Paleobiology, 29(2), 2003, pp. 230–242

Stable isotopes, hypsodonty, and the paleodiet of *Hemiauchenia* (Mammalia: Camelidae): a morphological specialization creating ecological generalization

Robert S. Feranec

Abstract.—Morphological adaptations may indicate increased specialization (narrowing of ecological niche) or expansion of the suite of lifestyles available to an organism (increasing niche breadth). Hypsodonty in mammals generally has been interpreted as a specialization into a grazing niche from a browsing niche. Here I examine the feeding strategy of the extinct hypsodont camel *Hemiauchenia* through an analysis of stable carbon isotope values from its tooth enamel, which was used to clarify its feeding strategy and to resolve conflicting interpretations of dental versus muzzle attributes. The paleodiet of *Hemiauchenia* is then used to test whether hypsodonty correlates to grazing within fossil Lamini. This study focuses on fossils from Florida, which is geographically ideal because unlike other regions of the country almost all extant plants on which animals browse use the C_3 photosynthetic pathway. In contrast, most of the grasses and sedges utilized by grazers use the C_4 photosynthetic pathway. If *Hemiauchenia* was an obligate grazer, the stable carbon isotope values of tooth enamel should reflect primarily a diet of C_4 grass and sedge (>-1.3‰). If *Hemiauchenia* was mainly a browser, the isotopic value should be considerably more negative reflecting ingestion primarily of C_3 browse (<-7.9‰). The mean $\delta^{13}C$ values for *Hemiauchenia* during each time interval average more negative than -8.0‰, indicating a dominantly C_3 browse diet, and there is no evidence for abandonment of the browsing niche from the Hemphillian through the Rancholabrean North American Land Mammal Ages. However, an increase in the range of isotopic values indicates a diet with a higher proportion of C_4 grasses and sedges through time. This study therefore suggests that *Hemiauchenia* was a hypsodont *intermediate feeder with preference for browse* during the past 5 million years. Hypsodonty is not strictly associated with obligate grazing; instead it may, in this case, represent an adaptation to widen niche breadth that allowed grazing as well as browsing.

Robert S. Feranec. Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, California 94720. E-mail: feranec@socrates.berkeley.edu

Accepted: 31 October 2002

Introduction

Determining the diet of ancient animals has important implications for interpreting paleocommunity structure. For example, determining whether extinct herbivores are browsers, intermediate feeders, or grazers is required to understand details of resource partitioning, which ultimately influences diversity in ecosystems by affecting competition and allowing for the co-occurrence of species (Hutchinson 1958). The interpretation of feeding strategy for ungulates is that there was a progression through a pathway from browsing to intermediate feeding to grazing, with the ancestral state in diet being browsing and the derived state being grazing (Perez-Barberia et al. 2001). What has been unclear, however, is whether increasing hypsodonty indicates increased specialization for abrasive foods at the expense of browse, or an actual broadening of niche breadth by simply adding the ability to graze. At issue is whether extinct hypsodont animals were obligate grazers, or whether they continued to utilize browse plants in significant quantities and added a grazing component to their feeding strategy.

Because fossils are rarely preserved with any direct physical evidence of diet, indirect proxies are commonly used to assess feeding strategies. Dietary proxies include morphological characteristics of the skull, such as hypsodonty of teeth and shape of the muzzle. Such data, however, can lead to conflicting interpretations of diet (Webb 1974; Dompierre and Churcher 1996). A prime example of this conflict involves the feeding ecology of *Hemiauchenia*. *Hemiauchenia* is an extinct genus of llama that ranged from the late Barstovian (ca. 13 Ma) to the late Rancholabrean (ca. 0.01 Ma) North American Land Mammal Ages (NAL-

0094-8373/03/2902-0006/$1.00

MA) in North America (Honey et al. 1998). This genus has been suggested to comprise only browsers, according to morphological characteristics of the snout (Dompierre and Churcher 1996), or to include intermediate feeders with a preference for grasses, according to the presence of hypsodont teeth and abundant cementum (Webb 1974; Webb and Stehli 1995). This study uses stable carbon isotopes and measures of hypsodonty to determine the feeding strategy employed by *Hemiauchenia* during the past 5 million years. The results are then used to assess whether the attainment of hypsodonty within the Lamini evolved through the progression of browsing to intermediate feeding to grazing, and whether hypsodont animals are specialized grazers.

Background Information

As mentioned above, hypsodonty and the shape of the ungulate muzzle are but two morphological proxies used to interpret paleodiet. Generally, more hypsodont animals tend to feed on grasses and live in open habitats. Because the spread of grasslands during the Miocene appears roughly coincident with widespread hypsodonty, it has been hypothesized that hypsodonty evolved as a coevolutionary response to the spread of phytolith-laden grasses, and as an adaptation to deal with grit and dirt that typically coats plants in open habitats (McNaughton et al. 1985; Janis 1988, 1989, 1995; MacFadden 1997). With respect to the shape of the muzzle in ungulates, grazers have a broad muzzle capable of feeding on large quantities of low-lying forage, and browsers generally have narrow muzzles for manipulating through branches to select choice, succulent forage. Intermediate feeders generally have muzzle widths in between (Janis and Ehrhardt 1988; Solounias et al. 1988; Dompierre and Churcher 1996).

