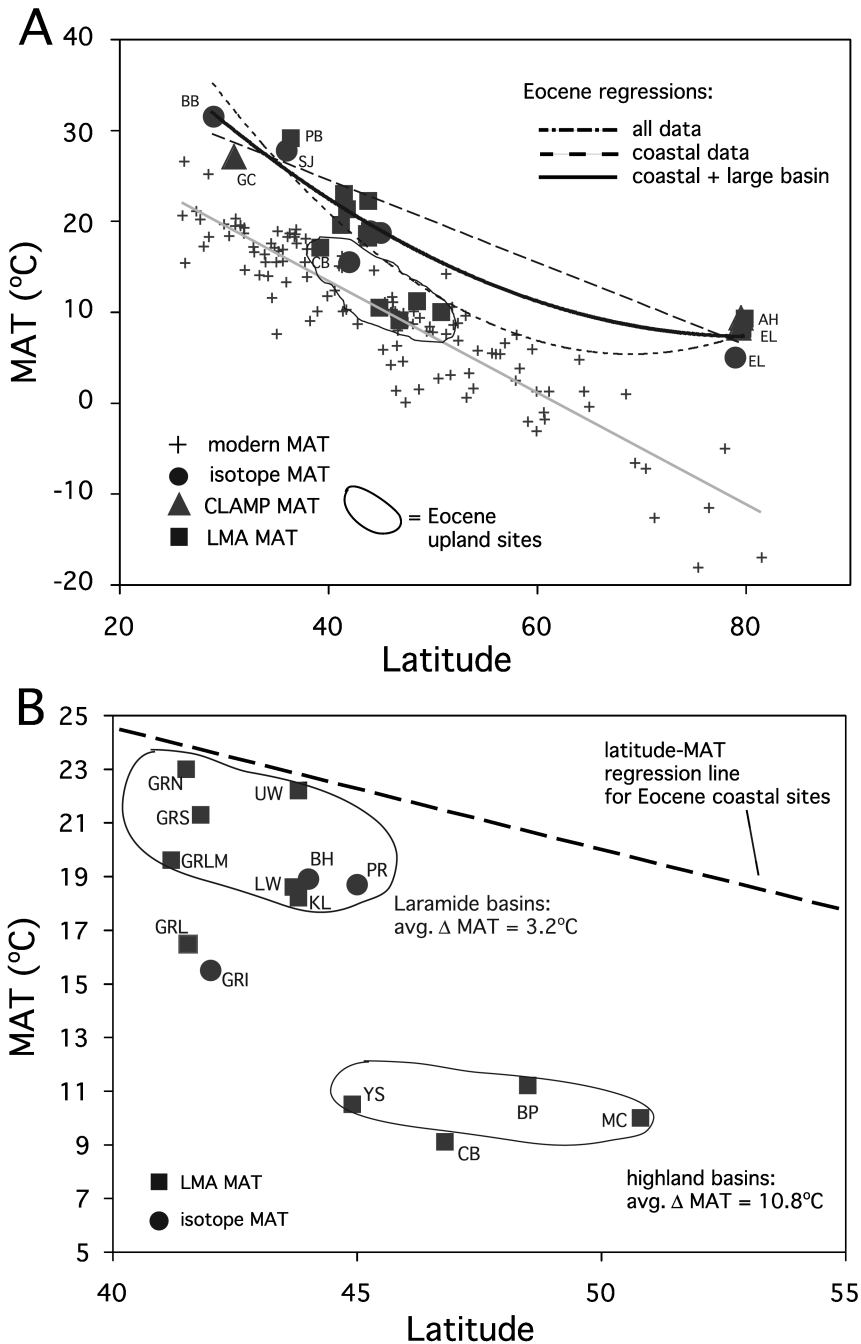


Fig. 5. (A) Estimated MAT versus paleolatitude for the present day (crosses; $y = -0.61x + 37.89$, $R^2 = 0.84$) and for North American northern localities of the early Eocene. Eocene MAT is estimated using oxygen isotopes (circles), leaf margin analysis (squares), and corrected multiple regression analysis (triangles). Circled data points overlap with modern temperatures, and some may represent localities at higher elevation. Short dash line is a regression through all Eocene data points. Long dash line is a regression that only includes coastal localities at ~ 30 and 80°N latitude ($y = -0.45x + 42.68$, $R^2 = 0.87$). Solid only black line is a regression which includes coastal localities and those from large Wyoming basin localities. The gray line is the regression through modern data (equation given). BB = Big Bend; GC = Gulf

(Wolfe, 1992). If Eocene localities from the Pacific Northwest represent such near-coastal localities, then it is possible that previous elevations of the Wyoming basins are overestimated.

To minimize the impact of relying on a single 'coastal' temperature, it is possible to predict a set of northern hemisphere *mean* coastal temperatures for the 'early Eocene' using the regression line for coastal localities of Ellesmere Island, Texas, and Puyyear-Buchanan in figure 5A. Temperature differences between inland Eocene localities and this coastal regression line at the latitude of the inland site can then be used to investigate differences in paleoelevation. In the case of our localities from Laramide basins, temperature differences range from 0.6 to 12.3°C (fig. 5B), and they appear to correspond with general geologic differences between basins themselves. The paleo-MAT estimates that are the farthest below the 'sea level' regression line (for example, Yellowstone, Bear's Paw, and McAbee) are from deposits associated with regional volcanic highlands (for example, Fritz and Harrison, 1985), and are 10.0 to 12.3°C cooler than (avg. 10.8°C \pm 1.3 1 σ) presumed coastal sites at ~41 to 45 degrees latitude. Depending on lapse rate, the average difference in MAT implies that these areas may have been anywhere from 1.8 to 3.6 km higher than coastal localities. Chalk Bluff is presently located in the foothills of the Sierra Nevada mountains in California, and is also estimated to have been 1 to 2 km above sea level during the Eocene. In contrast, the large intermontane basins of Wyoming (for example, Bighorn, Green River, Powder River, Wind River basins) are within 1 to 5°C (avg. 3.2°C \pm 1.6 1 σ) of presumed coastal temperatures at ~41 to 45 degrees latitude. Using the average temperature difference of 3.2°C and endmember lapse rates, paleoelevations are estimated to have only been ~0.6 to 1.3 km above sea level.

