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# Stable isotopes in early Eocene mammals as indicators of forest canopy structure and resource partitioning

Ross Secord, Scott L. Wing, and Amy Chew

*Abstract*.—The three dimensional structure of vegetation is an important component of ecosystems, yet it is difficult to reconstruct from the fossil record. Forests or woodlands prevailed at mid-latitudes in North America during the early Eocene but tree spacing and canopy structure are uncertain. Here we use stable carbon isotope values ($\delta^{13}C$ ) in early Eocene mammalian faunas to infer canopy structure. We compare $\delta^{13}C$ values in two diverse fossil assemblages from the central Bighorn Basin to values predicted for mammals in a variety of open and closed habitats, based on modern floras and faunas. We conclude that these early Eocene faunas occupied an open canopy forest. We also use carbon and oxygen isotopes to infer diet and microhabitat. Three higher level taxa have significantly different mean $\delta^{13}C$ values, and values are negatively correlated with body mass. The pattern suggests diets high in leaves for larger mammals, and fruit or other non-foliar plant organs for small ones. A preference in the larger mammals for wetter habitats with high water availability to plants may also have contributed to the pattern.

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## Introduction

The three-dimensional structure of vegetation is important for many reasons. It affects the albedo of land surfaces, hydrologic cycling, atmospheric circulation near the earth's surface, and carbon storage, all of which affect climate and biogeochemical cycles on a global scale. Vegetation also forms the habitat in which terrestrial organisms move, and over time influences the evolution of their locomotor adaptations. In spite of the climatic, biogeochemical, and evolutionary importance of vegetational structure, it is difficult to reconstruct. Inferences about past vegetation structure generally rely on rare instances of exceptional preservation or ecological analogies between living and ancient organisms. Such inferences, however, become increasingly tenuous as older biotas are considered.

We consider the structure of early Eocene forests or woodlands in the Bighorn Basin of Wyoming. Occasional fossilized tree stumps indicate the presence of trees, but tree spacing and canopy structure are less certain. Van Houten (1945) argued from the prevalence of hoofed mammals that savanna-like habitats prevailed in the early Eocene of the Rocky Mountain region. Upchurch and Wolfe (1987), however, inferred from paleobotanical evidence that midlatitude Eocene forests were similar to modern closed canopy tropical rain forests. On the basis of mammalian body mass distributions (cenograms), Gunnell (1997) also concluded that closed canopy forests were present. Subsequent paleobotanical work suggests, however, that early Eocene climates at midlatitudes were not tropical, but rather were warm-temperate to subtropical (Wing et al. 1991; Wilf 2000; Wing et al. 2000). Moreover, leaf-area analyses suggest mean annual precipitation of only ~120–140 cm (Wilf 2000), which is lower than in modern tropical rain forests and may have been inadequate to support a closed canopy.

We use a new approach to infer canopy structure and develop a simple model that uses stable carbon isotope values ($\delta^{13}C$) in mammalian tooth enamel and modern plants.

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The model predicts expected $\delta^{13}C$ values for fossil tooth enamel (hydroxylapatite) from a variety of habitats and microhabitats, ranging from closed canopy forests to savannas. (In this paper ''habitat'' refers broadly to vegetation structure, such as open or closed canopy, whereas ''microhabitat'' refers to areas within a habitat, such as the understory in a closed canopy forest). We infer canopy structure by comparing predicted to measured $\delta^{13}C$ values from two early Eocene mammalian assemblages.

These assemblages also provide a glimpse into the evolution of mammalian herbivory about 12 Myr after the beginning of the Cenozoic mammalian radiation. Faunas at this time contained a mixture of ''archaic'' ungulates (e.g., condylarths, tillodonts) and the first representatives of the extant ungulate clades Perissodactyla and Artiodactyla. These faunas pre-date the spread of grasslands (e.g., Strömberg 2004) and contain a higher proportion of omnivores and browsers than most post-Eocene faunas (Janis 2000). Dental specializations such as hypsodonty and selenodonty were rare. Thus, herbivores may have partitioned resources less and had more broadly overlapping diets than younger faunas. We make the first attempt to recognize resource partitioning in faunas of this antiquity by using stable isotopes.

## Materials and Methods

*Diet and Locomotion.*—Most of the mammals included in this study are considered herbivores, but a few may have been omnivores (e.g., Gunnell et al. 1995). Diets inferred from other studies, on the basis of dental morphology and body size, are summarized in the Appendix (online at http://dx.doi.org/10.1666/06049.s1) and discussed for selected taxa in the ''Resource Partitioning'' section. Although postcrania are poorly known for many species, it is clear that most were ground-dwelling ungulates. Exceptions are *Cantius*, which is thought to have been arboreal, and *Esthonyx*, which had both arboreal and terrestrial adaptations. *Didelphodus* was also probably arboreal. Rose (2001) summarized known postcrania and locomotor interpretations for early Eocene mammals from North American.

*Specimen Provenance.*—Specimens are early Eocene in age (Wasatchian land-mammal age, Fig. 1) and are from overbank floodplain deposits in the Willwood Formation in the central Bighorn Basin, Wyoming (Wing et al. 1991; Bown et al. 1994). Teeth are from two discrete stratigraphic intervals in the Elk Creek composite section. The lower and upper assemblages are from the Upper *Haplomylus-Ectocion* and *Heptodon* biozones, respectively, of the Wasatchian land-mammal age (Schankler 1980). The lower and upper assemblages occur at times of moderately cool and warm climates, respectively, according to mean annual temperature estimates (MAT) from leaf margin analyses and $\delta^{18}O$ values in hematite (Wing et al. 2000). Although MAT during the cool interval was lower than that of bounding intervals (Fig. 1), it was still considerably warmer than in this region today. The lower assemblage was collected from a thicker stratigraphic interval (~22 m) over a greater geographic area than the upper one (~4 m; thicknesses assume that most localities sample an interval of ~4 m). However, although total thickness for the lower assemblage is ~22 m, 76% of the specimens were collected from an interval of only ~8 m. Sediment accumulation rates for the upper and lower assemblages were ~215 and 422 m/Myr, respectively, according to interpretations of paleosol maturity (Bown and Kraus 1993). This implies time-averaging of ~37,000 and 10,000 years for the lower and upper assemblages, respectively. Seventy-nine percent of the specimens in the lower assemblage were collected from a geographic area of ~1.5 $km^2$. Another 15% are from a ~1 $km^2$ area about 5 km farther north (D-1415, D-1417) and 6% are from a small locality (D-1299) about 3 km southwest of the main area. The upper assemblage is from a series of localities distributed over ~1 $km^2$.

*Stable Isotope Conventions.*—Stable isotope ratios are expressed using delta notation in units of parts per thousand (per mil, ‰): $\delta^{13}C$ or $\delta^{18}O = \{[R_{sample}/R_{standard}] - 1)\} \cdot 10^3$, where $R = {}^{13}C/{}^{12}C$ for carbon, and the standard is Cretaceous belemnite shell from the PeeDee Formation (vPDB); $R = {}^{18}O/{}^{16}O$ for oxygen, and

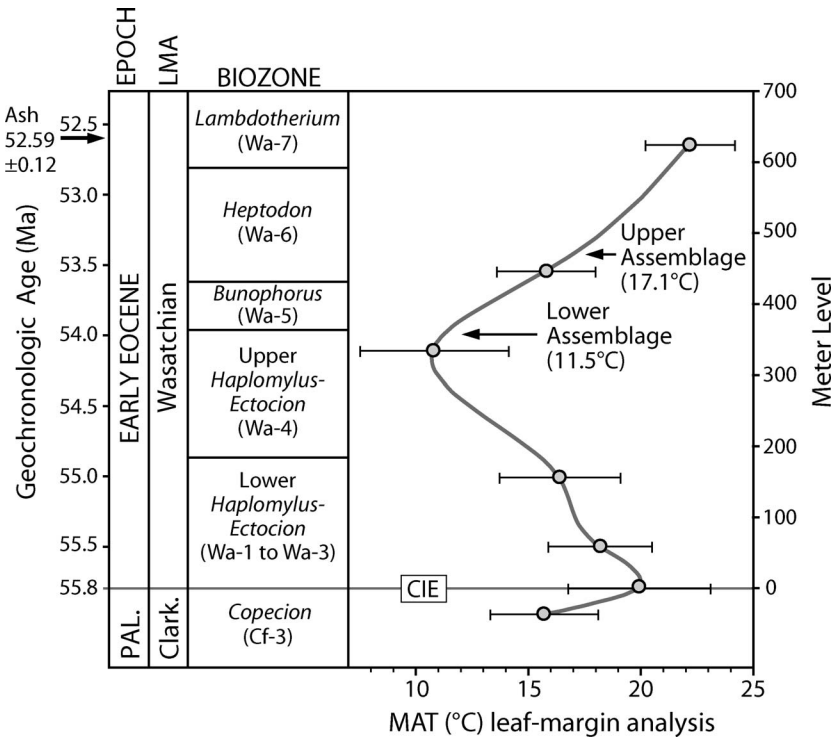


FIGURE 1. Geochronology and stratigraphic positions of biozones, faunal assemblages, and MAT estimates in Elk Creek and Cabin Fork sections, central and southern Bighorn Basin (except Paleocene MAT estimate from northern Bighorn Basin). Meter levels are relative to base of Willwood Formation. Geochronologic ages are based on linear interpolation between ages for CIE (Ogg and Smith 2004) and a volcanic ash (upper left) (Wing et al. 1991; Smith et al. 2004). MAT estimates for assemblages are based on spline interpolation (see Secord et al. 2006) between leaf-margin MAT estimates from Wing et al. (2000, 2005). MAT error bars are 95% confidence. Mammalian biozones are based on Schankler (1980), Gingerich (1983, 2001a), and Secord et al. (2006). Spline curves were generated with PetroPlot software (Su et al. 1999–2002). **CIE**, carbon isotope excursion; **Clark.**, Clarkforkian; **LMA**, Land-mammal age; **MAT**, mean annual temperature; **PAL.**, Paleocene.