Modern Ungulate Feeding Categories.—Hofmann and Stewart (1972) used forage composition and stomach structure, to characterize modern ungulate feeding strategy into three main types: *concentrate selectors* (*browsers*), which focus feeding on flora other than grasses and sedges (browse); *bulk and roughage feeders* (*grazers*), which concentrate feeding on grasses and sedges; *intermediate feeders*, which have a composite diet of grasses and sedges, and browse. These three categories have been adopted in much of the paleoecological literature for interpretation of paleoungulate diets, and for use in paleoenvironment interpretation (e.g., Janis 1988; Quade et al. 1992; Solounias et al. 1995; MacFadden and Cerling 1996; Janis et al. 2000). In using these three categories alone, much of the complexity in feeding in ungulates is obscured; for example, an intermediate feeder does not necessarily have a diet midway between a browser and a grazer. Hofmann and Stewart (1972) suggested further subcategories within the three main categories to reflect some of this complexity. Thus, concentrate selectors can be subdivided into *tree and shrub foliage eaters* and *fruit and dicot foliage eaters.* Bulk and roughage feeders include the subcategories *roughage grazers, fresh grass grazers,* and *dry region grazers.* Within intermediate feeder are the subcategories *preferring grasses* and *preferring forbs, shrubs, and tree foliage.* However, these subcategories are seldom used in paleobiological studies because it generally is difficult to determine the percent of a particular forage type within the diet of an extinct ungulate. Whereas one can observe the forage and droppings of modern ungulates, it is often difficult or impossible to link paleobotanical remains and/or coprolites to particular extinct animals. However, as is explained below, in a restricted geographical area in which the flora is relatively well known, the analysis of stable carbon isotopes in the tooth enamel of extinct herbivores provides a means for determining the percentage of certain forage in the diet. This proxy can be used to distinguish browsers, grazers, intermediate feeder with a preference for grasses and sedges, and intermediate feeder with a preference for browse.

Carbon Isotopes and Diet.—The carbon isotope values of fossil teeth are useful in paleodiet studies because different photosynthetic pathways impart different ratios of $^{13}C/^{12}C$ in different kinds of plants, which are ultimately reflected in the animals that eat them. Plants can be grouped into three main photosynthetic pathways: C_3, C_4, and Crassulacean Acid Metabolism (CAM). Tropical, warm-season sedges and grasses using the Hatch-Slack photosynthetic pathway (C_4) are enriched in the heavy carbon isotope (^{13}C). Conversely, Calvin cycle plants (C_3), including most browse and high-latitude grasses, are enriched in the light carbon isotope (^{12}C). The third pathway, the CAM pathway, is characteristic of succulents and incorporates intermediate ratios of ^{12}C and ^{13}C (O'Leary 1988; Ehleringer et al. 1991; Ehleringer and Monson 1993). Animals that feed upon these various kinds of plants will reflect the isotope ratio ($^{13}C/^{12}C$) ingested (DeNiro and Epstein 1978; Quade et al. 1992). The $^{13}C/^{12}C$ ratio of tooth enamel is further enriched by a consistent amount, which is about +14‰ for the tooth enamel of medium- to large-bodied mammals (Cerling and Harris 1999). Although post-depositional diagenesis can overprint carbon isotope values in bone (Schoeninger and DeNiro 1982), tooth enamel is not prone to diagenetic alteration and thus reliably reflects isotope values derived from feeding (Quade et al. 1992; Wang and Cerling 1994; Koch et al. 1997). As a general guide, grazers are predominantly C_4 feeders, browsers are predominantly C_3 foragers, and intermediate and CAM feeders utilize both C_3 and C_4 plants. Care must be taken when interpreting carbon isotopic values in herbivore tissue because some grasses, especially those above 43°N latitude, use the C_3 pathway; some browse uses the C_4 pathway, especially in lower latitudes and drier climates; and animals that are strict CAM feeders can show values similar to either C_3 or C_4 feeders (Teeri and Stowe 1976; Stowe and Teeri 1978; O'Leary 1988; Tieszen et al. 1997). Because CAM flora is generally only dominant in xeric habitats (Ehleringer et al. 1991), it is assumed that *Hemiauchenia* did not use this flora as a significant proportion of its diet.

Florida as a Model Location.—Florida is ideal for this study because (1) the flora eliminates many of the discrepancies that can occur when interpretation is based on isotopic values, and (2) because *Hemiauchenia* is abundant in late Tertiary through Quaternary deposits. Nearly all present-day browse in Florida is C_3 (>97% [Stowe and Teeri 1978]), whereas most of the grasses and sedges are C_4 (>63% for Poaceae, and up to 43% for Cyperaceae [Teeri and Stowe 1976; Teeri et al. 1980; Sage et al. 1999]). Two studies of modern floral composition on sites near fossil localities within this study show that even though C_3 grasses and sedges may be present and represent up to 40% of the species richness of grasses, C_3 grasses are generally confined to wet and marshy areas and are not widespread on the landscape (Easley and Judd 1990; Huffman and Judd 1998). Many of the fossil localities within this study are suggested to have floras similar to the interglacial floras of today (Webb 1991; Rich and Newsom 1995), and models of past floras during glacial stages would suggest the spread of grasslands and an increase in dominance of grasses and sedges using C_4 photosynthesis due to decreasing CO_2 levels (Webb 1991; Ehleringer et al. 1997; Cowling 1999). This would suggest that percentages of C_3 grasses in Florida are unlikely to have been significantly greater during the past, and because C_4 browse is rare, it is unlikely that these percentages have significantly changed.