Although such comparisons of inland and predicted coastal MATs suggest broad-scale differences in paleoelevation between areas, we do not give paleoelevation estimates for specific sites for two reasons. First, it is difficult to establish coeval deposition of coastal and inland fossils. In the case of the Green River basin, MAT varied significantly over the early Eocene (fig. 4), and when compared to a single, 'early Eocene' temperature estimate from the coast, temperature differences (fig. 5B), and hence estimates of paleoelevation, fluctuate wildly (for example, estimated paleoelevation ranges from 133 to 1350 m using lapse rate of 6°C/1000 m). Which, if any, of these estimates is accurate cannot be determined in the absence of well-dated localities in both coastal and upland areas. Second, estimates of paleoelevation have high error because of uncertainty in individual estimates of MAT. The LMA estimate from the Camel's Butte Flora of North Dakota (Hickey, 1977) falls farther below the regression line than any other (fig. 5B). The geological setting of this paleoflora, far from any Cenozoic uplift and in a sequence of fine-grained, horizontal strata, makes it very unlikely that the assemblage was deposited at a paleoaltitude much higher than sea-level. The cool MAT estimate for the Camel's Butte flora more likely reflects low precision related to the small number of species (15, SE=3.5°C), to the higher

Fig. 5 (continued). Coast; SJ = San Juan basin; PB = Puyyear-Buchanan; CB = Chalk Bluff; AH = Axel Heiberg; EL = Ellesmere Island. (B) Detail of figure 5A illustrating temperature differences (ΔT) between regression line for Eocene coastal localities (long dash) and individual North American sites. Oxygen isotopes temperature estimates are illustrated by circles, LMA estimates by squares. GRN = Green River (Niland); GRS = Green River (Sourdough); GRLM = Green River (Little Mtn.); GRL = Green River (Latham); GRI = Green River, isotope; UW = Upper Willwood; BH = Bighorn basin, isotope; LW = Lower Willwood; KL = Kisinger Lakes; PR = Powder River, isotope; YS = Yellowstone; BP = Bear's Paw; MC = McAbee. Data from larger Laramide basins are grouped together and are on average 3.2°C lower than presumed coastal temperatures, while three localities associated with volcanic highlands have a larger average temperature difference of 10.8°C. MATs from GR, GRL, and CB are anomalously low; the Green River estimates likely reflect changes in Wyoming temperature over time rather than drastic changes in elevation, while the CB estimate is likely low due to small number of plant taxa present (see text for details).

proportion of toothed species generally present in wetland vegetation (Kowalski and Dilcher, 2003), or to taphonomic factors.

Latitudinal Temperature Gradient and Warming Mechanisms

If we set aside low MAT values from Camel's Butte, Yellowstone, Bear's Paw and McAbee as reflecting relatively high elevations or other factors, we can construct a third latitudinal MAT gradient from data points that represent coastlines and large (presumably lower) intermontane basins of Wyoming (solid black, fig. 5A). Differences between this regression (1), that for all Eocene data points (2), and that for coastal Eocene localities alone (3), have important climatic implications. If all data points are considered, two separate gradients are observed, one steeper than at present in the middle latitudes, and one much shallower than at present at higher latitudes. Such a situation is not comparable to global gradients of the modern icehouse world (fig. 5A) or to global gradients of the middle Cretaceous hothouse world (for example, Huber and others, 1995, 2002). If this "two-slope" gradient fairly represents North American climate during the early Eocene, it requires mechanisms that preferentially cool only middle latitudes (or preferentially heat only tropical and polar regions).

In contrast, the reduced latitudinal gradient in MAT produced when only considering coastal Eocene localities requires mechanisms that preferentially warm or retain heat at the poles relative to the tropics and lower middle latitudes. Similarly, the MAT- latitude regression that includes both data from coastlines and from larger intermontane basins of Wyoming is slightly curvilinear (solid line, fig. 5A), and indicates that although all of North America was warmer during the Eocene, this warmth was concentrated specifically in polar regions (60–80 degrees latitude). Modeling studies of the effect of elevated CO₂ on Eocene climate suggest that greenhouse gases alone should not have led to preferential warming at polar latitudes, except for ice-albedo feedbacks related to seasonal melting of Arctic Ocean sea ice (for example, Sloan and others, 1995). Paleontological data from Ellesmere, Axel Heiberg, and Spitsbergen (Hickey and others, 1983; McIver and Basinger, 1999; Golovneva, 2000) suggest that the Arctic Ocean was not frozen over, so the preferential high-latitude warming predicted by the models is not likely to have taken place.