the standard is mean ocean water (vSMOW). Diet-to-enamel $^{13}$C-enrichment was calculated using an enrichment factor ($\varepsilon^*$): $\varepsilon^*_{\text{diet-enamel}} = \{[1000 + \delta^{13}C_E]/[1000 + \delta^{13}C_{\text{diet}}] - 1\}$. For our data, $\varepsilon^*$ usually differs from $\delta^{13}C_E - \delta^{13}C_{\text{diet}}$ by only a few tenths per mil, but using $\varepsilon^*$ has the advantage of being independent of scale (Cerling and Harris 1999).

*Sampling and Pretreatment.*—Tooth enamel was sampled from 11 species in the lower assemblage and 17 in the upper (Appendix). Nearly all specimens were isolated teeth, and all but *Coryphodon* and *Hexacodus* were adequate for specific identification. At least three individuals were sampled for species that were abundantly represented. To ensure that isotope values represent an adult diet we avoided sampling first molars and deciduous premolars whenever possible, because these teeth could have pre-weaning values (e.g., Boisseriea et al. 2005). Samples of enamel hydroxylapatite weighing 2–3 mg were pretreated to remove organic matter and nonstructural carbonate following Koch et al. (1997). Our protocol differed only in that samples were baked at 200°C after pretreatment under vacuum for one hour to remove volatile contaminants and water, rather than being lyophilized. Experiments at the University of Michigan Stable Isotope Laboratory (UMSIL) showed a mean decrease in $\delta^{18}O$ of 0.98 ± 0.35‰ (2 σ; $p < 0.001$) when unbaked or lyophilized samples were baked, while $\delta^{13}C$ values were unchanged. Fourier transform infrared spectroscopy (FTIR) indicated that $H_2O$ and OH were removed from samples when baked, suggesting that baking is necessary to remove water that may otherwise contribute

to $^{18}O$ enrichment (L. Wingate and K. C. Lohmann, UMSIL, personal communication 2005).

*Isotope Analysis.*—Samples were reacted with phosphoric acid at 76° ± 2°C in a Finnigan MAT Kiel automated carbonate reaction device at UMSIL. $\delta^{13}C$ and $\delta^{18}O$ values of the resulting $CO_2$ were measured on a Finnigan MAT 251 triple collector isotope-ratio-monitoring mass spectrometer. We assume that the fractionation factor between hydroxylapatite carbonate and $CO_2$ is the same as for calcite and $CO_2$ (1.008818), following common practice. Our lab standard (LOX; from modern elephant enamel, courtesy of D. L. Fox) yielded the following values: $\delta^{18}O = 31.03 \pm 0.18‰$ and $\delta^{13}C = -5.80 \pm 0.06‰$ (SD; $n = 31$). Replicates were not run for the data presented here, but the mean, median, and range of differences among replicates of Bighorn Basin pretreated fossil enamel are 0.10, 0.08, and 0.00–0.21‰, respectively for $\delta^{13}C$, and 0.11, 0.08, and 0.00–0.41‰, respectively for $\delta^{18}O$ ($n = 35$) (unpublished data). Analytical precision based on international standards for carbonate (NBS-18, NBS-19) is $< \pm 0.1‰$ (SD) for $\delta^{18}O$ and $\delta^{13}C$ values.

### Inferring Canopy Structure from Carbon Isotopes in Herbivorous Mammals

Carbon in plants is derived from atmospheric $CO_2$ fixed during photosynthesis. Plants discriminate against $^{13}C$ in $CO_2$ to varying degrees as a result of using different photosynthetic pathways. Modern floras consist of plants that use $C_3$, CAM (crassulacean acid metabolism), and/or $C_4$, photosynthetic pathways. Resulting $\delta^{13}C$ values are lowest in $C_3$ plants (−37‰ to −21‰), intermediate in CAM plants, and highest in $C_4$ plants (−19‰ to −9‰) (e.g., Vogel 1993; Cerling and Ehleringer 2000). Although plant fossils with living CAM or $C_4$ relatives are known from Paleogene floras in the Bighorn Basin (including cycads, the aquatic lycopod *Isoetites*, and pollen similar to modern Chenopodiaceae; Wing et al. 1995; Wing and Harrington 2001), all published $\delta^{13}C$ values of dispersed organic matter, fossil plants, and fossil mammals are consistent with $C_3$ vegetation.

Natural variation of $\delta^{13}C$ values in $C_3$ plants results mostly from environmental factors, such as light, temperature, soil nutrients, and water availability (e.g., Broadmeadow and Griffiths 1993; Heaton 1999). Studies of vegetation along light and water gradients show that the $\delta^{13}C$ value in leaves decreases with increasing humidity or precipitation, and increases with increasing irradiance (Ehleringer et al. 1986; Stewart et al. 1995). Both open and closed canopy forests exhibit a stratification of $\delta^{13}C$ leaf values, whereby values decrease from the upper canopy to the base of the forest (van der Merwe and Medina 1991; Cerling et al. 2004). This phenomenon is sometimes called the ''canopy effect'' and results largely from decreased irradiance below the canopy (Ehleringer et al. 1986; Hanba et al. 1997; Heaton 1999), although recycling of $^{13}C$-depleted $CO_2$ under the canopy also contributes (Vogel 1978; van der Merwe and Medina 1989, 1991). The lowest $\delta^{13}C$ values in non-aquatic plants occur in understory leaves in closed canopy forests, and mean values increase as the canopy becomes more open (Ehleringer et al. 1987). Thus, the presence of a closed canopy can be inferred by distinctively low $\delta^{13}C$ values in understory leaves or by mean floral values, which are recorded in the teeth of herbivorous mammals (Cerling et al. 2004).

The carbon isotope composition of mammalian tooth enamel ($\delta^{13}C_E$) is strongly correlated to the mammal's diet and serves as a proxy for the $\delta^{13}C$ value of vegetation (Lee-Thorp and van der Merwe 1987; Cerling and Harris 1999; Passey et al. 2005). Carbon isotope values from a diversity of herbivores feeding within different microhabitats should reflect the mean value of local vegetation. This is exemplified in the Ituri closed canopy forest in tropical Africa (Cerling et al. 2004). If we assume a diet-enamel enrichment factor of 13.7‰, based on a 65/35% composition of ruminants and non-ruminants (see below), Ituri mammalian enamel accurately reflects mean values for vegetation in the entire habitat and in microhabitats, with the exception of understory browsers (Fig. 2). The mean value predicted for mammals from understory vegetation is ~2‰ higher than the actual value but the latter is based on only three individuals,

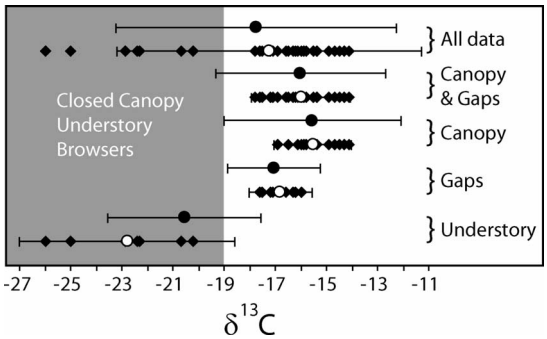


FIGURE 2. Comparison of mean $\delta^{13}C_E$ values for mammals from the Ituri closed canopy forest (open circles) with mean values predicted for mammals from Ituri vegetation (solid circles). Prediction is based on diet-enamel $\varepsilon^*$ of 13.7‰ (see text). Canopy, Gaps (local open areas), and Understory are microhabitats within the Ituri forest. Note close agreement between actual and predicted mean $\delta^{13}C_E$ values for all but understory. Primary data are from Cerling et al. (2004). Solid diamonds show individuals. Error bars ± 2 SD.

one of which (dwarf antelope; *Neotragus batesi*) had unusually low values (−26.0‰, −25.2‰).

