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Seasonal variability in Arctic temperatures during early Eocene time

Jaelyn J. Eberle [a,*], Henry C. Fricke [b], John D. Humphrey [c], Logan Hackett [c], Michael G. Newbrey [d], J. Howard Hutchison [e]

[a] University of Colorado Museum of Natural History and Department of Geological Sciences, University of Colorado, Boulder, USA
[b] Department of Geology, Colorado College, Colorado Springs, USA
[c] Department of Geology and Geological Engineering, Colorado School of Mines, Golden, USA
[d] Department of Biological Sciences, University of Alberta, Edmonton, and Royal Tyrrell Museum of Palaeontology, Drumheller, Canada
[e] University of California Berkeley Museum of Paleontology, 1101 Valley Life Sciences, Berkeley, USA

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ABSTRACT

As a deep time analog for today's rapidly warming Arctic region, early Eocene (52–53 Ma) rock on Ellesmere Island in Canada's High Arctic (~79°N.) preserves evidence of lush swamp forests inhabited by turtles, alligators, primates, tapirs, and hippo-like *Coryphodon*. Although the rich flora and fauna of the early Eocene Arctic imply warmer, wetter conditions than at present, the quantification of Eocene Arctic climate has been more elusive. By analyzing oxygen isotope ratios of biogenic phosphate from mammal, fish, and turtle fossils from a single locality on central Ellesmere Island, we infer early Eocene Arctic temperatures, including mean annual temperature (MAT) of ~8 °C, mean annual range in temperature of ~16.5–19 °C, warm month mean temperature of 19–20 °C, and cold month mean temperature of 0–3.5 °C. Our seasonal range in temperature is similar to the range in estimated MAT obtained using different proxies. In particular, relatively high estimates of early Eocene Arctic MAT and SST by others that are based upon the distribution of branched glycerol dialkyl glycerol tetraether (GDGT) membrane lipids in terrestrial soil bacteria and isoprenoid tetraether lipids in marine Crenarchaeota fall close to our warm month temperature, suggesting a bias towards summer values. From a paleontologic perspective, our temperature estimates verify that alligators and tortoises, by way of nearest living relative-based climatic inference, are viable paleoclimate proxies for mild, above-freezing year-round temperatures. Although for both of these reptilian groups, past temperature tolerances probably were greater than in living descendants.

1. Introduction

Today's Arctic region has undergone unprecedented warming, with temperatures rising at almost twice the rate as the rest of the world (ACIA, 2005). As warming is predicted to continue well into the future (Zhang and Walsh, 2006), there is critical need for climatic and ecologic analogs of a mild, ice-free Arctic. Among the best deep time analogs, early Eocene (~52–53 Ma) sediments on central Ellesmere Island, Arctic Canada (~76°N. Paleolat.; Fig. 1) preserve fossil evidence of lush swamp forests (McIver and Basinger, 1999) inhabited by alligators, giant tortoises, varanid lizards, and fish (Estes and Hutchison, 1980), as well as a diverse mammalian fauna that included tapirs, brontotheres, primates, and hippo-like *Coryphodon* (Dawson et al., 1993; Eberle, 2005, 2006). This fauna shares most of its genera with contemporaneous mid-latitude faunas (Estes and Hutchison, 1980; Eberle and McKenna, 2002), and some of the large mammals appear to have lived year-round in the High Arctic (Eberle et al., 2009).

The existence of dense forests inhabited by a rich vertebrate fauna implies much warmer and wetter climate in the Arctic than at present. Quantitative estimates of early Eocene climatic conditions at high latitudes (Table 1), however, are rare and often contradictory. For example, estimates of mean annual temperature (MAT) in continental settings range from 4 to 20 °C (e.g., Basinger et al., 1994; Greenwood and Wing, 1995; Fricke and Wing, 2004; Weijers et al., 2007), which is equivalent to the range of MAT from present-day Canada to Florida. Further, very few estimates of other important climatic variables such as mean annual range in temperature (MART), cold monthly mean temperature (CMMT) and warm monthly mean temperature (WMMT) have been published (Basinger et al., 1994; Greenwood and Wing, 1995; Table 1). Information regarding these variables is particularly important when considering the early Eocene as an analog for the future because many aspects of biodiversity, such as patterns of species richness (Currie, 2001) and geographic ranges of species (Letcher and Harvey, 1994), are related less to mean annual temperatures than to seasonal differences and ranges. The two proxy-

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* Corresponding author. University of Colorado Museum of Natural History, 265 UCB, Boulder, CO 80309, USA. Tel.: +1 303 492 8069; fax: +1 303 735 2347.
E-mail addresses: Jaelyn.Eberle@Colorado.edu (J.J. Eberle), hfricke@ColoradoCollege.edu (H.C. Fricke), jhumphre@Mines.edu (J.D. Humphrey), michael.newbrey@ualberta.ca (M.G. Newbrey), hutch@color-country.net (J.H. Hutchison).