A more likely possibility is an increase in the export of moisture, and hence latent heat, from tropics to the poles (Sloan and others, 1995), and $\delta^{18}\text{O}$ values of river water inferred from *Coryphodon* tooth enamel support such a mechanism (Fricke, 2003). In addition, it has been suggested that the formation of polar stratospheric clouds might preferentially warm polar regions relative to the tropics (Sloan and Pollard, 1998). These authors suggest that high biological productivity in polar regions might have resulted in an increased input of methane to the overlying atmosphere, resulting in high-altitude cloud formation, and a trapping of out-going long-wavelength radiation near the poles (Sloan and Pollard, 1998). Of these two mechanisms, polar stratospheric clouds provide a more likely explanation for the curvilinear gradient (fig. 5A, solid line) as they focus warming on the poles, while warming by atmospheric water vapor should apply equally strongly at low and low-middle latitudes and would produce a more linear gradient (fig. 5A, long dashed line).

In order to advance our understanding of what mechanisms were most important in influencing Eocene climate, it is necessary to move beyond qualitative descriptions of MAT- latitude gradients (that is "low" gradient versus "high" gradient). Instead, we need to define the shape of the gradient more precisely. We hope that more geographically extensive data, such as presented here, will yield a more resolved picture of the latitudinal temperature gradient and that these can be compared explicitly with output from GCMs that invoke specific causes for Eocene warmth.

$\delta^{18}\text{O}_{\text{pt}}$ -MAT Relation During the Eocene

In this paper we have relied on combined isotopic measurements from coexisting mammals and fish to estimate MAT. Previous authors have estimated paleo-MAT simply using relations between $\delta^{18}\text{O}_{\text{pt}}$ and MAT (for example, Norris and others, 1996, 2000; Ferguson and others, 1999; Dettman and Lohmann, 2000; Nordt and others, 2003). The present-day spatial correlation between $\delta^{18}\text{O}_{\text{pt}}$ and MAT occurs because ^{18}O is preferentially incorporated into condensate as water is precipitated and removed from cooling air masses. Resulting patterns in $\delta^{18}\text{O}$ of precipitation include a regular decrease in $\delta^{18}\text{O}_{\text{pt}}$ as air masses cool while moving from tropical source areas to polar sinks (fig. 6A). To study the past, oxygen isotope ratios of authigenic materials of various ages are used as a proxy for $\delta^{18}\text{O}$ of ancient precipitation, and in turn the $\delta^{18}\text{O}_{\text{pt}}$ -MAT relation is used to estimate past temperatures. Results from this and other studies, however, indicate that there are two potential problems with this approach.

Hydrological effects.—Except for ice, no geologic source of oxygen isotopes forms directly from precipitation, and therefore isotopic values of past precipitation can only be inferred indirectly. Soil carbonates, bivalve aragonite, and tooth enamel apatite form from surface reservoirs of precipitation like soil water, rivers and lakes (precipitation as sampled by the entire river watershed). This point is important because $\delta^{18}\text{O}$ of surface waters can be modified relative to precipitation by hydrological processes such as evaporation or variable recharge rates, and a direct comparison of $\delta^{18}\text{O}$ of geologic materials with $\delta^{18}\text{O}$ of modern precipitation may not be valid.

As a case in point, $\delta^{18}\text{O}$ of precipitation and of river water from the same area is clearly different, and the former has a steeper slope when plotted against MAT than does global precipitation (fig. 6A). A plausible explanation for the high $\delta^{18}\text{O}$ of surface waters relative to $\delta^{18}\text{O}_{\text{pt}}$ at latitudes below $\sim 35^\circ\text{N}$ is that there is intense evaporation associated with high-pressure belts. These regions are characterized by a mean annual evaporative input of water from the surface to the atmosphere that is greater than water loss from air masses via precipitation ($\text{P-E} < 0$; Peixoto and Oort, 1992). This leads to a net transfer of lighter ^{16}O to the atmosphere, thus increasing $\delta^{18}\text{O}$ of surface waters. At middle and high latitudes, two factors should lead rivers to have lower $\delta^{18}\text{O}$ than precipitation. First, precipitation exceeds evaporation ($\text{P-E} > 0$; Peixoto and Oort, 1992), so there is no net transfer of lighter ^{16}O to the atmosphere. Second, there is a seasonal bias in river recharge, with isotopically heavier summer precipitation being quickly returned to the atmosphere by means of plant transpiration, and isotopically lighter winter and spring precipitation infiltrating and recharging ground and surface waters. Therefore if the shell of a river-dwelling bivalve indicates that it formed from water with $\delta^{18}\text{O}$ of -17 permil, and the $\delta^{18}\text{O}_{\text{pt}}$ -MAT relation is used to estimate MAT, instead of the more appropriate $\delta^{18}\text{O}_{\text{river}}$ -MAT relation, an MAT of below 0°C would be inferred mistakenly (fig. 6A).

Offset in relations.—Even if hydrological processes can be accounted for by using modern relations between $\delta^{18}\text{O}_{\text{river}}$ (or $\delta^{18}\text{O}_{\text{carbonate}}$, $\delta^{18}\text{O}_{\text{clay}}$, *et cetera*) and MAT, a second problem remains: that $\delta^{18}\text{O}$ -MAT relations change as climate states change over time. This possibility can be investigated by using combined *Coryphodon*/gar isotope and temperature data presented in table 2 to reconstruct an approximate $\delta^{18}\text{O}_{\text{river}}$ -MAT relation for the early Eocene. Large parts of the Green River Formation are characterized by deposition of evaporites (Smoot, 1983), which suggests that the oxygen isotope ratios of surface-formed minerals from this basin should be anomalously high; therefore these data are not included in the regression. The result is presented in figure 6B and indicates a statistically significant offset does exist between $\delta^{18}\text{O}_{\text{river}}$ -MAT relations of the Eocene and present day.

