

ABSTRACT

STABLE ISOTOPE RECORDS OF INLAND CALIFORNIA MEGAFUNA – NEW INSIGHTS INTO PLEISTOCENE PALEOECOLOGY AND PALEOENVIRONMENTAL CONDITIONS

Paleodietary studies of California megafauna have focused primarily on the coastal late Pleistocene Rancho La Brea tar seeps (RLB) in Los Angeles, while other sites remain understudied. This study examined two Pleistocene fossil localities from inland California (San Joaquin Valley) and report $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values measured from tooth enamel of mammalian megafauna at both sites. The late Pleistocene McKittrick tar seeps in Kern County have a similar fauna to RLB. The middle Irvingtonian (~700,000 year old) Fairmead Landfill site, near Chowchilla, contains a megafaunal assemblage dominated by *Equus*, *Camelops* and *Mammuthus*.

This study uses stable isotope values measured in carnivore and herbivore tooth enamel to investigate paleodietary and paleoecological patterns at both sites. The $\delta^{13}\text{C}$ values of tooth enamel are controlled by diet and can be used to investigate resource usage and partitioning among and between taxa. In large mammals $\delta^{18}\text{O}$ ratios are controlled by drinking water, and by proxy, climate. Ontogenetic serial tooth $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ reveal seasonal trends in resource usage, from which we can infer patterns of forage availability.

Stable carbon values from 16 taxa, reveal significant differences both between taxa and between localities. Faunal $\delta^{13}\text{C}$ differ significantly ($p < 0.001$) between Fairmead and McKittrick, ranging from -13.5‰ to -8.2‰ and -11.8 to -0.7‰, respectively. No significant differences were detected in $\delta^{18}\text{O}$ between sites ($p = 0.7$).

Fairmead Landfill $\delta^{13}\text{C}$ values are consistent with an environment dominated by C_3 vegetation. *Platygonus* and *Camelops* had the lowest and highest $\delta^{13}\text{C}$, respectively. *Camelops* exhibited the most variable $\delta^{13}\text{C}$ among herbivores, though several other taxa are represented by single individuals, thus lacking dietary ranges. Among carnivores, *Smilodon* had the lowest $\delta^{13}\text{C}$ values (-13.4‰) and *Canis latrans* the highest (-10.7‰). Carnivore $\delta^{13}\text{C}$ values only partially overlap the observed range of herbivore values suggesting that not all herbivores were consumed with the same frequency.

In comparison to Fairmead, $\delta^{13}\text{C}$ values from McKittrick show a significant shift in isotopic values suggesting greater C_4 plant availability from middle to late Pleistocene. *Camelops* showed the greatest shift towards C_4 plants values, while *Cervus* had the most negative $\delta^{13}\text{C}$ value indicating the presence of woodland C_3 resources. Within the carnivore guild, *Panthera* and *Arctodus* had specialized diets trending towards forested habitats, while canids exhibit generalist diets.

Serially sampled teeth from both sites were used to investigate seasonality and temporal resource usage among megafauna. *Equus* from both localities showed little variation in $\delta^{13}\text{C}$, while at McKittrick *Camelops* diet included variable amounts of C_4 resources throughout a seasonal cycle. We also report the first ever serially sampled *Tetrameryx* tooth; $\delta^{13}\text{C}$ variation throughout the tooth is low suggesting a stable diet. Comparing similarly aged inland McKittrick and coastal RLB faunas reveal significant differences ($p < 0.001$). *Bison*, *Equus* (Feranec et al., 2009) and *Panthera* show statistically similar dietary $\delta^{13}\text{C}$ while *Camelops*, *Canis dirus*, *Canis latrans* and *Mammuth* show significant differences from previously reported RLB analogs (Coltrain et al., 2004).

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MEGAFUNA – NEW INSIGHTS INTO PLEISTOCENE
PALEOECOLOGY AND PALEOENVIRONMENTAL
CONDITIONS

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INTRODUCTION AND BACKGROUND

Paleodietary studies of fossil mammals from California have focused primarily on the coastal, Pleistocene megafauna of the Rancho La Brea tar seeps (Coltrain et al., 2004; Feranec, 2004; Feranec et al., 2009). Currently no detailed studies exist for inland faunas. Paleodiet is reconstructed using a variety of methods. Tooth morphology and breakage has been used to study both herbivore and carnivore diet (Van Valkenburgh and Hertel, 1993; Dompierre and Churcher, 1996; Anyonge and Baker, 2006), while mesowear and microwear analyses provide detailed windows into broad feeding habits (Anyonge, 1996; Green et al., 2005; Semprebon and Rivals, 2010). Coprolites and dental impacta (Akersten et al., 1988; Lepper et al., 1991) accurately identify dietary preferences, however these remains are relatively rare in the fossil record. Stable isotope analysis of fossil animal tissues is commonly used to investigate paleodietary and paleoecological questions. Extracted collagen is used for late Pleistocene localities, however it decays quickly, making it unsuitable for older localities (Clementz, 2012). Tooth enamel, composed bioapatite, is resistant to diagenesis (Koch et al., 1997; Kohn and Cerling, 2002) and accurately preserves the isotopic composition of an animal's diet. Since enamel forms incrementally and is not remodeled after mineralization, it preserves a sequential record of diet and climate for the period of tooth formation (Passey and Cerling, 2002; Hoppe et al., 2004b). For most taxa this should amount to a few months to a few years of growth. Using a combination of single bulk and multiple serial samples, this study reports $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from tooth enamel from two San Joaquin Valley, California, fossil localities: the middle Irvingtonian Fairmead Landfill site and the late Rancholabrean McKittrick asphalt seeps. This study uses stable carbon isotopes to

investigate niche partitioning between taxa within localities and between localities to explore shifts in megafaunal diet from the middle to late Pleistocene. Serial samples from both carnivores and herbivores are used to examine the relative seasonality at both localities and its effects on diet. Lastly, by comparing the McKittrick fauna to published data sets for Rancho La Brea fauna, this study investigates geographic effects on megafaunal diet in the late Pleistocene.

The McKittrick Asphalt Seeps

The McKittrick asphalt seeps, Kern County, (Fig. 1) produce a faunal assemblage similar to Rancho La Brea. Radiocarbon analysis of three University of California Museum of Paleontology specimens; UCMP 153245 (*Arctodus simus*) = 11,040±310, UCMP 153241 (*Panthera atrox*) = 15,290±510, UCMP 153257 (*Cervus elaphus*) = 11230±60, date the site to late Rancholabrean. The later two individuals were also included in stable isotope analysis for this study. During the late Pleistocene tar seeps were active at the site, permeating surficial sediments and entrapping animals. Schultz (1938) summarized the mammalian fauna. Subsequent publications focus on birds, insects, and reptiles, leaving the mammalian megafauna largely unstudied (DeMay, 1942; Miller, 1942; Brattstrom, 1953; Miller, 1982; Fox-Dobbs et al., 2006). MacFadden et al. (1999) report the only published $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for McKittrick mammalian fauna; a single *Equus* tooth was sampled as part of a larger study of C_3/C_4 distributions in North America.

Six plant taxa are recorded from McKittrick. *Pinus* (Pine), *Juniperus* (Juniper), *Atriplex* (saltbush), *Arctostaphylos* (manzanita) and *Echinocystis* (wild cucumber) are represented as macrofossils (Mason, 1944). Pollen profiles from Tulare Lake, located 50 miles north of McKittrick are dominated by *Artemisia*

(sagebrush) and *Sarcobatus* (greasewood), with *Quercus* (oak) and *Sequoiadendron* (giant sequoia) less common (Davis, 1999). Taken together, these flora suggest an open scrub/grassland with an upland juniper-pine woodlands.

Fairmead Landfill

Fairmead Landfill, Chowchilla, (Fig. 1) sits on the distal edge of the Chowchilla river alluvial fan. Fossils are recovered from the upper unit of the Turlock Lake Formation. The sediments are magnetically normal (Dundas et al., 1996), and contain the friant pumice (750.1 ± 5 ka) (Sarna-Wojcicki et al., 2000) constraining the age to $\sim 700,000$ ka. Fossils occur from 4 m to 20 m below surface over a 40-acre area. The sediments represent a distal alluvial fan channel, with overbank flood, marsh and lacustrine deposits being common (Marchand and Allwardt, 1981). The presence of *Clemmys marmorata* (pond turtle) and *Archoplites interruptus* (perch) suggest an intermittent fluvial-lacustrine environment that collected vertebrate remains (Dundas et al., 1996).

Macrofossil evidence of Fairmead's floral community is limited, represented by a single mold of *Xanthium* (cocklebur). Preliminary pollen analysis reveals that grass and pine were the most common plants, although pine pollen transports great distances and may not have a local origin. Pollen of chenopods (chenopodiaceae and amaranthaceae), cattails (Typhaceae), sedges, willow, oak, spruce, juniper, and sagebrush were also recovered. This evidence suggests a lush prairie ecosystem with occasional oak and pine woodlands. The Fairmead Landfill faunal collection is dominated by grazing and mixed feeding herbivores (e.g., *Equus*, *Mammuthus columbi*, *Camelops* and *Paramylodon*) further supporting this interpretation.

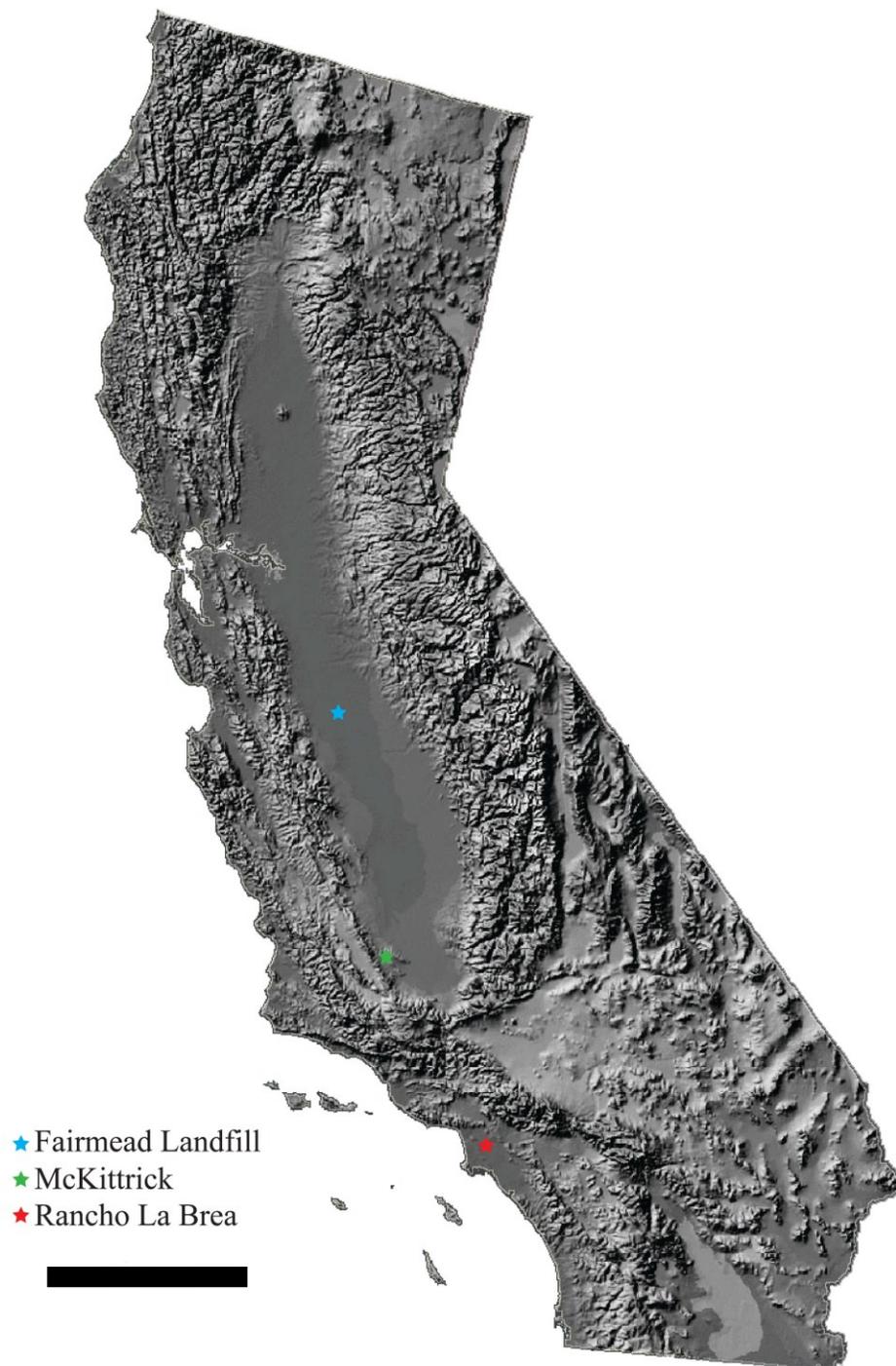


Figure 1. Map of localities. Scale bar is 100 miles.

METHODOLOGY

Stable Isotope Theory and Usage

All values are reported in the standard delta notation, where X is either ‰ or $\delta^{18}\text{O}$ and R is $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$. Stable carbon and oxygen are reported relative to the Vienna Pee Dee Belemnite (V-PDB) and Vienna Standard Mean Ocean Water (V-SMOW), respectively.

$$X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

The carbon isotopic ratio of mammalian enamel is controlled by diet, and in herbivores reflects the types of plants they eat (DeNiro and Epstein, 1978). Three photosynthetic pathways control the isotopic values of plants. The Calvin-Benson cycle (C_3) is used by most trees and shrubs, and some cool season grasses, producing average $\delta^{13}\text{C}$ values of -27.0‰ but ranging between -22‰ and -37‰ (Kohn, 2010). The range of $\delta^{13}\text{C}$ values exhibited by C_3 plants can be used to infer habitat structure with values decreasing with both increased canopy cover and water availability (Passey et al., 2002; MacFadden and Higgins, 2004). The Hatch-Slack cycle (C_4) is used by warm season grasses and a small number of dicots (e.g., *Atriplex* sp.). $\delta^{13}\text{C}$ values range from -11.4‰ to -12.7‰ and average -12.5‰ (Cerling et al., 1997). The third pathway, the Crassulacean Acid Metabolism (CAM), may produce $\delta^{13}\text{C}$ values similar to either C_3 or C_4 photosynthetic processes. However, considering floral data from both Fairmead Landfill and McKittrick, CAM plants, which are primarily succulents, likely did not contribute a significant portion of herbivore diet.

Fractionation of $\delta^{13}\text{C}$ from diet to enamel is controlled by digestive physiology and gut methane production with $\Delta^{13}\text{C}$ values of +14.6‰_{enamel-diet} and +13.3‰_{enamel-diet} for ruminant and nonruminant herbivores (Passey et al., 2005).

Carnivores reflect the $\delta^{13}\text{C}$ values of their prey with a $\Delta^{13}\text{C}$ value of -1.3‰ (Clementz et al., 2009). Materials from animals living before industrialization are expected to be $+1.5\text{‰}$ enriched versus modern analogs due to a shift in atmospheric $\delta^{13}\text{C}$ from the burning of fossil fuels (Tippie et al., 2010). Thus, a herbivore feeding entirely on C_3 plants would have an enamel $\delta^{13}\text{C}$ more negative than -8.0‰ while a C_4 feeder would show isotopic values more positive than 0.0‰ (Cerling et al., 1997). For herbivores with an intermediate value, a simple mixing equation can be used to calculate the percentage diet of both C_3 and C_4 plants. Therefore:

$$\delta^{13}\text{C} = f_1 \delta^{13}\text{C}_1 + f_2 \delta^{13}\text{C}_2$$

$$f_1 + f_2 = 1$$

Where f_1 and f_2 represent the percentage contribution from C_3 and C_4 plants and, $\delta^{13}\text{C}_1$ and $\delta^{13}\text{C}_2$ are the expected $\delta^{13}\text{C}$ values for these plants. $\delta^{13}\text{C}_{\text{enamel}}$ is the measured tooth value, corrected for fractionation to dietary values. While this equation provides an approximation of the input from each dietary source, both C_3 and C_4 plants produce a range of $\delta^{13}\text{C}$ values. By using -8.0‰ , an enamel value that corresponds to most positive C_3 plants consumption mixing calculations may underestimate the contribution C_4 biomass in the diet (Cerling et al., 1997; Phillips and Gregg, 2001; Phillips, 2012).

In large mammals, the oxygen isotopic composition of tooth enamel is primarily controlled by the composition of ingested water. In herbivores this water comes from two sources: drinking water and water contained within forage. The $\delta^{18}\text{O}$ value of meteoric waters is controlled largely by temperature (Dansgaard, 1964) and several studies have shown that the $\delta^{18}\text{O}$ of tooth enamel correlates well to mean meteoric water values (Kohn, 1996; Kohn and Cerling, 2002; Hoppe, 2006). Plant $\delta^{18}\text{O}$ values are generally enriched relative to meteoric water and are

also affected by relative humidity (Bryant and Froelich, 1995). Large herbivores are predicted to be more sensitive to changes in plant $\delta^{18}\text{O}$ since they derive more of their water from forage than carnivores. Carnivores $\delta^{18}\text{O}$ values are less affected by humidity are predicted to have similar $\delta^{18}\text{O}$ values to their prey (Kohn, 1996).

The range of $\delta^{18}\text{O}$ values in precipitation for the western United States is $\sim 10\text{‰}$ seasonally with summer $\delta^{18}\text{O}$ values being more positive and winter values being more negative (Henderson and Shuman, 2009). Since it forms in a two-part process (Passey and Cerling, 2002), enamel time average $\delta^{18}\text{O}$ values and does not reflect the total variation in meteoric waters. Despite this, the expected pattern if not the magnitude, of seasonal variation is preserved (Koch et al., 1989; 1995; Bryant et al., 1996; Feranec, 2004; Feranec et al., 2009). Seasonal variation in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values is investigated by collecting multiple samples in series along the growth axis of a tooth. Idealized $\delta^{18}\text{O}$ values should reflect the seasonal variation and produce a sinusoidal curve with $\delta^{18}\text{O}$ plotted against position on tooth, with peaks and valleys representing warm and cool seasons, respectively (Fig. 2). By comparing the apparent seasonality of $\delta^{18}\text{O}$ to dietary $\delta^{13}\text{C}$ values, this study investigates resource usage by taxa.