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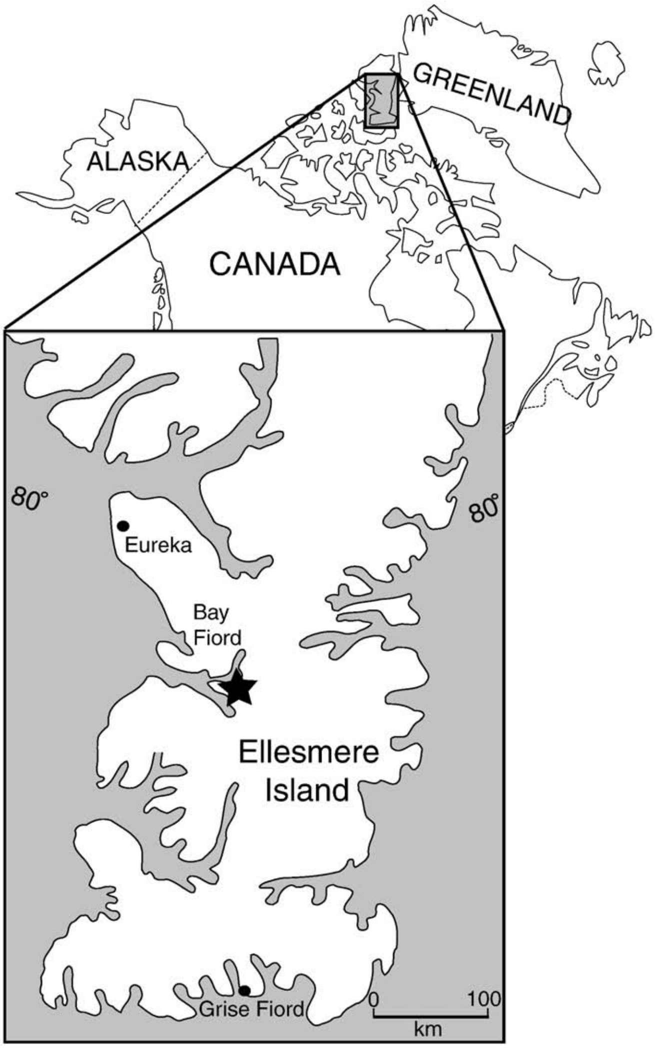

Fig. 1. Map of Ellesmere Island, Nunavut, Arctic Canada showing location of CMN locality 76-44 (star) at approximately 79°N. Paleogeographic reconstructions indicate that this locality was just a few degrees further south than its present latitude (~76°N. Paleolat.; Irving and Wynne, 1991).

based estimates of seasonal range in temperature and CMMT for the early Eocene Arctic are based upon the climatic preferences of nearest living relatives of fossil taxa and multiple regression (MR) analyses of leaf physiognomic variables in North American Eocene floras (Basinger et al., 1994; Greenwood and Wing, 1995). In these studies, the authors considered a below-freezing CMMT to be too low, in part because the MR method attributed deciduousness to temperature seasonality when in fact this feature may be induced by light. Further, because high latitude Paleogene megafloras are typically low in diversity (<20 species/site), multiple regression estimates are not as reliable as those derived from mid-latitude floras with higher species numbers (Basinger et al., 1994).

Our goal is to provide quantitative information regarding early Eocene climate at high latitudes, in particular annual range of temperature and warm and cold month means. To do so, we utilize a combination of oxygen isotope ratios from fossil bone and tooth enamel phosphate of co-occurring mammal, fish, and turtle from Ellesmere Island. Using this seasonal information, we suggest that it is possible to reconcile the wide range in MAT estimates that have been obtained using other proxy methods. Lastly, we use our climate data to test the hypothesis that fossil alligators and tortoises such as those that inhabited the Eocene Arctic are reliable paleoclimate proxies.

2. Oxygen isotope ratios, vertebrate fossils, and climate

Vertebrate bone and tooth enamel, consisting largely of biogenic apatite ($Ca_5(PO_4,CO_3)_3(OH,CO_3)$), can be used as a proxy for past climate because oxygen isotope ratios of the carbonate and phosphate components depend primarily on (1) oxygen isotope ratio of ingested water; and (2) temperature of bioapatite precipitation. The nature of these relations, however, differs for different animals. We can take advantage of the fact that co-existing animals can have different physiologies, and thus ‘solve’ for environmental temperatures of the past.