Materials and Methods

Definitions and Feeding Strategies.—*Grazers* are strictly defined in this study as animals that eat grasses and sedges (Poaceae and Cyperaceae) as at least 90% of their diet. *Browsers* are considered here to have diets consisting nearly exclusively of non-grasses and sedges, that is browse (>90%). Intermediate feeders eat both grasses and sedges, and browse (i.e., >10% grasses and sedges, and browse). This type of designation is appropriate because anatomical and physiological differences characterize animals that focus feeding on grasses and sedges and/or browse. Grazers, for example, must deal with abundant abrasive phytoliths and grit from feeding close to the ground, and accordingly develop strategies to deal with tooth abrasion. Browsers, on the other hand, ingest more anti-herbivory chemicals such as tannins (McNaughton 1991; Heckathorn et al. 1999), which necessitate strategies to deal with these secondary chemicals, but tooth abrasion offers less of a selective pressure than it does for grazers. The definitions used in this paper parallel the cate-

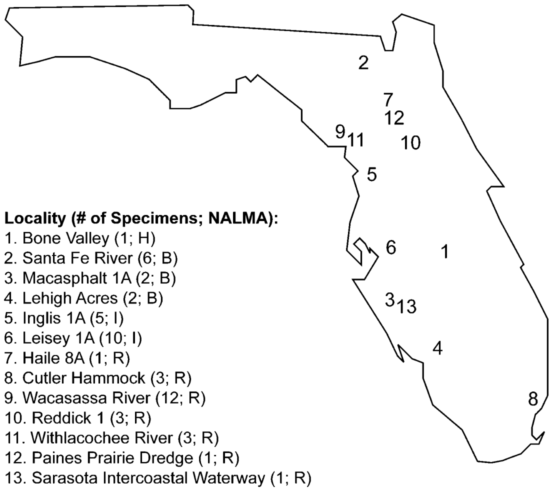

FIGURE 1. Fossil localities in Florida of the *Hemiauchenia* samples used in this study. Items in parentheses refer to the number of specimens from the locality and to the North American Land Mammal Age. Abbreviations as follows: H = Hemphillian, B = Blancan, I = Irvingtonian, R = Rancholabrean.

gories of Hofmann and Stewart (1972) for ease in comparison with modern ungulate analogs and other paleoecological studies. Where possible the subcategories *prefers grasses and sedges* and *prefers browse* similar to Hofmann and Stewart (1972) are also used for intermediate feeders.

Stable Isotope Analysis.—*Hemiauchenia* molars were obtained from the Vertebrate Paleontology collection at the Florida Museum of Natural History (FLMNH) and include four species: *H. vera*, *H. blancoensis*, *H. seymourensis*, and *H. macrocephala*. The teeth range in age from the latest Hemphillian (ca. 5 Ma) to the latest Rancholabrean (ca. 10 Ka) NALMAs and were taken from sites extending through the entire peninsula of Florida (Fig. 1). The ages of the included localities were determined biochronologically by assignment to North American Land Mammal Ages (Lundelius et al. 1987; Woodburne 1987; MacFadden and Cerling 1996). The Leisey Shell Pit locality has also been paleomagnetically dated at 1.5 Ma (MacFadden 1995).

The general method for stable isotope sampling followed MacFadden and Cerling (1996) and Koch et al. (1997). Because the goal of the study was to recognize the feeding strategy of adult animals, sampling focused on but was not confined to the second through fourth premolars and third molar. These teeth are among the last ones to develop, mineralize, and erupt (Hillson 1986; Bryant et al. 1996 a,b). Sampling involved drilling 20–30 mg of pristine enamel powder off the tooth along a non-occlusal surface parallel to the growth axis and across its entire length using a 0.3-mm inverted cone carbide drill bit and a variable speed Dremel ™ rotary tool. The powder was first collected and treated with 35% hydrogen peroxide for 24 hours to remove organics. It then was decanted and washed with distilled water and soaked in 0.1 N acetic acid for another 24 hours to remove any diagenetic carbonate. The following day it was again decanted and washed with distilled water, rinsed with 100% ethyl alcohol, and dried overnight.

After treatment, the samples were analyzed by using an ISOCARB automated carbonate preparation system attached to a Micromass Optima gas source mass spectrometer within the Department of Earth and Ocean Sciences at the University of California, Santa Cruz. The ~1-mg samples were dissolved in 100% phosphoric acid at 90°C to create CO_2. The results are expressed in standard δ-notation: $X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is the $\delta^{13}C$ value, and $R = {}^{13}C/{}^{12}C$. All isotope values are reported relative to V-PDB. The precision for the analysis was ±0.1‰. A total of 31 samples were collected, prepared, and analyzed along with the data for 19 samples obtained from the published literature (MacFadden and Cerling 1996; Feranec and MacFadden 2000). Mean differences in *Hemiauchenia* between NALMAs were compared by post hoc LSD tests, which are similar to *t*-tests but take into account multiple comparisons. Statistical analyses were run on Microsoft Excel 2000 and SPSS Student Version 8.0 for Windows, with significance set at $p < 0.05$.

Carbon Isotope Values in Paleoecology.—As noted above, herbivores will reflect the carbon isotope values of plants ingested. Modern C_3 plants—trees, shrubs, and high-latitude grasses—have a carbon isotope value of −27.0‰ ± 3.0‰, whereas modern C_4 plants—tropical sedges and grasses—have a mean isotopic value of −13.0‰ ± 2.0‰

(O'Leary 1988; Quade et al. 1992; Koch et al. 1998). Because of the +14.0‰ fractionation from plant material to tooth enamel in large herbivores (Cerling and Harris 1999), modern C_3 feeders will show enamel carbon isotope values between −16.0‰ and −10.0‰, whereas modern C_4 feeders display isotopic values between −1.0‰ and +3.0‰. These enamel isotope values are based on the $\delta^{13}C$ value of the modern atmosphere, which has decreased from about −6.5‰ to about −8.0‰ as a result of fossil fuel burning over the last two hundred years (Friedli et al. 1986; Marino and McElroy 1991; Marino et al. 1992). Because $\delta^{13}C$ values of past glacial and interglacial periods are different from those of today, fossil enamel isotope values are about 0.5‰ to 1.3‰ more positive than in the modern taxa (Koch et al. 1998). For fossil enamel then, a diet of pure C_3 plants would not have an isotopic value more positive than −8.7‰, and a diet of pure C_4 plants would not have an isotopic value more negative than −0.5‰. Using these values as a continuum between 100% C_3 feeding and 100% C_4 feeding, values more negative than −7.9‰ are interpreted to indicate primarily browsing (<10% C_4 diet), values more positive than −1.3‰ are interpreted to signal primarily grazing (<10% C_3 diet), and values between −7.9‰ and −1.3‰ result from intermediate feeding strategies.