The range of $\delta^{13}C_E$ values is also important, but harder to predict. In order to reflect the full range of $\delta^{13}C$ values in a flora, some individuals would have to feed exclusively on vegetation at both extremes. Because most herbivores exploit a variety of vegetation, however, we expect that the range in mammals will be smaller than that of the flora. This was demonstrated in a recent study that showed decreased variance in $\delta^{13}C$ from producer to consumer (Bump et al. 2007). In the Ituri Forest, the ranges of $\delta^{13}C_E$ values for canopy, gap (open area), or canopy and gap feeders are all considerably smaller than predicted by the flora (using 4 SD, capturing 95% of the variability), but for the fauna as a whole (all data, Fig. 2) the actual range is greater than predicted. This is due partly to the extremely low $\delta^{13}C_E$ values in *N. batesi*, which suggest it was eating vegetation ~3‰ lower than any sampled. If *N. batesi* is removed, the range is smaller than predicted. The range of $\delta^{13}C_E$ values in the Ituri fauna (~12‰) probably represents a maximum that will only be found in $C_3$ habitats with extreme heterogeneity, such as closed canopy tropical rain forests. The range of $\delta^{13}C_E$ values in the combined canopy and gap feeders (~4‰) should be similar to, or slightly less than, what would be found in an open $C_3$ habitat with no appreciable understory, such as a savanna or woodland. An intermediate range should be found in a fauna from an open canopy forest where trees are more closely spaced and lower irradiance causes greater $^{13}C$-depletion in the understory.

Significance of differences in range can be approximated by comparing variance. Some data sets we compare are not normally distributed, such as the Ituri fauna, and standard parametric tests of variance (e.g., *F*-test, Levene's test) are sensitive to small departures from normality. Thus, we use Conover's (1999) nonparametric squared ranks test of variance. We use species $\delta^{13}C_E$ averages in order to meet the test assumption that data are independent within the samples being compared.

## Predicting Carbon Isotope Values for Early Eocene Mammals

We develop a model to predict expected $\delta^{13}C_E$ values in herbivores from a variety of early Eocene habitats. Far more $\delta^{13}C$ values have been published for extant plants than for extant mammals, and no study has reported $\delta^{13}C_E$ values for a diverse fauna from an open canopy forest. Thus, we use data from extant plants. We normalize values for modern vegetation to parameters for the early Eocene of the Bighorn Basin. Factors that need to be considered are (1) diet-enamel enrichment; (2) the effects of latitude and altitude on $\delta^{13}C$ values in vegetation; and (3) changes in the composition of atmospheric $CO_2$ ($\delta^{13}C_A$) between the early Eocene and present.

*Diet-Enamel Enrichment*.—The large-bodied component of many modern faunas is dominated by ruminants, for which $\varepsilon^*_{\text{diet-enamel}}$ = 14.1 ± 0.5‰ (1 SD) for individuals larger than 5 kg (Cerling and Harris 1999). Other mammals have a lower $\varepsilon^*$, probably caused by lower methane production (Passey et al. 2005), which is correlated to body mass ($p < 0.001$, $r = 0.73$; data from Langer 2002; both variables logged). Our faunas are composed primarily of non-artiodactyls, and therefore non-ruminants. A controlled diet study found that pigs and rabbits, which bracket the body sizes of most species in our Eocene assemblages, had $\varepsilon^*$ = 13.3 ± 0.3‰ and $\varepsilon^*$ = 12.8 ± 0.7‰, re-

spectively (Passey et al. 2005). Thus, we use a mean non-ruminant $\varepsilon^*_{\text{diet-enamel}}$ of 13.1‰.

*Latitude Correction.*—A mean increase of ~0.3‰/10° latitude in $\delta^{13}C$ values occurs in leaves receiving the same amount of light and water (our calculation; data from Körner et al. 1991). Körner et al. attributed the effect to air temperature. To compensate, we normalized modern data to 37°N, where present-day mean annual temperature (MAT) in the southern United States is similar to that estimated for the Bighorn Basin at the time of our assemblages (average MAT ~14°C; Fig. 1).

*Altitude Correction.*—A mean increase in $\delta^{13}C$ values of ~1.2 ± 0.90‰/km of elevation was found in 12 plant species sampled at different elevations (Körner et al. 1988: Table 3). However, when mean values for a much wider diversity of $C_3$ species are considered, the increase is considerably less (~0.65‰/km [our calculation]; data from Körner et al. 1988). Fricke and Wing (2004: p. 627) estimated an early Eocene paleoelevation of 0.6–1.3 km (mean = 0.95 km) for intermontane basins in Wyoming on the basis of modern lapse rates and MAT estimates from leaf-margin analyses. Accordingly, we normalized modern data to a mean elevation of 0.95 km using the more conservative rate of 0.65‰/km.

*Atmosphere Correction.*—Changes in atmospheric $\delta^{13}C$ ($\delta^{13}C_A$) can be estimated from the tests of fossil foraminifers because they incorporate dissolved carbon with predictable fractionation from vital effects (Koch et al. 1995; Passey et al. 2002). Carbon is rapidly exchanged between the atmosphere and surface ocean in near equilibrium. In turn, surface and deep waters are mixed over centuries or millennia (Sundquist 1993). Thus, benthic foraminifers should be in approximate isotopic equilibrium with the atmosphere. We used data compiled by Zachos et al. (2001) from two lineages of benthic foraminifers, adjusted for vital effects, to calculate changes in $\delta^{13}C_A$. The mean foraminifer value at the time of our assemblages is only 0.2 ± 0.5‰ more negative than the mean pre-industrial value for the last 1000 years.

Fractionation between $\delta^{13}C_A$ values and the surface ocean is, however, moderately temperature dependent. Because the latitudinal temperature gradient in the early Eocene was lower than today, the difference in MAT would have been greater at higher latitudes. Taking into account that surface area decreases from the equator to the poles, we calculate that global MAT was ~7°C warmer in the early to middle Eocene (data from Greenwood and Wing 1995; Fricke and Wing 2004). Because of higher MAT, fractionation between dissolved carbon in the ocean and atmospheric carbon would have been ~0.8‰ lower (based on Mook 1986; Lynch-Stieglitz et al. 1995). This translates to a 0.6‰ greater $\delta^{13}C_A$ value in the early Eocene, when the 0.2‰ temporal difference in foraminifers is subtracted. Of greater impact is a decrease of ~1.5‰ in the $\delta^{13}C_A$ value caused by industrialization over the last two centuries (Friedli et al. 1986). Taken together these effects imply that the $\delta^{13}C_A$ value at the time of our assemblages was ~2.1‰ more positive than today.

An additional factor is the influence that the carbonate ion concentration ($[CO_3^{2-}]$) of marine water has on $\delta^{13}C$ values in foraminiferal tests. Spero et al. (1997) showed that in two species of planktonic foraminifera $\delta^{13}C$ values in tests were negatively correlated with $[CO_3^{2-}]$. Recent studies suggest that $[CO_3^{2-}]$ was lower in the Eocene (Tyrrell and Zeebe 2004; Locklair and Lerman 2005), which could have resulted in higher $\delta^{13}C$ values in tests. Lower $[CO_3^{2-}]$ was presumably the result of higher atmospheric $CO_2$ concentrations (Tyrrell and Zeebe 2004). Although this suggests that a correction for the $[CO_3^{2-}]$ effect is needed, there is considerable variability in the amount of effect in the two modern species studied, and the effect has not been documented in benthic species. Also problematic is the observation that the massive influx of $CO_2$ (~4500 Gt) into the atmosphere during the Paleocene/Eocene boundary thermal maximum (PETM) appears to have had little effect on the magnitude of the carbon isotope excursion in foraminifers. An increase in $CO_2$ should cause a decrease in $[CO_3^{2-}]$, resulting in an increase in $\delta^{13}C$ values in foraminifers and a muting of the carbon isotope excursion (CIE). The muting should be greater in planktonic species, but the magnitude of the CIE is actually lower in benthic species (Bowen et al. 2004). For

these reasons we refrain from correcting for [$CO_3^{2-}$], which would result in lower predicted $\delta^{13}C$ values for early Eocene mammals.

The sum of latitudinal, altitudinal, and atmospheric differences results in adjustments of +1.5 to +2.9‰ in $\delta^{13}C$ values of modern vegetation. After applying an enrichment factor of 13.1‰, the predicted mean $\delta^{13}C_E$ value for early Eocene herbivores in a closed canopy forest is $\leq -14$‰, and for an open canopy is between −10‰ and −13.5‰, with values in the upper range ($\geq -12$‰) representing dry, open forest, woodland, or savanna, and values in the lower range ($\leq -13$‰) representing mesic and/or dense open canopy forest. Values for individual understory browsers in a closed canopy forest range from −18‰ to −23‰, and for confident recognition must be $< -17$‰.