This result is not surprising, as recent modeling (for example, Boyle, 1997; Rowley and others, 2001) and empirical investigations (for example, Fricke and O'Neil, 1999;

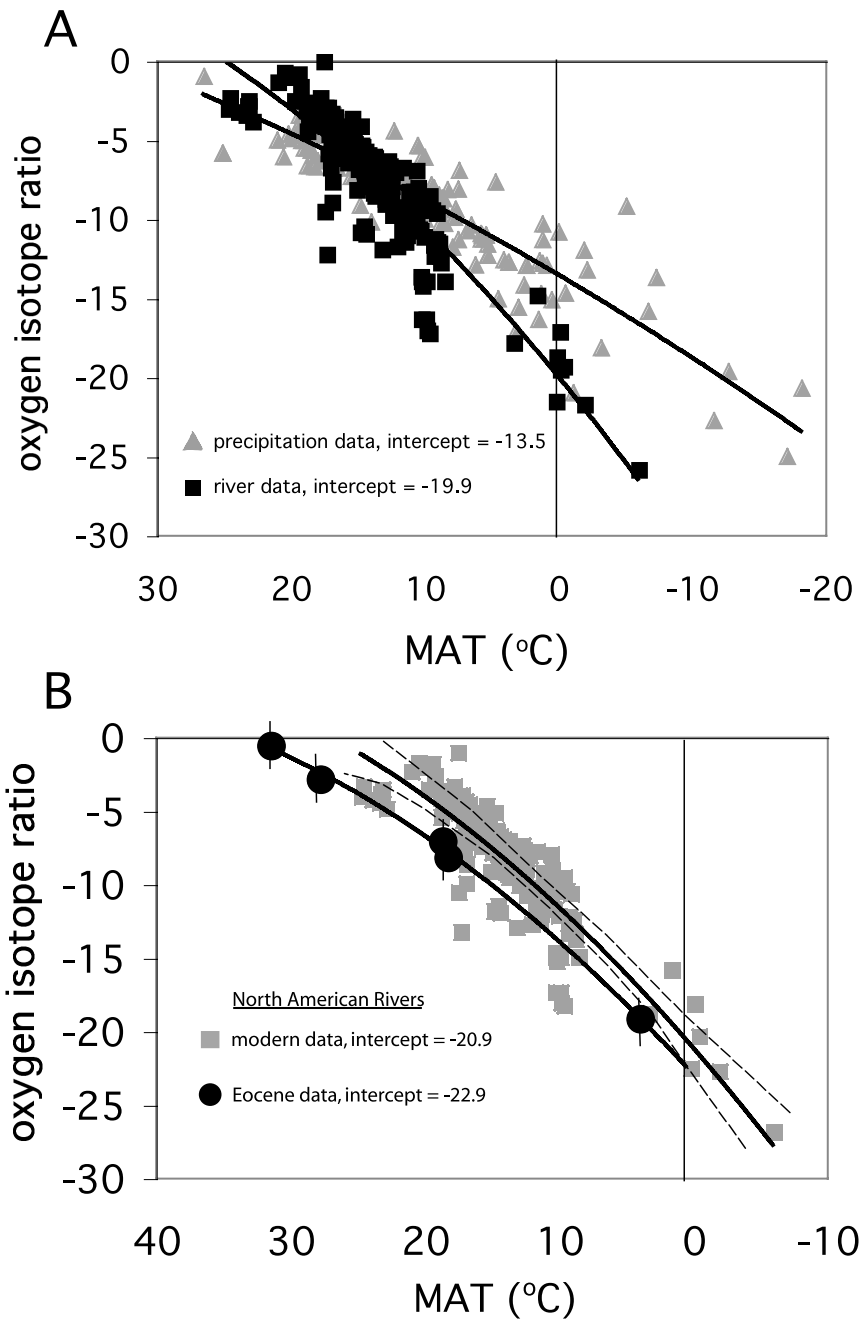


Fig. 6. (A) MAT versus oxygen isotope ratio of modern rivers of North America (squares; Coplen and Kendall, 2000; $y = -0.01x^2 + 1.03x - 19.94$, $R^2 = 0.81$) versus modern precipitation (triangles; Rozanski and others, 1993; $y = 0.5x - 13.53$, $R^2 = 0.81$). Intercepts of these relations are different, and reflect the influence of hydrologic variables such as evaporation, transpiration, seasonal runoff and stream mixing on oxygen isotope ratios of river water. (B) MAT versus oxygen isotope ratio of modern rivers of North America (squares; $y = -0.01x^2 + 1.03x - 20.94$, $R^2 = 0.81$) versus those estimated for the early Eocene (circles; $y = -0.01x^2 + 1.0x - 22.91$, $R^2 = 1.0$). To facilitate comparison with pre-ice sheet time periods, modern river data have been shifted by 1 ‰ to lower values (Miller and others, 1987). For modern data, dashed lines are 95% confidence intervals around the regression line. The Eocene regression line is nearly identical to the lower 95% confidence interval around the modern data set. For Eocene data, solid vertical lines represent uncertainty (1 σ) of the position of the regression line associated with the physiological model utilized. Note that both regression lines are steeper than that for modern MAT versus oxygen isotope ratio of precipitation (fig. 6A).