Hypsodonty Measurements.—Hypsodonty measurements for *Hemiauchenia* teeth were taken on specimens at the FLMNH and compiled from the published literature (Webb 1974; Webb and Stehli 1995). Most measurements come from second lower molars, and when possible the same teeth were sampled isotopically. Measurements of crown height and width were taken on teeth that were relatively unworn, and represent the greatest height and width for each tooth. Tooth crown measurements (height and width) for extant camelids, *Camelus*, *Lama*, and *Vicugna*, were acquired from the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley. The Hypsodonty Index (HI) was calculated as HI = Crown Height/Crown Width. Even though relatively unworn teeth were measured when possible, the HI represents a conservative estimate because any wear or incomplete eruption reduces the numerator, crown height. Because of wear and small sample sizes, these measurements are intended to show that *Hemiauchenia* was hypsodont but not to show the level of hypsodonty for any particular species or at any particular time. Relative degree of hypsodonty among species is provided by Webb (1974).

Modern Camelids and Modern Analogs.—Understanding the diets of modern camelids aids in determining the feeding strategy of *Hemiauchenia*. Modern camelids can be placed within three genera and up to six species: *Camelus* (including *C. bactrianus* and *C. dromedarius*), *Lama* (including *L. guanicoe*, *L. glama*, and *L. pacos*), and *Vicugna* (including *V. vicugna*). It is still uncertain whether the two identified species of *Camelus* or the three species of *Lama* are conspecific (Nowak 1999). Because of these taxonomic similarities and the similarity in morphology and ecology between the modern species (Nowak 1999), I treat them on the generic level. Studies on modern *Camelus* suggest that it is mainly a browser feeding predominantly, if not solely, on trees and shrubs, but is capable of feeding and subsisting on a significant quantity of grasses (>30%) when necessary (Gauthier-Pilters 1984; Newman 1984; Migongo-Bake and Hansen 1987; Kohler-Rollefson 1991; Nowak 1999). *Camelus* is therefore classified as an intermediate feeder with preference for browse. Modern *Lama* has been suggested to be an ''adaptable mixed feeder'' (Puig et al. 1996: p. 221) showing a preference for feeding on grasses, but fully able to feed on browse (Puig et al. 1996, 1997; Fraser 1998, 1999; Nowak 1999). *Lama* is classified here as an intermediate feeder with preference for grasses and sedges. Koford (1957) suggested that the main food of the *Vicugna* is grass, but that other forage such as forbs and the legume *Astragalus* was a prized food when it was, though rarely, available. *Vicugna* is classified here as a grazer. Isotopically, all modern camelid genera would be expected to exhibit a C_3 diet. This is because C_3 grass genera predominate where camelids live (Koford 1957; Puig et al. 1996, 1997; Fraser 1998, 1999; Sage et al. 1999).

This study also uses a modern analog comparison similar to the Extant Phylogenetic Bracket (EPB) method to determine if HI is an

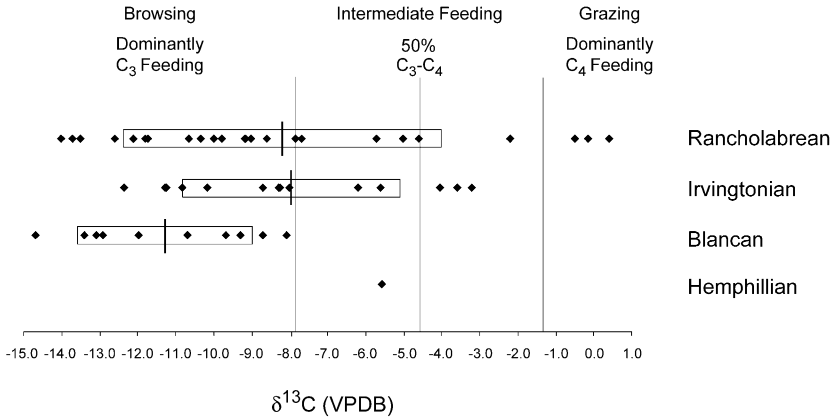

FIGURE 2. Stable carbon isotope values of *Hemiauchenia* from the Hemphillian through the Rancholabrean of North America.

osteological correlate that may be ''causally related'' to obligate grazing (Witmer 1995: p. 23). The comparison in this study differs from an EPB comparison in that a cladistic analysis with hypsodonty characters was not completed and is beyond the scope of this study. The modern analog comparison should nonetheless work in the same fashion as the EPB methodology. Therefore, if hypsodonty is a good osteological correlate for obligate grazing within fossil Lamines, then all taxa that have high-crowned teeth (the osteological correlate) should be grazers, or at least intermediate feeders with preference for grasses and sedges (the behavior or ecology). The stable isotope value of fossil enamel can be used as an independent indicator for grazing as suggested above. In this study, I use the phylogeny proposed by Honey et al. (1998), (*Camelus*, (*Hemiauchenia*, (*Lama*, *Vicugna*))), where the fossil genus *Hemiauchenia* is bracketed by the extant genera *Camelus* and *Lama-Vicugna*.

Results

Stable Carbon Isotope Analysis.—Of the 11 specimens of *Hemiauchenia* sampled from the Tertiary of Florida, one was from the Hemphillian and ten were from the Blancan. The Hemphillian specimen, from the Bone Valley Formation in Florida had a δ^{13}C value of -5.6‰ (Fig. 2, Appendix 1). The Blancan specimens had a mean δ^{13}C value of -11.3‰ and a standard deviation of 2.3‰. The isotopic values ranged from -8.1‰ to -14.7‰.