### Isotopic Differences Among Species

Isotopic differences in $\delta^{13}C$ values among mammalian herbivores can result from feeding in different microhabitats or on different foods. Fruit, seeds, flowers, or bark generally have higher mean $\delta^{13}C$ values than leaves from the same habitat. Young, tender leaves also have higher $\delta^{13}C$ values than mature leaves (e.g., Sobrado and Ehleringer 1997). Mean $\delta^{13}C$ values were 1.4–1.7‰ lower for leaves than for other organs in $C_3$ plants from tropical rain forest and savanna biomes, and canopy fruit exposed to direct sunlight had some of the highest values (Cerling et al. 2004; Codron et al. 2005). Thus, we expect folivores to have lower mean $\delta^{13}C_E$ values than frugivores. Low values are also expected for mammals feeding in microhabitats that are dark or where water is easily available to vegetation, such as riparian and paludal settings.

Oxygen isotopes in mammals reflect the $\delta^{18}O$ composition of local surface and plant water, with varying degrees of $^{18}O$-enrichment (e.g., Bryant and Froelich 1995; Kohn 1996). Oxygen isotope values in tooth enamel ($\delta^{18}O_E$) in carnivorous mammals and species that are associated with water and are obligate drinkers have been shown to reflect meteoric water values, whereas values in species that derive a significant portion of water from leaves and/or live in arid regions are sometimes $^{18}O$-enriched (Ayliffe and Chivas 1990; Iacumin and Longinelli 2002; Balasse et al. 2003; Levin et al. 2006). This is due to enrichment of leaf water in dry climates where evapotranspiration rates are high and to enrichment of the mammal's body water through physiological processes. Levin et al. (2006) showed that $\delta^{18}O_E$ increased with increasing aridity in evaporation-sensitive (ES) species, but not in evaporation-insensitive (EI) ones. They quantified the magnitude of enrichment between ES and EI species ($\varepsilon_{ES\text{-}EI}$) and suggested that it could be used to predict differences in water deficit among habitats.

Of the early Eocene mammals studied here, *Coryphodon* is the best EI candidate because it was probably semiaquatic or at least closely associated with water (see below). However, it is unclear which, if any, of the fossil species were aridity sensitive. Thus, we refrain from using the $\varepsilon_{ES\text{-}EI}$ relationship to estimate water deficit. We note, however, that the overall range of $\delta^{18}O_E$ values in a fauna should increase in arid regions because of $^{18}O$-enrichment in ES taxa, and compare the range of $\delta^{18}O_E$ assemblage values with those in the modern faunas considered by Levin et al. (2006).

## Results

Figure 3 shows mean $\delta^{13}C_E$ and $\delta^{18}O_E$ values for mammal species in the lower and upper assemblages. Isotopic values and descriptive statistics are reported in the Appendix and in Table 1, respectively. The range of $\delta^{13}C_E$ values is slightly smaller in the lower assemblage, but the range of $\delta^{18}O_E$ values is nearly identical in both. Variance in neither $\delta^{13}C_E$ nor $\delta^{18}O_E$ values, however, is significantly different between the assemblages ($p = 0.16$, $p = 0.20$, respectively).

Mean $\delta^{13}C_E$ and $\delta^{18}O_E$ values increased by 0.3‰ and 1.6‰, respectively, from the lower to upper assemblage, but only the increase in $\delta^{18}O_E$ values was significant with 95% confidence (*t*-tests: $p = 0.08$ and $p < 0.001$, respectively). The increase in $\delta^{18}O_E$ values is consistent with the direction expected from $\delta^{18}O$ values in hematite sampled from the same stratigraphic sections, which should track surface water values (Bao et al. 1999). It is also consis-

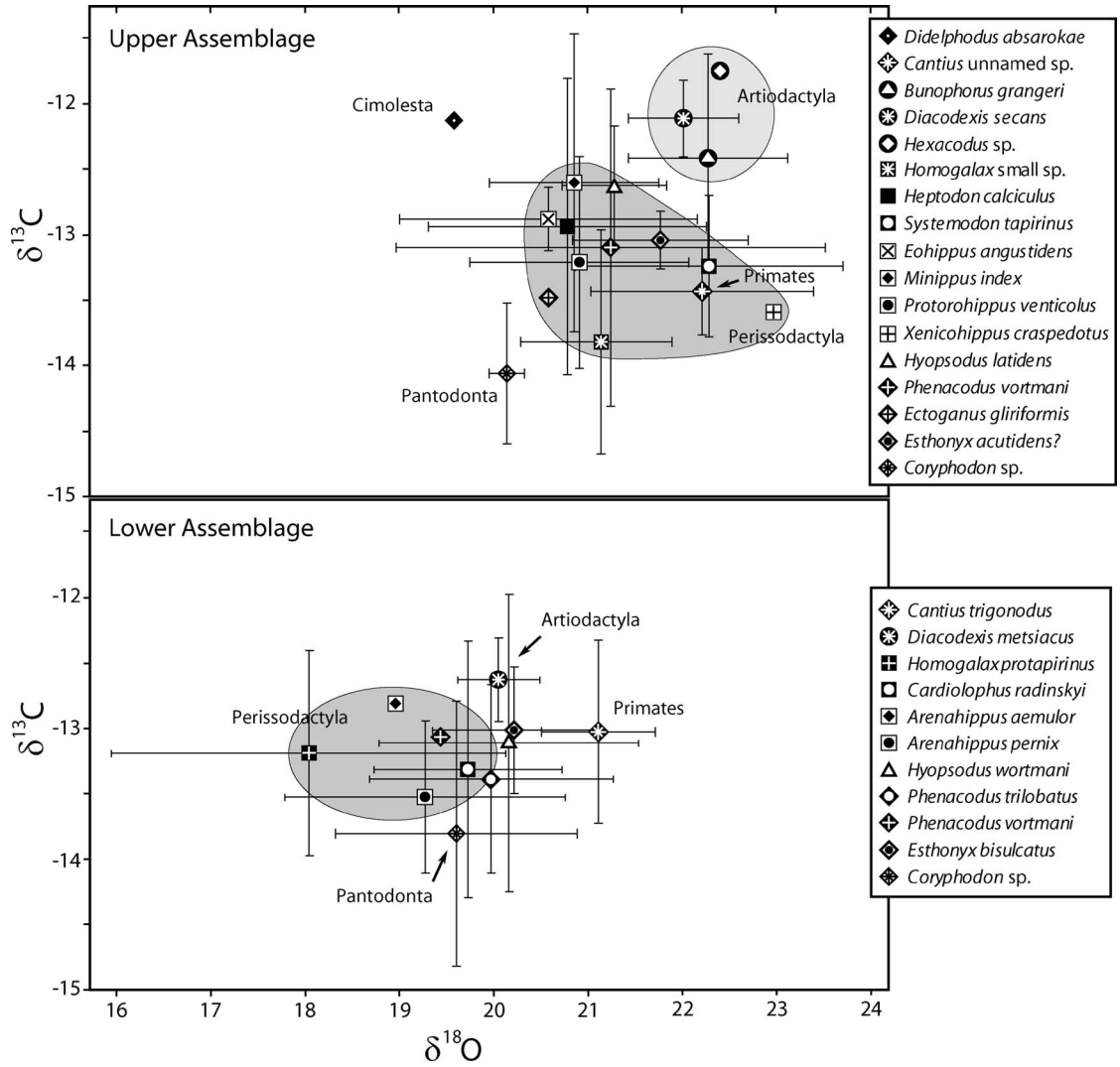


FIGURE 3. Mean $\delta^{13}C_E$ and $\delta^{18}O_E$ values for mammals from the upper and lower fossil assemblages. Error bars 1 SD. Species without bars are represented by a single sample, except *Didelphodus* (upper assemblage), which is based on three combined samples. Artiodactyls are shown as circles and perissodactyls as squares (tapiroids black, equids white background). Shaded areas show regions within which mean values for artiodactyl or perissodactyl species occur. Note close grouping and elevated mean $\delta^{13}C_E$ values for Artiodactyla in upper assemblage.

TABLE 1. Descriptive statistics for $\delta^{13}C$ and $\delta^{18}O$ values from lower (LA) and upper (UA) assemblages.

| | $\delta^{13}C_{(vPDB)}$ | | $\delta^{18}O_{(vSMOW)}$ | |
|---|---|---|---|---|
| | LA | UA | LA | UA |
| *n* | 33 | 52 | 33 | 52 |
| Mean | −13.2 | −13.0 | 19.7 | 21.4 |
| Minimum | −15.0 | −14.8 | 16.8 | 18.6 |
| Maximum | −12.1 | −11.3 | 21.7 | 23.7 |
| Range | 3.0 | 3.5 | 4.9 | 5.0 |
| SD | 0.74 | 0.83 | 1.28 | 1.21 |
| SE | 0.13 | 0.11 | 0.22 | 0.17 |
| Skew | −0.55 | −0.13 | −0.69 | −0.33 |

tent with the increase in MAT inferred from leaf-margin analyses (Fig. 1) (Wing et al. 2000). Oxygen isotopes in modern precipitation are strongly correlated to MAT at mid and high latitudes (Dansgaard 1964; Kohn and Welker 2005), and although the slope of the $\delta^{18}O_{meteoric\ water}$/MAT relationship may have been different in the past (Boyle 1997), a positive correlation is still expected.