Materials and Methods

All teeth sampled are housed in either the Madera County Paleontology Collection (MCPC) or the University of California Museum of Paleontology (UCMP). When available, teeth of a taxon were chosen from the same position in all individuals selected (e.g., P2 for *Equus*). At Fairmead Landfill, where excavation is known, teeth were selected from different stratigraphic levels when duplicates at the same tooth position were not available. This was done to

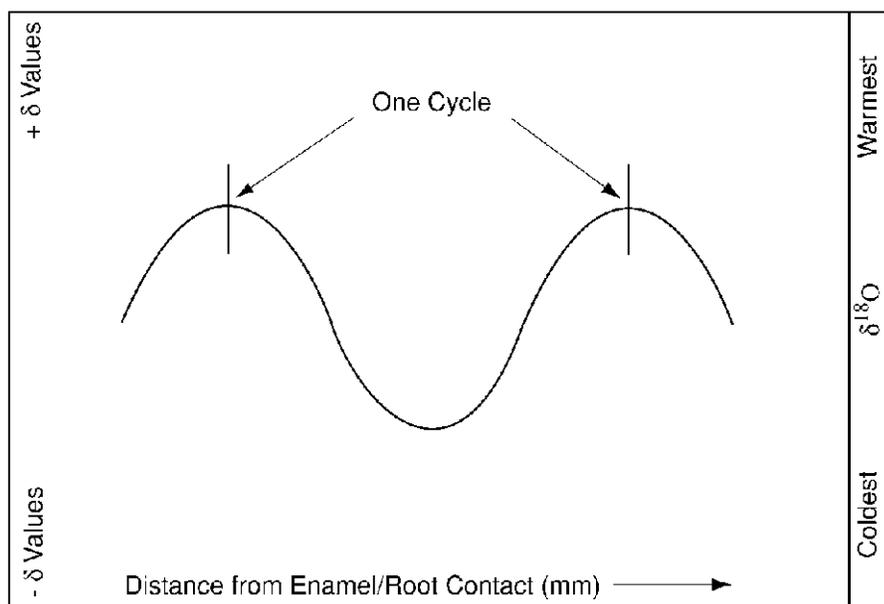


Figure 2. The expected pattern of seasonal variation in tooth enamel. One cycle should represent approximately one year. After Feranec and MacFadden (2000).

ensure that each bulk sample represented a discrete individual. In addition, it has been suggested that teeth formed during nursing may not accurately reflect environmental isotope values due to milk consumption. However, the exact magnitude of this effect is unclear (Boisserie et al., 2005). To minimize the possibility of a “nursing signal,” late erupting teeth, reflecting formation post weaning, were chosen.

Tooth enamel was sampled according to established protocols (Koch et al., 1997). All teeth were cleaned with a carbide burr and rinsed with ethanol to remove surficial material before sampling. Sampling involved drilling 10-20 mg of pristine enamel powder off of the tooth using a Dremel® rotary tool and either a 0.5 mm or 0.3 mm inverted cone carbide dental drill bit. For bulk samples, a single continuous groove was drilled perpendicular to the growth axis, the length of the available enamel. Serial samples were drilled parallel to the growth axis of the tooth for the length of the axis (Fig. 3).

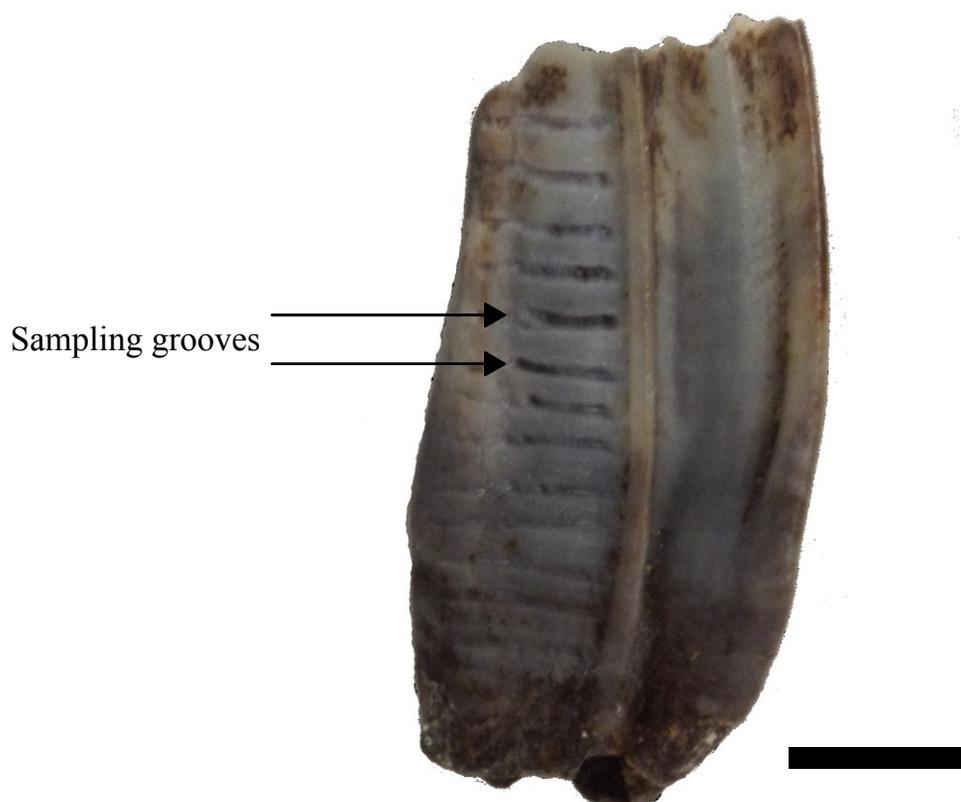


Figure 3. Serial sampled *Tetrameryx irvingtonensis* upper third molar. Note the parallel sampling grooves. Scale bar is 1 cm.

After drilling, enamel powder was collected and treated with 30% hydrogen peroxide (H_2O_2) overnight to remove residual mobile organics. The hydrogen peroxide was decanted, the powder was washed twice with distilled water and soaked with 0.1 N acetic acid (CH_3COOH) overnight to remove any adsorbed carbonate. The acetic acid was decanted, the powder rinsed twice with distilled water then dried in a vacuum oven at 40° for 48 hours.

After treatment, samples were analyzed using a ThermoScientific Kiel IV carbonate device coupled to a ThermoScientific MAT-253 isotope ratio mass

spectrometer (IRMS) at the University of California, Santa Cruz Stable Isotope Facility. Samples were reacted at 75° with phosphoric acid to generate CO₂ and H₂O. The water was removed and the remaining CO₂ measured by the IRMS. All values are reported in standard delta notation relative to the international PeeDee Belemnite (PDB) standard and VSMOW for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ respectively.

For taxa where $n > 1$, ANOVA tests were used to compare mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values both between taxa and between localities, and t-tests between individual taxa.

Carnivore $\delta^{13}\text{C}$ values were corrected using a $\Delta^{13}\text{C}$ of -1.3‰ to account for trophic level effects. Collagen data from Coltrain et al. (2004) were corrected to dietary values using a $\Delta^{13}\text{C}_{\text{collagen-diet}}$ of 5‰ (Koch, 1998) and then to enamel values, to allow direct comparison between bioapatite and collagen. Statistical analyses were performed using TC-Statistics for iPad and Numbers '09 with significance set at $p < 0.05$.

PALEOBIOLOGY OF SAMPLED TAXA

While some of the sampled taxa (Table 1) in this study are extant, the majority are extinct, and thus less is known about their paleoecology. Dietary information for extinct taxa comes from several sources; in herbivores, gut contents and coprolites provide direct evidence of diet, while mesowear, microwear, and hypsodonty show broader dietary preferences. For carnivores, morphologic adaptations may suggest different hunting strategies. By summarizing the paleobiology of the taxa included in this study, it is possible to make greater inferences about diet than $\delta^{13}\text{C}$ values alone allow.

Table 1. Sampled Taxa at Fairmead Landfill and McKittrick.

Fairmead Landfill	McKittrick
<i>Arctodus simus</i>	<i>Arctodus simus</i>
<i>Canis dirus</i>	<i>Canis dirus</i>
<i>Canis latrans</i>	<i>Canis latrans</i>
<i>Homotherium</i> sp.	<i>Panthera atrox</i>
<i>Smilodon</i> sp.	<i>Camelops hesternus</i>
<i>Miracinonyx inexpectatus</i>	<i>Hemiauchenia macrocephala</i>
<i>Camelops</i> sp.	<i>Bison</i> sp.
<i>Hemiauchenia</i> sp.	<i>Cervus elaphus</i>
<i>Platygonus vetus</i>	<i>Equus</i> sp.
<i>Capromeryx</i> sp.	<i>Mammut americanum</i>
<i>Tetrameryx irvingtonensis</i>	
<i>Equus</i> sp.	
<i>Mammuthus columbi</i>	

Arctodus simus (Giant Short Faced Bear)

Arctodus simus had an estimated mean body mass of 700-800 kg (Christiansen, 1999) making it the largest known bear species. Limb proportions of *Arctodus simus* are slightly elongate compared to extant ursids (Emslie and

Czaplewski, 1985) and the rostrum is broad, producing the illusion of a “short face.” While these characteristics have led to inferences that *Arctodus simus* was a cursorial predator, its diet has been widely debated.

Extant brown bears (*Ursus arctos*) are solitary omnivores. They consume a variety of plants including grasses, herbs, flowers, tubers, and berries. Insects, fungi, birds and small mammals also contribute to diet. Large ungulates are also commonly hunted or consumed as carrion (Pasitschniak-Arts, 1993).

Wear patterns of *Arctodus simus* carnassials and its great body size led Emslie and Czaplewski (1985) to conclude that *Arctodus simus* was primarily herbivorous. *Mammuthus* remains co-occurring with *Arctodus simus* show gnaw marks consistent with predation or scavenging, suggesting an omnivorous diet (Gillette and Madsen, 1992). Matheus (1995) Used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from bone collagen, to determine that Beringian *Arctodus simus* were primarily a scavenger which used its bulk to drive off other carnivores from kills. However, isotopic evidence alone cannot distinguish between predation and scavenging. A reevaluation of these data, coupled with new data for several potential herbivore prey, indicate that high latitude *Arctodus simus* had a highly specialized diet, focused on *Rangifer*. Additionally, *Arctodus simus* may have displaced other large carnivores from its range (Fox-Dobbs et al., 2008).

Recent morphologic analyses suggest that *Arctodus simus* specialized neither in scavenging or predation and was instead a versatile omnivore. The availability of carrion was likely higher during the Pleistocene due to the presence of *Homotherium* and *Smilodon*, who rarely fed close to the bone, leaving large amounts of flesh on their kills. Dietary components would have varied based on availability, not unlike extant brown bears (Figueirido et al., 2010).

Canis dirus (Dire Wolf)

Canis dirus were common throughout much of North America during the Pleistocene (Dundas, 1999). *Canis dirus* was 25% heavier than extant grey wolf (*Canis lupus*), with a mean body mass of 60 kg (Anyonge and Roman, 2006). Body proportions are similar to *Canis lupus* although with a larger head and more robust dentition (Dundas, 1994). *Canis dirus* exhibits a similar level of sexual dimorphism as *Canis lupus*. Coupled with the large number of individuals recovered from Rancho La Brea relative to prey species, it is likely that *Canis dirus* was a social canid similar to modern wolves (Stock and Harris, 1992).

The exact hunting and feeding method of *Canis dirus* is unclear. Tooth breakage frequencies in *Canis dirus* are consistent with bone crunching or gnawing (Van Valkenburgh and Hertel, 1993). Through comparisons to spotted hyena, Hill (1991) determined that *Canis dirus* lacked adaptations of a habitual bone crusher. Dundas (1994b) suggests that *Canis dirus* hunted similarly to modern wolves, but made greater use of its jaws to hold struggling prey resulting in higher stresses on its canines. This is supported by Anyonge and Baker (2006) who conclude that *Canis dirus* was only an occasional bone cracker and essentially functioned similarly to extant wolves.

Pack hunting canids commonly take prey much larger than themselves. Maximum prey size for *Canis dirus* was about 600 kg (Van Valkenburgh and Hertel, 1998), a weight only adult proboscideans, and some species of *Bison* and ground sloth exceed (Stuart, 1991). Mixing models using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from bone collagen from Rancho la Brea, *Canis dirus* shows that *Equus* was the most important contributor to diet, comprising 41-69% of wolf diet while *Paramylodon*, *Bison*, *Camelops* and *Mammut* made up the remaining portion. The contributions of *Paramylodon* and *Mammut* is likely evidence of either scavenging

or of preying on juvenile animals or weak/old individuals as healthy adults are larger than the predicted maximum weight of prey (Fox-Dobbs et al., 2007).

Canis latrans (Coyote)

The only extant carnivore in this study, *Canis latrans* is widespread throughout North America, occurring from northern Mexico, throughout the United States and Canada. Males are somewhat larger than females, ranging in weight from 10.6-15.8 kg and 8.0-14.2 kg, respectively (Bekoff, 1977; Bekoff and Gese, 2003). Pleistocene *Canis latrans* was larger than modern individuals with size decreasing during the late Pleistocene (Kurtén and Anderson, 1980). *Canis latrans* occur in a large number of habitats including grasslands, deserts, forests and mountains. A major limiting factor of *Canis latrans*' ability to colonize new habitats is the presence of other large carnivores. Both *Canis lupus* and *Puma concolor* have been documented to kill *Canis latrans* where their ranges overlap. *Canis latrans* are less social than wolves and are frequently solitary, but may form groups of up to 10 individuals if there is availability of large prey (Bekoff and Gese, 2003).

Canis latrans is a generalist feeder, with a highly variable diet based on food availability. Mammals comprise about 90% of overall diet in extant *Canis latrans*. Large ungulates, including deer, elk and sheep, are consumed as carrion, while small mammals, birds, reptiles, amphibians and insects are hunted. Fruits and other vegetable matter is also included in the diet (Bekoff, 1977; Bekoff and Gese, 2003). The frequency of canine breakage in Pleistocene *Canis latrans* is higher than in modern individuals. This suggests that the Pleistocene individuals may have hunted large prey with a higher frequency, perhaps facilitated by their increased body size (Van Valkenburgh and Hertel, 1993).

Isotopic reconstructions of *Canis latrans* diet are hindered by a lack of data for small mammals. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from bone collagen indicate they occupied the expected omnivore niche at Rancho La Brea, with variable $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ intermediate between herbivores and large carnivores (Coltrain et al., 2004).

Homotherium (Scimitar Cat)

A machirodont felid, *Homotherium* was similar in size to modern lions, weighing 146-231 kg (Anyonge, 1993). The forelimb proportions are similar to those of extant cheetahs, while the hind limbs are shorter and the back sloped to the hindquarters, giving *Homotherium* a hyena-like appearance. An enlarged nasal opening is also present, a feature that increases oxygen intake during running. This combination of features suggests that *Homotherium* was moderately cursorial (Rawn-Schatzinger, 1992). *Homotherium* canines are smaller and more heavily serrated than those of *Smilodon*, and may have been more effective at slashing or ripping flesh (Anyonge, 1996). The front incisors often show heavy wear suggesting they were used to carry heavy prey (Rawn-Schatzinger, 1992).

Friesenhahn Cave, Texas, has produced a minimum of 20 adult and 13 juvenile *Homotherium*. Other large carnivores are rare by comparison, and so the cave is inferred to have been a *Homotherium* den. Modern felids that occupy dens are usually solitary, implying that *Homotherium* was a solitary hunter (Rawn-Schatzinger, 1992).

Along with numerous *Homotherium*, the Friesenhahn Cave assemblage contains remains of *Platygonus*, *Mylohyus*, *Odocoileus*, *Camelops*, *Bison*, *Tapirus*, *Equus*, *Mammuthus* and *Mammuthus*. Juvenile *Mammuthus* are the most common, with a minimum of 300 individuals, outnumbering all other taxa combined.

Because the herbivore assemblage in the cave is presumed to represent carnivore transport and not natural accumulation, *Mammuthus* calves appear to have been a favorite prey (Rawn-Schatzinger, 1992). Extant lions occasionally hunt juvenile elephants, although the kills can take over an hour and require multiple lions. This is seemingly at odds with the inferred solitary nature of *Homotherium*. However, in contrast with modern lions, the enlarged canines of *Homotherium* would allow a single individual to deliver a killing bite (Turner and Antón, 1997). *Homotherium* is commonly found in association with juvenile proboscideans or *Rhinoceros* across its range implying that this was not a localized dietary choice (Rawn-Schatzinger, 1992).

Fox-Dobbs et al. (2008) reconstructed Beringian *Homotherium* diet using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from bone collagen. The authors used data from several prey species; *Rangifer*, *Ovibos*, *Bos*, *Mammuthus*, *Equus* and *Bison* to determine the contribution of each potential prey species to *Homotherium* diet. *Equus* and *Bison* isotope values were indistinguishable from the expected generalist dietary values and were combined into one category. Eight of 11 sampled *Homotherium* were either *Equus/Bison* specialists or generalists, while the remaining three were either *Ovibos* or *Bos* specialists. Curiously, *Mammuthus* did not contribute to Beringian *Homotherium* diet.

Smilodon (Saber-Toothed Cat)

Two species of *Smilodon* occur in Pleistocene North America. The Plio-Pleistocene *Smilodon gracilis* was similar in size to modern jaguars, with a body mass of 55-100 kg. The late Pleistocene *Smilodon fatalis* was comparable to the largest extant felid, the Siberian tiger (*Panthera tigris*), with mass estimates of 160-280 kg (Christiansen and Harris, 2005). Body proportions of *Smilodon* are

similar to modern forest dwelling felids, with short powerful limbs, and may represent an affinity for similar habitats (Gonyea, 1976), although *Smilodon* occurs more frequently at localities interpreted as grassland or woodland margin habitats. The large number of individuals recovered from Rancho La Brea has made *Smilodon* one of the best known Pleistocene carnivores (Turner and Antón, 1997).

The most recognizable feature of *Smilodon*, its elongate “saber” canines, would have made it a formidable predator. The large number of individuals recovered from Rancho La Brea, relative to prey species, provides evidence that *Smilodon* may been a social hunter (Stock and Harris, 1992). *Smilodon* had an overall stocky build, with short powerful limbs, more suited to ambush than rapid pursuits. The muscular forelimbs were used to immobilize prey, while the sabers were used to stab or sheer at either the neck or soft underbelly (Gonyea, 1976; Van Valkenburgh et al., 1990b). The canines show low amounts of wear, suggesting they were used only during hunting and not for feeding. Canine breakage frequencies and a low amount of pits and scratches are consistent with little bone cracking or consumption (Van Valkenburgh and Hertel, 1993; Anyonge, 1996). If *Smilodon* avoided contact between its canines and bone, this would limit its ability to completely consume a kill, leaving carcasses for scavengers. Van Valkenburgh et al. (1990b) noted that this may have led to a coevolutionary relationship between *Smilodon* and hyena, and after the extinction of hyena in North America, *Canis dirus*.

Carbon isotope reconstructions of diet have proposed several prey/habitat choices for *Smilodon*. Kohn et al. (2005) proposed a woodland margin occupancy consuming both woodland and grassland prey. Florida *Smilodon gracilis* show $\delta^{13}\text{C}$ values overlap with *Hemiauchenia* and *Platygonus*, making them likely prey

(Feranec, 2005). *Smilodon fatalis* from Rancho La Brea competed directly with both *Panthera atrox* and *Canis dirus*, with all three preferring C₃ feeding ruminant prey (Coltrain et al., 2004). Similarly, Feranec (2004) showed no evidence of consumption of C₄ feeding prey in Rancho La Brea *Smilodon*.