Within the Quaternary of Florida, *Hemiauchenia* is represented by 39 specimens. Fifteen Irvingtonian samples were analyzed, yielding a mean δ^{13}C value of -8.0‰ and a standard deviation of 2.9‰. The isotopic values ranged from -3.2‰ to -12.4‰. Of the 15 specimens, five specimens had values suggesting the incorporation of C_4 forage and three had isotopic values suggesting feeding on more than 50% C_4 (Fig. 2, Appendix 1). Twenty-four Rancholabrean specimens were sampled, and demonstrated a mean δ^{13}C value of -8.3‰ and a standard deviation of 4.3‰. The range in isotopic values was from $+0.4$‰ to -14.0‰. Of the 24 specimens, nine had values suggesting the incorporation of some C_4 forage into the diet. Five of these specimens had values suggesting feeding on 50% or more C_4, three of which indicated 100% C_4 feeding. The three specimens feeding on 100% C_4 were from the latest Rancholabrean (ca. 11 Ka [Emslie and Morgan 1995]) Cutler Hammock locality of southern Florida.

Post hoc LSD tests did show significant differences between the Blancan and Irvingtonian ($p = 0.032$), and between the Blancan and the Rancholabrean ($p = 0.036$).

Hypsodonty Indices.—The Hypsodonty Index (HI) in the Hemphillian for the single specimen of *Hemiauchenia* was 1.36 with a crown height of 18.1 mm and width of 13.3 mm (Table 1). The Blancan specimens had a mean HI of 1.03 with a mean height and width of 15.4 mm and 15.0 mm, respectively. The Ir-

TABLE 1. Hypsodonty measurements for *Hemiauchenia* from Florida. Most measurements were taken directly from the literature (Webb 1974; Webb and Stehli 1995). The Leisey Shell Pit 1A data are means from 18 specimens. Crown height measurements were taken from the base of the enamel to the occlusal surface of the individual tooth. Abbreviations: m1 = lower first molar; m2 = lower second molar.

Localities	Specimen number	Tooth	Crown height (mm)	HI
Hemphillian				
Bone Valley	UF 23946	m1	18.1	1.36
Blancan				
Inglis 1A	UF 18223	m2	12.3	0.78
Macasphalt Shell Pit	UF 104500	m2	18.5	1.31
Irvingtonian				
Leisey Shell Pit 1A	18 specimens	m2	35.1	2.22
Rancholabrean				
Cutler Hammock	UF 206866	m2	21.5	1.82
Waccasassa River	UF 47439	m2	30.7	2.24

vingtonian specimens had a HI of 2.22 with a height of 35.10 mm and a width of 15.80 mm. The Rancholabrean specimens had a mean HI of 2.04 with a mean height of 26.1 mm and a mean width of 12.75 mm.

Within the extant camelids, the *Camelus* sample had a mean HI of 1.48 with a mean height of 29.9 mm and a mean width of 20.2 mm (Table 2). The *Lama* sample had a mean HI of 1.30 with a mean height of 14.6 mm and a mean width of 11.6 mm. The *Vicugna* sample had a mean HI of 1.60 mm with a mean height of 14.2 mm and a mean width of 9.3 mm. The HI of both the modern and the fossil taxa identifies these animals as hypsodont, especially in view of the fact that wear or incomplete eruption means the values for HI are conservative.

Discussion

The stable carbon isotope values displayed by *Hemiauchenia* from the Late Tertiary through the Quaternary of Florida suggest that it most commonly fed as a browser but was fully capable of having a varied diet inclusive of grasses and sedges. *Hemiauchenia* is therefore classified here as an intermediate feeder with preference for browse. Those specimens with more positive $\delta^{13}C$ values conceivably were eating C_4 browse, but this is unlikely because <3% of browse species in Florida are C_4 today, and the same would have been the case through the time spanned by this study.

Comparison with Previous Isotopic Studies.—The data presented here for *Hemiauchenia* are similar to those presented by Feranec and MacFadden (2000), which showed a significant difference in carbon isotope values across the Blancan/Irvingtonian boundary. Feranec and MacFadden (2000) further suggested a change in feeding strategy from a pure browsing strategy to an intermediate feeding strategy. The data here suggest that *Hemiauchenia* maintained a predominantly browsing feed-

TABLE 2. Hypsodonty measurements for the extant camelid genera *Camelus, Lama*, and *Vicugna*. Abbreviations: m1 = lower first molar; m2 = lower second molar; L = left; R = right.

Species	Specimen number	Tooth	Crown height (mm)	HI
Camelus dromedarius	MVZ 101026	Lm1	26.8	1.37
Camelus bactrianus	MVZ 74673	Rm1	33.0	1.59
Lama sp.	MVZ 119831	Lm2	13.6	1.11
Lama sp.	MVZ 116807	Rm2	13.1	1.16
Lama guanicoe	MVZ 116318	Rm2	17.2	1.51
Vicugna vicugna	MVZ 184198	Rm2	11.8	1.13
Vicugna vicugna	MVZ 116208	Lm2	16.6	2.05

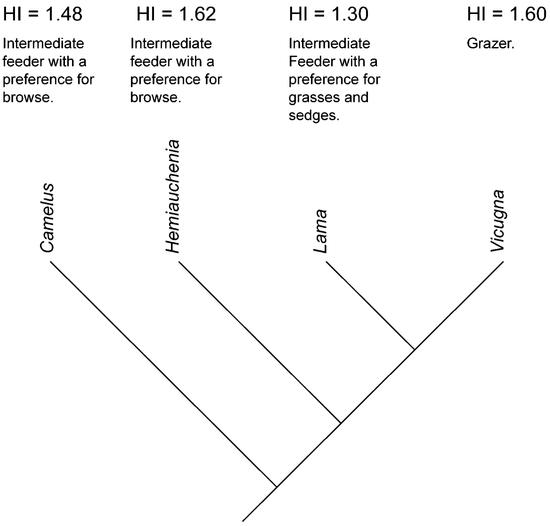

FIGURE 3. Phylogenetic relationships of *Hemiauchenia* with the mean Hypsodonty Index (HI) ''measured'' in this study and feeding strategy of the genera included. Feeding data on the extant genera are from modern studies, and those for *Hemiauchenia* come from stable carbon isotope values and knowledge of the Floridian flora. These HI values indicate that each genus is hypsodont; they are not intended to show the exact HI values for specific taxa. Because these genera are all hypsodont but are not all grazers, hypsodonty is not causally related to grazing and should not be used by itself as an indicator of paleodiet.