Body mass is significantly negatively correlated with mean $\delta^{13}C_E$ values for species in the upper assemblage, using either parametric

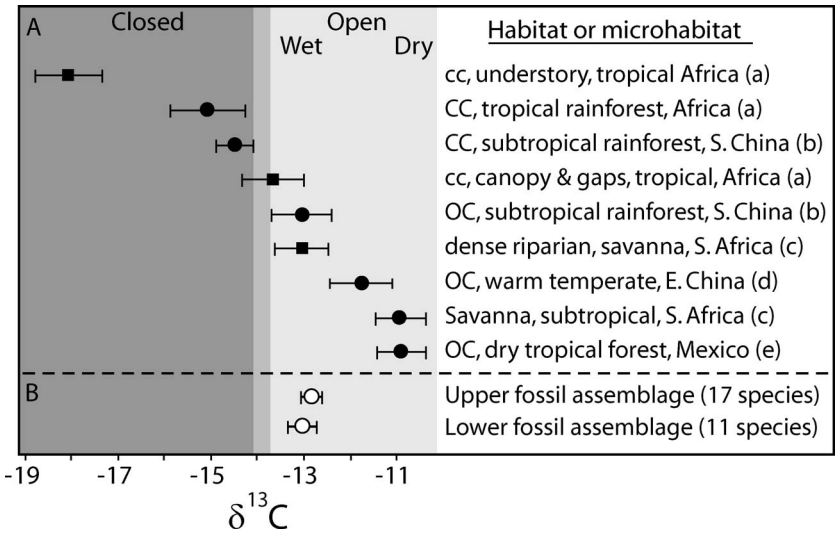


FIGURE 4. Comparison of mean $\delta^{13}C_E$ values. A, Predicted mean values for diverse mammal faunas from various habitats (solid circles) and microhabitats (solid squares). B, Data from fossil assemblages (open circles). Note that fossil means plot in the area expected for an open canopy fauna. Predictions are based on $\delta^{13}C$ values from modern floras, normalized to 37°N latitude, 950 m elevation, corrected for a 2.1‰ difference in atmospheric $\delta^{13}C$ values, and a diet-enamel $\varepsilon^*$ of 13.1‰ (see text). ''Wet'' and ''dry'' refer to water availability for vegetation. Error bars show 95% confidence of mean (±1.96 SE). CC, closed canopy; OC, open canopy. Data sources: a, Cerling et al. (2004); b, Ehleringer et al. (1987); c, Codron et al. (2005); d, Yan et al. (1999); e, Mooney et al. (1989).

(Fisher's least significant difference [LSD]; $p = 0.006$; $r = -0.65$) or nonparametric tests (Spearman's rank correlation; $p = 0.001$, $r = -0.75$) (Body size transformed to natural log in both). The Shapiro-Wilk test suggests normal distribution ($p \geq 0.24$), but even if possible body mass outliers (*Coryphodon* and *Didelphodus*) are removed, correlation is still significant at $\alpha = 0.05$. Body mass is also significantly negatively correlated with $\delta^{13}C$ values in the lower assemblage (Fisher's LSD; $p = 0.02$, $r = -0.66$). The correlation is only marginally significant using Spearman's rank correlation ($p = 0.08$, $r = -0.55$), but the Shapiro-Wilk test suggests normal distribution ($p \geq 0.29$). Body mass is negatively correlated with $\delta^{18}O_E$ values in both assemblages, but neither correlation is significant (all data; lower: $p = 0.38$, $r = -0.30$; upper: $p = 0.78$, $r = -0.07$; without body mass outliers; lower: $p = 0.25$, $r = -0.40$; upper: $p = 0.37$, $r = -0.25$; all tests parametric).

Figure 4 compares mean $\delta^{13}C_E$ values for the fossil assemblages with those predicted for early Eocene herbivorous faunas feeding in various habitats. Mean $\delta^{13}C_E$ values for both fossil assemblages plot in the area for open canopy forest, and 95% confidence intervals do not overlap with closed forest. Figure 5 shows the predicted range of $\delta^{13}C$ values for various habitats and microhabitats. The range of $\delta^{13}C_E$ values in both fossil assemblages is narrower than expected for closed canopy forest, but consistent with open forest. No individual fossil values are in the area predicted for closed canopy understory browsers (≤17‰). The distribution of fossil values is nearly even (skew = −0.55, −0.13; Table 1); this contrasts with the Ituri fauna, which has a long left tail resulting from understory browsers (skew = −1.65).

We perform a pairwise comparison of all genera and orders represented by three or more isotope values in each assemblage using analysis of variance tests (ANOVA). Fisher's LSD test indicates that many taxa have significantly different mean $\delta^{13}C_E$ and $\delta^{18}O_E$ values (Table 2, Fig. 6). However, this test does not adjust for the large number of pairs being considered (e.g., Sokal and Rohlf 1997). A comparison of 11 genera (55 pairs) will result in a false indication of significance for 2.8 pairs at $\alpha = 0.05$ using standard ANOVAs. Thus, we also apply Tukey's post hoc test, which adjusts

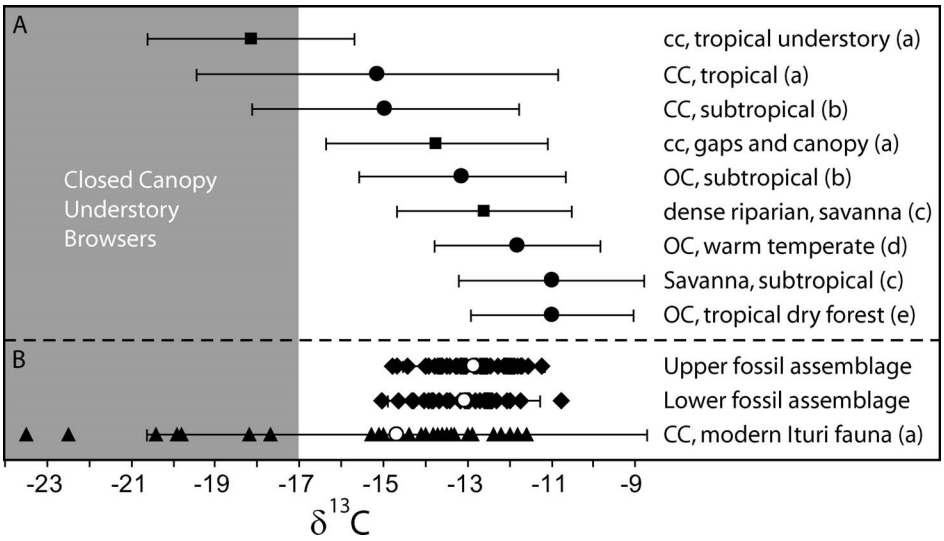


FIGURE 5. Comparison of $\delta^{13}C_E$ ranges. A, Predicted ranges for various early Eocene habitats (means: solid circles) and microhabitats (means: solid squares). Predicted range is ±1.6 SD of floral range (see text). B, Actual ranges for fossil assemblages (solid diamonds) and the modern Ituri fauna (solid triangles) (means: open circles). Note how range narrows from closed to open habitats and that no fossil $\delta^{13}C_E$ value plots in the range for unequivocal understory browsers (shaded area). See Figure 4 for normalization of mean values for plants and Ituri mammals, and for abbreviations.

for number of pairs, and find that several pairs remain significant. In the upper assemblage, $\delta^{13}C_E$ values in Artiodactyla are significantly elevated above those in Perissodactyla and Pantodonta ($p$ = 0.004, 0.002, respectively), and marginally above Primates ($p$ = 0.08). At the generic or specific level *Diacodexis* is significantly elevated above *Coryphodon* ($p$ = 0.009), and *Bunophorus* is marginally higher ($p$ = 0.07). Differences in $\delta^{18}O$ values were marginally significant for Artiodactyla-Pantodonta ($p$ = 0.08). Using Tukey's test for the lower assemblage, we find no pairs with significantly different $\delta^{13}C$ values, but Primates and *Cantius* have significantly higher $\delta^{18}O_E$ values than Perissodactyla and *Homogalax*, respectively ($p$ = 0.06, 0.04).

## Discussion

*Interpretation of Forest Structure.*—Our interpretation relies on several assumptions that warrant discussion: (1) the assemblages contained mammals capable of consuming understory leaves; (2) the numbers of species and individuals sampled were great enough to detect understory browsers; and (3) results were not biased by diagenetic alteration or time averaging.

Regarding (1), the tapiroid perissodactyls and *Coryphodon* had moderate to well-developed molar shearing lophs, which are used in modern mammals to slice mature leaves and other tough vegetation with high fiber content (e.g., Collinson and Hooker 1991). The equoid perissodactyls also had shearing lophs, although weakly developed. This implies that almost half of the individuals sampled were capable of masticating at least some mature leaves. Moreover, young leaves are softer and easier to digest than mature leaves, and would have been available to an even wider range of species. Young leaves have $\delta^{13}C$ values ~2‰ higher than mature leaves of the same plant (Sobrado and Ehleringer 1997), but mammals eating young leaves in a closed canopy understory should still record an understory signal.

