# Lower-latitude mammals as year-round residents in Eocene Arctic forests

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## ABSTRACT

The Arctic is undergoing rapid warming, but the impact on the biosphere, in particular on large terrestrial mammals, is not clear. Among the best deep time laboratories to assess biotic impacts of Arctic climate change, early Eocene (ca. 53 Ma ago) fossil assemblages on Ellesmere Island, Nunavut (~79°N), preserve evidence of forests inhabited by alligators, tortoises, and a diverse mammalian fauna most similar to coeval lower-latitude faunas in western North America. By analyzing carbon and oxygen isotope ratios of mammalian tooth enamel, we show that large herbivores were year-round inhabitants in the Arctic, a probable prerequisite to dispersal across northern high-latitude land bridges. If present-day warming continues, year-round occupation of the Arctic by lower-latitude plants and animals is predicted.

## INTRODUCTION

In the Arctic, the most abundant large mammals today are caribou that survive primarily by migrating south up to 1000 km to overwinter below the Arctic Circle. There is, however, evidence that Arctic regions are changing, with temperatures rising at almost twice the global average. This climate change begs the question of how large terrestrial mammals will respond: will they migrate or live year-round in the Arctic?

From a paleontological perspective, the study of how ancient biota responded to past global warming is a way to address this question. One such warm interval occurred during the early Eocene (ca. 50–55 Ma ago), when mean annual temperatures in the Arctic may have been 40 °C warmer than today (Sluijs et al., 2006). The Arctic contained swamp forests of predominantly deciduous conifer (McIver and Basinger, 1999) and a warm-weather fauna of alligators, tortoises, lizards, snakes, and a diversity of mammals (Estes and Hutchison, 1980; Eberle and McKenna, 2002). As the relevant fossil-bearing rocks on Ellesmere Island were ~77° N paleolatitude (Irving and Wynne, 1991), this environment underwent months of continuous sunlight as well as darkness.

The early Eocene Arctic mammal fauna shares most genera with coeval mid-latitude faunas thousands of kilometers to the south in western North America (Eberle and McKenna, 2002). These similarities suggest that animals from lower latitudes were either adapted to living in polar regions or were migratory. We use oxygen and carbon isotope ratios of fossil tooth enamel to test the hypothesis that some Eocene lower-latitude mammals lived year-round in the Arctic. In so doing, our study provides a deep time analog from which to predict the consequences of imminent global warming on today's Arctic biota.

## Stable Isotopes, Behavior, and Ecology

Animals record the isotopic characteristics of ancient landscapes when they ingest organic material and drink from surface water reservoirs and then form bioapatite [$Ca_5(PO_4, CO_3)_3(OH, CO_3)$]. Carbon in the carbonate phase of bioapatite is related to ingested organic material such as plants in the case of herbivores (Kohn, 1996). In turn, carbon isotope compositions of Eocene plants varied primarily in response to environmental conditions and plant-specific differences in carbon isotope discrimination during photosynthesis. Environmental conditions influence the opening of leaf stomata, which control the concentration of $CO_2$ and thus the ability of plants to discriminate between carbon isotopes (Farquhar et al., 1989). The result is higher isotopic ratios for plants living in hot, dry, and nutrient-poor settings. Moreover, carbon isotope fractionation is taxon specific; for example, gymnosperms typically have higher carbon isotope ratios than angiosperms (Heaton, 1999).

Although oxygen in mammalian bioapatite has sources in ingested water and atmospheric oxygen, isotopic variations in ingested water play a primary role in corresponding variations in isotopic ratios of bioapatite (Kohn, 1996). Oxygen isotope ratios of ingested waters from streams, lakes, and leaves vary in response to environmental factors, particularly aridity, as $^{16}O$ is preferentially incorporated into the vapor phase during evaporation. The other major control on oxygen isotope ratios of surface waters is the hydrological history of air masses that supply precipitation. Preferential incorporation and removal of $^{18}O$ into condensate from cooling air masses results in a decrease in oxygen isotope ratios of precipitation as air masses move from tropical sources to polar sinks (Rozanski et al., 1993). Latitudinal temperature gradients, and thus latitudinal gradients in isotopic ratios of precipitation, vary with season, and larger seasonal temperature ranges at high latitudes result in larger seasonal isotopic ranges in precipitation (Fricke and O'Neil, 1999).