White and others, 2001) have indicated that spatial relations between $\delta^{18}\text{O}_{\text{pt}}$ and MAT vary. One possible reason for the offset in $\delta^{18}\text{O}_{\text{pt}}$ -MAT relations is that extra-tropical precipitation from air masses (that is distillation of ^{18}O) began at higher temperatures during the Eocene. Compared to the present day, a greater proportion of ^{18}O would have been lost from Eocene air masses by the time a given lower temperature was reached, and therefore $\delta^{18}\text{O}_{\text{pt/river}}$ would have been lower (fig. 6B). The direction and magnitude of the Eocene offset is consistent with the prediction of Fricke and O'Neil (1999) based on modern seasonal data, and reflects the linkages between temperature, latitude, and water vapor content in air masses.

It is also possible that $\delta^{18}\text{O}_{\text{river}}$ -MAT relations are different in the Eocene and today because of hydrological changes over time. As mentioned above, river watersheds can capture precipitation from large areas, but not all of this precipitation makes it to rivers because evaporation in soils and transpiration by plants can return a large proportion of precipitation back to the atmosphere. Thus if hydrological parameters such as intensity of evaporation and seasonal distribution of rainfall change along with global changes in climate, $\delta^{18}\text{O}_{\text{river}}$ -MAT relations for river water might also vary.

Variation in $\delta^{18}\text{O}_{\text{river}}$ -MAT relations over time has important implications for estimating paleotemperature from $\delta^{18}\text{O}$ data. Specifically, during greenhouse climate states low $\delta^{18}\text{O}_{\text{river}}$ values may be associated with relatively high MATs, as is the case for Ellesmere Island where $\delta^{18}\text{O}_{\text{river}}$ is ~ -19.1 permil and MAT is $\sim 4^\circ\text{C}$ (or higher if leaf physiognomic estimates of MAT are used). Therefore even the lowest reported $\delta^{18}\text{O}$ values of river and lake water for the late Paleocene-early Eocene of -19 permil (lake carbonate; Norris and others, 1996, 2000) and -22 permil (river bivalve; Dettman and Lohmann, 2001) do not provide unambiguous evidence for MATs of less than 0°C . As a result the use of oxygen isotope ratios alone to infer below freezing temperatures at the poles and at high elevations during the Cretaceous and Eocene should be revisited, and complementary evidence that substantiates such cold temperatures is essential when studying ancient time periods.

SUMMARY

In an effort to increase the temporal and spatial resolution of terrestrial records of Eocene climate, we compared estimates of mean annual temperature obtained from two very different methods: leaf margin analysis and oxygen isotope ratios of co-existing mammals and fish. The similarity observed indicates that both methods provide comparable, and presumably reliable, results. The common occurrence of fish and mammal remains make the oxygen isotope approach widely applicable for Paleogene time, and thus a great complement to leaf margin analysis. As an example, combined paleobotanical-isotope temperature estimates in Wyoming capture a global warming event at the Paleocene-Eocene boundary that is not recorded by paleobotanical data alone.

Temperature estimates made using both methods were also combined from geographically widespread localities in order to describe latitudinal temperature gradients over North America during the Eocene. These gradients were shallower due to preferential warming of high latitudes, although uncertainty in the exact nature of latitudinal gradients makes it difficult to determine the specific cause of this warming. In addition to describing temperature gradients, the combined dataset of estimated temperatures suggests that some areas of western North America associated with volcanic edifices had substantial paleoelevations. Larger Laramide basins had lower elevations.

Lastly, we used temperature and isotope data presented here to reconstruct an oxygen isotope-MAT relation for the early Eocene. It is significantly different than the present-day relation, and likely reflects differences in the temperature-controlled removal of precipitation from air masses during the Eocene. As a result, it is not

possible to obtain reliable estimates of Eocene MAT using the modern oxygen isotope–MAT relation, and care must be taken when interpreting oxygen isotope data from authigenic materials in the absence of additional paleoclimatic information.