ing strategy but included more grasses and sedges in the diet in the Quaternary. This result may indicate a change in the flora occurring across the Blancan/Irvingtonian boundary to a more open habitat and a higher dominance of grasses and sedges. Alternatively, the result may indicate only sampling bias, with more closed-canopy sites sampled in the Blancan, and a wider range of habitats sampled in the Irvingtonian and the Rancholabrean. Because the localities from these NALMAs covers a wide geographical range (Fig. 1), a change in flora seems the more probable explanation.

Modern Analog Comparison.—All of the camelid species, both fossil and extant, had HI above 1.0, which is consistent with feeding on a higher percentage of grasses and sedges. Modern observations of extant camelids have shown them to be either intermediate feeders (*Camelus* and *Lama*) or pure grazers (*Vicugna*). The stable carbon isotope evidence and a high HI suggest that *Hemiauchenia* was a hypsodont intermediate feeder with a preference for browse (Table 1, Fig. 2). This result is similar to the findings of Dompierre and Churcher (1996), whose study used muzzle shape to determine feeding strategy and suggested that *Hemiauchenia* was a ''browser or browser-like intermediate feeder, similar to the Bactrian camel'' (Dompierre and Churcher 1996: p. 146). This study suggests that hypsodonty is not a good osteological correlate and not ''causally related'' to obligate grazing for ancient taxa within the Lamini (Fig. 3). Hypsodonty has been shown to be a spurious correlate to obligate grazing in previous studies on certain equid and proboscidean taxa as well (Cerling et al. 1999; MacFadden et al. 1999). These results are consistent, however, with the hypothesis that the ancestral ungulate feeding state is browsing, which then changes through intermediate feeding to the derived grazing strategy (Fig. 3) (Perez-Barberia et al. 2001).

Ecology of Hemiauchenia Species.—Because this study includes the species *H. vera*, *H. blancoensis*, *H. seymourensis*, and *H. macrocephala*, which occur in Florida during the Hemphillian, Blancan, Irvingtonian, and Rancholabrean, respectively, and these species are suggested to have increasing hypsodonty in that order (Webb 1974), it might be inferred that the differences seen in the carbon isotope values reveal species-level ecological differences and that hypsodonty between species does reflect those changes. This cannot be the case, however, because the least hypsodont taxa within this study, *H. vera*, has a carbon isotope value (-5.6‰) indicating an intermediate feeding diet, and the more hypsodont species *H. blancoensis* has isotopic values indicating a pure C_3 feeding strategy, i.e., browsing (Appendix 1).

Links between Hypsodonty and Grazing.—The diets of *Hemiauchenia* and many other species, which were based on the HI, have been used to infer environment and interpolate primary productivity in Nebraska (Janis et al. 2000). *Hemiauchenia* species were suggested in that study to be mesodont, and mesodont animals ''had a wider array of diets but for the most part depended on grass to a greater extent than did browsers'' (Janis et al. 2000: p. 7901). Those results are in accord with the results of this study. However, given the wide range in diet possible, as shown by the carbon isotope evidence, the link between hypsodonty and environment or amount of primary productivity in a particular area becomes weaker.

The increase in number of taxa having hypsodont dentitions has been used to suggest that C_3 grasslands became more widespread in the early Miocene (ca. 18 Ma [McNaughton et al. 1985; Janis 1989; MacFadden 1997]). New studies lend credence to this interpretation by suggesting that the abundance of grass phytoliths in sediment pushes the spread of grasslands back 10 Myr before the increase in taxa with hypsodont teeth (Strömberg et al. 2000; Strömberg 2002). Because the results reported here for *Hemiauchenia*, as well as information about equids and proboscideans (Cerling et al. 1999; MacFadden et al. 1999), indicate that hypsodonty is not always correlated with feeding on significant quantities of grasses and sedges, it may be that the development of hypsodonty primarily reflects a diet that became more generalized to include the newly widespread grasslands, rather than a strict shift from browsing to grazing.

Rates of Morphological Evolution and Diet.— This example from *Hemiauchenia* highlights the disjunction between the evolution of morphological characteristics, such as hypsodonty, and the current use of the morphology in determining an animal's ecology. In this particular example, the hypsodont morphology does not appear to reflect a specialization that restricts the animal to a grazing or primarily grass-dominated diet. This is not to say that hypsodont teeth did not evolve as an adaptation to feeding on grasses or on gritty material, but to suggest that previous feeding strategies on browse were not necessarily abandoned. This study demonstrates that a specialized dental morphology may in fact broaden the ecological niche that the organisms occupy, rather than restrict the niche. Therefore, interpretations based on assumptions that all specialized morphologies indicate a restricted ecology deserve further scrutiny using complementary lines of evidence. An important area of future investigation would be microwear studies to gain insights into the nature of the food that abraded animals teeth in the few days before they died. These studies are beyond the scope of this paper but are underway by other investigators.

Conclusions

Characterizing the diets of extinct herbivores is important before further inferences about paleoenvironment can be made. Classifying an animal or a group of animals into categories based upon a single specialization in morphology can be a useful approximation of ecological requirements. For maximal utility, however, a full understanding of the niche breadth in which the specialization is used must be ascertained. To accomplish this, multiple lines of evidence for determining the diet of the extinct animal must be used.