## METHODS

Arctic fossils for this study are from the Margaret Formation, Eureka Sound Group, on Ellesmere Island. An early Eocene (late Wasatchian; ca. 53 Ma ago) age is inferred for this fauna based upon fossil mammals (Dawson et al., 1993) and palynology (Norris and Miall, 1984). Rocks comprise coarsening-upward cycles of interbedded 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 conifer and broadleaf angiosperms (McIver and Basinger, 1999), contrasting with predominantly angiosperm forests at mid-latitudes (Wing et al., 1995).

Arctic mammal fossils are rare; only ~80 *Coryphodon*, 40 tapiroid, and 7 brontothere specimens are documented. We sampled tooth enamel from 9 *Coryphodon* and 5 perissodactyls (n = 3 for tapirs; n = 2 for brontotheres). A bulk sample was taken by drilling enamel from the base to the top of the tooth or tooth fragment. For six *Coryphodon* teeth, multiple samples were taken along the tooth's length to determine seasonal variations in isotope ratios. Oxygen and carbon isotope ratios were measured for the carbonate component of tooth enamel (see the GSA Data Repository[1] for details of sample preparation, isotopic analyses, and diagenesis). Stable isotope ratios are reported as $\delta^{13}C$ and $\delta^{18}O$ values, where $\delta = (R_{sample}/R_{standard} - 1) \times 1000‰$, and the standard is Vienna Peedee belemnite for carbon and Vienna standard mean ocean water for oxygen. Arctic isotopic data are compared to published data for three late Wasatchian

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[1]GSA Data Repository item 2009119, details of sample preparation, isotope analyses, and diagenesis; tables of stable isotope data from bulk samples of Arctic *Coryphodon* and perissodactyls, as well as sequential samples of Arctic *Coryphodon*; and Fig. DR1 (changes in seasonal range in $\delta^{18}O$ of precipitation with latitudinal differences), is available online at www.geosociety.org/pubs/ft2009. htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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(ca. 53 Ma ago) *Coryphodon* teeth from the Willwood Formation, Bighorn Basin, Wyoming (Fricke et al., 1998). Strata consist of channel sands, floodplain siltstones, and mudstones, with variable paleosol development characterized by red beds and carbonate nodules that imply seasonal fluctuation of water table (Kraus, 2001).

## RESULTS AND DISCUSSION

### Isotopic Differences Among Arctic Herbivores

Figure 1 shows $\delta^{18}O$ and $\delta^{13}C$ for bulk samples of tooth enamel from Arctic *Coryphodon* and perissodactyls (Table DR1). Overlapping $\delta^{18}O$ among Arctic *Coryphodon* and perissodactyls suggest a humid early Eocene High Arctic, consistent with sedimentology (e.g., abundant coal seams and absence of red beds; Miall, 1986) and swamp forest flora. Humidity controls the degree to which leaves are enriched in $^{18}O$ over surface water, due to preferential evaporation of $^{16}O$. In dry climates, $\delta^{18}O$ of vegetation is higher and more variable, and because different browsers consume different plant species, there is less likelihood of overlap in their $\delta^{18}O$ values.

Mid-latitude studies reveal that *Coryphodon* has lower $\delta^{13}C$ than coexisting herbivores, a difference that, along with lower variability in $\delta^{18}O$ than other taxa, probably reflects a semiaquatic lifestyle (Secord et al., 2008). Arctic *Coryphodon* tends to have lower $\delta^{13}C$ than Arctic perissodactyls, suggesting similar niche partitioning.