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REFERENCES

- Alexander, R. B., Ludtke, A. S., Fitzgerald, K. K., and Schertz, T. L., 1996, Data from selected U.S. Geological Survey national stream water-quality monitoring networks (WQN) on CD-ROM: USGS Open-File Report 96-337.
- Ayliffe, L. K., Chivas, A. R., and Leakey, M. G., 1994, The retention of primary oxygen isotope compositions of fossil elephant skeletal phosphate: *Geochimica et Cosmochimica Acta*, v. 58, p. 5291–5298.
- Barrera, E., and Savin, S. M., 1999, Evolution of late Campanian–Maastrichtian marine climates and oceans, *in* Barrera, E., and Johnson, C. C., editors, *Evolution of the Cretaceous ocean–climate system: Geological Society of America Special paper 332*, p. 245–282.
- Barrick, R. E., Fischer, A. G., and Showers, W. J., 1999, Oxygen isotopes from turtle bone: Applications for terrestrial paleoclimates?: *Palaios*, v. 14, p. 186–191.
- Bocherens, H., Koch, P. L., Mariotti, A., Geraads, D., and Jaeger, J. J., 1996, Isotopic biogeochemistry (^{13}C , ^{18}O) of mammalian enamel from African Pleistocene Hominid sites: *Palaios*, v. 11, p. 306–318.
- Boyle, E. A., 1997, Cool tropical temperatures shift the global $\delta^{18}\text{O}$ -T relationship: *Geophysical Research Letters*, v. 24, p. 273–276.
- Bryant, J. D., and Froelich, P. N., 1995, A model of oxygen isotope fractionation in body water of large mammals: *Geochimica et Cosmochimica Acta*, v. 59, p. 4523–4537.
- Burnham, R. J., 1989, Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany: *Review of Palaeobotany and Palynology*, v. 58, p. 5–32.
- Burnham, R. J., Pitman, N. C. A., Johnson, K. R., and Wilf, P., 2001, Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest: *American Journal of Botany*, v. 88, p. 1096–1102.
- Chase, C. G., Gregory-Wodzicki, K. M., Parrish, J. T., and DeCelles, P. G., 1998, Topographic history of the western cordillera of North America and controls on climate, *in* Crowley, T. J., and Burke, K. C., editors, *Tectonic Boundary Conditions for Climatic Reconstructions: Oxford Monographs on Geology and Geophysics*, v. 39, p. 73–100.
- Clementz, M. T., and Koch, P. L., 2001, Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel: *Oecologia*, v. 129, p. 461–472.
- Clementz, M. T., Hoppe, K. A., and Koch, P. L., 2003, A paleoecological paradox: the habitat and dietary preferences of the extinct tethythere *Desmostylus*, inferred from stable isotope analysis: *Paleobiology*, v. 29, p. 506–519.
- Coplen, T. B., and Kendall, C., 2000, Stable hydrogen and oxygen isotope ratios for selected sites of the I.S. Geological Survey's NASQUAN and benchmark surface-water networks: *United States Geological Survey*, p. 424.
- Dansgaard, W., 1964, Stable isotopes in precipitation: *Tellus*, v. 16, p. 436–468.
- Davies-Vollum, S. K., and Wing, S. L., 1998, Sedimentological, taphonomic, and climatic aspects of Eocene swamp deposits (Willwood Formation, Bighorn Basin, Wyoming): *Palaios*, v. 13, p. 28–40.
- Dettman, D. L., and Lohmann, K., 2000, Oxygen isotope evidence for high-altitude snow in the Laramide Rocky Mountains of North America during the Late Cretaceous and Paleogene: *Geology*, v. 28, p. 243–246.
- Ferguson, K. M., Gregory, R. T., and Constantine, A., 1999, Lower Cretaceous (Aptian–Albian) secular changes in the oxygen and carbon isotope record from high paleolatitude, fluvial sediments, southeast Australia: comparisons to the marine record, *in* Barrera, E., and Johnson, C. C., editors, *Evolution of the Cretaceous ocean–climate system: Geological Society of America Special paper 332*, p. 59–72.
- Fricke, H. C., 2003, $\delta^{18}\text{O}$ of geographically widespread mammal remains as a means of studying water vapor transport and mountain building during the early Eocene: *Geological Society of America Bulletin*, v. 115, p. 1088–1096.
- Fricke, H. C., and O'Neil, J. R., 1996, Inter- and intra-tooth variations in the oxygen isotope composition of mammalian tooth enamel: Some implications for paleoclimatological and paleobiological research: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 126, p. 91–99.