Consider the situation where co-occurring mammals and fish are found from a single locality and stratigraphic horizon (Fig. 2). It is possible to estimate the mean annual temperature of river water using oxygen isotope ratios of biogenic apatite from fish, oxygen isotope ratios of the river, and the fractionation equation between water and phosphate (Kolodny et al., 1983; Fricke et al., 1998a; Fricke and Wing, 2004). This method works because fish are characterized by a large through-put of water, and the $\delta^{18}O$ values of their apatite reflect that of their aqueous environment (Kolodny et al., 1983). Freshwater fish are also ectothermic and do not regulate their body temperatures internally. While most species have a restricted range of growth temperatures (Patterson et al., 1993), some groups such as bowfins (amiids; used in this study) grow year-round, and bulk samples taken from their bones capture an annual (or multi-year) amount of deposition. In short, oxygen isotope ratios of fish bone apatite are impacted by changes in environmental/water temperature as well as by the oxygen isotope ratio of ingested water.

Table 1
Eocene High Arctic continental temperature estimates. All are early Eocene, with exception of palynological data from the Norwegian–Greenland Sea that are middle Eocene in age.

Location	Paleolat.	MAT	MART	WMMT	CMMT	Method
Lomonosov R.	~75°N	18–20 °C	–	–	–	Bacterial membrane lipids[a]
Norwegian–Greenland Sea	~75°N	14 °C	–	18–24 °C	>5 °C	Palynology[b] NLR
Ellesmere Is.	~76°N	8.2 °C	14 °C	–	−2 °C	Paleofloral analyses[c] MR
Ellesmere and Axel Heiberg Is.	~76°N	12–15 °C	20–25 °C	>25 °C	0–4 °C	Paleofloral analyses[d] NLR
Ellesmere Is.	~76°N	4.0 °C	–	–	–	$\delta^{18}O$ analyses[e]
Ellesmere Is.	~76°N	8 °C	16.5–19 °C	19–20 °C	0–3.5 °C	$\delta^{18}O$ analyses THIS PAPER

Note: MAT is mean annual temperature, CMMT is cold month mean temperature, WMMT is warm month mean temperature, MART is mean annual range of temperature, MR is multiple regression leaf physiognomic analyses, and NLR is Nearest Living Relatives method (see Basinger et al., 1994). MAT estimated from soil-derived bacterial membrane lipids has standard error of approximately ±5 °C (Weijers et al., 2007); MAT estimated from spore and pollen assemblages has an error of ±3 °C(Eldrett et al., 2009); climate parameters estimated from paleofloral analyses, and specifically multiple regression models of physiognomic characters in paleoflora have standard errors of: MAT ±2.0 °C; CMMT +3.6 °C; and MART ±5.1 °C (Greenwood and Wing, 1995); and MAT and CMMT estimated from $\delta^{18}O_{river}$ values that are determined from $\delta^{18}O$ analyses of mammalian fossils incorporated into a physiological model have a range of uncertainty of approximately ±7 °C. Turtle-derived WMMT has an estimated error of ±2.5 °C (see discussion).

[a] Weijers et al. (2007).
[b] Eldrett et al. (2009).
[c] Greenwood and Wing (1995).
[d] Basinger et al., 1994.
[e] Fricke and Wing (2004).

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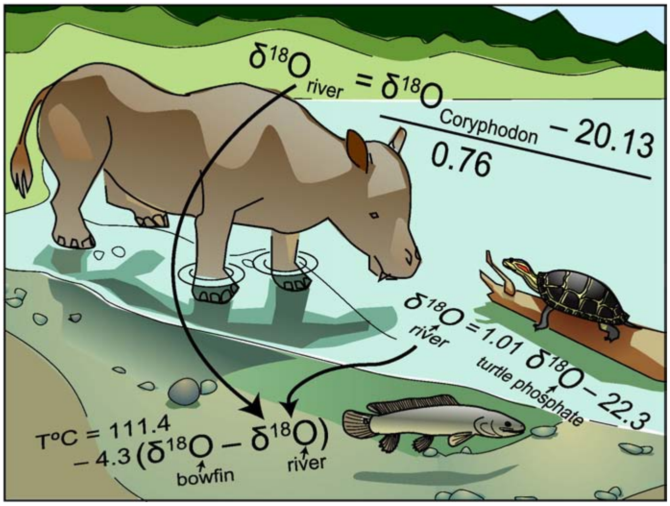