Figure 2. A: Oxygen and carbon isotope ratios for mid-latitude *Coryphodon* (Fricke et al., 1998) have positive correlation coefficient of 0.32. VPDB—Vienna Peedee belemnite; VSMOW—Vienna standard mean ocean water. B, C: Oxygen and carbon isotope ratios versus tooth position (distance from base) for mid-latitude samples. Cyclic isotopic variations from low to high occurring over ~50 mm are consistent with summer to early winter changes in isotope ratios of ingested water and plants (Table DR2; see footnote 1).
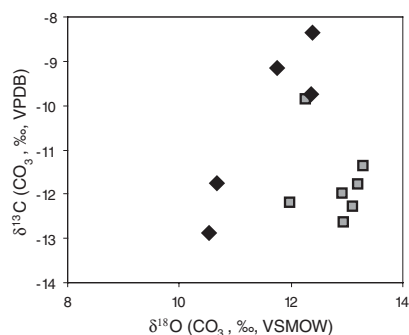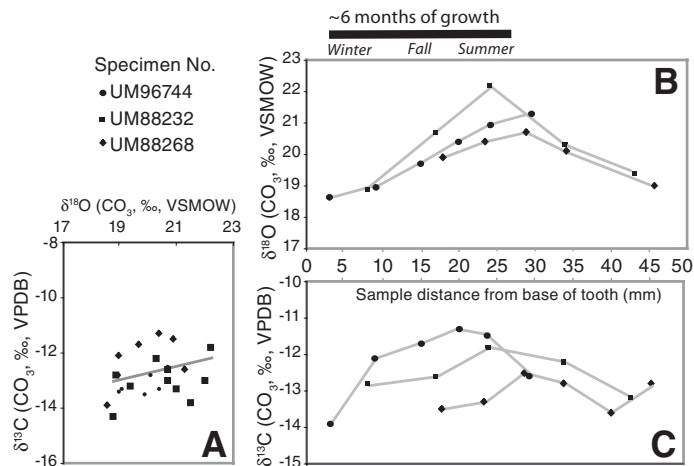


Figure 1. Stable isotope data from bulk samples of Arctic *Coryphodon* (gray squares, n = 7) and perissodactyls (black diamonds, n = 5). See Table DR1 (see footnote 1). VPDB—Vienna Peedee belemnite; VSMOW—Vienna standard mean ocean water.

### Isotopic Differences Among *Coryphodon*

Focusing on intratooth isotope data of *Coryphodon* from mid-latitudes (Fig. 2) and the Arctic (Fig. 3), there are several similarities and differences that reflect environmental conditions and animal behavior. Arctic *Coryphodon* have lower average $\delta^{18}O$ and higher $\delta^{13}C$ that are consistent with broad geographic differences. Lower $\delta^{18}O$ (x axis, Fig. 3A) reflects the decrease in $\delta^{18}O$ of precipitation that occurs as air masses cool and lose water during transport from tropical sources to polar sinks (Rozanski et al., 1993). The magnitude of this decrease during the Eocene was much less than at present, and reflects warmer temperatures, a shallower equator to pole temperature gradient (Fricke and Wing, 2004), and a probable increase in polar transport of atmospheric water vapor at that time (Fricke, 2003). Regarding carbon data (y axis, Fig. 3A), slightly higher $\delta^{13}C$ in Arctic *Coryphodon* may reflect a larger proportion of gymnosperms relative to angiosperms available for forage in Arctic settings.

It is also possible to compare how the $\delta^{13}C$ and $\delta^{18}O$ of food and water ingested by *Coryphodon* varied seasonally at middle and high latitudes. Seasonal variations in $\delta^{13}C$ and $\delta^{18}O$ can be studied because enamel forms sequentially during tooth eruption, at rates estimated at ~50 mm/a for large modern herbivores (Sharp and Cerling, 1998) and *Coryphodon* (Fricke et al., 1998). Enamel that formed first is at the tip of the tooth, and enamel that formed last is at the base. Therefore, an intratooth sequence
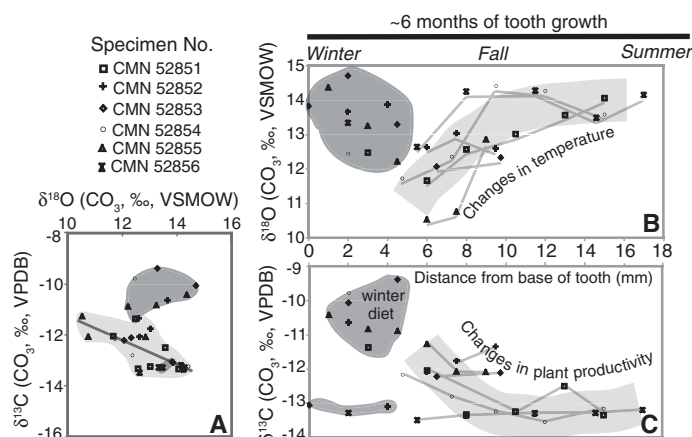