Miracinonyx inexpectatus (Cheetah Like Cat)

While morphologically similar to true cheetahs (*Acinonyx*), *Miracinonyx* was more closely related to extant *Puma concolor* (cougar) (Van Valkenburgh et al., 1990a; Barnett et al., 2005). *Miracinonyx* was lightly built and estimated to weigh 70 kg (Van Valkenburgh et al., 1990a). The nasal cavity is enlarged and the limbs are elongated, both cursorial adaptations (Adams, 1979). *Miracinonyx* is rare in the fossil record (Dundas, 1994); however, co-occurrences with both *Smilodon* and *Panthera onca* are common, suggesting that resources were partitioned among the three felids similar to the modern cheetah, lion and leopard relationship in Africa (Van Valkenburgh et al., 1990).

Little direct dietary evidence exists for *Miracinonyx* (Adams, 1979). Chorn et al. (1988) suggested *Antilocapra americana* as a preferred prey. In the late Pleistocene *Miracinonyx trumani* was highly cursorial, an adaptation that may have co-evolved along with the running speed of Antilocapridae. $\delta^{13}\text{C}$ values from Wyoming *Miracinonyx trumani* are consistent with this interpretation suggesting both *Antilocapra americana* and undifferentiated cervids as potential prey (Kohn and McKay, 2012).

Panthera atrox (American Lion)

Once considered a subspecies of extant lions (*Panthera leo*), recent morphologic and genetic analyses has shown *Panthera atrox* to be a distinct species (Barnett et al., 2009; Christiansen and Harris, 2009). *Panthera atrox* was

the largest North American felid, estimated to weigh 344-543 kg (Anyonge, 1993). Extant lion are gregarious and live and hunt in prides. *Panthera atrox* shows a high degree of cephalization, a feature usually associated with social carnivores. However, the relatively low number of individuals relative to other carnivores recovered from Rancho La Brea, coupled with higher proportion of males, suggest that *Panthera atrox* was solitary (Stock and Harris, 1992).

The massive build of *Panthera atrox* suggests that it was able to hunt the largest herbivores in North America, possibly including sub-adult proboscideans (Anyonge, 1993). Using a dietary mixing model with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from bone collagen from both *Panthera atrox* and multiple possible prey species, Fox-Dobbs et al. (2008) showed that Beringian *Panthera atrox* consumed *Equus*, *Bison* and *Rangifer*, as well as exhibiting a generalist diet in some cases. At Rancho La Brea, *Panthera atrox*, *Smilodon fatalis* and *Canis dirus* competed for prey (Coltrain et al., 2004), leading to a higher frequency of tooth breakage as a result of tooth-bone contact (Van Valkenburgh and Hertel, 1993).

Camelops (Camel)

Estimated to weigh 580 kg (Stuart, 1991), *Camelops* superficially resembled extant dromedary camels (*Camelus dromedarius*), although the limbs were 20% longer (Webb, 1965). Modern camels travel in small herds of up to 20 individuals (Köhler-Rollefson, 1991), are well adapted to arid habitats with diets dominated by 70 to 90% browse (Newman, 1984), and have large ranges to avoid over-browsing. Camels have relatively low daily food requirements (Gauthier-Pilters, 1984). Camels require 45-60 g of dietary salt a day, leading to high consumption of halophyte plants, which can make up to one-third of their diet (Köhler-Rollefson, 1991).

Hypsodont cheek teeth led Webb (1965) to conclude that *Camelops* was primarily a grazer, though he speculated that its long neck and limbs would facilitate occasional browsing. Premaxillary shape index (PSI) measurements correlate with diet in ungulate herbivores. A PSI of 67.5% in late Pleistocene *Camelops hesternus* suggest that it was a mixed feeder (Dompierre and Churcher, 1996). Considering tooth wear patterns and hypsodonty index measurements, Semprebon and Rivals (2010) concluded that *Camelops* was primarily a browser. This is supported by dental boluses extracted from Rancho La Brea *Camelops hesternus*, which indicate that diet consisted of 90% non-monocots (Akersten et al., 1988). Coltrain et al. (2004) likewise concluded that Rancho La Brea *Camelops hesternus* did not consume C₄ vegetation. C₄ grasses were rare in late Pleistocene Nevada leading Vetter et al. (2007) to interpret high $\delta^{13}\text{C}$ values in Nevada *Camelops* as evidence of halophyte consumption.

Hemiauchenia (Llama)

Hemiauchenia resembled modern llamas, although they were larger, had longer limbs, an elongate cranium (Webb, 1965) and an estimated mean mass of 100 kg (Stuart, 1991). Extant *Lama* are opportunistic feeders and vary their diet based on forage availability (Puig et al., 1997). Grasses are the preferred food but browse is also commonly eaten (Fraser, 1998, 1999). Premaxillary shape index (PSI) values from modern *Lama* are correspondingly high (72.5%), consistent with an intermediate feeder with a preference for grazing. The measured PSI of *Hemiauchenia* (46%), lower than extant *Lama*, is closer to the expected value for a pure browser (Dompierre and Churcher, 1996). Microwear analysis of *Hemiauchenia* teeth also suggest it was either a mixed feeder or leaf browser,

although a single Miocene individual was classified as a grazer (Semprebon and Rivals, 2010).

Hemiauchenia is commonly included in stable isotope studies of diet. Irvingtonian *Hemiauchenia* from Florida have $\delta^{13}\text{C}$ values consistent with a mixed C_3 - C_4 feeding strategy. Feranec and MacFadden (2000) included Irvingtonian and Rancholabrean *Hemiauchenia* in a larger study of the expansion of grazers in Florida. Irvingtonian and early Rancholabrean *Hemiauchenia* have $\delta^{13}\text{C}$ values consistent with mixed feeding, however a single late Rancholabrean individual appears to have been a C_4 grazer. A shift from browsing to mixed feeding is also seen in *Hemiauchenia* from Pliocene and Pleistocene Florida, respectively (DeSantis et al., 2009). South Carolina *Hemiauchenia* also exhibit $\delta^{13}\text{C}$ values expected of opportunistic woodland browsers (Kohn et al., 2005). Feranec (2003) reports both hypsodonty index and $\delta^{13}\text{C}$ values for Florida *Hemiauchenia*, concluding that it was an intermediate feeder that preferred to browse.

Bison (Bison)

Multiple species of *Bison* were present in Pleistocene North America. Body mass estimates of 630-900 kg show that *Bison* were the largest artiodactyl herbivores present, with only the proboscideans and some ground sloths exceeding them in size (Stuart, 1991). Extant *Bison bison* form mixed sex migratory herds. Grasslands are the most common habitat but *Bison bison* also occasionally inhabit boreal forests and montane habitats. Migration distance changes with habitat, varying between 14-240 km from closed and open habitats, respectively (Meagher, 1986). Grasses are the most common food in modern *Bison bison* diet, contributing 56-89% year round. Sedges are more important in winter and spring making up 17-44%, however they become less common in winter and fall and

contribute only 11-16% of total forage. Forbs are the least important food and never comprise more than 2% of total diet (Coppedge et al., 1998). *Bison bison* in Yellowstone National Park, a C₃ dominated environment, have collagen, scat, and enamel $\delta^{13}\text{C}$ values consistent with open environment C₃ grazing (Feranec, 2007).

Bison latifrons was less common than *Bison antiquus* in Pleistocene California. *Bison latifrons* was the largest known bison, with an impressive horn span of up to 6.5 feet (Stock and Harris, 1992). A woodland and forest clearing habitat is suggested for *Bison latifrons*, similar to the largest extant cervid, *Alces alces* (moose). Forest habitats reduce the practicality of large herds, suggesting that unlike other bison, *Bison latifrons* was relatively solitary. Likewise, closed habitats necessitate a mixed feeding strategy, incorporating more browse into the diet (McDonald, 1981).

Bison antiquus was more common in California and resembled extant *Bison bison*, though it was larger (Stock and Harris, 1992). McDonald (1981) suggested a savanna or wooded steppe habitat, forming herds similar to modern bison. Social animals are more commonly recovered from Rancho La Brea and *Bison antiquus* is represented there by at least 300 individuals, while *Bison latifrons* is rare (Stock and Harris, 1992). Discontinuous age groupings indicate that Rancho La Brea *Bison antiquus* were migratory, changing habitats seasonally (Jefferson and Goldin, 1989).

Dental boluses extracted from Rancho La Brea *Bison antiquus* show they relied on grasses much less than modern bison. Of 18 individuals sampled, boluses averaged only 13% monocots, showing a higher percentage of browse and C₃ grasses (Akersten et al., 1988). Carbon isotope values from Rancho La Brea are consistent with these dietary preferences, in most cases showing less than 25% C₄

plant consumption (Coltrain et al., 2004; Feranec et al., 2009). $\delta^{18}\text{O}$ values agree with the inferred migratory behavior of *Bison antiquus* (Feranec et al., 2009).

Platygonus vetus (Liedy's Peccary)

Larger than extant peccaries, and with longer limbs, *Platygonus* had a mean weight of 110 kg (Stuart, 1991). *Platygonus* was wide ranging and tolerated widely varying environments (Stock and Harris, 1992), but was likely best adapted to semiarid habitats. Modern peccaries range from the southwestern deserts of the United States to closed canopy rain forests of South America. They live in small herds of up to 10 with an average herd size of 4 (Mayer and Brandt, 1982).

Platygonus had low crowned cheek teeth (Stock and Harris, 1992) and is assumed to have a diet similar to extant peccaries. Modern peccaries are omnivores, consuming flowers, fruits, tubers, insects, carrion and most significantly, cacti. Modern *Tayassu tajacu* (collared peccary) vary the amount of cacti in their diets by season, with *Opuntia* (prickly pear) making up between 25-40% of total diet. Forbs are also commonly eaten and can make up 55% of diet in winter months. Carrion is eaten less regularly, suggesting that it is an opportunistic food (Corn and Warren, 1985). South American *Catagonus wagneri* (Chacoan peccary) exhibit similar dietary choices, consuming large amounts of cacti, fruits and insects. Paedophagy is also common in winter months (Mayer and Wetzel, 1987).

Isotopic interpretations of *Platygonus* diet are complicated due to the possibility of cacti consumption. Cacti are CAM plants which produce $\delta^{13}\text{C}$ values intermediate to, and spanning the range of, C_3 and C_4 plants. *Platygonus* from Pliocene and Pleistocene Florida have $\delta^{13}\text{C}$ values that indicate either a C_3/C_4

mixed feeder or CAM browser, consistent with modern peccary diet (MacFadden and Cerling, 1996).

Capromeryx (Dwarf Pronghorn) and *Tetrameryx*
irvintonensis (Irvington Pronghorn)

Capromeryx stood 60 cm at the shoulder and weighed about 10 kg (Stuart, 1991). Its diminutive size would have made it appealing prey for large carnivores. Stock and Harris (1992) suggested multiple strategies for carnivore avoidance. *Capromeryx* may have preferred a semi-open habitat, sheltering in shrubs or they may have grouped together in large herds similar to extant African antelope. White and Morgan (2011) compared *Capromeryx* to habitat and feeding categories for African antelope (Jarman, 1974), concluding that *Capromeryx* relied on hiding as its primary strategy for carnivore avoidance. Hiding is the predominant strategy in extant *Antilocapra americana* fawns, which approximate *Capromeryx* in size (Byers, 1997).

Little is known of the habits of *Tetrameryx*, though it is assumed to be similar to those of *Antilocapra americana*, which it resembles in size and form. Modern pronghorn have a mean mass of 47 kg (Stuart, 1991) and travel in herds of about 25 individuals. Adult pronghorn have been observed to run at speeds up to 86.5 kmh for short bursts and are capable of sustaining speeds of 72 kmh for several minutes (Byers, 1997). *Antilocapra americana* is hypothesized to have been common prey for *Miracinonyx* (Chorn, et al., 1988), a role *Tetrameryx* likely filled as well.

Both *Capromeryx* and *Tetrameryx* have high-crowned teeth similar to those of *Antilocapra americana* and have been assumed to have similar foraging preferences. Although they have high crowned teeth, observations of wild pronghorn show that they feed primarily of forbs and shrubs, with grasses

comprising less than 15% of total diet (McInnis and Vavra, 1987; Krueger, 1991). Pronghorns are selective feeders, often specializing on specific parts of a plant, moving from plant to plant rapidly (Byers, 1997). Carbon isotope data collected from Wyoming *Antilocapra americana* scat and bone collagen are consistent with a scrubland browser. DeSantis et al. (2009) reported enamel $\delta^{13}\text{C}$ values for two Florida *Capromeryx*, concluding they were C_3 browsers. Connin et al. (1998) reported enamel $\delta^{13}\text{C}$ values for two Nevada *Tetrameryx*, also consistent with a diet of C_3 browse.

Cervus elaphus (Elk)

Cervus elaphus have a mean mass of 390 kg making them the second largest cervid in North America (Stuart, 1991). Elk travel in herds with as many as 400 individuals.

Cervus elaphus are mixed feeders, consuming forbs, grasses, sedges and leaves extensively (Cook, 2002). Modern *Cervus elaphus* from California consume between 56-76% grasses and sedges. Browse and forbs comprise 23-42% of total diet seasonally (Harper et al., 1967). Nevada *Cervus elaphus* also vary their diet seasonally, with forbs making up 59-78% of summer forage, while spring diet contains 18-60% grasses, 10-35% woody browse, and 30-55% forbs (Beck and Peek, 2005). *Cervus elaphus* also occur in Europe, locally known as Red Deer. The diet of European *Cervus elaphus* differs from North American populations, with grasses and sedges making up one-third of diet, and woody browse becoming more prominent (Gebert and Verheyden-Tixier, 2001).

Being rare in the fossil record (O'Gara and Dundas, 2002), *Cervus elaphus* are rarely included in stable isotope studies of diet. Feranec (2007) investigated niche partitioning among modern ungulates in Yellowstone National Park,

Wyoming. Yellowstone National Park is a C₃ dominated ecosystem, leading habitat choice to play an important role in $\delta^{13}\text{C}$ values. Tooth enamel, bone collagen and scat were analyzed for $\delta^{13}\text{C}$. Of taxa sampled, *Cervus elaphus* had the widest range of resource use.

Equus (Horse)

Equus is one of the most common taxa found in Pleistocene North America. Several species existed, however most are similar in form and are assumed to have behaved similarly. Mean mass estimates for multiple species of Pleistocene *Equus* average 300 kg (Stuart, 1991), similar in size to extant domestic horse and zebra. Extant equids occupy a variety of habitats including deserts, grasslands, tundra, scrubland and forests. They travel in herds, usually consisting of an adult stallion, about five mares, and several foals (Grubb, 1981; Penzhorn, 1988; Bennett and Hoffmann, 1999). Equids have hypsodont teeth and are generally considered grazers. Feral *Equus* in North America consume up to 90% grass, although they will preferentially choose browse when availability is high (Hoppe et al., 2004a).

Equids are one of the most commonly used taxa for stable isotope studies. Detailed understanding of tooth mineralization (Hoppe et al., 2004b) makes them ideal to test a wide range of topics including the expansion of C₄ grasses (MacFadden et al., 1999), estimating rain shadow effects (Crowley et al., 2008) and multiple paleodietary studies (Passey et al., 2002; Wang et al., 2008). Rancho La Brea *Equus occidentalis* consumed low amounts of C₄ grasses. Extracted dental boluses show that 56% of diet came from nonmonocotyledons, suggesting a mixed graze-browse diet (Akersten et al., 1988). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of bone collagen and $\delta^{13}\text{C}$

from tooth enamel confirm this result and show less than 15% C₄ consumption (Coltrain et al., 2004; Feranec et al., 2009).

Mammut americanum (American Mastodon)

Smaller than *Mammuthus columbi*, *Mammut americanum* weighed 4000 kg (Stuart, 1991) and stood about 2 m at the shoulder. *Mammut* had a more stocky build than *Mammuthus* but it retained the basic proboscidean characteristics. *Mammut* were browsers that preferred open woodlands and forests (Lepper et al., 1991; Stock and Harris, 1992). Pollen associated with Arizona *Mammut* indicate a pine forest environment (Minckley et al., 1997).

Mammut have distinctive molars made up of pairs of conical cusps. The alternating peaks and valleys of the upper and lower molars interlock, ideal for sheering and crushing vegetation (Saunders, 1977; Stock and Harris, 1992). Preserved gut contents from an Ohio *Mammut americanum* consisting of twigs, leaves, marsh plants and moss indicating a browsing diet. Pollen recovered from the molars of the associated skeleton was primarily from sedges, grasses and aquatic plants (Lepper et al., 1991). Stomach contents recovered from several eastern North America localities show that *Mammut* commonly consumed hemlock, cedar, pine and other conifers (Dreimanis, 1968).

Microwear analysis of *Mammut americanum* molars is consistent with a browsing diet. Microwear features associated with grass consumption were low while features associated with bark consumption were high. Fruit was also consumed occasionally (Green et al., 2005).

Mammut americanum stable isotopic data also support a browsing diet. Florida *Mammut americanum* consumed less than 20% C₄ plants (Koch et al., 1998). In addition, diet appears to remain stable between glacial and interglacial

periods (DeSantis et al., 2009). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from bone collagen from Rancho La Brea *Mammuthus* show a diet unlike other larger herbivores from the locality. Low $\delta^{15}\text{N}$ suggest a reliance on nitrogen fixing plants, while low $\delta^{13}\text{C}$ values indicate browsing. Similarly to Florida, Rancho La Brea *Mammuthus* show little change in diet over time (Coltrain et al., 2004).

Mammuthus columbi (Columbian Mammoth)

The largest herbivore in Pleistocene North America, *Mammuthus columbi* is estimated to weigh 8000 kg (Stuart, 1991), about 25% larger than an African elephant bull. Extant elephants, the closest relatives of *Mammuthus*, are extremely adaptable, commonly found in deserts, grasslands and forest. Elephants are social animals forming herds of up to 70 individuals (Laursen and Bekoff, 1978).

Mammuthus is thought to have grazed more heavily than modern elephants. The molars consist of several tightly packed enamel plates, ideal for grinding tough grasses (Stock and Harris, 1992). Modern elephants graze heavily, however, they also browse, consuming tree bark, leaves, and whole branches (Laursen and Bekoff, 1978). Recovered dung from Utah *Mammuthus columbi* show that grasses and sedges were the major constituents of diet, making up about 90%. Twigs and needles of fir trees, pollen from multiple broadleaf trees, and *Atriplex* were also recovered, showing that *Mammuthus* occasionally included halophytes and browse in its diet (Gillette and Madsen, 1993).

Mammuthus was widespread in Pleistocene North America, and are commonly included in stable isotopic studies. Hoppe et al. (1999) used $^{87}\text{Sr}/^{86}\text{Sr}$ ratios to track migration patterns of Florida *Mammuthus*, concluding they had a range of 120-300 km. Using $\delta^{13}\text{C}$ values from tooth enamel, Koch et al. (1998) investigated the diet of *Mammuthus* from several localities in Pleistocene Florida.

C₄ consumption was high, ranging from 49-90% of total diet. Since *Mammuthus* grazed heavily, they can be used as a proxy for the amount of C₄ biomass in an environment. *Mammuthus* tooth enamel $\delta^{13}\text{C}$ values from the Great Basin and southwestern United States localities vary from pure C₃ to pure C₄ values, suggesting that *Mammuthus* had very adaptable diets (Connin et al., 1998).