Regarding (2), we targeted taxa that were most likely to be understory browsers, judging from dental morphology and body size. A total of 85 individuals were sampled, representing 11 species in the lower assemblage and 17 the upper one. Because some species may have browsed in both closed and open habitats, as do some modern species (e.g., *Hylochoerus meinertzhageni*), the number of indi-

TABLE 2. Matrices of pairwise probabilities of mean differences in $\delta^{13}C_E$ and $\delta^{18}O_E$ values among higher level taxa (A, B, E, F) and genera (C, D, G, H) in upper and lower assemblages. Values shown in bold indicate significance for $\alpha \leq 0.05$. using Fisher's least significant difference test. Pairs that were significant using Tukey's post hoc test are indicated by asterisks (*$\alpha \leq 0.10$, **$\alpha \leq 0.05$).

| A. $\delta^{13}C_E$ | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Upper Assemblage | | | | | | |
| 1. Artiodactyla | 1.000 | | | | | |
| 2. Condylarthra | 0.060 | 1.000 | | | | |
| 3. Pantodonta | **0.001**** | **0.014** | 1.000 | | | |
| 4. Perissodactyla | **0.001**** | 0.292 | **0.040** | 1.000 | | |
| 5. Primates | **0.008*** | 0.214 | 0.274 | 0.516 | 1.000 | |
| 6. Tillodontia | 0.065 | 0.658 | 0.079 | 0.799 | 0.495 | 1.000 |

| B. $\delta^{18}O_E$ | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Upper Assemblage | | | | | | |
| 1. Artiodactyla | 1.000 | | | | | |
| 2. Condylarthra | 0.104 | 1.000 | | | | |
| 3. Pantodonta | **0.008*** | 0.156 | 1.000 | | | |
| 4. Perissodactyla | **0.025** | 0.928 | 0.128 | 1.000 | | |
| 5. Primates | 0.928 | 0.232 | **0.030** | 0.163 | 1.000 | |
| 6. Tillodontia | 0.607 | 0.521 | 0.084 | 0.435 | 0.635 | 1.000 |

| C. $\delta^{13}C_E$ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Upper Assemblage | | | | | | | | | | | |
| 1. *Bunophorus* | 1.000 | | | | | | | | | | |
| 2. *Cantius* | **0.050** | 1.000 | | | | | | | | | |
| 3. *Coryphodon* | **0.002*** | 0.269 | 1.000 | | | | | | | | |
| 4. *Diacodexis* | 0.454 | **0.009** | **0.001**** | 1.000 | | | | | | | |
| 5. *Eohippus* | 0.356 | 0.331 | **0.043** | 0.112 | 1.000 | | | | | | |
| 6. *Esthonyx* | 0.217 | 0.489 | 0.078 | 0.057 | 0.776 | 1.000 | | | | | |
| 7. *Heptodon* | 0.236 | 0.328 | **0.031** | **0.047** | 0.913 | 0.834 | 1.000 | | | | |
| 8. *Hyopsodus* | 0.647 | 0.132 | **0.010** | 0.238 | 0.627 | 0.431 | 0.503 | 1.000 | | | |
| 9. *Phenacodus* | 0.180 | 0.554 | 0.095 | **0.044** | 0.700 | 0.920 | 0.747 | 0.372 | 1.000 | | |
| 10. *Protorohippus* | 0.120 | 0.696 | 0.139 | **0.026** | 0.558 | 0.762 | 0.585 | 0.270 | 0.840 | 1.000 | |
| 11. *Systemodon* | 0.081 | 0.717 | 0.127 | **0.013** | 0.496 | 0.705 | 0.511 | 0.212 | 0.786 | 0.956 | 1.000 |

| D. $\delta^{18}O_E$ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Upper Assemblage | | | | | | | | | | | |
| 1. *Bunophorus* | 1.000 | | | | | | | | | | |
| 2. *Cantius* | 0.938 | 1.000 | | | | | | | | | |
| 3. *Coryphodon* | **0.014** | **0.030** | 1.000 | | | | | | | | |
| 4. *Diacodexis* | 0.695 | 0.802 | **0.021** | 1.000 | | | | | | | |
| 5. *Eohippus* | **0.046** | 0.084 | 0.630 | 0.072 | 1.000 | | | | | | |
| 6. *Esthonyx* | 0.541 | 0.633 | 0.083 | 0.752 | 0.202 | 1.000 | | | | | |
| 7. *Heptodon* | **0.013** | **0.032** | 0.852 | **0.020** | 0.742 | 0.095 | 1.000 | | | | |
| 8. *Hyopsodus* | 0.195 | 0.285 | 0.190 | 0.303 | 0.418 | 0.571 | 0.222 | 1.000 | | | |
| 9. *Phenacodus* | 0.215 | 0.297 | 0.235 | 0.324 | 0.474 | 0.567 | 0.277 | 0.964 | 1.000 | | |
| 10. *Protorohippus* | 0.104 | 0.164 | 0.404 | 0.161 | 0.722 | 0.352 | 0.479 | 0.665 | 0.717 | 1.000 | |
| 11. *Systemodon* | 0.988 | 0.930 | **0.017** | 0.703 | 0.055 | 0.550 | **0.017** | 0.213 | 0.231 | 0.117 | 1.000 |

| E. $\delta^{13}C_E$ | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Lower Assemblage | | | | | | |
| 1. Artiodactyla | 1.000 | | | | | |
| 2. Condylarthra | 0.226 | 1.000 | | | | |
| 3. Pantodont | 0.189 | 0.724 | 1.000 | | | |
| 4. Perissodactyla | 0.141 | 0.795 | 0.852 | 1.000 | | |
| 5. Primates | 0.462 | 0.653 | 0.492 | 0.484 | 1.000 | |
| 6. Tillodontia | 0.504 | 0.665 | 0.508 | 0.514 | 0.983 | 1.000 |

TABLE 2. Continued

| F. $\delta^{18}O_E$ | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Lower Assemblage | | | | | | |
| 1. Artiodactyla | 1.000 | | | | | |
| 2. Condylarthra | 0.929 | 1.000 | | | | |
| 3. Pantodont | 0.948 | 0.867 | 1.000 | | | |
| 4. Perissodactyla | 0.214 | 0.122 | 0.186 | 1.000 | | |
| 5. Primates | 0.248 | 0.136 | 0.277 | **0.006*** | 1.000 | |
| 6. Tillodontia | 0.866 | 0.772 | 0.917 | 0.148 | 0.328 | 1.000 |

| G. $\delta^{13}C_E$ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| Lower Assemblage | | | | | | | | | |
| 1. *Arenahippus* | 1.000 | | | | | | | | |
| 2. *Cantius* | 0.481 | 1.000 | | | | | | | |
| 3. *Cardiolophus* | 0.901 | 0.581 | 1.000 | | | | | | |
| 4. *Coryphodon* | 0.976 | 0.517 | 0.890 | 1.000 | | | | | |
| 5. *Diacodexis* | 0.176 | 0.487 | 0.233 | 0.215 | 1.000 | | | | |
| 6. *Esthonyx* | 0.504 | 0.984 | 0.595 | 0.532 | 0.528 | 1.000 | | | |
| 7. *Homogalax* | 0.728 | 0.773 | 0.823 | 0.735 | 0.360 | 0.772 | 1.000 | | |
| 8. *Hyopsodus* | 0.626 | 0.877 | 0.721 | 0.643 | 0.428 | 0.870 | 0.900 | 1.000 | |
| 9. *Phenacodus* | 0.885 | 0.594 | 0.985 | 0.876 | 0.240 | 0.607 | 0.837 | 0.734 | 1.000 |

| H. $\delta^{18}O_E$ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| Lower Assemblage | | | | | | | | | |
| 1. *Arenahippus* | 1.000 | | | | | | | | |
| 2. *Cantius* | **0.022** | 1.000 | | | | | | | |
| 3. *Cardiolophus* | 0.513 | 0.103 | 1.000 | | | | | | |
| 4. *Coryphodon* | 0.293 | 0.270 | 0.660 | 1.000 | | | | | |
| 5. *Diacodexis* | 0.328 | 0.242 | 0.713 | 0.947 | 1.000 | | | | |
| 6. *Esthonyx* | 0.244 | 0.321 | 0.582 | 0.916 | 0.863 | 1.000 | | | |
| 7. *Homogalax* | 0.176 | **0.002**** | 0.067 | **0.037** | **0.043** | **0.030** | 1.000 | | |
| 8. *Hyopsodus* | 0.270 | 0.293 | 0.623 | 0.961 | 0.908 | 0.955 | **0.033** | 1.000 | |
| 9. *Phenacodus* | 0.422 | 0.133 | 0.886 | 0.758 | 0.813 | 0.675 | 0.052 | 0.719 | 1.000 |

viduals sampled may be more important than the number of species. Also important is the number of individuals with lophodont dentitions, which we assume were most likely to consume leaves. We sampled a total of 46 individuals with lophodont or proto-lophodont dentitions, 27 in the lower assemblage and 19 in the upper one. These individuals represent species with body masses ≥5 kg (online appendix) that are thought to have been terrestrial, except for possibly *Esthonyx* (Rose 2001). With regard to diversity, the lower and upper assemblages contain nine and 19 species, respectively, that exhibit some degree of lophodonty. We sampled six (67%) and nine (47%) of the most common of these species, respectively. This sample size should be more than adequate to detect understory browsers.