Fig. 2. Illustration of how oxygen isotope ratios from three vertebrate taxa living in a single riverine environment can be used to estimate local temperature variables. Biogenic phosphate in mammals, including large, hippo-like *Coryphodon* shown here, is formed at a constant temperature and is used in a physiological model (Kohn, 1996) to estimate the $\delta^{18}O$ of the river water ($\delta^{18}O_{river}$) (upper right equation). This $\delta^{18}O_{river}$ value is then substituted along with $\delta^{18}O$ of biogenic phosphate in bowfin bones ($\delta^{18}O_{bowfin}$) into the phosphate–water fractionation equation of Longinelli and Nuti (1973; lower left equation) to estimate mean annual temperature (MAT) of the river. To estimate the warm monthly mean temperature (WMMT), the $\delta^{18}O$ of biogenic phosphate from emydid turtle bone ($\delta^{18}O_{turtle\ phosphate}$) is first used in the regression equation for modern emydid turtles by Barrick et al. (1999) that estimates $\delta^{18}O_{river}$ during summer months when turtle shell growth occurs. The $\delta^{18}O_{river}$ is then used with $\delta^{18}O_{bowfin}$ in the phosphate–water fractionation equation (lower left) to estimate a WMMT of the river. Because today's North American rivers are ~1 °C warmer than the atmosphere, our estimates of atmospheric MAT and WMMT are ~1 °C cooler than those estimated for the river.

The remaining unknown in the fractionation equation is the oxygen isotope ratio of ingested, or river, water (Fig. 2). This isotope ratio can be inferred by means of the oxygen isotope ratio of co-existing mammals. Unlike fish, oxygen utilized by mammals has two primary sources — ingested water (~75%) and atmospheric oxygen (~25%) — but isotopic variations in ingested water play the primary role in corresponding variations in isotopic ratios of bioapatite (Kohn, 1996). Mammals are endothermic homeotherms (warm-blooded), and exhibit a relatively constant body temperature, regardless of the air temperature. The range of body temperature among extant placental mammals correlates with phylogeny and is approximately 32–38 °C, with xenarthrans (edentates) falling at the low end, while carnivorans and ungulates exhibit the highest mammalian body temperatures (Clarke and Rothery, 2008). Biogenic phosphate in a mammal's teeth and bones forms from body water at a constant temperature, and any change in the oxygen isotope ratio of biogenic apatite should reflect a change only in the oxygen isotope ratio of water ingested from surface reservoirs sourced by local precipitation (Fricke et al., 1998a,b). When the oxygen isotope ratio of biogenic apatite is measured, these values can be used to estimate the oxygen isotope ratio of ingested water using a physiological model (Kohn, 1996). In turn, these estimates of the oxygen isotope ratio of river water can be inserted into the isotope fractionation equation to estimate mean annual river temperature (Fig. 2).

Using a similar approach, it is also possible to estimate summer temperatures. In this case, we rely on the fact that turtles are able to control their body temperature via behavioral modifications such as basking. As a result, they can be considered effective homeotherms. Furthermore, shell growth in non-equatorial regions occurs only during the summer months (Barrick et al., 1999), and consequently the oxygen isotope ratio of turtle shell can be used to estimate the warm month mean temperature (WMMT) of a locality (Fig. 2). Analyses of living pond turtles (emydids) indicate covariation of $\delta^{18}O_{turtle\ phosphate}$ with $\delta^{18}O_{river}$ (Barrick et al., 1999). Oxygen isotope ratios of rivers estimated from turtle shell phosphate can be incorporated along with measured oxygen isotope ratios of fish into the phosphate–water fractionation equation of Longinelli and Nuti (1973) to provide an estimate of the temperature of shell deposition (Barrick et al., 1999), which in the Arctic, would be in summer.

Lastly, it is also possible to estimate the seasonal range in temperature for a region using the modern empirical relation between it and the seasonal range in $\delta^{18}O$ of surface water (Fricke et al., 1998a). Because mammalian tooth enamel mineralizes incrementally over time scales of months, seasonal variations in $\delta^{18}O$ of ingested water can be estimated by intra-tooth sampling (Fricke et al., 1998a,b), or by taking a number of bulk tooth enamel samples from multiple animals at a single locality (Clementz and Koch, 2001), and using a physiological model (e.g., Kohn, 1996). In general, seasonal changes in $\delta^{18}O$ of tooth enamel reflect changes in $\delta^{18}O$ of precipitation-sourced drinking water that occur in response to temperature changes, with higher $\delta^{18}O$ corresponding to summer (Fricke and O'Neil, 1999).

3. Samples

Arctic fossils for this study were recovered from the Margaret Formation, Eureka Sound Group near Bay Fiord on central Ellesmere Island (Fig. 1). An early Eocene (late Wasatchian; ~52–53 Ma) age is inferred for this fauna, based upon mammalian biostratigraphy and correlation to mid-latitude faunas (Dawson et al., 1993) and palynology (Norris and Miall, 1984). Rocks of the Margaret Formation comprise coarsening-upward cycles of interbedded cross-bedded sandstone, siltstone, mudstone and coal, interpreted as a proximal delta front to delta plain environment with abundant channels and coal swamps (Miall, 1986). Macrofloral assemblages indicate a mostly deciduous swamp forest of taxodioid conifer and broadleaf angiosperm taxa (McIver and Basinger, 1999). This macroflora, along with oxygen isotope analyses of teeth of mammalian taxa (Eberle et al., 2009) and sedimentology (Miall, 1986), indicates a humid environment, in stark contrast to today's polar desert.