RESULTS

The Appendix contains a full specimen list, including data for bulk (Table A1) and serial sampling (Table A2). Mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for serial sampled teeth were included in statistical analyses of bulk data. Taxa with single specimens ($n = 1$) were excluded from statistical analyses and instead compared to the mean ($\pm 1\text{S.D.}$) of other taxa. Trophic level corrections were not included in figures unless otherwise stated.

Fairmead Landfill $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ Values

The mean, range and standard deviations of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for Fairmead Landfill bulk isotope sampling of the 59 individuals sampled are reported in Table 2. Stable carbon values range from -13.5‰ to -8.1‰, with a mean of -10.9‰ (Fig. 4). Pooled mean values of the carnivores and herbivores are -12.2‰ and -10.3‰, respectively.

Fairmead herbivore $\delta^{13}\text{C}$ values show statistically significant differences between taxa (ANOVA, $p < 0.01$). Pairwise comparisons (Table 3) reveal that *Camelops* differs significantly from all other herbivores, while excluding *Camelops* reveals no significant differences among the remaining herbivore taxa (ANOVA, $p = 0.90$). Similarly, no significant differences were detected among carnivores (ANOVA, $p = 0.95$). Adjusting for trophic level differences, pairwise comparisons of $\delta^{13}\text{C}$ values between taxa reveal that all carnivore and herbivore taxa are statistically indistinguishable, except for *Camelops*, which differs significantly from all other taxa.

Five taxa are represented by single individuals and were not included in the statistical analyses. *Capromeryx*' $\delta^{13}\text{C}$ value is within one standard deviation of the means for *Tetrameryx irvingtonensis*, *Mammuthus columbi*, *Equus*, *Smilodon*,

Table 2. Descriptive Statistics for Fairmead Landfill Taxa.

Taxa	<i>n</i>	Min $\delta^{13}\text{C}$ (‰)	Max $\delta^{13}\text{C}$ (‰)	Mean $\delta^{13}\text{C}$ (‰)	S.D. $\delta^{13}\text{C}$ (‰)	Min $\delta^{18}\text{O}$ (‰)	Max $\delta^{18}\text{O}$ (‰)	Mean $\delta^{18}\text{O}$ (‰)	S.D. $\delta^{18}\text{O}$ (‰)
<i>Arctodus simus</i>	1	-11.9	-11.9	-11.9	-	25.0	25.0	25.0	-
<i>Canis dirus</i>	8	-13.1	-10.8	-12.1	0.9	26.8	34.4	29.3	2.6
<i>Canis latrans</i>	5	-13.1	-10.7	-12.3	0.9	24.9	31.6	28.3	3.0
<i>Homotherium</i> sp.	1	-13.5	-13.5	-13.5	-	26.8	26.8	26.8	-
<i>Smilodon</i> sp.	3	-13.4	-11.2	-12.2	1.1	24.3	27.9	25.9	1.8
<i>Miracinonyx inexpectatus</i>	1	-11.6	-11.6	-11.6	-	23.8	23.8	23.8	-
<i>Camelops</i> sp.	16	-11.7	-8.1	-9.4	1.0	24.8	30.6	27.4	1.5
<i>Equus</i> sp.	7	-12.8	-8.5	-11.0	1.7	24.4	28.2	26.7	1.3
<i>Hemiauchenia</i> sp.	3	-13.3	-9.3	-11.4	2.0	27.8	34.4	31.2	3.3
<i>Mammuthus columbi</i>	7	-12.2	-9.3	-10.7	1.0	22.4	28.1	24.8	2.1
<i>Platygonus vetus</i>	1	-13.5	-13.5	-13.5	-	29.1	29.1	29.1	-
<i>Tetrameryx irvingtonensis</i>	4	-11.5	-10.5	-11.0	0.4	28.6	33.3	30.3	2.1
<i>Capromeryx</i> sp.	1	-11.1	-11.1	-11.1	-	26.6	26.6	26.6	-

Note: Bold *p*-values indicate significant differences. Carnivore values were adjusted by 1.3‰ to correct for trophic level fractionation (Clementz et al., 2009).

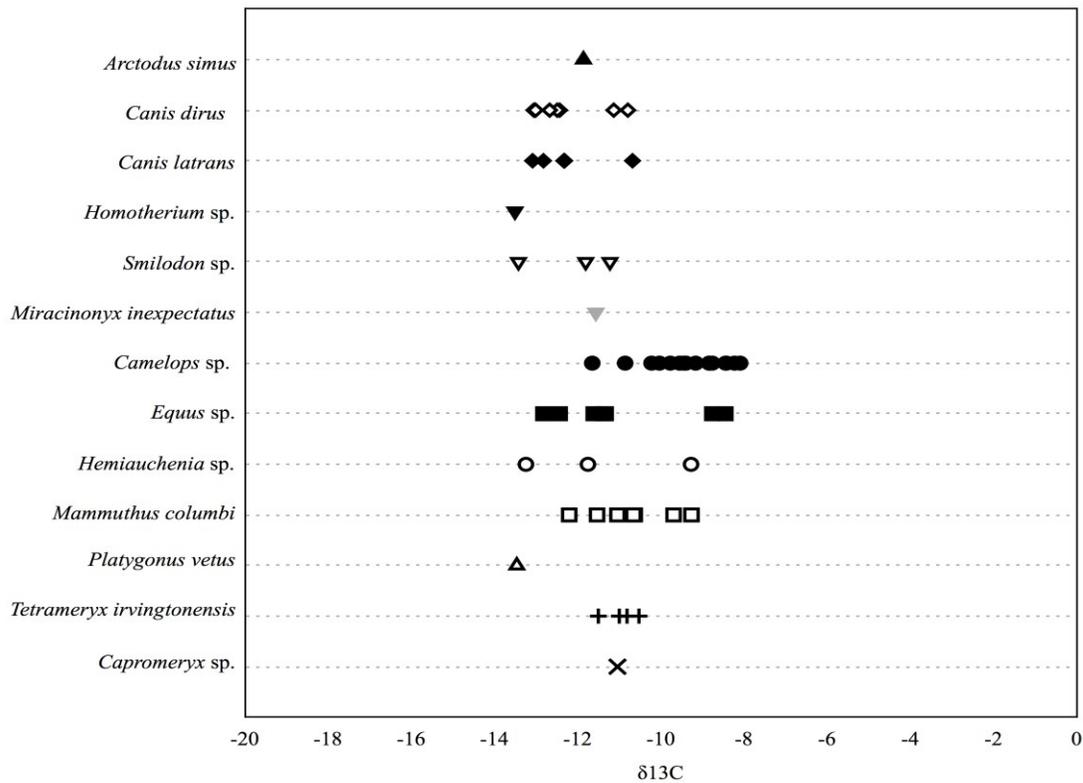


Figure 4. Stable carbon isotope values for Fairmead Landfill taxa.

and both canids. *Platygonus vetus* is the most negative herbivore, and does not overlap with the means \pm 1 S.D. of any other taxa. *Miracinonyx inexpectatus* $\delta^{13}\text{C}$ is within one standard deviation of the means for *Hemiauchenia*, *Equus*, *Smilodon*, *Camelops*, and both canids are within the range of *Tetrameryx irvingtonensis*. The $\delta^{13}\text{C}$ of *Homotherium* is within one standard deviation of both the *Equus* and *Hemiauchenia* means and overlaps with both *Smilodon* and *Mammuthus columbi*. *Arctodus simus* $\delta^{13}\text{C}$ falls within one standard deviation of all other taxa ($n > 1$) except *Tetrameryx irvingtonensis* and is negligibly different from *Miracinonyx inexpectatus*.

Fairmead $\delta^{18}\text{O}$ values for the 59 bulk samples ranged from 22.4‰ to 34.4‰ and have a mean of 27.5‰. Pooled carnivore and herbivores means are

Table 3. Significant Differences in Stable Carbon Between Taxa from Fairmead Landfill.

	<i>Canis dirus</i>	<i>Canis latrans</i>	<i>Smilodon</i> sp.	<i>Camelops</i> sp.	<i>Equus</i> sp.	<i>Hemiauchenia</i> sp.	<i>M. columbi</i>	<i>T. irvingtonensis</i>
<i>Canis dirus</i>		0.77	0.07	0.01	0.80	0.47	0.89	0.73
<i>Canis latrans</i>			0.90	0.01	0.98	0.65	0.70	0.98
<i>Smilodon</i> sp.				0.03	0.92	0.69	0.86	0.86
<i>Camelops</i> sp.					0.01	0.01	0.01	0.01
<i>Equus</i> sp.						0.72	0.74	0.99
<i>Hemiauchenia</i> sp.							0.46	0.66
<i>Mammuthus columbi</i>								0.66

Note: Bold *p*-values indicate significant differences. Carnivore values were adjusted by 1.3‰ to correct for trophic level fractionation (Clementz et al., 2009).

Table 4. Significant Differences in Stable Oxygen Between Taxa from Fairmead Landfill.

	<i>Canis dirus</i>	<i>Canis latrans</i>	<i>Smilodon</i> sp.	<i>Camelops</i> sp.	<i>Equus</i> sp.	<i>Hemiauchenia</i> sp.	<i>M. columbi</i>	<i>T. irvingtonensis</i>
<i>Canis dirus</i>		0.52	0.07	0.03	0.03	0.33	< 0.01	0.52
<i>Canis latrans</i>			0.27	0.37	0.25	0.24	0.04	0.30
<i>Smilodon</i> sp.				0.15	0.43	0.07	0.46	0.03
<i>Camelops</i> sp.					0.34	< 0.01	< 0.01	< 0.01
<i>Equus</i> sp.						0.01	0.06	0.01
<i>Hemiauchenia</i> sp.							0.01	0.67
<i>Mammuthus columbi</i>								< 0.01

Note: Bold *p*-values indicate significant differences.

similar at 27.3‰ and 27.8‰, respectively. Pairwise comparisons between taxa do not reveal a significant correlation between significance in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (Table 4).

Three herbivore taxa were selected for serial sampling. Ninety samples total were collected serially from the teeth of three *Equus* (MCPC A1355a, A579, A1902a (Figs. 5, 6, 7), one *Camelops* (MCPC A282) (Fig. 8) and one *Tetrameryx irvingtonensis* (UCMP 197567) (Fig. 9) tooth. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for these teeth are reported in (Table A2). Pooled serial sampling $\delta^{13}\text{C}$ values demonstrate significant differences among taxa (ANOVA, $p = 0.02$). Pairwise comparisons between taxa again reveal that *Camelops* differs significantly from both *Equus* (ANOVA, $p = 0.024$) and *Tetrameryx irvingtonensis* (ANOVA, $p \ll 0.001$) while *Equus* and *Tetrameryx irvingtonensis* are indistinguishable (ANOVA, $p = 0.41$). Pooled $\delta^{13}\text{C}$ values for three *Equus* teeth range from -8.0‰ to -14.0‰, although individuals displayed considerably less variation with inter-tooth variation of 0.8‰, 1.2‰, and 1.8‰ for MCPC A1902a, A579 and A1355a, respectively. *Tetrameryx irvingtonensis* $\delta^{13}\text{C}$ values ranged from -9.5‰ to -11.2‰ and *Camelops* (MCPC A282) -8.3‰ to -9.9‰.

The $\delta^{18}\text{O}$ values for all three taxa show significant differences (ANOVA, $p \ll 0.001$). *Tetrameryx irvingtonensis* has the highest total range of $\delta^{18}\text{O}$ values of 6.4‰. Total variation in *Equus* teeth is lower; 3.1‰, 3.3‰ and 2.0‰ for MCPC A1355a, MCPC A579 and MCPC A1902a, respectively. MCPC A282 (*Camelops*) exhibits a total $\delta^{18}\text{O}$ variation of 2.2‰.

A single *Homotherium* (UCMP 197566) canine was sampled serially. Variation in $\delta^{13}\text{C}$ values was low, ranging from -11.9‰ to -14.4‰. Total variation in $\delta^{18}\text{O}$ was higher than observed in most herbivores, with a total variation of 5.2‰ (Fig. 10).

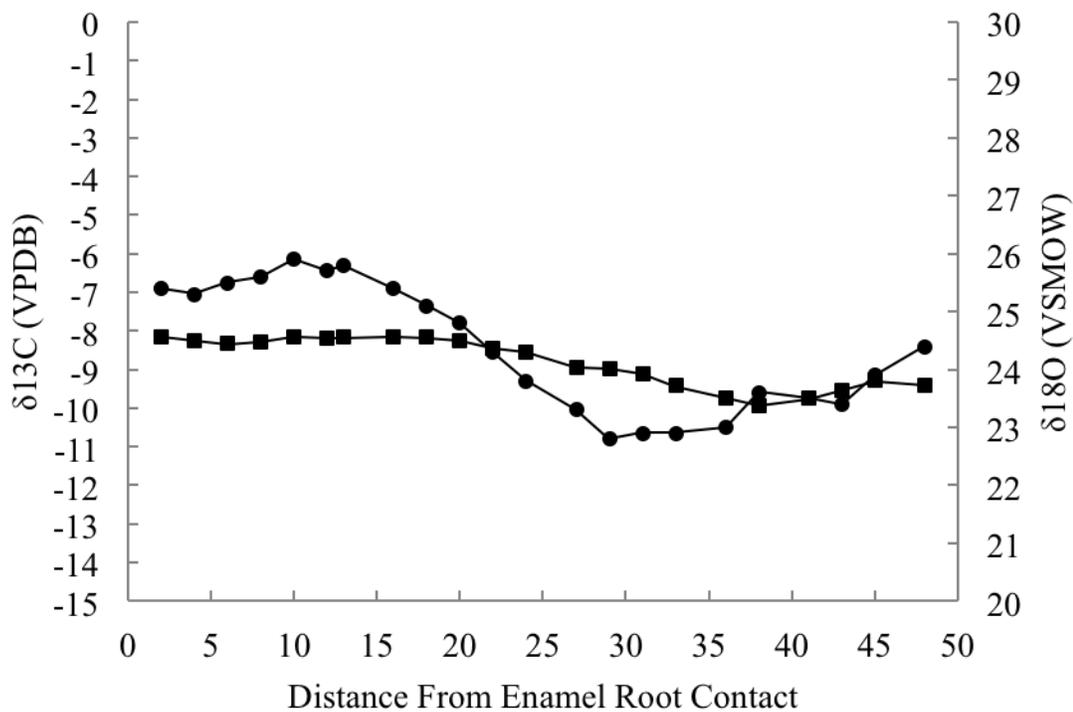


Figure 5. Stable carbon (■) and oxygen (●) for MCPC A1355a (*Equus*).

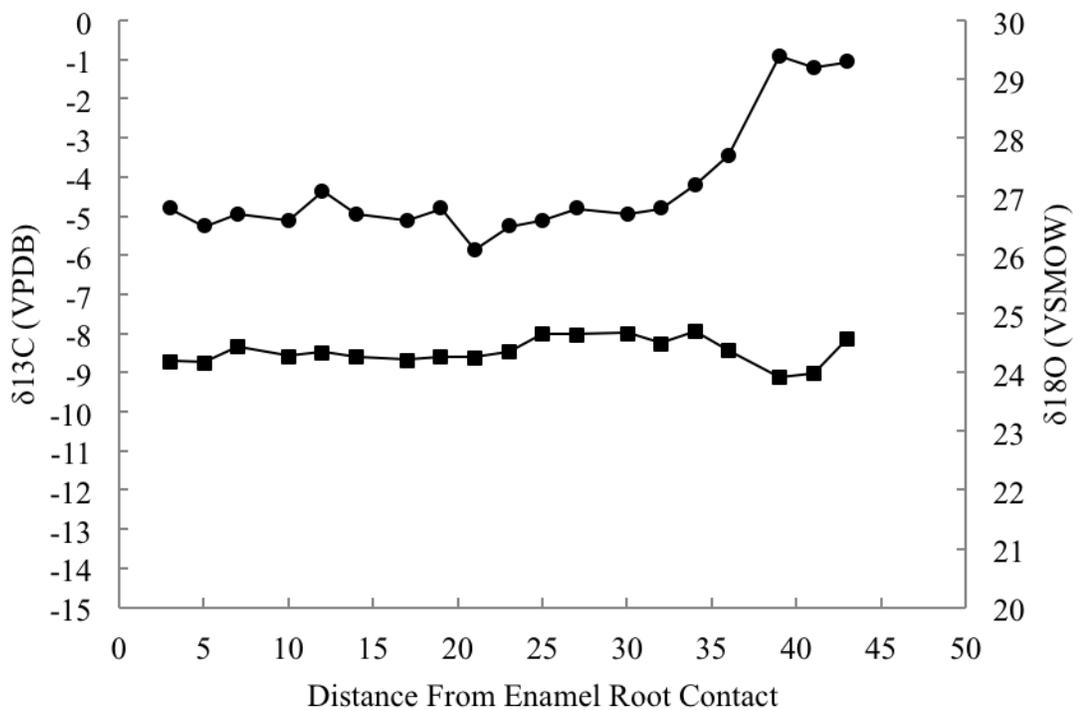


Figure 6. Stable carbon (■) and oxygen (●) for MCPC A579 (*Equus*).