Figure 3. A: Oxygen and carbon isotope ratios for Arctic *Coryphodon*. VPDB—Vienna Peedee belemnite; VSMOW—Vienna standard mean ocean water. B, C: Ratios versus tooth position. Samples in light shading are characterized by negative correlation coefficient of –0.71 (gray line in A) and interpreted to represent diet and ingested water that tracks summer to fall changes in plant productivity (increase in $\delta^{13}C$ of terrestrial plants) and temperature (decrease in $\delta^{18}O$ of precipitation). Samples in dark shading are poorly correlated and interpreted as complex diet and ingested water from nonprecipitation sources during dark polar winter (Table DR2; see footnote 1).

represents a temporal sequence of isotopic data. In general, seasonal changes in $\delta^{18}O$ of 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). Seasonal changes in $\delta^{13}C$ of enamel reflect changes in plant productivity, environmental stresses acting on plants, and kinds of plants available for forage.

Seasonal ranges in $\delta^{18}O$ and $\delta^{13}C$ are similar in both regions (~3‰ and ~2.5‰, respectively; see Figs. 2B, 2C, 3B, and 3C). Ranges in enamel $\delta^{18}O$ are dampened relative to that of ingested water because ~25% of oxygen in a mammal's body has an atmospheric rather than hydrologic source (Kohn, 1996). Therefore, seasonal ranges in $\delta^{18}O$ of enamel from

both regions correspond to a range of ~4‰ in $\delta^{18}O$ of ingested surface water. What differs between regions is the correlation between $\delta^{13}C$ and $\delta^{18}O$. Canine tusks from mid-latitudes exhibit a weak positive correlation between $\delta^{13}C$ and $\delta^{18}O$ (Fig. 2). Incisors from the Arctic have more complicated intratooth patterns; there is a subset of samples characterized by high $\delta^{13}C$ and a wide range of $\delta^{18}O$ (Fig. 3, dark shading). Setting these aside (see following), a negative correlation between $\delta^{13}C$ and $\delta^{18}O$ is clear and statistically significant (Z-test, correlation coefficient = −0.713; $p < 0.0001$; $n = 23$).

Positive correlation between $\delta^{13}C$ and $\delta^{18}O$ in Wyoming (Fig. 2A) is likely due to summer-season warmth and aridity. Co-occurrence of paleosol carbonates and hematite in Bighorn Basin paleosols implies seasonal changes in environmental conditions (Kraus, 2001), particularly decrease in water availability and/or drying during summer months. Increased evaporation results in an increase in $\delta^{18}O$ of surface waters, while water stress is a plausible cause of higher $\delta^{13}C$ of plants during the same period, resulting in a positive correlation between $\delta^{13}C$ and $\delta^{18}O$ for *Coryphodon*. Seasonal changes in plant productivity or proportion of angiosperm to gymnosperm plants ingested by *Coryphodon* are unlikely to be important, as productivity of subtropical forests, such as those characteristic of mid latitudes during the Eocene, is relatively constant (Poussart and Schrag, 2005), and angiosperms dominated mid-latitude forests (Wing et al., 1995).