The hippo-like mammal *Coryphodon* as well as bones of bowfin (amiid fish) and emydid (pond) turtle from CMN locality 76-44 on central Ellesmere Island are the focus of this study. This is in contrast to an earlier study by Fricke and Wing (2004) in which *Coryphodon* and fish samples came from multiple sites separated by space and possibly time. *Coryphodon* was probably semiaquatic (Secord et al., 2008), and therefore most ingested water probably came from the river, with only minor contributions from terrestrial plant/leaf water which can have $\delta^{18}O$ values much higher than $\delta^{18}O_{river}$ (Sternberg, 1989). Bowfins are freshwater fishes limited today to North America. Like their living relatives, the Eocene Arctic bowfins grew year-round, indicated by the presence of both summer and winter bone deposition on the vertebrae and dentary sampled in this study as well as similar growth profiles to living bowfin *Amia calva* (see online Supplementary materials). Emydid turtles are the most abundant and speciose turtles in North America today, they comprise mostly freshwater species, and they include box turtles and sliders (Stephens and Wiens, 2003). The Eocene Arctic emydids were small turtles (<20 cm in length; Estes and Hutchison, 1980).

Arctic fossils are rare and consequently the number of specimens sampled from CMN locality 76-44 is small. Multiple samples were taken from two *Coryphodon* teeth (NUFV specimens 399 and 18), an emydid shell fragment (CMN 52771), as well as two vertebrae and a jaw fragment of bowfin (NUFV 400, NUFV 401, CMN 32395). Intra-tooth sampling of *Coryphodon* teeth was used to estimate the seasonal range in $\delta^{18}O$. Each sample of approximately 3–5 mg was removed using a Dremel© tool with diamond-tipped bits. Elsewhere we reported on oxygen and carbon isotope ratios for the carbonate component of tooth enamel from Eocene Arctic mammals and the

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paleoecologic implications (Eberle et al., 2009). Here, however, we utilize oxygen isotope ratios measured from the phosphate component of bone and tooth enamel to estimate paleotemperature. Although tooth enamel is considered the most reliable vertebrate tissue for paleoenvironmental studies, in vertebrates that lack teeth such as turtles, the phosphate $\delta^{18}O$ in their bones has been shown to be relatively unaltered and more pristine than carbonate $\delta^{18}O$ (Matson and Fox, 2008). Our phosphate data are reported as $\delta^{18}O$ values, where $\delta = (R_{sample}/R_{standard} - 1) * 1000‰$; the standard is VSMOW (see online Supplementary materials for details of sample preparation and isotopic analyses as well as discussion of diagenesis).

5. Results

Results are provided in Table 2. We calculated the mean annual $\delta^{18}O_{river}$ and seasonal range in $\delta^{18}O_{river}$ by incorporating isotopic data from *Coryphodon* ($\delta^{18}O_{Coryphodon}$) into Kohn's (1996) physiologic model for generalized mammalian herbivores: $\delta^{18}O_{river} = (\delta^{18}O_{Coryphodon} - 20.13)/0.76$, assuming a relative humidity of 75% (see Fig. 2). This model accounts for oxygen input and output amounts and shows a good fit with published data from modern mammals, with estimated uncertainty range of ±1.39‰ due to physiological factors (Kohn, 1996).

Our mean $\delta^{18}O_{bowfin}$ is from two vertebrae (from fishes aged 6 years; see online Supplementary materials) and a dentary that averages 2–3 years of bone deposition, although it is somewhat biased towards warmer seasons because more bone growth occurred then. Assuming the bowfin and *Coryphodon* ingested water from the same Eocene Arctic river, the $\delta^{18}O_{river}$ estimated from $\delta^{18}O_{Coryphodon}$ is used alongside $\delta^{18}O_{bowfin}$ in the phosphate–water fractionation equation to estimate mean annual temperature (MAT) for the early Eocene Arctic river at ~9 °C (Fig. 2). Due to the uncertainty of ±1.39‰ associated with using $\delta^{18}O_{Coryphodon}$ and the physiological model of Kohn (1996) to estimate $\delta^{18}O_{river}$, our MAT for the early Eocene Arctic river has an estimated uncertainty range of at least ±7 °C. Today's North American rivers are, on average, 1° warmer than the atmosphere, and we assume that this relationship existed for the Eocene as well (Fricke et al., 1998b). Consequently, we estimate early Eocene Arctic atmospheric MAT to be about 8 °C.