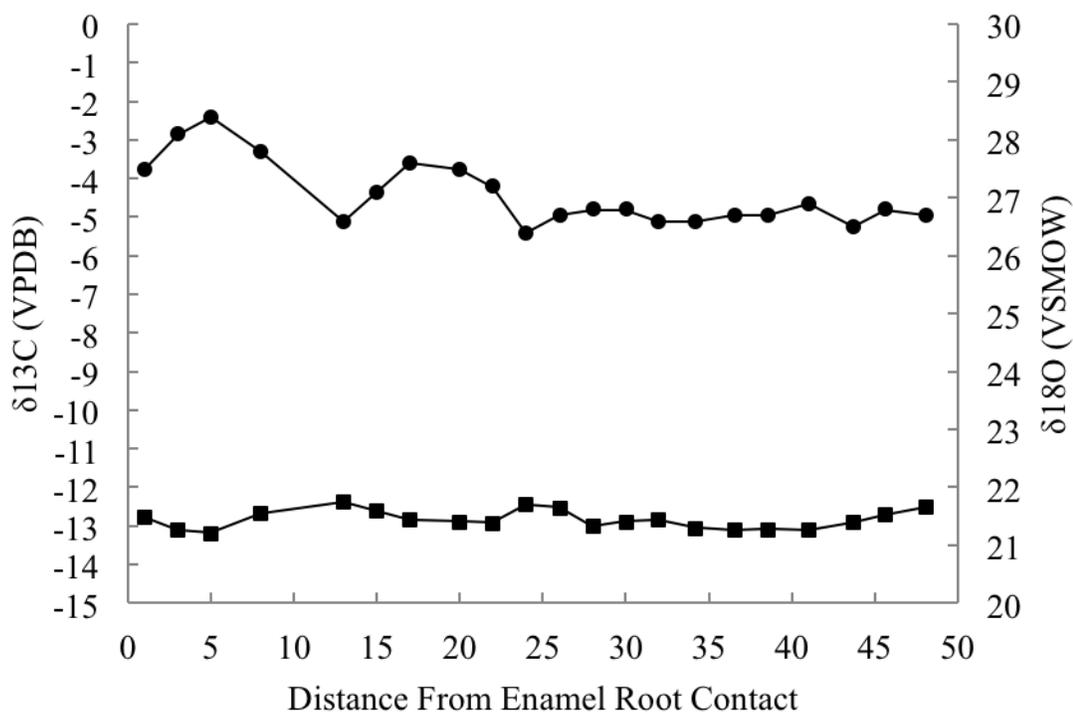


Figure 7. Stable carbon (■) and oxygen (●) for MCPC A1902a (*Equus*)

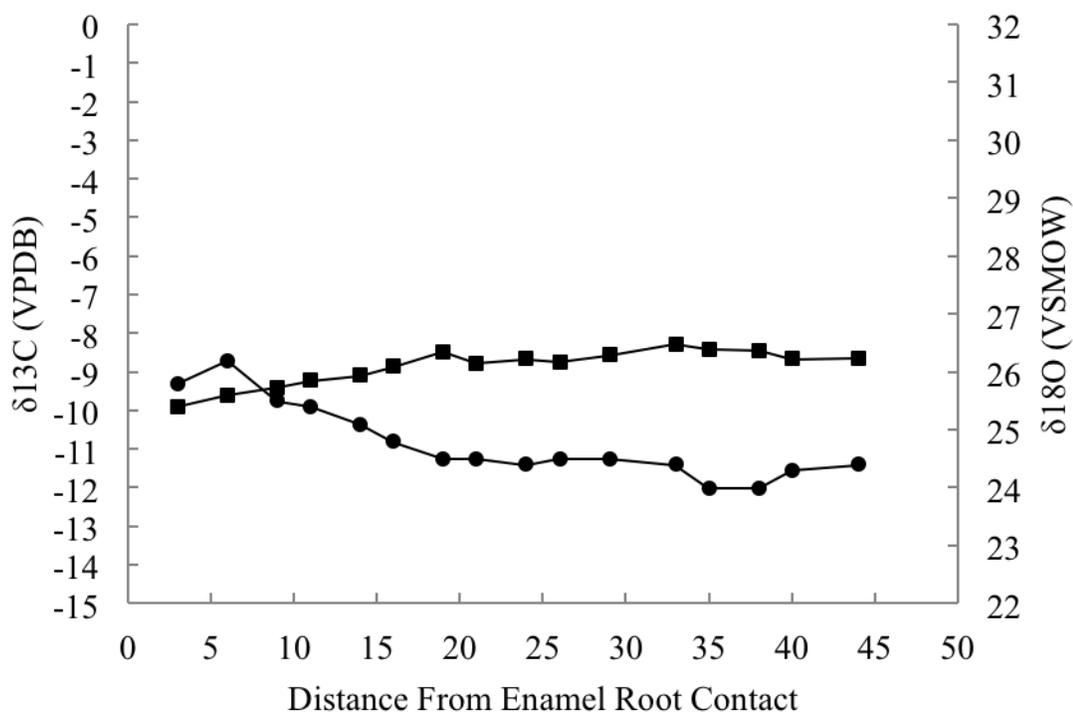


Figure 8. Stable carbon (■) and oxygen (●) for MCPC A282 (*Camelops*)

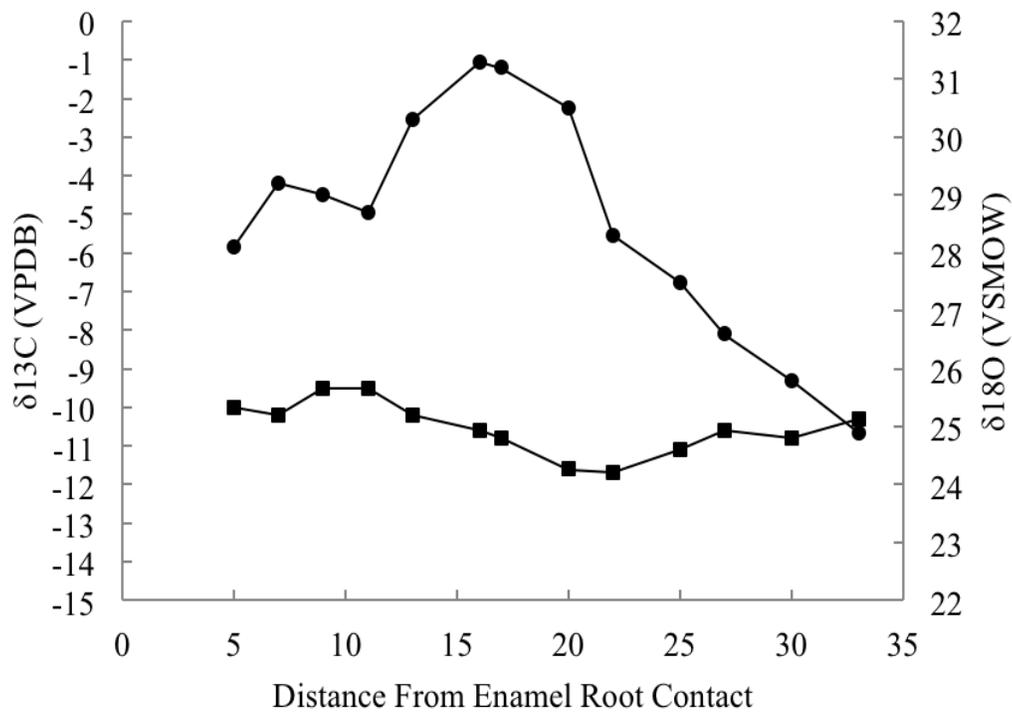


Figure 9. Stable carbon (■) and oxygen (●) for UCMP 197567 (*Tetrameryx irvingtonensis*)

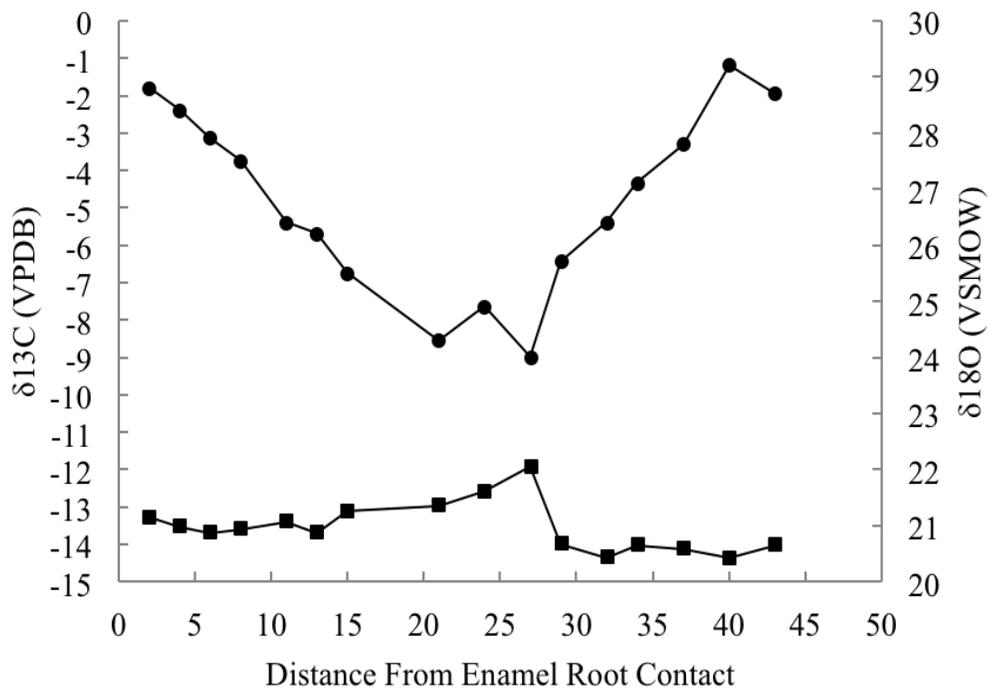


Figure 10. Stable carbon (■) and oxygen (●) for UCMP 197566 (*Homotherium*)

McKittrick Asphalt Seep $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ Values

Descriptive statistics for McKittrick asphalt seep fauna are reported in Table 5. The $\delta^{13}\text{C}$ values (Fig. 11) of the 33 sampled individuals range from -11.8‰ to -0.7‰ with a mean of -5.8‰. Carnivores exhibit a mean value of -6.1‰ while the herbivore mean is 5.4‰.

Camelops hesternus and *Equus* $\delta^{13}\text{C}$ values are significantly different (ANOVA, $p < 0.01$). Among the carnivore guild, $\delta^{13}\text{C}$ values differed significantly only between *Canis latrans* and *Panthera atrox* (ANOVA, $p < 0.01$), while both do not differ from *Canis dirus*. Pairwise comparisons between taxa are reported in Table 6.

Arctodus simus, *Bison*, *Cervus elaphus*, *Hemiauchenia macrocephala* and *Mammut americanum* are all represented by single individuals. *Mammut americanum* $\delta^{13}\text{C}$ falls within one standard deviation of the means for both *Panthera atrox* and *Equus*, although it falls outside the range of the latter. *Hemiauchenia macrocephala* $\delta^{13}\text{C}$ are within both one standard deviation of the means and within the observed ranges of *Canis latrans*, *Canis dirus*, and within the range of *Camelops hesternus*. *Bison* $\delta^{13}\text{C}$ is within one standard deviation of the means of *Equus* and both canids. The $\delta^{13}\text{C}$ of *Arctodus simus* is within both the range and one standard deviation of *Panthera atrox*, and within the range of *Canis dirus*. *Cervus elaphus* is the most negative herbivore and falls outside the range and does not overlap with the means ± 1 S.D of all taxa, although it differs from the most negative *Panthera atrox* individual by only 0.8‰.

McKittrick $\delta^{18}\text{O}$ values range from 23.7‰ to 33.7‰, have a mean value of 27.9‰, all within 1‰ of the Fairmead results but show significant differences between taxa (ANOVA $p < 0.01$). Carnivores and herbivores have mean $\delta^{18}\text{O}$ values of 28.8‰ and 26.9‰, respectively. Pairwise comparisons (Table 7) show

Table 5. Descriptive Statistics for McKittrick Asphalt Seep Taxa.

Taxa	<i>n</i>	Min $\delta^{13}\text{C}$ (‰)	Max $\delta^{13}\text{C}$ (‰)	Mean $\delta^{13}\text{C}$ (‰)	S.D. $\delta^{13}\text{C}$ (‰)	Min $\delta^{18}\text{O}$ (‰)	Max $\delta^{18}\text{O}$ (‰)	Mean $\delta^{18}\text{O}$ (‰)	S.D. $\delta^{18}\text{O}$ (‰)
<i>Arctodus simus</i>	1	-10.9	-10.9	-10.9	-	27.0	27.0	27.0	-
<i>Canis dirus</i>	7	-11.8	-1.7	-5.3	3.5	24.2	30.3	27.2	1.9
<i>Canis latrans</i>	7	-7.2	-1.6	-4.6	1.8	28.0	33.7	31.2	2.1
<i>Panthera atrox</i>	3	-11.8	-7.8	-9.9	2.0	25.1	29.8	27.1	2.5
<i>Bison</i> sp.	1	-4.9	-4.9	-4.9	-	23.9	23.9	23.9	-
<i>Camelops hesternus</i>	5	-4.8	-0.7	-2.6	1.5	26.2	30.8	28.2	2.1
<i>Cervus elaphus</i>	1	-11.3	-11.3	-11.3	-	24.8	24.8	24.8	-
<i>Equus</i> sp.	6	-7.7	-2.3	-6.4	2.1	23.7	27.5	26.5	1.4
<i>Hemiauchenia macrocephala</i>	1	-4.3	-4.3	-4.3	-	27.6	27.6	27.6	-
<i>Mammut americanum</i>	1	-8.4	-8.4	-8.4	-	27.4	27.4	27.4	-

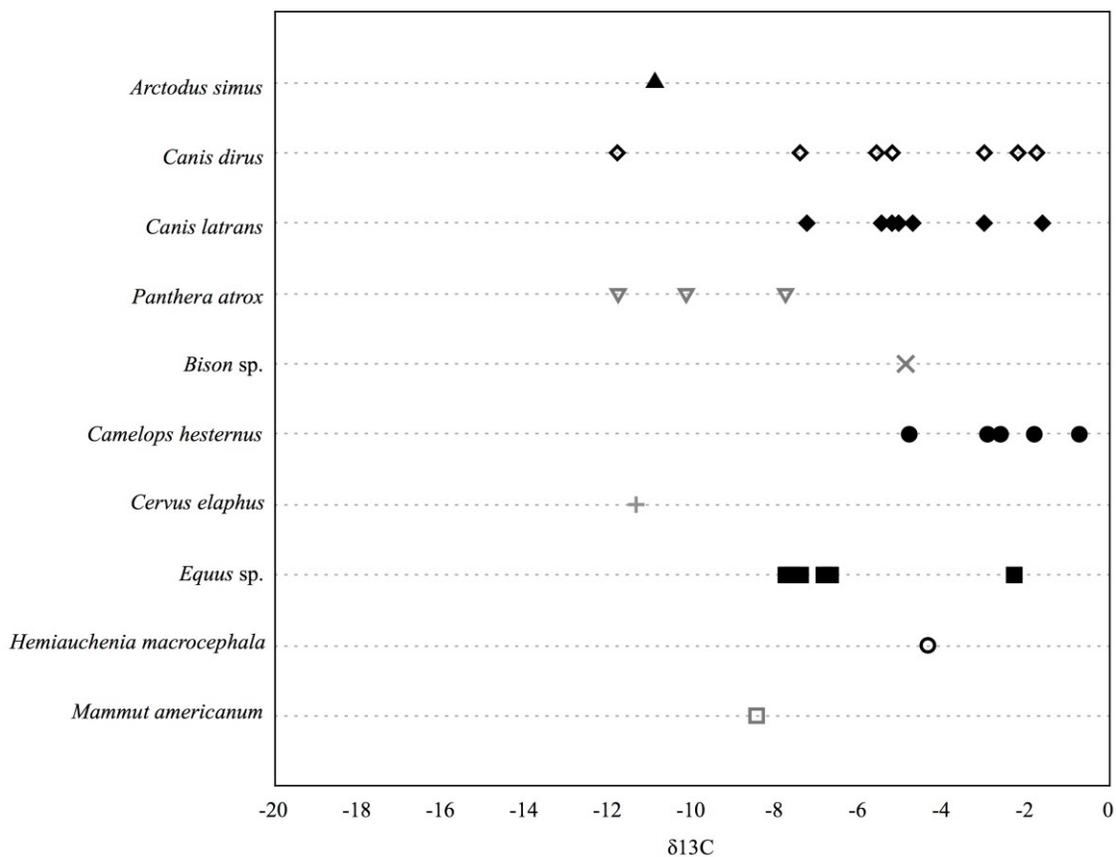


Figure 11. Stable Carbon for McKittrick asphalt seep taxa.

Table 6. Significant Differences in Stable Carbon Between Taxa from the McKittrick Asphalt Seeps.

	<i>Canis latrans</i>	<i>Canis dirus</i>	<i>Panthera atrox</i>	<i>Camelops hesternus</i>	<i>Equus sp.</i>
<i>Canis dirus</i>		0.67	0.07	0.43	0.16
<i>Canis latrans</i>			< 0.01	0.47	< 0.01
<i>Panthera atrox</i>				< 0.01	0.18
<i>Camelops hesternus</i>					< 0.01

Note: Bold *p*-values indicate significant differences. Carnivore values were adjusted by 1.3‰ to correct for trophic level fractionation (Clementz et al., 2009).

that *Canis latrans* differs significantly from all other taxa and excluding it from comparisons reveals no significant differences in the remaining taxa (ANOVA, $p = 0.69$).

Table 7. Significant Differences in Stable Oxygen Between Taxa from the McKittrick Asphalt Seeps.

	<i>Canis dirus</i>	<i>Canis latrans</i>	<i>Panthera atrox</i>	<i>Camelops hesternus</i>	<i>Equus</i> sp.
<i>Canis dirus</i>		< 0.01	0.90	0.45	0.47
<i>Canis latrans</i>			0.03	0.04	< 0.01
<i>Panthera atrox</i>				0.52	0.69
<i>Camelops hesternus</i>					0.16

Note: Bold p -values indicate significant differences.

Sixty-one total serial samples from one *Camelops hesternus* (Fig. 12) and two *Equus* teeth (Figs. 13, 14) exhibit significant differences in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values between taxa (ANOVA, $p < 0.001$). *Camelops hesternus* (UCMP 212893) has the highest variation in both isotopes with $\delta^{13}\text{C}$ ranging from -6.1‰ to -2.8‰ and $\delta^{18}\text{O}$ varying by 3.1‰. *Equus* displays slightly less variation in both isotopes; with UCMP 212874 $\delta^{13}\text{C}$ ranging from -7.9‰ to -6.1‰ and UCMP 212872 ranging from -8.7‰ to -7.1‰. Both individuals show similar changes in $\delta^{18}\text{O}$ with values varying by 2.6‰ and 2.4‰, respectively.

Inter-Locality Isotopic Variability

Both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ show significant differences between Fairmead Landfill and the McKittrick asphalt seeps (ANOVA, $p < 0.001$). Comparisons between shared taxa at the genus level reveal that all $\delta^{13}\text{C}$ values differ significantly between localities (Table 8). *Arctodus simus* shows the lowest difference in $\delta^{13}\text{C}$, varying by only 1.0‰ between Fairmead Landfill and McKittrick.

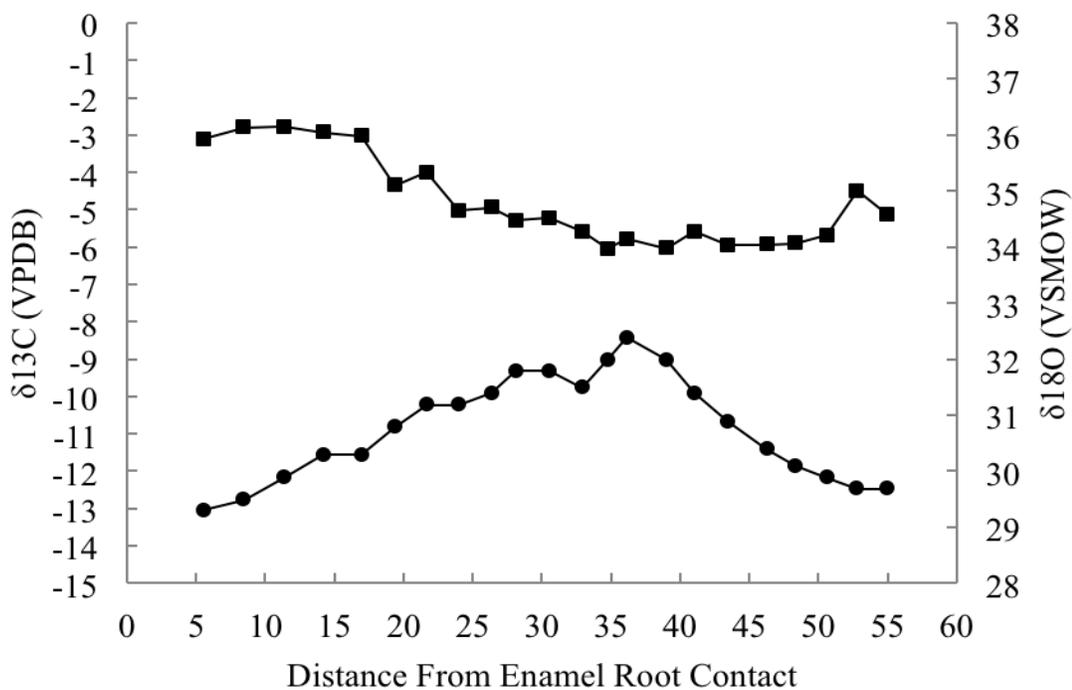


Figure 12. Stable carbon (■) and oxygen (●) for UCMP 212893 (*Camelops hesternus*).