The data presented here for *Hemiauchenia* from the Late Tertiary through the Quaternary in Florida show that even though it had hypsodont teeth, it most commonly was an *intermediate feeder with a preference for browse.* The modern analog comparison suggests that hypsodonty is not causally related to obligate grazing in this genus of llama, or within the Lamini in general. The results are consistent with the findings of Dompierre and Churcher (1996), who inferred intermediate feeding from muzzle width, and with the hypothesis that feeding evolved from browsing through intermediate feeding and ultimately to grazing (Perez-Barberia et al. 2001). Because hypsodonty tells little about floral species that were eaten, it is only a coarse tool to interpret feeding ecology in fossil taxa: hypsodonty may make grazing possible, but it does not unequivocally mean the animal was a ''grazer.'' In fact, hypsodonty in *Hemiauchenia* appears to have widened its niche breadth relative to ancestral browsers. Whether such an interpretation reflects a general relationship between attainment of a specialization and widening of niche space remains to be tested by further studies on a variety of taxa.

Acknowledgments

This study was improved thanks to discussions and comments from A. D. Barnosky, B. J. MacFadden, C. M. Janis, D. Fox, J. Quade, H. Dompierre, M. A. Carrasco, L. Witmer, S. D. Webb, E. B. Davis, P. D'Girolamo, S. S. B. Hopkins, D. Ruez, and K. C. Smith. Funding was provided by Sigma Xi Grants-in-Aid-of-Research, the Department of Integrative Biology, and the University of California Museum of Paleontology. I thank the Florida Museum of Natural History for access to the Vertebrate Paleontology Collections, the Museum of Vertebrate Zoology at UC Berkeley for access to the ungulate collections, and P. L. Koch for running the isotope samples. This is UC Contribution to Paleobiology No. 1792.

Literature Cited

Bryant, J. D., P. N. Froelich, W. J. Showers, and B. J. Genna. 1996a. A tale of two quarries: biologic and taphonomic signatures in the oxygen isotopic composition of tooth enamel phosphate from modern and Miocene equids. Palaios 11:397–408.

———. 1996b. Biologic and climatic signals in the oxygen isotopic composition of Eocene-Oligocene equid enamel phosphate. Palaeogeography, Palaeoclimatology, Palaeoecology 126:75–89.

Cerling, T. E., and J. M. Harris. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120:347–363.

Cerling, T. E., J. M. Harris, and M. G. Leakey. 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia 120:364–374.

Cowling, S. A. 1999. Simulated effects of low atmospheric CO$_2$ on structure and composition of North American vegetation at the Last Glacial Maximum. Global Ecology and Biogeography 8:81–93.

DeNiro, M. J., and S. Epstein. 1978. Carbon isotopic evidence for different feeding patterns in two hyrax species occupying the same habitat. Science 201:906–908.

Dompierre, H., and C. S. Churcher. 1996. Premaxillary shape as an indicator of the diet of seven extinct late Cenozoic New World camels. Journal of Vertebrate Paleontology 16:141–148.

Easley, M. C., and W. S. Judd. 1990. Vascular flora of the southern upland property of Paynes Prairie State Preserve, Alachua County, Florida. Castanea 55:142–186.

Ehleringer, J. R., and R. K. Monson. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annual Review of Ecology and Systematics 24:411–439.

Ehleringer, J. R., R. F. Sage, L. B. Flanagan, and R. W. Pearcy. 1991. Climate change and the evolution of C$_4$ photosynthesis. Trends in Ecology and Evolution 6:95–99.

Ehleringer, J. R., T. E. Cerling, and B. R. Helliker. 1997. C$_4$ photosynthesis, atmospheric CO$_2$, and climate. Oecologia 112: 285–299.

Emslie, S. D., and G. S. Morgan. 1995. Taphonomy of a late Pleistocene carnivore den, Dade County, Florida. Pp. 65–83 *in* D. W. Steadman and J. I. Mead, eds. Late Quaternary environments and deep history: a tribute to Paul S. Martin. Scientific Papers, Vol. 3. The Mammoth Site of Hot Springs, Hot Springs, S. Dak.

Feranec, R. S., and B. J. MacFadden. 2000. Evolution of the grazing niche in Pleistocene mammals from Florida: evidence from stable isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology 162:155–169.

Fraser, M. D. 1998. Diet composition of guanacos (*Lama guanicoe*) and sheep (*Ovis aries*) grazing in grassland communities typical of UK uplands. Small Ruminant Research 29:201–212.

———. 1999. A comparison of the diet composition of guanacos (*Lama guanicoe*) and sheep when grazing swards with different clover: grass ratios. Small Ruminant Research 32:231–241.

Friedli, H., H. Lötscher, H. Oeschger, U. Seigenthaler, and B. Stauffer. 1986. Ice core record of the ^{13}C/^{12}C ratio of atmospheric CO$_2$ in the past two centuries. Nature 324:237–238.

Gauthier-Pilters, H. 1984. Aspects of dromedary ecology and ethology. Pp. 412–430 *in* W. R. Cockrill, ed. The camelid: an all-purpose animal. Scandinavian Institute of African Studies, Uppsala.

Heckathorn, S. A., S. J. McNaughton, and J. S. Coleman. 1999. C$_4$ plants and herbivory. Pp. 285–312 *in* R. F. Sage and R. K. Monson, eds. C$_4$ plant biology. Academic Press, New York.

Hillson, S. 1986. Teeth. Cambridge University Press, Cambridge.

Hofmann, R. R., and D. R. M. Stewart. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36:226–240.

Honey, J. G., J. A. Harrison, D. R. Prothero, and M. S. Stevens. 1998. Camelidae. Pp. 439–462 *in* C. M. Janis, K. M. Scott, and L. L. Jacobs, eds. Evolution of Tertiary mammals of North America, Vol. 1. Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge University Press, New York.