Regarding (3), the strongest evidence that primary $\delta^{13}C_E$ values are preserved in the Willwood Formation is a consistent decrease of ~3–4‰ in $\delta^{13}C_E$ values in three mammal lineages during the CIE associated with the Paleocene/Eocene boundary (Koch et al. 1995; Fricke et al. 1998). $\delta^{13}C$ values in carbonate paleosol nodules (Bowen et al. 2001) and organic carbon (Magioncalda et al. 2004) from the same stratigraphic interval as the teeth also decrease in the CIE. All of these materials obtain their primary $\delta^{13}C$ signal from plants, leaving little doubt that $\delta^{13}C_E$ values preserve a primary shift in atmospheric $CO_2$ composition (Koch et al. 2003). Paleosol carbonate nodules bracketing our assemblages provide additional evidence. Unaltered paleosol carbonate is enriched in $^{13}C$ through pedogenic processes by ~15‰, relative to local vegetation (Koch 1998). Thus, paleosol nodules should be ~2‰ higher than mean $\delta^{13}C_E$ values, assuming an enrichment factor of 13‰ for mammals. These values should converge through diagenesis. Mean $\delta^{13}C$ values in paleosol carbonates stratigraphically bracketing our assemblages (localities D1200, D1493, D1289 for

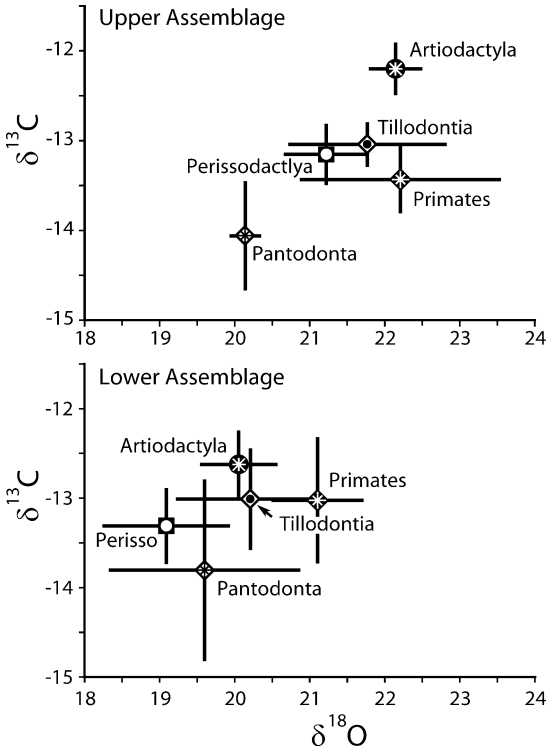


FIGURE 6. Values of $\delta^{13}C_E$ and $\delta^{18}O_E$ for higher-level taxa in the fossil assemblages. Symbols indicate means; error bars show 95% confidence (±1.96 SE). Artiodactyla and Pantodonta have, respectively, the highest and lowest $\delta^{13}C_E$ values in both assemblages. See Table 2 for significance matrix.

lower; D1162, D1250, D1204 for upper; $\delta^{13}C$ data from Koch et al. 2003) are 2.8‰ and 2.6‰ higher, respectively, than $\delta^{13}C_E$ mean faunal values. This agrees well with expectations for unaltered enamel.

Our interpretation of canopy structure does not appear to have been affected by temporal or spatial averaging. The home ranges of the species sampled would probably have been less than 1 km$^2$, according to body size, except for *Coryphodon*, which would have been ~6 km$^2$ (Jetz et al. 2004). Time-averaging, however, could have substantially increased this area. A fauna derived from multiple stratigraphic levels might sample different microhabitats or habitats, effectively increasing the sampling area. Climate variation through the sampled interval could also result in mixing mammals from different climatic regimes. In any of these cases the effect would be to increase overall isotopic variability in the assemblages. The range of variability is narrow in both assemblages (Table 1, Fig. 5), however, and the range in the lower assemblage, which is from a thicker stratigraphic interval and was collected over a larger geographic area (see ''Methods''), is narrower than that in the upper one. This is consistent with the smaller number of species and specimens sampled, but not with the idea that temporal or spatial averaging increased the range of isotopic values.

Our results suggest that early Eocene forests in the Bighorn Basin had an open canopy. The faunal assemblages plot closest to the values predicted from a subtropical open canopy forest in southern China (Ehleringer et al. 1987) and a riparian microhabitat in a South African savanna (Fig. 4) (Codron et al. 2005). The former receives monsoonal rainfall, with ~200 cm mean annual precipitation (MAP). Rainfall in the Bighorn Basin may also have been seasonal (Bown and Kraus 1981; Kraus and Riggins 2007). The southern China open forest is a localized patch with a well-exposed understory, adjacent to closed canopy forest. Although this is essentially a microhabitat, Ehleringer et al. (1987) sampled a high diversity of plants species ($n$ = 23) and forms, and the mean value should be comparable to that of a more regional mesic open forest. The riparian microhabitat had the lowest mean $\delta^{13}C$ value of any in the savanna. The area receives low MAP (30–50 cm). The low $\delta^{13}C$ values were attributed to high water availability due to close proximity to a perennial water source (Codron et al. 2005, p. 1765). Because many of the mammals used in our study occur in floodplain deposits, it is probable that they inhabited riparian areas where water was also readily available to plants. Thus, part of the $\delta^{13}C$ signal may be related to riparian microhabitat. Although riparian areas typically have dense vegetation, mean $\delta^{13}C_E$ assemblage values would be expected to be even lower if a closed canopy had been present. Moreover, no individual values are low enough to suggest feeding in a closed canopy understory (Fig. 5).

An open canopy is also suggested by the even distribution and narrow range of $\delta^{13}C_E$ values. Both of these parameters are indepen-

dent of changes in atmospheric $\delta^{13}C$ values. If a closed canopy had been present, we would expect a left tail on the overall distribution because of $^{13}C$-depletion in understory browsers (Fig. 5, Ituri fauna). Instead, the distributions are almost even, especially in the upper assemblage, which contains the greatest numbers of species and individuals. The range of values is lower than expected for a closed canopy forest, which should have greater heterogeneity between the understory and other microhabitats (e.g., Cerling et al. 2004). Variance in both fossil assemblages is significantly lower than in the Ituri fauna ($p < 0.001$). Thus, all parameters in both assemblages are consistent with a dense open canopy forest where water is readily available to vegetation.

A mesic habitat with high relative humidity is also suggested by the narrow range of $\delta^{18}O_E$ values in both assemblages (4.9, 5.0‰, Table 1). The range is smaller than in any of the modern faunas with a comparable sample size reported by Levin et al. (2006). Of these, Nakuru has the lowest range of $\delta^{18}O_E$ values (6.8‰, vSMOW) and a low water deficit (448 mm). However, only six species were sampled, and additional species may increase the range. Ituri (including all 22 species from Cerling et al. 2004) had the lowest water deficit (−80 mm) but a moderately high $\delta^{18}O_E$ range (10‰, vSMOW). However, the range is more than doubled by two extreme positive outliers of *Colobus*. The high values in these folivorous monkeys suggest dependence on an evaporated water source, such as leaves (Cerling et al. 2004). Without *Colobus* the range of $\delta^{18}O_E$ values is 4.4‰ (vSMOW, $n = 35$), which is only slightly below that of the fossil assemblages. In contrast, less diverse samples from regions with greater water deficits show a greater range of $\delta^{18}O_E$ values. For example, Mpala (12 species, $n = 105$), Tsavo (12 species, $n = 128$), and Turkana (9 species, $n = 40$) have water deficits of 751, 1059, 1588 mm and $\delta^{18}O_E$ ranges of 11.0, 10.5, and 14.3‰, respectively (data from Levin et al. 2006). Because of outliers, differing sample size, and differing species diversity, it is difficult to evaluate these differences statistically. Nevertheless, an interpretation of a mesic, humid habitat for the assemblages is consistent with other proxies, such as leaf-area analyses, which suggest moderately high precipitation (~120–140 cm) (Wilf 2000), and a cenogram analysis, which suggests a humid climate in the early Eocene of the Bighorn Basin (Gunnell 1997).