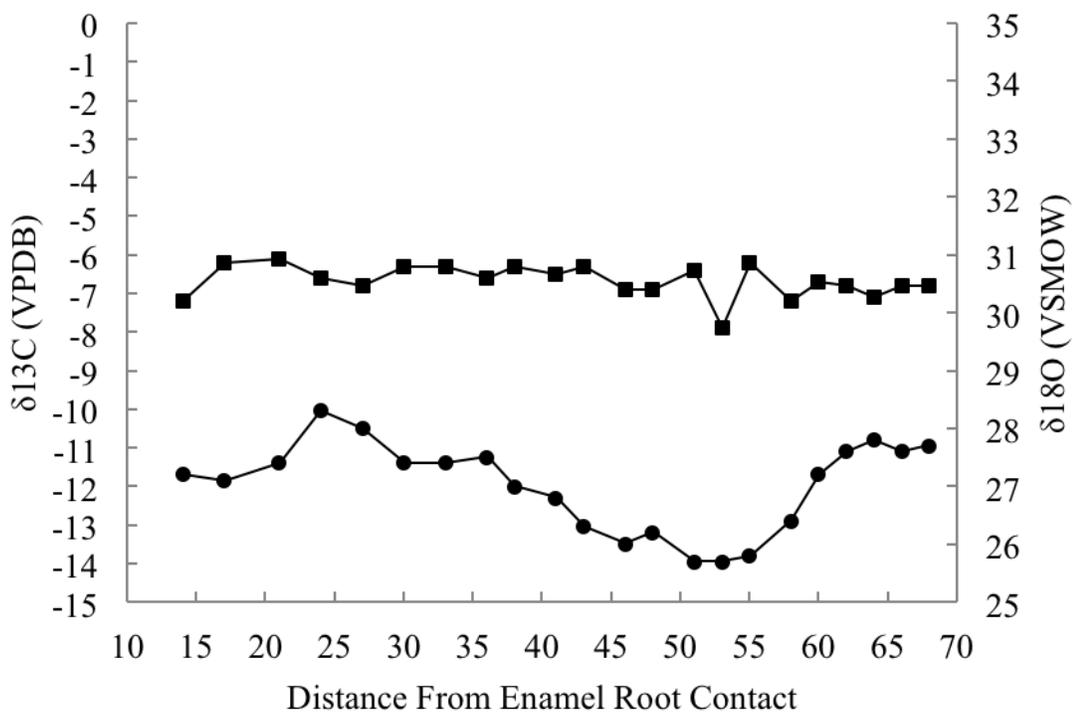


Figure 13. Stable carbon (■) and oxygen (●) for UCMP 212872 (*Equus*).

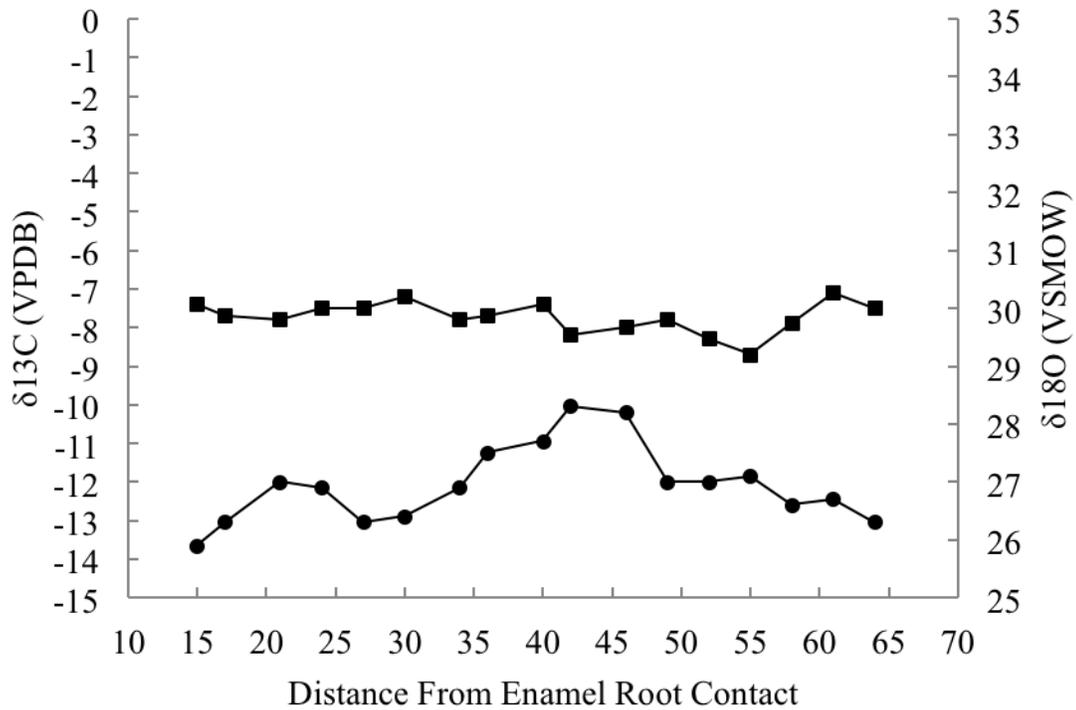


Figure 14. Stable carbon (■) and oxygen (●) for UCMP 212874 (*Equus*).

Table 8. Significant Differences in Stable Carbon Between Shared Taxa from Fairmead Landfill and McKittrick.

	<i>Canis dirus</i>	<i>Canis latrans</i>	<i>Camelops hesternus</i>	<i>Equus</i> sp.
<i>Canis dirus</i>	< 0.001			
<i>Canis latrans</i>		< 0.001		
<i>Camelops</i> sp.			< 0.001	
<i>Equus</i> sp.				< 0.01

Note: Bold *p*-values indicate significant differences. Carnivore values were adjusted by 1.3‰ to correct for trophic level fractionation (Clementz et al., 2009).

DISCUSSION

Differentiating habitats within a C₃ dominated environment based solely on $\delta^{13}\text{C}$ values is difficult since there is considerable overlap between habitat types. However, general trends allow some conclusions. Habitats can be referred to as either open (grassland, savanna) or closed (mosaic woodland, forest) based on the general relationship between environmental factors and $\delta^{13}\text{C}$ in C₃ plants. Habitat type can be associated with feeding strategy, with open and closed environments favoring grazers and browsers, respectively. Within a C₃ dominated environment, variations in $\delta^{13}\text{C}$ is largely controlled by physiological differences between plants and the degree of aridity. More positive $\delta^{13}\text{C}$ values are expected from plants with either higher water use efficiency or from more open or arid environments (Ehleringer et al., 1992; Ehleringer and Monson, 1993). Plants of the same species may vary by ~2‰ depending on microhabitat and water availability (Ehleringer and Cooper, 1988). Closed environments are associated with more negative $\delta^{13}\text{C}$ values due to the “canopy effect”, resulting from CO₂ recycling and lower light levels (van der Merwe and Medina, 1991; Cerling et al., 2004).

Fairmead Landfill Herbivore Diet and Habitat

All Fairmead Landfill herbivore $\delta^{13}\text{C}$ values are consistent with a diet of pure C₃ vegetation. Sedimentologic evidence indicates a distal alluvial fan setting with channel, flood plain and some marshy lacustrine environments (Dundas et al., 1996). Recovered pollen indicates a predominantly grassland habitat with some riparian vegetation and occasional trees and shrubs.

Two herbivores, *Camelops* and *Platygonus vetus*, exhibit the highest and lowest $\delta^{13}\text{C}$ values, respectively, and differ significantly from the remaining taxa. *Camelops* is the best represented taxon in this study and its $\delta^{13}\text{C}$ values differ

significantly from all other herbivore taxa. *Camelops* also exhibits the most positive $\delta^{13}\text{C}$ value, suggesting a preference for more open habitats. Stable carbon values are high for a C_3 browser, with the most positive individuals within 0.1‰ of the predicted boundary for mixed C_3 - C_4 feeding. Serial sampling of MCPC A282 reveals a low temporal variability in $\delta^{13}\text{C}$ values of 1.6‰, indicating that *Camelops* had narrow dietary preferences. Extant camels commonly include halophytic plants in their diet to satisfy their high salt requirements (Köhler-Rollefson, 1991). Salinity stress and water use efficiency drive $\delta^{13}\text{C}$ more positive, a trait exhibited by modern C_3 halophytes (Guy et al., 1980). If *Camelops* commonly consumed these plants, then they would be expected to have higher $\delta^{13}\text{C}$ values than other C_3 feeding herbivores. *Platygonus vetus*, the most negative herbivore, was a C_3 browser, with an apparent preference for closed habitats.

Hemiauchenia and both antilocaprids exhibit indistinguishable $\delta^{13}\text{C}$ values, suggesting similar dietary niches. Niche partitioning within C_3 dominated environments has been demonstrated within both modern (Feranec, 2007) and extinct faunas (Feranec and MacFadden, 2006). The lack of significant differences between taxa suggests that either resource abundance was high (Gordon and Illius, 1989) or that taxa partitioned resources in ways not preserved in their $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ values for *Tetrameryx irvingtonensis* and *Capromeryx* are typical of a C_3 browsing diet and consistent with other isotopic reconstructions of antilocaprid diet (Connin et al., 1998; DeSantis et al., 2009). Serial samples from a single *Tetrameryx irvingtonensis* tooth (UCMP 197467) reveal a low variability in $\delta^{13}\text{C}$ of 2.2‰, suggesting only slight variations in diet seasonally. Although *Mammuthus columbi* $\delta^{13}\text{C}$ is indistinguishable from both antilocaprids and *Hemiauchenia*, it probably included more C_3 grasses in its diet.

Equus $\delta^{13}\text{C}$ values are consistent with a bimodal distribution, although more sampling may be required to confirm this result. Serial sampled individuals from both groups do not exhibit overlapping values. Excavation data reveal that five of the seven sampled *Equus* were recovered from the same bone bed, including both of the individuals exhibiting higher $\delta^{13}\text{C}$ values. This suggests that the differences are may not result from temporal separation. A variation of $\sim 2.5\%$ between groups suggests that the *Equus* may have occupied multiple microhabitats, leading to these differences. Alternatively, Dundas et al. (1996) suggests the presence of two species of *Equus*, although examination of the teeth sampled for this study cannot confirm this.

Fairmead Landfill Carnivore-Herbivore Interactions

Carbon isotope values for Fairmead Landfill carnivores indicate a diet of exclusively C_3 feeding herbivores. *Canis dirus* and *Canis latrans* exhibit generalist diets, potentially feeding on *Equus*, *Mammuthus*, *Hemiauchenia* and antilocaprids. Due to the lack of significant differences among these herbivore taxa, carnivore dietary interpretations are difficult and require considering factors besides $\delta^{13}\text{C}$ values. *Equus* were major dietary components of both *Canis dirus* (Fox-Dobbs et al., 2007) and *Canis lupus* (Fox-Dobbs et al., 2008) during the late Pleistocene and $\delta^{13}\text{C}$ values for Fairmead Landfill *Canis dirus* support this preference. *Hemiauchenia* $\delta^{13}\text{C}$ values are indistinguishable from *Equus*, making their contribution to carnivore diet unclear. However, *Equus* represents two-thirds of all specimens recovered at Fairmead Landfill and was likely more abundant than other herbivores (Asami et al., 2011), likely making them the most commonly available prey. The contribution of *Mammuthus columbi* to *Canis dirus* diet at Fairmead Landfill is uncertain. Fox-Dobbs et al. (2008) interprets the presence of

Mammuthus columbi in the diets of late Pleistocene *Canis lupus* as evidence of scavenging, not direct predation. Indeed, healthy adult proboscideans would have been too large for *Canis dirus* to hunt. Modern wolves occasionally hunt *Antilocapra americana*, although infrequently and with little success due largely to the great speed of *Antilocapra americana* (Byers, 1997). Interactions between *Canis dirus* and *Tetrameryx irvingtonensis* were presumably similar, with only older, weaker individuals and fawns being killed. *Canis latrans* exhibits similar $\delta^{13}\text{C}$ values to *Canis dirus*. Dietary interpretations of *Canis latrans* are complicated by the lack of data for small animals that comprise a large portion of its diet. Modern *Canis latrans* occasionally hunt deer (Bekoff, 1977; Bekoff and Gese, 2003) and *Antilocapra americana* fawns (Byers, 1997). *Odocoileus virginianus* (white-tailed deer) is present in the Fairmead Landfill collection, however no teeth were available for analysis. *Tetrameryx irvingtonensis* fawns and *Capromeryx* are potential prey for *Canis latrans*, as is carrion from any of the other large herbivores, however the total contribution of each to *Canis latrans* diet is uncertain.

Of the three felids sampled, only *Smilodon* is represented by multiple individuals. Carbon isotope values are indistinguishable from both canids suggesting a similar, generalist diet. Feranec (2005) suggests *Platygonus* and *Hemiauchenia* as likely prey for Florida *Smilodon gracilis*, while Coltrain et al. (2004) shows a preference for large ruminants in Rancho La Brea *Smilodon fatalis*. Fairmead Landfill *Smilodon* $\delta^{13}\text{C}$ values suggest that *Equus* and *Hemiauchenia* were the most common prey. As is the case with canids, the contribution of *Mammuthus columbi* to *Smilodon* diet is unclear. *Homotherium*, which at Fairmead Landfill exhibits $\delta^{13}\text{C}$ similar to *Smilodon*, is strongly associated with predation of juvenile *Mammuthus* (Rawn-Schatzinger, 1992). The

similarities between the $\delta^{13}\text{C}$ of both machairodonts, suggest a diet of *Equus*, *Hemiauchenia* and possibly *Mammuthus columbi*. Neither *Smilodon* or *Homotherium* was highly cursorial, which likely limited their ability to prey on antilocaprids. The association of late Pleistocene *Miracinonyx trumani* and *Antilocapra americana* coupled with the highly cursorial build of the former lead Chorn et al. (1988) to suggest antilocaprids as favored prey. While *Miracinonyx inexpectatus* is represented at Fairmead Landfill by a single individual, its $\delta^{13}\text{C}$ values overlap with those of *Tetrameryx irvingtonensis*. *Miracinonyx inexpectatus* $\delta^{13}\text{C}$ also overlaps with *Equus*, *Camelops*, *Mammuthus* and *Hemiauchenia*. Extant cheetah rarely hunt large ungulates (Krausman and Morales, 2005) and instead focus on medium to small prey. *Miracinonyx* was considerably smaller than *Homotherium* and *Smilodon* and likely coexisted by pursuing smaller, faster quarry suggesting antilocaprids and *Hemiauchenia* as prey.

Overlap between the $\delta^{13}\text{C}$ of *Arctodus simus*, *Mammuthus columbi*, and large ungulates, except *Tetrameryx irvingtonensis*, suggest all as potential prey or scavenge. *Arctodus simus* likely included large amounts of vegetation in its diet (Figueirido et al., 2010) as well, making conclusive dietary interpretations unclear.

McKittrick Asphalt Seep Herbivore Diet and Habitat

Kohn et al. (2005) interpreted a range of $\delta^{13}\text{C}$ values similar to those of McKittrick fauna as evidence for a mixed woodland-grassland environment. The presence of *Cervus elaphus* and *Mammut americanum* suggest the presence of closed woodland habitats, which is supported by recovered *Pinus* and *Juniperus* macrofossils (Mason, 1944). The abundance of the mixed feeder and grazers (*Bison*, *Equus*, *Hemiauchenia macrocephala* and *Camelops hesternus*) indicates the presence of open grasslands.

The McKittrick asphalt seep mammalian megafauna display a considerably greater range in $\delta^{13}\text{C}$ values than Fairmead Landfill, with some taxa exhibiting values consistent with C_4 feeding. Herbivores can be divided into three categories, C_3 browsers, mixed feeders and C_4 feeders. Dietary interpretations are again limited by the use of a single isotopic system ($\delta^{13}\text{C}$). The addition of $\delta^{15}\text{N}$ would allow for more detailed dietary comparisons between taxa, however multiple attempts to extract viable collagen from McKittrick asphalt seep fauna produced C:N ratios outside the acceptable range of < 3.6 (Ambrose, 1990). This is similar to the results of France (2008) who recovered little viable collagen from McKittrick specimens. Fox-Dobbs et al. (2006) reported collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for avian megafauna from McKittrick, suggesting that further attempts may produce viable collagen.

Cervus elaphus, the most negative McKittrick herbivore, has a $\delta^{13}\text{C}$ value consistent with C_3 browsing. *Mammuth americanum* also exhibits a $\delta^{13}\text{C}$ value consistent with C_3 browsing. *Mammuth americanum* is strongly associated with closed habitats (Lepper et al., 1991; Stock and Harris, 1992) suggesting the presence of woodland habitats near McKittrick. Conifers are known to contribute to *Mammuth americanum* diet (Dreimanis, 1968; Lepper et al., 1991) and are present in the McKittrick deposits (Mason, 1944), implicating them as a potential food source. Conifers have $\delta^{13}\text{C}$ values $\sim 2\text{‰}$ higher than other woody plants (Diefendorf et al., 2010), which may explain the relatively high $\delta^{13}\text{C}$ value for *Mammuth americanum*.

The remaining McKittrick herbivores taxa have $\delta^{13}\text{C}$ values indicative of mixed C_3 - C_4 feeding, although some individuals consumed almost entirely C_4 plants. *Bison* and *Hemiauchenia macrocephala* are both represented by single individuals with modeled percentages of C_4 vegetation in their diets of 39% and

46% C₄ plants, respectively. *Equus* consumed a mean of 20% C₄ plants although one individual (UCMP 212973) consumed 72%. Both serial sampled *Equus* (UCMP 212874, UCMP 212872) show low temporal variability in $\delta^{13}\text{C}$, suggesting that diet changed little seasonally.

Camelops hesternus is the most positive herbivore in the McKittrick fauna, with C₄ plants comprising an average of 68% of diet, and one individual consuming 91%, suggesting a dominantly C₄ grazing diet. Extant *Camelus* consume large amounts of *Atriplex* (Köhler-Rollefson, 1991), a C₄ halophyte, and the presence of *Atriplex lentiformis* in the McKittrick deposits (Mason, 1944) provides a potential food source for *Camelops hesternus*. Serial samples from UCMP 212893 show higher temporal variability than seen in *Equus*, with the C₄ contribution to diet varying from 24% to 65%. Seasonal variation in the diet may indicate migratory behavior (Feranec et al., 2009), although a larger sample size is needed to solidify this conclusion.