To estimate warm monthly mean temperature (WMMT), we utilize $\delta^{18}O$ from emydid turtle shell and $\delta^{18}O$ bowfin fossils (Table 2). This works because turtle shell growth in non-equatorial regions occurs only during the summer months (Barrick et al., 1999). Using the regression equation of Barrick et al. (1999, fig. 1d) for modern turtles: $\delta^{18}O_{river} = 1.01\delta^{18}O_{turtle\ phosphate} - 22.3$ (Fig. 2), where the slope is unity and the correlation coefficient is 0.98, a $\delta^{18}O_{river}$ for the summer months can be calculated, with a standard error of approximately ±0.58‰. Whereas the composition of food is the most important factor contributing to the total uncertainty range in $\delta^{18}O$ of herbivorous mammals (Kohn, 1996), the advantage to using freshwater turtles in these analyses is that regardless of species, the majority of their diet has $\delta^{18}O$ values in equilibrium with the $\delta^{18}O$ of the water they inhabit (Barrick et al., 1999). The $\delta^{18}O_{river}$, in turn, is used with $\delta^{18}O_{bowfin}$ in the phosphate–water fractionation equation to estimate a WMMT of approximately 21 °C (±2.5 °C) for the early Eocene Arctic river (~20 °C for atmospheric MAT). Although the $\delta^{18}O_{bowfin}$ represents a bulk sample from year-round bone deposition, it is somewhat biased towards warmer seasons because more bone growth occurred then, and consequently we expect that its substitution in the phosphate–water fractionation equation would not prejudice the WMMT significantly.

Both CMMT and WMMT can be estimated in another manner by comparing low and high $\delta^{18}O$ values from *Coryphodon* along with $\delta^{18}O$ values from the bowfin. The highest value of $\delta^{18}O_{Coryphodon}$ (6.61‰; Table 2), hypothesized to represent summer deposition of tooth enamel (Fricke and O'Neil, 1999; Eberle et al., 2009), can be substituted into the physiological model to calculate $\delta^{18}O_{river}$ during the summer months. Similarly, the lowest value of $\delta^{18}O_{Coryphodon}$ (3.30‰; Table 2), hypothesized to represent winter deposition of tooth enamel (Fricke and O'Neil, 1999; Eberle et al., 2009), can be used in the model to estimate $\delta^{18}O_{river}$ during the winter months. These estimates can, in turn, be used with $\delta^{18}O_{bowfin}$ in the phosphate–water fractionation equation to estimate a river WMMT of ~20 °C and a CMMT of ~1 °C (~19 °C and 0 °C, respectively, for atmospheric WMMT and CMMT). Although the absolute uncertainty of these estimates is ±7 °C, the congruence of the *Coryphodon*-derived WMMT with the turtle-derived WMMT lends more credence to these results. It should be noted that this approach relies on the bulk sampling of the bowfin vertebrae, which means that an *annual* average $\delta^{18}O$ of bowfin was used to calculate a *seasonal* temperature. Because more bone was deposited during the summer months (see online Supplementary materials), $\delta^{18}O_{bowfin}$ probably had minimal effect on the WMMT, although our CMMT estimates are likely to be slightly low.

A final means of estimating the seasonal range in temperature utilizes the observed inter-tooth range in $\delta^{18}O$ values of biogenic phosphate. Because of the role of atmospheric oxygen in 'dampening' the seasonal signal (Kohn, 1996), the observed 3.3‰ range in $\delta^{18}O_{Coryphodon}$ (Table 2) corresponds to an approximately 4.1‰ range in $\delta^{18}O_{river}$. This range is the same as that obtained via serial sampling of Eocene Arctic *Coryphodon* teeth and the isotopic analysis of the carbonate component of tooth enamel (Eberle et al., 2009). Furthermore, this seasonal range in $\delta^{18}O$ agrees with that inferred from isotopic analyses of wood cellulose in Eocene Arctic trees (Jahren and Sternberg, 2008).

At the present time, the seasonal range in oxygen isotope composition of precipitation is strongly correlated to seasonal range in temperature (MART; Fricke et al., 1998a, fig. 1). Applying this relation to the seasonal 4.1‰ range in $\delta^{18}O$ of Eocene water yields a MART of approximately 16.5 °C. A range of 16.5° considered alongside the estimated mean annual temperature of 8 °C suggests a cold month mean of about freezing. However, subtracting 16.5 °C from the turtle-estimated WMMT (which has a lower range of uncertainty than the mammal-derived WMMT; see discussion above) suggests a cold month mean of ~3.5 °C.

Table 2
$\delta^{18}O$ of *Coryphodon*, amiid (bowfin), and emydid (pond turtle) from early Eocene CMN loc. 76-44, central Ellesmere Island, Nunavut, Arctic Canada, as well as estimates of $\delta^{18}O_{river}$.