- 1999, The correlation between $^{18}\text{O}/^{16}\text{O}$ ratios of meteoric water and surface temperature: its use in investigating terrestrial climate change over geologic time: *Earth and Planetary Science Letters*, v. 170, p. 181–196.
- Fricke, H. C., and Rogers, R. R., 2000, Multiple taxon-multiple locality approach to providing oxygen isotope evidence for warm-blooded theropod dinosaurs: *Geology*, v. 28, p. 799–802.
- Fricke, H., Clyde, W., O'Neil, J. R., and Gingerich, P., 1998a, Evidence for rapid climate change in North America during the latest Paleocene thermal maximum: Oxygen isotope composition of biogenic phosphate from the Bighorn Basin (Wyoming): *Earth and Planetary Science Letters*, v. 160, p. 193–208.
- 1998b, Intra-tooth variation in $\delta^{18}\text{O}$ of mammalian tooth enamel as a record of seasonal changes in continental climate variables: *Geochimica et Cosmochimica Acta*, v. 62, p. 1839–1851.
- Fritz, W. J., and Harrison, S., 1985, Early Tertiary volcanoclastic deposits of the northern Rocky Mountains, *in* Flores, R. M., and Kaplan, S. S., editors, *Cenozoic Paleogeography of the West-central United States*. Denver, Colorado: Rocky Mountain Section Society of Economic Paleontologists and Mineralogists, p. 383–402.
- Golovneva, L. B., 2000, Palaeogene climates of Spitsbergen: *GFF (Geological Society of Sweden)*, v. 122, p. 62–63.
- 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., and Wing, S. L., 1995, Eocene continental climates and latitudinal temperature gradients: *Geology*, v. 23, p. 1044–1048.
- Greenwood, D. R., Wilf, P., Wing, S. L., and Christophel, D. C., 2004, Paleotemperature Estimation Using Leaf-Margin Analysis: Is Australia Different?: *Palaios*, v. 19, p. 129–142.
- 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.
- Gregory-Wodzicki, K. M., 1997, The late Eocene House Range Flora, Sevier Desert, Utah: Paleoclimate and paleoelevation: *Palaios*, v. 12, p. 552–567.
- 2000, Relationships between leaf morphology and climate, Bolivia: implications for estimating paleoclimate from fossil floras: *Paleobiology*, v. 26, p. 668–688.
- Hickey, L. J., 1977, Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota: *Geological Society of America Memoir* 150, p. 1–181.
- Hickey, L. J., West, R. M., Dawson, M. R., and Choi, D. K., 1983, Arctic terrestrial biota: paleomagnetic evidence of age disparity with mid-northern latitudes during the late Cretaceous and Early Tertiary: *Science*, v. 221, p. 1153–1156.
- Huber, B. T., Hodell, D. A., and Hamilton, C. P., 1995, Mid- to Late Cretaceous climate of the southern high latitudes: Stable isotopic evidence for minimal equator-to-pole thermal gradients: *Geological Society America Bulletin*, v. 107, p. 1164–1191.
- Huber, B. T., Norris, R. D., and MacLeod, K. G., 2002, Deep-sea paleotemperature record of extreme warmth during the Cretaceous: *Geology*, v. 30, p. 123–126.
- Jacobs, B. F., 1999, Estimation of rainfall variables from leaf characters in tropical Africa: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 145, p. 231–250.
- 2002, Estimation of low-latitude paleoclimates using fossil angiosperm leaves: examples from the Miocene Tugen Hills, Kenya: *Paleobiology*, v. 28, p. 399–421.
- Kennedy, E. M., Spicer, R. A., and Rees, P. M., 2002, Quantitative palaeoclimate estimates from Late Cretaceous and Paleocene leaf floras in the northwest of the South Island, New Zealand: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 184, p. 321–345.
- Koch, P. L., Fisher, D. C., and Dettman, D., 1989, Oxygen isotope variation in the tusks of extinct proboscideans: A measure of season of death and seasonality: *Geology*, v. 17, p. 515–519.
- Koch, P. L., Zachos, J. C., and Dettman, D. L., 1995, Stable isotope stratigraphy and paleoclimatology of the Paleogene Bighorn Basin (Wyoming, USA): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 61–89.
- Kohn, M. J., 1996, Predicting animal $\delta^{18}\text{O}$: Accounting for diet and physiological adaption: *Geochimica et Cosmochimica Acta*, v. 60, p. 4811–4829.
- Kolodny, Y., Luz, B., and Navon, O., 1983, Oxygen isotope variations in phosphate of biogenic apatite, I: Fish bone apatite: *Earth and Planetary Science Letters*, v. 64, p. 398–404.
- Kornexl, B. E., Gehre, M., Hofling, R., and Werner, R. A., 1999, On-line $\delta^{18}\text{O}$ measurement of organic and inorganic substances: *Rapid Communications in Mass Spectrometry*, v. 13, p. 1685–1693.
- Kowalski, E. A., 2002, Mean annual temperature estimation based on leaf morphology: a test from tropical South America: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 188, p. 141–165.
- Kowalski, E. A., and Dilcher, D. L., 2003, Warmer paleotemperatures for terrestrial ecosystems: *Proceedings of the National Academy of Sciences*, v. 100, p. 167–170.
- Lee-Thorpe, J. A., and Van der Merwe, N. J., 1991, Aspects of the chemistry of modern and fossil biogenic apatites: *Journal of Archaeological Science*, v. 18, p. 343–354.
- Longinelli, A., 1984, Oxygen isotopes in mammal bone phosphate: A new tool for paleohydrological and paleoclimatological research?: *Geochimica et Cosmochimica Acta*, v. 48, p. 385–390.
- Longinelli, A., and Nuti, S., 1973, Revised phosphate-water isotopic temperature scale: *Earth and Planetary Science Letters*, v. 19, p. 373–376.
- Luz, B., and Kolodny, Y., 1985, Oxygen isotope variations in phosphates of biogenic apatites, IV: Mammal teeth and bones: *Earth and Planetary Science Letters*, v. 75, p. 29–36.
- Markwick, P. J., 1995, “Equability”, continentality, and Tertiary “climate”: The crocodylian perspective: *Geology*, v. 22, p. 613–616.
- McIver, E. E., and Basinger, J. F., 1999, Early Tertiary floral evolution in the Canadian high Arctic, *in* Crane, P. R., and Herendeen, P. S., editors: *Annals of the Missouri Botanical Garden*, v. 86, p. 523–545.