McKittrick Asphalt Seep Carnivore-Herbivore Interactions

While Fairmead Landfill carnivore $\delta^{13}\text{C}$ values overlap with all herbivore taxa, McKittrick carnivores particularly the most negative individuals of *Canis dirus*, *Panthera atrox* and *Arctodus simus* do not overlap with most herbivore prey. There are multiple possible explanations for this discrepancy; 1) there are several herbivore taxa that were not available for analysis. *Tapirus* and *Odocoileus* both occurred at McKittrick. Both taxa are deep forest herbivores and potential prey sources for closed habitat carnivores. Similarly, a larger sample of *Cervus elaphus* and *Mammuth americanum* may fill in some of the “gaps.” 2) Closed habitat herbivores occur in lower numbers in the McKittrick deposits than open habitat herbivores (Schultz, 1938) suggesting that they occurred less frequently in

the vicinity of the asphalt seeps. If some carnivore populations preferred these closed habitat herbivores then they would also be expected to be only occasionally entrapped.

Of the four carnivores sampled, *Canis dirus* had the most generalist diet and shows $\delta^{13}\text{C}$ overlap with all herbivore taxa. This is similar to both Rancho La Brea *Canis dirus* (Fox-Dobbs et al., 2007) and late Pleistocene Beringian *Canis lupus* (Fox-Dobbs et al., 2008), both of which demonstrated generalist diets even though *Equus* was the most common prey. McKittrick *Canis dirus* likely consumed all available herbivores although any contributions from *Mammot americanum* to diet likely came as carrion.

Canis latrans exhibits a similar diet to *Canis dirus*, but with a narrower range. Extant *Canis latrans* compete poorly with *Canis lupus* (Bekoff, 1977; Bekoff and Gese, 2003), and only hunt large game in the absence of the larger canid. All sampled herbivore taxa were likely too large for *Canis latrans* to hunt successfully although they were probably eaten as carrion. Significant differences between *Canis latrans* and *Equus* exclude the latter as a major contributor to diet. Similarly to Fairmead Landfill, the lack of data for small animals limits dietary interpretations of *Canis latrans*.

Panthera atrox exhibits the most negative $\delta^{13}\text{C}$ values of the McKittrick carnivores and has a narrower range than either canid. In contrast to *Canis dirus* and *Canis latrans*, *Panthera atrox* primarily consumed C_3 feeding prey. This preference suggests that *Panthera atrox* either preferred closed habitats or at least preyed upon closed habitat herbivores. *Panthera atrox* has occasionally been reconstructed as a kind of “giant jaguar” and shows morphologic similarities to both extant lions and jaguars, although it remains a distinct species (Christiansen and Harris, 2009). Jaguar are forest dwelling felids, and $\delta^{13}\text{C}$ values for

McKittrick *Panthera atrox* suggest a similar habitat. *Cervus elaphus* and *Mammuth americanum* are both pure C₃ feeders making them the most likely prey. Some individual *Equus* primarily consumed C₃ plants and may have contributed to *Panthera atrox* diet.

Arctodus simus $\delta^{13}\text{C}$ does not overlap with any measured herbivores making interpretations of diet unclear. Data for Beringian *Arctodus simus* show *Rangifer* to be the most common prey (Fox-Dobbs et al., 2008) and a similar relationship between McKittrick *Arctodus simus* and *Cervus elaphus* is possible.

Seasonal Effects at Fairmead and McKittrick

The magnitude of $\delta^{18}\text{O}$ seasonal variation in serial sampled teeth varies between taxa, possibly a result of taxon specific metabolic effects. By comparing serial sampled $\delta^{18}\text{O}$ to the predicted pattern (Figure 2) the length of formation for each serial sampled tooth was estimated. At Fairmead Landfill, MCPC A1355a (*Equus*) displays the clearest seasonal cycle of ~1 year. The remaining *Equus* individuals are more difficult to interpret; MCPC A579 appears to show a dampened seasonal cycle while MCPC A1902a does not exhibit the predicted sinoidal pattern. McKittrick *Equus* show slightly less variability in $\delta^{18}\text{O}$, although a seasonal cycle of 12-16 months is apparent in both individuals (UCMP 212874, UCMP 212872). While the sampled McKittrick *Camelops hesternus* (UCMP 212893) shows clear evidence of seasonal variation, Fairmead Landfill *Camelops* (MCPC A282) does not. *Tetrameryx irvingtonensis* has the highest variability in $\delta^{18}\text{O}$ over a period estimated to be 10-12 months. With the exception of the McKittrick *Camelops hesternus*, the variation in $\delta^{13}\text{C}$ values of herbivore teeth from both localities is low, suggesting little in floral abundances between summer and winter at both localities.

The total variation in $\delta^{18}\text{O}$ values differs between taxa. While the cause of this effect is unclear, it may result from 1) taxon specific enamel maturation time, i.e., *Tetrameryx irvingtonensis* enamel may mineralize more quickly than *Equus* and thus exhibits less time averaging of $\delta^{18}\text{O}$ values (Passey and Cerling, 2002), 2) temporal effects. At Fairmead Landfill the individuals with the highest variation in $\delta^{18}\text{O}$ values (*Tetrameryx irvingtonensis* and *Homotherium*) were both recovered from a different bone bed than other serial sampled and may have experienced greater seasonal variability than individuals recovered from other bone beds.

Tooth eruption sequences in *Homotherium serum* were similar to extant *Panthera leo* (Rawn-Schatzinger, 1983) although canine growth rates in felids appear to be species specific (Feranec, 2008). Variation in *Homotherium* $\delta^{18}\text{O}$ values suggest mineralization of the sampled enamel over a period of 10-12 months. Sixteen samples were collected over 41 mm of enamel suggesting an upper canine growth rate of 3.4 mm per month, similar to the rate of 2.8 mm per month reported for *Homotherium serum*, and faster than the rates of *Panthera atrox* and *Panthera leo* (Feranec, 2008). The rate of growth is considerably slower than reported rate of 7 mm per month for *Smilodon fatalis* (Feranec, 2004).

Inter-locality Dietary Trends

All shared taxa between Fairmead Landfill and McKittrick exhibit significantly different diets. The McKittrick fauna have higher $\delta^{13}\text{C}$ values than the Fairmead Landfill fauna. The overall range of $\delta^{13}\text{C}$ values at McKittrick is approximately twice that of Fairmead landfill, suggesting a more varied habitat or diverse flora. The shift towards C_4 consumption seen at McKittrick indicates the presence of a more arid grassland habitat although with some woodlands.

Comparisons between the inland McKittrick fauna and the coastal fauna of Rancho La Brea reveal significant differences (ANOVA, $p < 0.001$). Comparative data were selected from two published data sets. *Equus* and *Bison* were compared to data from Feranec et al. (2009). These authors report serial sampled $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for both *Equus* and *Bison* tooth enamel. While Coltrain et al. (2004) reports a larger data set for both taxa, the authors' $\delta^{13}\text{C}$ data are from collagen, which averages diet over several years (Hedges et al., 2007), potentially obscuring some contributions to diet. However, in the absence of published enamel data for Rancho La Brea, *Panthera atrox*, *Canis latrans*, *Canis dirus* and *Camelops hesternus* collagen data from Coltrain et al. (2004) were used for comparisons for these taxa. For these taxa, collagen data were corrected to dietary values using a $\delta^{13}\text{C}_{\text{collagen-diet}}$ offset of 5‰ (Koch, 1998). Carnivore collagen values were adjusted by an additional 1.3‰ (Fox-Dobbs et al., 2007) to account for trophic fractionation. Values were then corrected to equivalence with enamel using the appropriate fractionation factors. *Camelops hesternus*, *Canis dirus* and *Canis latrans* are significantly different between localities. *Panthera atrox* and *Equus* do not differ significantly (Table 9). The McKittrick *Bison* $\delta^{13}\text{C}$ falls within the observed range of $\delta^{13}\text{C}$ values, while McKittrick *Mammuth americanum* falls outside the mean (± 1 S.D) of their Rancho La Brea analogs.

Rancho La Brea was more mesic during the late Pleistocene, with a flora dominated by coastal sage scrub and chaparral (Stock and Harris, 1992). C_4 plant consumption at Rancho La Brea was broadly similar to McKittrick, with obligate grazers (*Bison*, *Equus*) from both localities feeding on a mix of C_3 and C_4 grasses.

Table 9. Significant Differences in Stable Carbon Between Shared Taxa from Rancho La Brea and McKittrick.

	<i>Canis dirus</i>	<i>Canis latrans</i>	<i>Camelops hesternus</i>	<i>Equus</i> sp.	<i>Panthera atrox</i>
<i>Canis dirus</i>	<0.001				
<i>Canis latrans</i>		<0.001			
<i>Camelops hesternus</i>			<0.001		
<i>Equus</i> sp.				0.06	
<i>Panthera atrox</i>					0.35

Note: Bold *p*-values indicate significant differences. *Equus* sp. data from Feranec et al. (2009). All other comparative data from Coltrain et al. (2004).

While the individual $\delta^{13}\text{C}$ values for the presumed browser, *Mammuth americanum*, are distinctly different between localities, both are consistent with a diet of C_3 browse. Curiously, McKittrick *Camelops hesternus* consumed far more C_4 plants than Rancho La Brea individuals. Dental boluses from Rancho La Brea *Camelops hesternus* indicate a browsing diet (Akersten et al., 1988). *Camelops* was not an obligate grazer (Dompierre and Churcher, 1996; Semperebon and Rivals, 2010) and likely only included C_4 grasses in its diet when sufficient browse was unavailable.

Unlike *Canis dirus* (Fox-Dobbs et al., 2007), there are no detailed dietary reconstructions of Rancho La Brea *Panthera atrox*, although the $\delta^{13}\text{C}$ values of the two taxa are statistically indistinguishable, suggesting a similar diet of C_3 ruminants (Coltrain et al., 2004). McKittrick *Panthera atrox* shows similar dietary preferences, although precise comparisons of diet are difficult without dietary $\delta^{15}\text{N}$ values.

Conclusions

Faunas from the middle Irvingtonian Fairmead Landfill and the late Rancholabrean McKittrick asphalt seeps yielded $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tooth enamel that allows the investigation of their paleoecology. Fairmead Landfill is a C_3

dominated grassland, although with some scrub and tree cover as indicated by the pollen and presence of antilocaprids and *Platygonus vetus*. Herbivores exhibit little variability $\delta^{13}\text{C}$ values, suggesting similar diet although forms of partitioning that are not revealed using stable isotope analysis are possible; i.e. being active at different times or choosing different parts of the same plant. Similarly, Fairmead Landfill carnivores display similar diets.

The late Rancholabrean McKittrick asphalt seeps preserve a mixed $\text{C}_3\text{-C}_4$ habitat with the presence of both woodlands and grasslands. Herbivore diets differed more significantly with a larger separation between browsers and grazers. McKittrick canids continued opportunistically feeding, while *Panthera atrox* retained a narrower range of $\delta^{13}\text{C}$ values, similar to that observed for the Fairmead Landfill felids. The abundance of data for the coastal Rancho La Brea fauna allowed comparison between it and inland McKittrick, revealing shifts in the diets of both canids and *Camelops hesternus*, while browsers and obligate grazers had similar diets.

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APPENDIX

Table A1. Bulk Sample Data.

Collection	#	Locality	Tooth	Taxa	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
MCPC	A2604	Fairmead	LC	<i>Arctodus simus</i>	-11.9	25
MCPC	A2202	Fairmead	rC	<i>Canis dirus</i>	-12.5	26.8
UCMP	156048	Fairmead	rm2	<i>Canis dirus</i>	-10.8	27.6
UCMP	140265	Fairmead	rm2	<i>Canis dirus</i>	-12.5	34.4
MCPC	A2209	Fairmead	rm1	<i>Canis dirus</i>	-11.1	27.4
MCPC	A2605	Fairmead	lp4	<i>Canis dirus</i>	-11.1	28.5
UCMP	156047	Fairmead	lm1	<i>Canis dirus</i>	-13.1	28.9
MCPC	A576	Fairmead	pm	<i>Canis dirus</i>	-12.7	29.1
MCPC	A948	Fairmead	lp4	<i>Canis dirus</i>	-13	31.9
UCMP	140413	Fairmead	m2	<i>Canis latrans</i>	-10.7	30.6
MCPC	A1762	Fairmead	C	<i>Canis latrans</i>	-13.1	28.9
MCPC	A2606	Fairmead	lm2	<i>Canis latrans</i>	-12.3	31.6
MCPC	A19	Fairmead	lM1	<i>Canis latrans</i>	-12.8	25.4
MCPC	A7	Fairmead	lc	<i>Canis latrans</i>	-12.4	24.9
UCMP	197566 (mean)	Fairmead	C	<i>Homotherium serum</i>	-13.5	26.8
MCPC	A2210	Fairmead	II	<i>Smilodon sp.</i>	-13.4	24.3
MCPC	A2201	Fairmead	C	<i>Smilodon sp.</i>	-11.8	25.6
MCPC	A1757	Fairmead	I	<i>Smilodon sp.</i>	-11.2	27.9
UCMP	140618	Fairmead	LP4	<i>Miracinonyx sp.</i>	-11.6	23.8
MCPC	A1937	Fairmead	rM2	<i>Camelops sp.</i>	-8.4	27.7
MCPC	A1832	Fairmead	lM2	<i>Camelops sp.</i>	-9.5	25.5
MCPC	A523	Fairmead	lp4	<i>Camelops sp.</i>	-8.8	27.2
UCMP	140400	Fairmead	rm3	<i>Camelops sp.</i>	-10.1	27.2
UCMP	212866	Fairmead	rm2	<i>Camelops sp.</i>	-8.9	28.8
UCMP	212867	Fairmead	lm3	<i>Camelops sp.</i>	-8.1	30.6

Collection #	Locality	Tooth	Taxa	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
UCMP 212868	Fairmead	rm3	<i>Camelops sp.</i>	-10.2	27.9
MCPC A282 (mean)	Fairmead	rM2	<i>Camelops sp.</i>	-8.9	24.8
UCMP 197886	Fairmead	lm2	<i>Camelops sp.</i>	-10.9	27.4
UCMP 197888	Fairmead	lm2	<i>Camelops sp.</i>	-9.4	27.9
MCPC A978	Fairmead	P4	<i>Camelops sp.</i>	-11.7	29.4
MCPC A98	Fairmead	lM2	<i>Camelops sp.</i>	-9.8	25.9
MCPC A629	Fairmead	lm1	<i>Camelops sp.</i>	-8.5	26.6
MCPC A1307	Fairmead	lm3	<i>Camelops sp.</i>	-9.2	25.5
MCPC A989	Fairmead	lm2	<i>Camelops sp.</i>	-9.6	27.9
MCPC A993	Fairmead	lm2	<i>Camelops sp.</i>	-8.2	27.8
UCMP 212864	Fairmead	lP2	<i>Equus sp.</i>	-11.6	27.6
UCMP 212865	Fairmead	lP2	<i>Equus sp.</i>	-11.4	28.2
MCPC A1355a (mean)	Fairmead	lP2	<i>Equus sp.</i>	-8.8	24.4
MCPC A1902a (mean)	Fairmead	lP2	<i>Equus sp.</i>	-12.8	27
MCPC A579 (mean)	Fairmead	lP2	<i>Equus sp.</i>	-8.5	27.2
MCPC A311	Fairmead	lP2	<i>Equus sp.</i>	-12.5	26.8
MCPC A1285	Fairmead	lP2	<i>Equus sp.</i>	-11.3	25.9
UCMP 140397	Fairmead	rm1	<i>Hemiauchenia sp.</i>	-13.3	34.4
MCPC A391	Fairmead	rM2	<i>Hemiauchenia sp.</i>	-9.3	27.8
MCPC A1309	Fairmead		<i>Hemiauchenia sp.</i>	-11.8	31.5
MCPC A1197	Fairmead	Molar	<i>Mammuthus columbi</i>	-10.6	22.5
MCPC A267	Fairmead	Molar	<i>Mammuthus columbi</i>	-10.7	25.2
UCMP 141402	Fairmead	Molar	<i>Mammuthus columbi</i>	-11.1	26.6
MCPC A1339	Fairmead	Molar	<i>Mammuthus columbi</i>	-9.3	23.9
MCPC A320	Fairmead	Molar	<i>Mammuthus columbi</i>	-12.2	28.1
MCPC A2247	Fairmead	Molar	<i>Mammuthus columbi</i>	-11.6	24.9
MCPC A1286	Fairmead	Molar	<i>Mammuthus columbi</i>	-9.7	22.4

Collection #	Locality	Tooth	Taxa	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
MCPC A321	Fairmead	p4	<i>Platygonus vetus</i>	-13.5	29.1
UCMP 140410	Fairmead	lm2	<i>Tetrameryx irvingtonensis</i>	-10.8	30.2
MCPC A2253	Fairmead	lm3	<i>Tetrameryx irvingtonensis</i>	-11	29.2
MCPC A1065	Fairmead	lm1	<i>Tetrameryx irvingtonensis</i>	-11.5	33.3
UCMP 197567 (mean)	Fairmead	lm3	<i>Tetrameryx irvingtonensis</i>	-10.5	28.6
MCPC A1449	Fairmead	lm3	<i>Capromeryx</i>	-11.1	26.6
UCMP 33111	McKittrick	C	<i>Arctodus simus</i>	-10.9	27
UCMP 212885	McKittrick	rm2	<i>Canis dirus</i>	-2.2	24.2
UCMP 212889	McKittrick	rm2	<i>Canis dirus</i>	-5.6	26.8
UCMP 212887	McKittrick	rm2	<i>Canis dirus</i>	-1.7	30.3
UCMP 212891	McKittrick	rm2	<i>Canis dirus</i>	-11.8	27.1
UCMP 212890	McKittrick	rm2	<i>Canis dirus</i>	-3	26.5
UCMP 212888	McKittrick	rm2	<i>Canis dirus</i>	-5.2	28.6
UCMP 212886	McKittrick	rm2	<i>Canis dirus</i>	-7.4	27.3
UCMP 212877	McKittrick	rm2	<i>Canis latrans</i>	-5.5	28.9
UCMP 212882	McKittrick	rm2	<i>Canis latrans</i>	-5	33.7
UCMP 212883	McKittrick	rm2	<i>Canis latrans</i>	-3	31.7
UCMP 212878	McKittrick	rm2	<i>Canis latrans</i>	-5.2	31.1
UCMP 212881	McKittrick	rm2	<i>Canis latrans</i>	-1.6	31.7
UCMP 212879	McKittrick	rm2	<i>Canis latrans</i>	-4.7	33.6
UCMP 212884	McKittrick	rm2	<i>Canis latrans</i>	-7.2	28
UCMP 153243	McKittrick	lm1	<i>Panthera atrox</i>	-11.8	25.1
UCMP 153241	McKittrick	lc	<i>Panthera atrox</i>	-10.1	26.3
UCMP 153742	McKittrick	lm2	<i>Panthera atrox</i>	-7.8	29.8
UCMP 212876	McKittrick	lm3	<i>Bison sp.</i>	-4.9	23.9
UCMP 212895	McKittrick	lm3	<i>Camelops hesternus</i>	-2.9	26.5
UCMP 212897	McKittrick	lm3	<i>Camelops hesternus</i>	-2.6	26.2

Collection #	Locality	Tooth	Taxa	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
UCMP 212893 (mean)	McKittrick	lm2	<i>Camelops hesternus</i>	-4.8	30.8
UCMP 212894	McKittrick	lm2	<i>Camelops hesternus</i>	-0.7	30.2
UCMP 212896	McKittrick	lm3	<i>Camelops hesternus</i>	-1.8	27.1
UCMP 153257	McKittrick	rM3	<i>Cervus elaphus</i>	-11.3	24.8
UCMP 212870	McKittrick	rP2	<i>Equus sp.</i>	-6.8	26.7
UCMP 212873	McKittrick	rP2	<i>Equus sp.</i>	-2.3	23.7
UCMP 212871	McKittrick	rP2	<i>Equus sp.</i>	-7.4	27.4
UCMP 212875	McKittrick	rP2	<i>Equus sp.</i>	-7.6	27.5
UCMP 212874 (mean)	McKittrick	rP2	<i>Equus sp.</i>	-6.7	27
UCMP 212872 (mean)	McKittrick	rP2	<i>Equus sp.</i>	-7.7	27
UCMP 24258	McKittrick	rm3	<i>Hemiauchenia macrocephala</i>	-4.3	27.6
UCMP 235129	McKittrick	rm2	<i>Mammut americanum</i>	-8.4	27.4

Table A2. Data For Serial Sampled Taxa.