Species	N (samples)[a]	$\delta^{18}O_{phosphate}$ ‰ (σ)	$\delta^{18}O_{river}$ ‰[b]
Coryphodon	2 (9)	4.67 (1.19); range 3.3–6.61	−20.34
Emydid (pond turtle)	2 (2)	4.71 (0.23)	−17.54
Amiid fish (bowfin)	3 (9)	3.50 (0.65)	

[a] N = number of specimens, with number of samples in brackets; σ = Standard Deviation.

[b] $\delta^{18}O_{river}$ is calculated by substituting $\delta^{18}O_{phosphate}$ from bone and tooth enamel into physiologic models for mammals (Kohn, 1996) and turtles (Barrick et al., 1999), as outlined in Fig. 2.

6. Discussion

6.1. Comparison to previous studies

Oxygen isotope data from a number of physiologically-different taxa that are interpreted using a variety of assumptions and different empirical relations between water chemistry and climatic parameters provide remarkably consistent estimates of MAT (8 °C), WMMT (19–20 °C), and CMMT (0–3.5 °C). At first glance, these results, particularly MAT, appear to be at odds with those of Fricke and Wing (2004), who used similar approaches to provide a MAT estimate of 4 °C. Virtually all of the specimens used in this earlier study, however, lack locality and/or stratigraphic information, and it is probable that some

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specimens are older than the ones used in the current study. Thus, we no longer consider the Fricke and Wing (2004) estimate of MAT as valid.

When our paleotemperature estimates are compared to those made using multiple regression (MR) leaf physiognomic analyses (i.e., Greenwood and Wing, 1995) and nearest living relative (NLR) methods applied to the early–middle Eocene Arctic flora (Basinger et al., 1994), results are broadly similar. The primary difference is a below-freezing cold month mean temperature estimated by MR and a higher warm month mean temperature estimated from NLR. However, when the standard errors associated with MR (±3.6 °C for CMMT and ±5.1 °C for MART; Greenwood and Wing, 1995) and oxygen isotope analyses of co-occurring vertebrates (±7 °C) are taken into consideration, the temperature estimates overlap. The congruence of mean annual temperature, annual range of temperature, and cold month mean estimated by these two very different and independent proxies strengthens our confidence that our paleotemperature estimates are valid.

Our warm month mean temperature falls within the range of WMMT estimated from analysis (by NLR methods) of younger (middle Eocene), terrestrially-derived pollen and spore assemblages from marine sediments in the Norwegian–Greenland Sea (Eldrett et al., 2009), although these authors estimated a higher MAT (14° ± 3 °C) and CMMT (>5 °C) for the middle Eocene Arctic. Again, when the standard errors for both proxies are taken into consideration, there is overlap in the temperature estimates. Slight discrepancies may be due to changes in climate over time. Based upon correlation to the geomagnetic polarity timescale (specifically magnetochron C22N), the middle Eocene pollen and spore assemblages from Greenland are ~49 Ma (Eldrett et al., 2009) — several million years younger than the early Eocene localities on Ellesmere Island.

Of comparable age to the fossils analyzed in the current study, a relatively high SST of 17 °C (± 2 °C) was estimated for the early Eocene Arctic Ocean based upon the distribution of isoprenoid tetraether lipids in the abundant marine prokaryotes Crenarchaeota (TEX_{86} proxy; Sluijs et al., 2006). Although TEX_{86} values correlate with annual mean SST in today's non-polar oceans where water temperatures range from 5 to 30 °C (Kim et al., 2008), there are most likely seasonal biases in that TEX_{86} values record temperatures during the season when Crenarchaeota are most abundant on the ocean floor. In the Arctic Ocean, export of membrane lipids of Crenarchaeota to the sea floor is expected during the season of highest biological productivity, which is summer (Sluijs et al., 2006). That the early Eocene Arctic SST falls close to our warm month temperature estimate seems to confirm the summer season bias that was suggested for the TEX_{86} proxy by Sluijs et al. (2006).

Weijers et al. (2007) calculated a similarly high MAT of 18–20 °C (±5 °C) for the early Eocene Arctic, based upon analysis of the distribution of soil-derived branched GDGT lipids (combination of Methylation index of Branched Tetraethers or MBT and Cyclisation ratio of Branched Tetraethers or CBT indices; Weijers et al., 2007) from the same Arctic sediment core samples analyzed by Sluijs et al. (2006). Given the uncertainties concerning the original calibration between the MBT index and MAT and soil pH, origin of the MBT signal, and seasonal biases, Weijers et al. (2007) warned that absolute temperatures derived from distribution of soil-derived membrane lipids could have a seasonal bias. Our temperature estimates from $\delta^{18}O$ of co-occurring terrestrial vertebrates would seem to confirm the speculation made by Weijers et al. (2007) that the MBT/CBT proxy probably also estimates a summer temperature.