*Resource Partitioning and Microhabitats.*—The negative correlation between $\delta^{13}C_E$ values and body mass suggests that larger species consumed a greater portion of leaves than smaller ones. This is consistent with body size/diet relationships in extant mammals and with diets inferred from dental morphology. Small-bodied mammals have higher metabolic rates and therefore need to consume foods that are rich in nutrients and digest rapidly, such as fruit and insects. These foods are often not abundant enough to support large mammals, which must adapt to foods that take longer to digest and have lower nutrient content, such as mature leaves. Richard (1985: Fig. 5.13) described a general correspondence between body size and diet in euprimates. For body mass: insectivores < frugivores/insectivores < frugivores/folivores < folivores. Because fruit is more $^{13}C$-enriched than leaves (Codron et al. 2005), a negative correlation between body size and $\delta^{13}C_E$ values might result. The correlation would be enhanced if larger-bodied species were consuming aquatic vegetation, or feeding on leaves in darker and/or wetter areas, such as riparian or paludal microhabitats.

Differences in mean $\delta^{13}C_E$ values among taxa are significant only in the upper assemblage (Tukey's posthoc test; Table 2). This may be because of the smaller sample size, greater time-averaging, or greater homogeneity in the lower assemblage. Although time-averaging does not appear to have influenced our interpretation of canopy structure, it could have increased intraspecific variability (as discussed above), thereby decreasing the ability to distinguish among taxa. In spite of the reduced ability to distinguish among taxa in the lower assemblage, Artiodactyla and Pantodonta (i.e., *Coryphodon*) occupy the same relative positions in both assemblages. In both assemblages, Artiodactyla has the highest mean $\delta^{13}C_E$ value of any herbivore order, and Pantodonta has the lowest (Fig. 6). Mean $\delta^{13}C_E$ values in Artiodactyla are elevated above those in

Perissodactyla by 1.0‰ in the upper assemblage ($p = 0.004$, Table 2, Figs. 3, 6). Possible reasons for this are a higher diet-enamel $\varepsilon^*$ in Artiodactyla, differences in diet, and/or differences in microhabitat.

Higher $\varepsilon^*$ in modern ruminant artiodactyls appears to be caused by greater methanogenesis associated with rumination (Passey et al. 2005). Rumination provides a way of extracting nutrients from vegetation high in cellulose, such as mature leaves and unripe fruit. This is advantageous for large-bodied mammals, but mammals the size of *Diacodexis* and *Hexacodus* (≤2 kg, Appendix) would probably gain no advantage by ruminating (e.g., Janis 1976; Demment and Van Soest 1985). Diet is a more plausible cause for the higher $\delta^{13}C_E$ values in the artiodactyls. The artiodactyls had bunodont dentition, a condition that is not adapted to chewing tough vegetation. Thus, they would have selected foods with less fiber and higher nutrient content, such as fallen fruit or berries, buds, shoots, young leaves, and flowers. These items are generally enriched in $^{13}C$ above leaves from the same plant by ~1.4–1.7‰. Hence, higher $\delta^{13}C_E$ values are expected in artiodactyls if the perissodactyls were consuming mature leaves, as suggested by their dentition. Microhabitat preference could also be a factor if perissodactyls preferred more closed, and/or more poorly drained areas than artiodactyls. The postcranial morphology of early Eocene perissodactyls is most similar to that of modern tapirs (Janis 1984), which often prefer riparian habitats, frequently spend time in water or mud, and may consume semiaquatic plants (e.g., Nowak and Paradiso 1983). These habits should result in low $\delta^{13}C_E$ values, and although isotopes in modern tapirs are poorly known, Neogene tapirs have some of the lowest $\delta^{13}C$ values among contemporaneous species. (MacFadden and Cerling 1996; MacFadden et al. 1996; Koch et al. 1998). Thus, both diet and microhabitat are plausible contributors to the difference in $\delta^{13}C_E$ values between Perissodactyla and Artiodactyla.

The arboreal primate *Cantius* is widely thought to have been a frugivore, on the basis of its dentition (e.g., Covert 1995). However, its mean $\delta^{13}C_E$ value is lower than expected for a frugivore and is equivalent to those of folivores (Figs. 3, 6). Although this could be explained by a preference for fruit with lower than average $\delta^{13}C$ values, it is more probably the result of a lower enrichment factor in *Cantius*. Cerling et al. (2004) calculated $\varepsilon^* = 12.8 \pm 0.6$‰ for primates in the Ituri Forest, which is only slightly lower than the 13.1‰ that we assumed for our assemblages. However, the Ituri primates are anthropoids, are larger (mean ~16 kg), and are considerably more derived than *Cantius*. *Cantius* was a basal prosimian, similar to modern lemurs, and weighed only ~2–4 kg (Appendix). Also, no study has calculated $\varepsilon^*$ for primates on a controlled diet. Thus, the primate $\varepsilon^*$ from the Ituri Forest may not be valid for *Cantius*.

The high $\delta^{18}O_E$ values in *Cantius*, especially in the lower assemblage, suggest that it obtained water from an evaporated source. Extant arboreal primates often avoid drinking ground water and instead obtain a large portion of their water from arboreal cisterns and foods with high water content, such as fruit (Jolly 1985). Water in arboreal cisterns is likely to have elevated $\delta^{18}O$ values caused by evaporation, and fruit water is also enriched in $^{18}O$ relative to ground water (Dunbar and Wilson 1983). Thus, avoidance of ground water is a plausible explanation for the high $\delta^{18}O_E$ values in *Cantius*.

*Coryphodon* has the lowest mean $\delta^{13}C_E$ values in both assemblages and is by far the largest taxon (~600 kg). It is often considered semiaquatic (e.g., Simons 1960: p. 70). Its low $\delta^{13}C_E$ values are consistent with feeding on plants that lose little water from evapotranspiration, such as aquatic vegetation or plants around the periphery of a river or pond. Moreover, aquatic mammals are expected to have lower variability in $\delta^{18}O_E$ values than terrestrial mammals (Clementz and Koch 2001), and *Coryphodon* in the upper assemblage has the lowest variability of any taxon in this study (Figs. 3, 6). This is strong support for a semiaquatic interpretation. Teeth sampled from the upper assemblage were collected on different occasions from a single locality, and they appear to represent at least two individuals. Even for a single individual, however, the variability in $\delta^{18}O_E$ values would be markedly

low. Variability is considerably higher in *Coryphodon* in the lower assemblage and at other localities (Fricke et al. 1998), probably reflecting differences among water bodies. Variability in surface water is caused primarily by seasonal fluctuations in the $\delta^{18}O$ values of precipitation. In continental habitats seasonal variation is muted most in lakes or large ponds and to varying degrees in rivers, depending on input from groundwater (e.g., Dutton et al. 2005). Thus, the low variability of *Coryphodon* in the upper assemblage suggests that these individuals inhabited large ponds or large rivers with low seasonal fluctuation.

*Didelphodus* plots as an outlier from the main cluster in the upper assemblage by having the lowest mean $\delta^{18}O$ value, but a high $\delta^{13}C$ value (Fig. 3; mean based on combined samples from three individuals). Its tribosphenic molar design and small body size (160 g) indicate that *Didelphodus* had an insectivorous diet (e.g., Gunnell et al. 1995). Very little is known about isotopes in insectivores, but one study suggested that insectivores should have lower $\delta^{18}O$ values than herbivores (Sponheimer and Lee-Thorp 2001). The low $\delta^{18}O_E$ value in *Didelphodus* is consistent with this prediction.

## Conclusions

The carbon isotope composition of tooth enamel from both fossil assemblages suggests that early Eocene forests in the Bighorn Basin had an open canopy. Although some authors have suggested that Eocene forests had a closed canopy, no single $\delta^{13}C_E$ value is low enough to suggest feeding in the understory of a closed canopy forest, even though we sampled a large diversity of potential understory browsers. The range and distribution of $\delta^{13}C_E$ values in the herbivores, both of which are independent of changes in the composition of atmospheric $CO_2$, are also consistent with an open canopy. Mean $\delta^{13}C_E$ values fall at the low end of the range expected for open canopy forests, suggesting dense vegetation and/or high water availability to plants. Values compare closely to a riparian microhabitat, suggesting that many of these mammals consumed vegetation near rivers or ponds.

Overlap of isotopic values among most taxonomic groups is high in both assemblages and differences in $\delta^{13}C_E$ values are significant only in the better sampled upper assemblage. In the upper assemblage, the negative correlation between body size and $\delta^{13}C_E$ values is probably the result of larger species consuming greater portions of leaves, and smaller species more fruit and seeds. The significantly elevated $\delta^{13}C_E$ values in Artiodactyla suggest that fallen fruit, berries, and/or seeds were an important component of their diet. Differences between Artiodactyla and Perissodactyla may also have been amplified by a preference in the latter for microhabitats with high water availability to plants. The amount of resource partitioning in the ungulates at this stage of evolution appears to have been small, but studies of diverse modern faunas from $C_3$ habitats are needed for comparison. This study demonstrates that even in mammalian faunas of great antiquity resource partitioning can be recognized by using stable isotopes.

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