Collection #	Locality	Taxa	Position (mm)	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
MCPC 1902a.a	Fairmead	<i>Equus sp.</i>	1	-12.8	27.5
MCPC 1902a.b	Fairmead	<i>Equus sp.</i>	3	-13.1	28.1
MCPC 1902a.c	Fairmead	<i>Equus sp.</i>	5	-13.2	28.4
MCPC 1902a.d	Fairmead	<i>Equus sp.</i>	8	-12.7	27.8
MCPC 1902a.e	Fairmead	<i>Equus sp.</i>	13	-12.4	26.6
MCPC 1902a.f	Fairmead	<i>Equus sp.</i>	15	-12.6	27.1
MCPC 1902a.g	Fairmead	<i>Equus sp.</i>	17	-12.9	27.6
MCPC 1902a.h	Fairmead	<i>Equus sp.</i>	20	-12.9	27.5
MCPC 1902a.i	Fairmead	<i>Equus sp.</i>	22	-12.9	27.2
MCPC 1902a.j	Fairmead	<i>Equus sp.</i>	24	-12.5	26.4
MCPC 1902a.k	Fairmead	<i>Equus sp.</i>	26	-12.5	26.7
MCPC 1902a.l	Fairmead	<i>Equus sp.</i>	28	-13.0	26.8
MCPC 1902a.m	Fairmead	<i>Equus sp.</i>	30	-12.9	26.8
MCPC 1902a.n	Fairmead	<i>Equus sp.</i>	32	-12.9	26.6
MCPC 1902a.o	Fairmead	<i>Equus sp.</i>	34	-13.1	26.6
MCPC 1902a.p	Fairmead	<i>Equus sp.</i>	37	-13.1	26.7
MCPC 1902a.q	Fairmead	<i>Equus sp.</i>	39	-13.1	26.7
MCPC 1902a.r	Fairmead	<i>Equus sp.</i>	41	-13.1	26.9
MCPC 1902a.s	Fairmead	<i>Equus sp.</i>	44	-12.9	26.5
MCPC 1902a.t	Fairmead	<i>Equus sp.</i>	46	-12.7	26.8
MCPC 1902a.u	Fairmead	<i>Equus sp.</i>	48	-12.5	26.7
MCPC A579.a	Fairmead	<i>Equus sp.</i>	3	-8.7	26.8

Collection	#	Locality	Taxa	Position (mm)	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
MCPC	A579.b	Fairmead	<i>Equus sp.</i>	5	-8.8	26.5
MCPC	A579.c	Fairmead	<i>Equus sp.</i>	7	-8.3	26.7
MCPC	A579.d	Fairmead	<i>Equus sp.</i>	10	-8.6	26.6
MCPC	A579.e	Fairmead	<i>Equus sp.</i>	12	-8.5	27.1
MCPC	A579.f	Fairmead	<i>Equus sp.</i>	14	-8.6	26.7
MCPC	A579.g	Fairmead	<i>Equus sp.</i>	17	-8.7	26.6
MCPC	A579.h	Fairmead	<i>Equus sp.</i>	19	-8.6	26.8
MCPC	A579.i	Fairmead	<i>Equus sp.</i>	21	-8.6	26.1
MCPC	A579.j	Fairmead	<i>Equus sp.</i>	23	-8.5	26.5
MCPC	A579.k	Fairmead	<i>Equus sp.</i>	25	-8.0	26.6
MCPC	A579.l	Fairmead	<i>Equus sp.</i>	27	-8.0	26.8
MCPC	A579.m	Fairmead	<i>Equus sp.</i>	30	-8.0	26.7
MCPC	A579.n	Fairmead	<i>Equus sp.</i>	32	-8.3	26.8
MCPC	A579.o	Fairmead	<i>Equus sp.</i>	34	-8.0	27.2
MCPC	A579.p	Fairmead	<i>Equus sp.</i>	36	-8.4	27.7
MCPC	A579.q	Fairmead	<i>Equus sp.</i>	39	-9.1	29.4
MCPC	A579.r	Fairmead	<i>Equus sp.</i>	41	-9.0	29.2
MCPC	A579.s	Fairmead	<i>Equus sp.</i>	43	-8.1	29.3
MCPC	A1355a.a	Fairmead	<i>Equus sp.</i>	2	-8.1	25.4
MCPC	A1355a.b	Fairmead	<i>Equus sp.</i>	4	-8.3	25.3
MCPC	A1355a.c	Fairmead	<i>Equus sp.</i>	6	-8.3	25.5
MCPC	A1355a.d	Fairmead	<i>Equus sp.</i>	8	-8.3	25.6
MCPC	A1355a.e	Fairmead	<i>Equus sp.</i>	10	-8.2	25.9
MCPC	A1355a.f	Fairmead	<i>Equus sp.</i>	12	-8.2	25.7

Collection #	Locality	Taxa	Position (mm)	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
MCPC A1355a.g	Fairmead	<i>Equus sp.</i>	13	-8.2	25.8
MCPC A1355a.h	Fairmead	<i>Equus sp.</i>	16	-8.1	25.4
MCPC A1355a.i	Fairmead	<i>Equus sp.</i>	18	-8.2	25.1
MCPC A1355a.j	Fairmead	<i>Equus sp.</i>	20	-8.3	24.8
MCPC A1355a.k	Fairmead	<i>Equus sp.</i>	22	-8.5	24.3
MCPC A1355a.l	Fairmead	<i>Equus sp.</i>	24	-8.6	23.8
MCPC A1355a.m	Fairmead	<i>Equus sp.</i>	27	-8.9	23.3
MCPC A1355a.n	Fairmead	<i>Equus sp.</i>	29	-9.0	22.8
MCPC A1355a.o	Fairmead	<i>Equus sp.</i>	31	-9.1	22.9
MCPC A1355a.p	Fairmead	<i>Equus sp.</i>	33	-9.4	22.9
MCPC A1355a.q	Fairmead	<i>Equus sp.</i>	36	-9.7	23.0
MCPC A1355a.r	Fairmead	<i>Equus sp.</i>	38	-9.9	23.6
MCPC A1355a.s	Fairmead	<i>Equus sp.</i>	41	-9.8	23.5
MCPC A1355a.t	Fairmead	<i>Equus sp.</i>	43	-9.5	23.4
MCPC A1355a.u	Fairmead	<i>Equus sp.</i>	45	-9.3	23.9
MCPC A1355a.v	Fairmead	<i>Equus sp.</i>	48	-9.4	24.4
MCPC A282.a	Fairmead	<i>Camelops sp.</i>	3	-9.9	25.8
MCPC A282.b	Fairmead	<i>Camelops sp.</i>	6	-9.6	26.2
MCPC A282.c	Fairmead	<i>Camelops sp.</i>	9	-9.4	25.5
MCPC A282.d	Fairmead	<i>Camelops sp.</i>	11	-9.2	25.4
MCPC A282.e	Fairmead	<i>Camelops sp.</i>	14	-9.1	25.1
MCPC A282.f	Fairmead	<i>Camelops sp.</i>	16	-8.9	24.8
MCPC A282.g	Fairmead	<i>Camelops sp.</i>	19	-8.5	24.5
MCPC A282.h	Fairmead	<i>Camelops sp.</i>	21	-8.8	24.5

Collection #	Locality	Taxa	Position (mm)	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
MCPC A282.i	Fairmead	<i>Camelops sp.</i>	24	-8.7	24.4
MCPC A282.j	Fairmead	<i>Camelops sp.</i>	26	-8.7	24.5
MCPC A282.k	Fairmead	<i>Camelops sp.</i>	29	-8.6	24.5
MCPC A282.l	Fairmead	<i>Camelops sp.</i>	33	-8.3	24.4
MCPC A282.m	Fairmead	<i>Camelops sp.</i>	35	-8.4	24.0
MCPC A282.n	Fairmead	<i>Camelops sp.</i>	38	-8.5	24.0
MCPC A282.o	Fairmead	<i>Camelops sp.</i>	40	-8.7	24.3
MCPC A282.p	Fairmead	<i>Camelops sp.</i>	44	-8.6	24.4
UCMP 197567.a	Fairmead	<i>Tetrameryx irvingtonensis</i>	5	-10.0	28.1
UCMP 197567.b	Fairmead	<i>Tetrameryx irvingtonensis</i>	7	-10.2	29.2
UCMP 197567.c	Fairmead	<i>Tetrameryx irvingtonensis</i>	9	-9.5	29.0
UCMP 197567.d	Fairmead	<i>Tetrameryx irvingtonensis</i>	11	-9.5	28.7
UCMP 197567.e	Fairmead	<i>Tetrameryx irvingtonensis</i>	13	-10.2	30.3
UCMP 197567.f	Fairmead	<i>Tetrameryx irvingtonensis</i>	16	-10.6	31.3
UCMP 197567.g	Fairmead	<i>Tetrameryx irvingtonensis</i>	17	-10.8	31.2
UCMP 197567.h	Fairmead	<i>Tetrameryx irvingtonensis</i>	20	-11.6	30.5
UCMP 197567.i	Fairmead	<i>Tetrameryx irvingtonensis</i>	22	-11.7	28.3
UCMP 197567.j	Fairmead	<i>Tetrameryx irvingtonensis</i>	25	-11.1	27.5
UCMP 197567.k	Fairmead	<i>Tetrameryx irvingtonensis</i>	27	-10.6	26.6
UCMP 197567.l	Fairmead	<i>Tetrameryx irvingtonensis</i>	30	-10.8	25.8
UCMP 197567.m	Fairmead	<i>Tetrameryx irvingtonensis</i>	33	-10.3	24.9
UCMP 197566.a	Fairmead	<i>Homotherium sp.</i>	2	-13.3	28.8
UCMP 197566.b	Fairmead	<i>Homotherium sp.</i>	4	-13.5	28.4

Collection #	Locality	Taxa	Position (mm)	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
UCMP 197566.c	Fairmead	<i>Homotherium sp.</i>	6	-13.7	27.9
UCMP 197566.d	Fairmead	<i>Homotherium sp.</i>	8	-13.6	27.5
UCMP 197566.e	Fairmead	<i>Homotherium sp.</i>	11	-13.4	26.4
UCMP 197566.f	Fairmead	<i>Homotherium sp.</i>	13	-13.7	26.2
UCMP 197566.g	Fairmead	<i>Homotherium sp.</i>	15	-13.1	25.5
UCMP 197566.h	Fairmead	<i>Homotherium sp.</i>	21	-13.0	24.3
UCMP 197566.i	Fairmead	<i>Homotherium sp.</i>	24	-12.6	24.9
UCMP 197566.j	Fairmead	<i>Homotherium sp.</i>	27	-11.9	24.0
UCMP 197566.k	Fairmead	<i>Homotherium sp.</i>	29	-14.0	25.7
UCMP 197566.l	Fairmead	<i>Homotherium sp.</i>	32	-14.3	26.4
UCMP 197566.m	Fairmead	<i>Homotherium sp.</i>	34	-14.0	27.1
UCMP 197566.n	Fairmead	<i>Homotherium sp.</i>	37	-14.1	27.8
UCMP 197566.o	Fairmead	<i>Homotherium sp.</i>	40	-14.4	29.2
UCMP 197566.p	Fairmead	<i>Homotherium sp.</i>	43	-14.0	28.7
UCMP 212872.a	McKittrick	<i>Equus sp.</i>	64	-7.5	26.3
UCMP 212872.b	McKittrick	<i>Equus sp.</i>	61	-7.1	26.7
UCMP 212872.c	McKittrick	<i>Equus sp.</i>	58	-7.9	26.6
UCMP 212872.d	McKittrick	<i>Equus sp.</i>	55	-8.7	27.1
UCMP 212872.e	McKittrick	<i>Equus sp.</i>	52	-8.3	27.0
UCMP 212872.f	McKittrick	<i>Equus sp.</i>	49	-7.8	27.0
UCMP 212872.g	McKittrick	<i>Equus sp.</i>	46	-8.0	28.2
UCMP 212872.h	McKittrick	<i>Equus sp.</i>	42	-8.2	28.3
UCMP 212872.i	McKittrick	<i>Equus sp.</i>	40	-7.4	27.7
UCMP 212872.j	McKittrick	<i>Equus sp.</i>	36	-7.7	27.5

Collection #	Locality	Taxa	Position (mm)	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
UCMP 212872.k	McKittrick	<i>Equus sp.</i>	34	-7.8	26.9
UCMP 212872.l	McKittrick	<i>Equus sp.</i>	30	-7.2	26.4
UCMP 212872.m	McKittrick	<i>Equus sp.</i>	27	-7.5	26.3
UCMP 212872.n	McKittrick	<i>Equus sp.</i>	24	-7.5	26.9
UCMP 212872.o	McKittrick	<i>Equus sp.</i>	21	-7.8	27.0
UCMP 212872.p	McKittrick	<i>Equus sp.</i>	17	-7.7	26.3
UCMP 212872.q	McKittrick	<i>Equus sp.</i>	15	-7.4	25.9
UCMP 212874.a	McKittrick	<i>Equus sp.</i>	14	-7.2	27.2
UCMP 212874.b	McKittrick	<i>Equus sp.</i>	17	-6.2	27.1
UCMP 212874.c	McKittrick	<i>Equus sp.</i>	21	-6.1	27.4
UCMP 212874.d	McKittrick	<i>Equus sp.</i>	24	-6.6	28.3
UCMP 212874.e	McKittrick	<i>Equus sp.</i>	27	-6.8	28.0
UCMP 212874.f	McKittrick	<i>Equus sp.</i>	30	-6.3	27.4
UCMP 212874.g	McKittrick	<i>Equus sp.</i>	33	-6.3	27.4
UCMP 212874.h	McKittrick	<i>Equus sp.</i>	36	-6.6	27.5
UCMP 212874.i	McKittrick	<i>Equus sp.</i>	38	-6.3	27.0
UCMP 212874.j	McKittrick	<i>Equus sp.</i>	41	-6.5	26.8
UCMP 212874.k	McKittrick	<i>Equus sp.</i>	43	-6.3	26.3
UCMP 212874.l	McKittrick	<i>Equus sp.</i>	46	-6.9	26.0
UCMP 212874.m	McKittrick	<i>Equus sp.</i>	48	-6.9	26.2
UCMP 212874.n	McKittrick	<i>Equus sp.</i>	51	-6.4	25.7
UCMP 212874.o	McKittrick	<i>Equus sp.</i>	53	-7.9	25.7
UCMP 212874.p	McKittrick	<i>Equus sp.</i>	55	-6.2	25.8
UCMP 212874.q	McKittrick	<i>Equus sp.</i>	58	-7.2	26.4

Collection #	Locality	Taxa	Position (mm)	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
UCMP 212874.r	McKittrick	<i>Equus sp.</i>	60	-6.7	27.2
UCMP 212874.s	McKittrick	<i>Equus sp.</i>	62	-6.8	27.6
UCMP 212874.t	McKittrick	<i>Equus sp.</i>	64	-7.1	27.8
UCMP 212874.u	McKittrick	<i>Equus sp.</i>	66	-6.8	27.6
UCMP 212874.v	McKittrick	<i>Equus sp.</i>	68	-6.8	27.7
UCMP 212893.a	McKittrick	<i>Camelops hesternus</i>	6	-3.1	29.3
UCMP 212893.b	McKittrick	<i>Camelops hesternus</i>	8	-2.8	29.5
UCMP 212893.c	McKittrick	<i>Camelops hesternus</i>	11	-2.8	29.9
UCMP 212893.d	McKittrick	<i>Camelops hesternus</i>	14	-2.9	30.3
UCMP 212893.e	McKittrick	<i>Camelops hesternus</i>	17	-3.0	30.3
UCMP 212893.f	McKittrick	<i>Camelops hesternus</i>	19	-4.3	30.8
UCMP 212893.g	McKittrick	<i>Camelops hesternus</i>	22	-4.0	31.2
UCMP 212893.h	McKittrick	<i>Camelops hesternus</i>	24	-5.0	31.2
UCMP 212893.i	McKittrick	<i>Camelops hesternus</i>	26	-4.9	31.4
UCMP 212893.j	McKittrick	<i>Camelops hesternus</i>	28	-5.3	31.8
UCMP 212893.k	McKittrick	<i>Camelops hesternus</i>	31	-5.2	31.8
UCMP 212893.l	McKittrick	<i>Camelops hesternus</i>	33	-5.6	31.5
UCMP 212893.m	McKittrick	<i>Camelops hesternus</i>	35	-6.1	32.0
UCMP 212893.n	McKittrick	<i>Camelops hesternus</i>	36	-5.8	32.4
UCMP 212893.o	McKittrick	<i>Camelops hesternus</i>	39	-6.0	32.0
UCMP 212893.p	McKittrick	<i>Camelops hesternus</i>	41	-5.6	31.4
UCMP 212893.q	McKittrick	<i>Camelops hesternus</i>	43	-5.9	30.9
UCMP 212893.r	McKittrick	<i>Camelops hesternus</i>	46	-5.9	30.4
UCMP 212893.s	McKittrick	<i>Camelops hesternus</i>	48	-5.9	30.1

Collection #	Locality	Taxa	Position (mm)	$\delta^{13}\text{C}$ V-PDB	$\delta^{18}\text{O}$ V-SMOW
UCMP 212893.t	McKittrick	<i>Camelops hesternus</i>	51	-5.7	29.9
UCMP 212893.u	McKittrick	<i>Camelops hesternus</i>	53	-4.5	29.7
UCMP 212893.v	McKittrick	<i>Camelops hesternus</i>	55	-5.1	29.7

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