Intratooth patterns for Arctic teeth are unusual in that a large decrease in $\delta^{18}O$ occurs over a few millimeters near the base of the tooth before values gradually increase near the tip (Fig. 3B). This pattern is unlikely to represent an annual cycle, as it would reflect a tooth eruption rate only ~35% of that observed for modern mammals and *Coryphodon* canines. Instead, the gradual increase in $\delta^{18}O$ from 6 to 18 mm (Fig. 3B, light shading) is interpreted to represent seasonal change from early winter to summer that is consistent with tooth eruption rates of ~50 mm/a. What follows from this interpretation is that high $\delta^{18}O$ values at the base of teeth reflect winter and/or polar darkness conditions.

Focusing on the fall-summer samples (Fig. 3A, light shading), the negative correlation between $\delta^{18}O$ and $\delta^{13}C$ is likely influenced by seasonal changes in temperature and plant productivity, respectively. As in the case for modern precipitation, highest $\delta^{18}O$ values are interpreted to represent warmer summer months, while subsequent decrease in $\delta^{18}O$ reflects fall and winter cooling. The overall ~4‰ range in $\delta^{18}O$ of surface waters agrees with the range inferred from isotopic studies of wood cellulose from Eocene Arctic trees (Jahren and Sternberg, 2008). However, this range is unusual compared with the present day, as seasonal range in the Arctic is typically twice that of mid-latitudes (Fricke and O'Neil, 1999). The reduced seasonal range in $\delta^{18}O$ for the Eocene Arctic mirrors the reduced latitudinal gradient in $\delta^{18}O$ noted above, and both reflect major differences in global climate and atmospheric circulation patterns between the Eocene and today. In contrast to mid-latitudes, $\delta^{13}C$ of ingested plant matter increases by ~2‰ from summer to fall months (Fig. 3C, light shading). Likely reasons for this increase are a decrease in plant productivity and/or change in diet. Unlike trees in lower latitudes (Poussart and Schrag, 2005), $\delta^{13}C$ of cellulose from trees at high latitudes in both modern and Eocene time range by ~2‰–4‰, with low $\delta^{13}C$ associated with preferential uptake of $^{12}C$ from the atmosphere during warmer, more photosynthetically active and productive summer months (Jahren and Sternberg, 2008, and references therein). As temperature and light levels decrease from summer to fall, a corresponding increase in $\delta^{13}C$ of ingested plant material is expected. Alternatively, gymnosperm plants characterized by higher average $\delta^{13}C$ may have been a more important food source than angiosperms at that time.

The last intriguing aspect of the Arctic intratooth data is the subset of samples characterized by high $\delta^{18}O$ and a bimodal range in $\delta^{13}C$ (including highest values observed; Fig. 3, dark shading). Bimodal $\delta^{13}C$ values

suggest that *Coryphodon* diet was different and varied during dark winter periods. Possible food sources with high $\delta^{13}C$ include: (1) wood and leaf litter rather than live leaves, (2) evergreen conifers, and (3) fungi. Wood cellulose and leaf litter have $\delta^{13}C$ ~1‰–2‰ higher than leaves from the same trees (Martinelli et al., 1998) and are abundant at Eocene Arctic localities. Evergreen conifers typically have $\delta^{13}C$ values 2‰–3‰ higher than angiosperms (Heaton, 1999), and are known from the Eocene Arctic pollen record (McIver and Basinger, 1999). The $\delta^{13}C$ of fungi is enriched by 3‰–6‰ over bulk leaf $\delta^{13}C$ (Bowling et al., 2008). A combination of these dietary choices may explain high winter $\delta^{13}C$ of tooth enamel. In contrast, anomalously low $\delta^{13}C$ (Fig. 3) may be explained by a component of phytoplankton and freshwater vascular plants in the diet, both of which tend toward lower $\delta^{13}C$ than terrestrial vegetation (Cloern et al., 2002). In the case of oxygen, a rapid switch to high $\delta^{18}O$ suggests a concurrent change in sources of drinking water for *Coryphodon* during winter, from those that track precipitation closely (e.g., flowing streams) to those that may be shifted to higher $\delta^{18}O$ throughout the year by evaporation (e.g., standing water ponds). It is also possible that high $\delta^{18}O$ reflects a component of summer leaf water that is ingested by *Coryphodon* once it begins to eat leaf litter in winter.