Overall, similarities between some paleclimate estimates made using different proxies (e.g. isotopes and plants) lend support to the interpretation that they are valid despite relatively large uncertainties, while differences between these estimates and those of other proxies (e.g. TEX_{86} and MBT/CBT indices) suggest that the latter are not in fact representative of mean annual temperature in polar settings, but are instead biased towards summer conditions (Sluijs et al., 2006; Weijers et al., 2007). Recognition of these biases has important implications. For one, it follows then that care should be taken when using the TEX_{86} proxy to infer absolute values of SST, particularly at high latitudes. For example, TEX_{86}-based SSTs exceeding 30 °C for late early Eocene (~50–51 Ma), southern high latitude localities (~55°N.) in New Zealand (Hollis et al., 2009) should probably be reinterpreted as summer highs, rather than MAT, and incorporated into global climate models accordingly. When interpreted as mean annual SST, these anomalously high values (>30 °C) near the south pole present a major challenge to climate modelers whose general circulation models, even under hypergreenhouse conditions (>2200 ppm CO_2), cannot generate mean annual SST above 20 °C for New Zealand (Hollis et al., 2009). Secondly, multiple techniques using a variety of physiologically-different organisms should provide the most comprehensive paleotemperature dataset for the Arctic. In this light, at early–middle Eocene localities in the Canadian High Arctic where vertebrate fossils are rare and plant fossils more abundant, the deltaic depositional environment would appear to be quite conducive to using the MBT/CBT proxy alongside the paleofloral analyses.

6.2. Alligators and turtles as paleoclimate proxies

Our early Eocene Arctic temperature estimates imply that fossil alligators are valid paleoclimate proxies for mild, above-freezing year-round temperatures. Nevertheless, the Eocene Arctic alligators that inhabited evidently cooler winters (CMMT 0–3.5 °C) and summers (WMMT 19–20 °C) than what is implied by the present-day crocodilian distribution (Markwick, 1994) are intriguing. Observational and experimental data from captive zoo animals indicates that alligators are hardier than other crocodilians, and can survive short intervals of subfreezing temperatures through submergence in water (Asa et al., 1998). Along similar lines, the abundance of alligator fossils referred to *Allognathosuchus* at Eocene localities on Ellesmere Island (Estes and Hutchison, 1980), in the absence of other crocodilian taxa (that are known from coeval mid-latitude localities), implies that ancient populations of alligators were hardier and inhabited seasonally cooler environments than other crocodilians. Although our data suggest that Eocene alligators probably had a somewhat greater climatic window than that implied by today's crocodilian distribution, their occurrence in the fossil record is a reliable NLR climate proxy for above-freezing temperatures.

Turtles also are used widely as climate and environmental proxies. Nearly all of the Arctic turtles are aquatic whose living representatives survive cool winter temperatures, including freezes, by submerging themselves in water or burrowing. Consequently, our temperature estimates for the Eocene Arctic are not incompatible with the temperature ranges of today's aquatic turtles. In contrast, the occurrence of large land tortoises in the Eocene High Arctic is more puzzling because today's representatives inhabit areas such as the Galápagos Islands where the cold month mean is generally above 10 °C (Hutchison, 1982). During the late Pleistocene Ice Age, however, giant tortoises ranged as far north as Pennsylvania and Illinois (Holman, 1995), suggesting that today's distribution does not represent their fullest geographic range allowed by climate.

7. Conclusions

Far more important than MAT to the survival of many organisms is the seasonal range in temperature and warm and cold month mean temperatures, yet few studies capture these aspects of paleotemperature, particularly for polar regions. Utilizing a combination of oxygen isotope ratios from fossil bone and tooth enamel phosphate of co-occurring mammal, fish, and turtle from Ellesmere Island, Arctic Canada, we estimated early Eocene Arctic temperatures, including

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mean annual temperature (MAT) of ∼8 °C, mean annual range in temperature of ∼16.5–19 °C, warm month mean temperature of 19–20 °C, and cold month mean temperature of 0–3.5 °C. Our paleotemperature estimates are most similar to those derived from analyses of early Eocene Arctic flora (i.e., Greenwood and Wing, 1995). They suggest that high estimates of early Eocene Arctic MAT and SST that are based upon the distribution of branched glycerol dialkyl glycerol tetraether (GDGT) membrane lipids in terrestrial soil bacteria (Weijers et al., 2007) and isoprenoid tetraether lipids in marine Crenarchaeota (Sluijs et al., 2006) probably are biased towards summer values.

Although the animals themselves, by way of nearest living relative-based climatic inference, are valuable paleoclimate proxies, our isotopic study highlights the need to assess phenotypic plasticity in the physiology and behavior of such climate-sensitive animals as alligators and tortoises whose past temperature tolerances may have been somewhat greater than their living descendants.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.epsl.2010.06.005.

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