- 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.
- Nordt, L., Atchley, S., and Dworkin, S., 2003, Terrestrial evidence for two greenhouse events in the latest Cretaceous: *GSA Today*, v. 13, p. 4–9.
- Norris, R. D., Jones, L. S., Corfield, R. M., and Cartlidge, J. E., 1996, Skiing in the Eocene Uinta mountains? Isotopic evidence for snow melt and large mountains in the Green River Formation: *Geology*, v. 24, p. 406–403.
- Norris, R. D., Corfield, R. M., and Hayes-Baker, K., 2000, Mountains and Eocene climate, in Huber, B. T., MacLeod, K. G., and Wing, S. L. editors, *Warm climates in earth history*: Cambridge, Cambridge University Press, p. 161–197.
- O'Neil, J. R., Roe, L. J., Reinhard, E., and Blake, R. E., 1994, A rapid and precise method of oxygen isotope analysis of biogenic phosphate: *Israel Journal of Earth Sciences*, v. 43, p. 203–212.
- Palmqvist, P., Gocke, D. R., Arribas, A., and Farina, R. A., 2003, Paleoclimatological reconstruction of a lower Pleistocene large mammal community using biochemical ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, Sr:Zn) and ecomorphological approaches: *Paleobiology*, v. 29, p. 205–229.
- Patterson, W. P., Smith, G., and Lohmann, K. C., 1993, Continental Paleothermometry and seasonality using the isotopic composition of aragonitic otoliths of freshwater fishes, in Swart, P. K., Lohmann, K. C., McKenzie, J., and Savin, S., editors, *Climate change in continental climate records*: Geophysical Monograph 78, American Geophysical Union, p. 191–202.
- Peixoto, P., and Oort, A. H., 1992, *Physics of Climate*: New York, American Institute of Physics, p. 520.
- Pierrehumbert, R. T., and Roca, R., 1998, Evidence for control of Atlantic subtropical humidity by large scale advection: *Geophysical Research Letters*, v. 25, p. 4537–4540.
- Rowley, D. B., Pierrehumbert, R. T., and Currie, B., 2001, A new approach to stable isotope-based paleoaltimetry: implications for paleoaltimetry and paleohypsometry of the High Himalaya since the Late Miocene: *Earth and Planetary Science Letters*, v. 188, p. 253–268.
- Rozanski, K., Aragus-Araguas, L., and Gonfiantini, R., 1993, Isotopic patterns in modern global precipitation in Swart, P. K., Lohmann, K. C., McKenzie, J., and Savin, S., editors, *Climate change in continental climate records*: American Geophysical Union, Geophysical Monograph 78, p. 1–36.
- Savage, D. E., and Russell, D. E., 1983, *Mammalian Paleofaunas of the World*: New York, Addison-Wesley Publishing Company, p. 432.
- Scotese, C. R., 1999, *PGIS/Mac, version 4.0*.
- Sloan, L., and Pollard, D., 1998, Polar stratospheric clouds: a high latitude warming mechanism in an ancient greenhouse world: *Geophysical Research Letters*, v. 25, p. 3517–3520.
- Sloan, L. C., Walker, J. C. G., and Moore, T. C., 1995, Possible role of oceanic heat transport in early Eocene climate: *Paleoceanography*, v. 10, p. 347–356.
- 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*, v. 30, p. 801–827.
- Sternberg, L. da S. L., 1989, Oxygen and hydrogen isotope ratios in plant cellulose: Mechanisms and applications, in Rundel, P., Ehleringer, J. R., and Nagy, K., editors, *Application of Stable Isotopes to Ecological Research*: University of California, Ecological Series Monographs, v. 62, p. 124–141.
- Vennemann, T., Fricke, H. C., Blake, R. E., O'Neil, J. R., and Colman, A., 2002, Oxygen isotope analysis of phosphates: A comparison of techniques for analysis of Ag_3PO_4 : *Chemical Geology*, 185, p. 321–336.
- White, T., Gonzalez, L., Ludvigson, G., and Poulsen, C., 2001, Middle Cretaceous greenhouse hydrologic cycle of North America: *Geology*, v. 29, p. 363–366.
- Wilf, P., 1997, When are leaves good thermometers? A new case for Leaf Margin Analysis: *Paleobiology*, v. 23, p. 373–390.
- 2000, Late Paleocene-early Eocene climate changes in southwestern Wyoming: paleobotanical analysis: *Geological Society of America Bulletin*, v. 112, p. 292–307.
- Wilf, P., Wing, S. L., Greenwood, D. L., and Greenwood, C. L., 1998, Using fossil leaves as paleoprecipitation indicators: an Eocene example: *Geology*, v. 26, p. 203–206.
- Wing, S. L., and DiMichele, W. A., 1995, Conflict between local and global changes in plant diversity through geological time: *Palaaios*, v. 10, p. 551–564.
- Wing, S. L., and Greenwood, D. R., 1993, Fossils and fossil climate: The case for equable continental interiors in the Eocene: *London, Philosophical Transactions of the Royal Society*, v. 341, p. 243–252.
- Wing, S. L., Bown, T. M., and Obradovich, J. D., 1991, Early Eocene biotic and climatic change in interior western North America: *Geology*, v. 19, p. 1189–1192.
- Wing, S. L., Bao, H., and Koch, P. L., 2000, An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic, in Huber, B. T., MacLeod, K. G., and Wing, S. L., editors, *Warm climates in earth history*: Cambridge, Cambridge University Press, p. 197–237.
- 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, p. 1–37.
- 1992, An analysis of present-day lapse rates in the western conterminous United States and their significance to paleoaltitudinal estimates: *U.S. Geological Survey Bulletin*, v. 1964, p. 1–35.
- 1993, A method of obtaining climatic parameters from leaf assemblages: *U.S. Geological Survey Bulletin* 2040, p. 1–71.
- Wolfe, J. A., and Dilcher, D. L., 2000, Late Paleocene through middle Eocene climate in lowland North America: *GFF*, v. 122, p. 184–185.
- Wolfe, J. A., and Upchurch, G. R., 1987, North American nonmarine climates and vegetation during the late Cretaceous: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 61, p. 33–77.
- Worldclimate.com, 1996–2004, <http://www.worldclimate.com/>, Buttle and Tuttle Ltd.

- Zachos, J., Stott, L., and Lohmann, K.C., 1994, Evolution of early Cenozoic marine temperatures: Paleoclimatology, v. 9, p. 353–387.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001, Trends rhythms and aberrations in global climate 65 Ma to present: *Science*, v. 292, p. 686–693.
- Zazzo, A., Lecuyer, C., and Mariotti, A., 2004, Experimentally-controlled carbon and oxygen isotope exchange between bioapatites and water under inorganic and microbially-mediated conditions: *Geochimica et Cosmochimica Acta*, v. 68, p. 1–12.
- Ziegler, A. M., Rowley, D. B., Lottes, A. L., Sahagian, D. L., Hulver, M. L., and Gierlowski, T. C., 1985, Paleogeographic interpretation: with an example from the mid-Cretaceous of North America: *Annual Review Earth Planetary Science*, v. 13, p. 385–425.