### *Coryphodon* as a Year-Round Polar Resident

A behavioral possibility not yet addressed is that *Coryphodon* migrated from a paleolatitude of ~77°N to below the Arctic Circle (~67°N) during winter months, avoiding prolonged periods of darkness and associated ecological stress. In this case, *Coryphodon* would have been just a part-time Arctic resident. We do not think such "snow-bird" migrations occurred, for the following reasons. First, intratooth ranges in $\delta^{13}C$ and $\delta^{18}O$ are similar to those from nonmigratory trees that lived above the Arctic Circle during the Eocene (Jahren and Sternberg, 2008), so migration is not required to explain *Coryphodon* data. Second, it is difficult to provide a parsimonious interpretation of the subset of samples with high $\delta^{18}O$ and variable $\delta^{13}C$ if migration was occurring. Third, a southward migration of ~10° latitude should decrease seasonal range in $\delta^{18}O$ of ingested waters to the point where little would be observed (Fig. DR1). Patterns in polar isotopic data are consistent with *Coryphodon* utilizing Arctic resources year-round and inconsistent with a long southward migration.

Other evidence argues against long *Coryphodon* migrations. In particular, the high energy expenditures required to travel great distances over land would pose an obstacle for *Coryphodon* and the perissodactyls, as it precludes today's High Arctic Peary caribou from migrating south to subarctic forests (Pielou, 1994). Second, the presence of baby and juvenile *Coryphodon* and tapirs in the Eocene Arctic, evidenced by jaws with partly and entirely deciduous dentitions (Eberle, unpublished data; M. Dawson, 2008, personal commun.), is consistent with year-round residency. If these animals migrated to below the Arctic Circle within a couple months of calving, as do today's barren-ground caribou, we would not expect juveniles, but rather babies and adults exclusively.

## CONCLUSIONS

Our isotopic data suggest that *Coryphodon* lived above the Arctic Circle year-round during the early Eocene, and that perissodactyls probably did as well. Because the same (or similar) mammalian genera are found in the western United States, the implication is that they had an ecological flexibility that allowed them to adapt to Arctic habitats. There is isotopic evidence that they were able to eat available wood and leaf litter, evergreens, and fungi during winter months.

Among living ungulates, the ability to eat a wide range of organic material works best with the physiology of perissodactyls, whose digestive system utilizes hindgut fermentation that is advantageous where food is of limited quality and high in fiber, provided it occurs in large quantities (Macdonald, 1987). That perissodactyls had an adaptive advantage

is implied by the absence of artiodactyl fossils from the Eocene Arctic, despite their modest diversity in contemporaneous mid-latitude faunas. In the case of *Coryphodon*, there are no living pantodonts with which to compare them, but year-round presence in the Eocene Arctic indicates that its gut physiology was adapted to a poorer quality winter diet. Large body size probably was beneficial in that differences in metabolic rate allow larger herbivores to feed on less nutritious plant parts than smaller ones (Macdonald, 1987).

Adaptation of lower-latitude mammals to Arctic environments has a parallel among plants. Growth-chamber experiments on living *Metasequoia* under conditions simulating Paleogene seasonal temperature regimes and high-latitude photoperiods demonstrate that deciduousness in *Metasequoia* was acquired at lower latitudes and simply retained in the Arctic with no obvious advantage to polar light regime (Royer et al., 2003).

Year-round habitation of Arctic regions is a probable prerequisite for dispersal across northern high-latitude land bridges. Such migrations have occurred several times in the geologic past, and are hypothesized to explain the early Eocene appearance in North America of several modern mammalian orders presumed to have come from Asia, including perissodactyls (Beard and Dawson, 1999). Such polar dispersals are predicated on climatic conditions in Arctic regions that are wetter and warmer than those of today. If current warming trends continue, year-round occupation of polar regions by lower-latitude plants and animals is predicted.

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