Huffman, J. M., and W. S. Judd. 1998. Vascular flora of Myakka River State Park, Sarasota and Manatee Counties, Florida. Castanea 63:25–50.

Hutchinson, G. E. 1958. Concluding remarks. Cold Springs Harbor Symposium on Quantitative Biology 22:415–427.

Janis, C. M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. Pp. 367–387 *in* D. E. Russell, J. P. Santoro, and D. Sigogneau-Russell, eds. Teeth revisited: proceedings of the VIIIth international symposium on dental morphology, Paris 1986. Mémoires du Muséum National d'Histoire Naturelle C 53:367–387.

———. 1989. A climatic explanation for patterns of evolutionary diversity in ungulate mammals. Palaeontology 32:463–481.

———. 1995. Correlations between craniodental and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. Pp. 76–98 *in* J. J. Thomason, ed. Functional morphology in vertebrate paleontology. Cambridge University Press, New York.

Janis, C. M., and D. Ehrhardt. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. Zoological Journal of the Linnean Society 92: 267–284.

Janis, C. M., J. Damuth, and J. M. Theodor. 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? Proceedings of the National Academy of Sciences USA 97:7899–7904.

Koch, P. L., N. Tuross, and M. L. Fogel. 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. Journal of Archaeological Science 24:417–429.

Koch, P. L., K. A. Hoppe, and S. D. Webb. 1998. The isotopic ecology of late Pleistocene mammals in North America, Part 1. Florida. Chemical Geology 152:119–138.

Koford, C. B. 1957. The vicuña and the puna. Ecological Monographs 27:153–219.

Kohler-Rollefson, I. U. 1991. *Camelus dromedarius*. Mammalian Species 375:1–8.

Lundelius, E. L., T. Downs, E. H. Lindsay, H. A. Semken, R. J. Zakrzewski, C. S. Churcher, C. R. Harington, G. E. Shultz, and S. D. Webb. 1987. The North American Quaternary Sequence. Pp. 211–235 *in* M. O. Woodburne, ed. Cenozoic mammals of North America: geochronology and biostratigraphy. University of California Press, Berkeley.

MacFadden, B. J. 1995. Magnetic polarity stratigraphy and correlation of the Leisey Shell Pits, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:107–116.

———. 1997. Origin and evolution of the grazing guild in New World terrestrial mammals. Trends in Ecology and Evolution 12:182–187.

MacFadden, B. J., and T. E. Cerling. 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10-million-year sequence from the Neogene of Florida. Journal of Vertebrate Paleontology 16:103–115.

MacFadden, B. J., N. Solunias, and T. E. Cerling. 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. Science 283:824–827.

Marino, B. D., and M. B. McElroy. 1991. Isotopic composition of atmospheric CO_2 inferred from carbon in C_4 plant cellulose. Nature 249:127–131.

Marino, B. D., M. B. McElroy, R. J. Salawitch, and W. G. Spaulding. 1992. Glacial-to-interglacial variations in the carbon isotopic composition of atmospheric CO_2. Nature 357:461–466.

McNaughton, S. J. 1991. Evolutionary ecology of large tropical herbivores. Pp. 509–522 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, eds. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. Wiley-Interscience, New York.

McNaughton, S. J., J. L. Tarrants, M. M. McNaughton, and R. H. Davis. 1985. Silica as a defense against herbivory and a growth promoter in African grasses. Ecology 66:528–535.

Migongo-Bake, W., and R. M. Hansen. 1987. Seasonal diets of camels, cattle, sheep, and goats in a common range in eastern Africa. Journal of Range Management 40:76–79.

Newman, D. M. R. 1984. The feeds and feeding habits of Old and New World camels. Pp. 250–292 *in* W. R. Cockrill, ed. The camelid: an all-purpose animal. Scandinavian Institute of African Studies, Uppsala.

Nowak, R. M. 1999. Walker's mammals of the world, 6th ed. Johns Hopkins University Press, Baltimore.

O'Leary, M. H. 1988. Carbon isotopes in photosynthesis. BioScience 38:328–336.

Perez-Barberia, F. J., I. J. Gordon, and C. Nores. 2001. Evolutionary transitions among feeding styles and habitats in ungulates. Evolutionary Ecology Research 3:221–230.

Puig, S., F. Videla, S. Monge, and V. Roig. 1996. Seasonal variations in guanaco diet (*Lama guanicoe* Muller 1776) and food availability in northern Patagonia, Argentina. Journal of Arid Environments 34:215–224.

Puig, S., F. Videla, and M. I. Cona. 1997. Diet and abundance of the guanaco (*Lama guanicoe* Muller 1776) in four habitats of northern Patagonia, Argentina. Journal of Arid Environments 36:343–357.

Quade, J., T. E. Cerling, J. C. Barry, M. E. Morgan, D. R. Pilbeam, A. R. Chivas, J. A. Lee-Thorp, and N. J. van der Merwe. 1992. A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. Chemical Geology (Isotope Geosciences Section) 94:183–192.

Rich, F. J., and L. A. Newsom. 1995. Preliminary palynology and macroplant report for the Leisey Shell Pits, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:117–126.

Sage, R. F., D. A. Wedin, and M. Li. 1999. The biogeography of C_4 photosynthesis: patterns and controlling factors. Pp. 313–373 *in* R. F. Sage and R. K. Monson, eds. C_4 plant biology. Academic Press, New York.

Schoeninger, M. J., and M. J. DeNiro. 1982. Carbon isotope ratios of apatite from fossil bone cannot be used to reconstruct diets of ancient animals. Nature 297:577–578.

Solounias, N., M. Teaford, and A. Walker. 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. Paleobiology 14:287–300.

Solounias, N., M. C. Moelleken, and J. M. Plavcan. 1995. Predicting the diets of extinct bovids using masseteric morphology. Journal of Vertebrate Paleontology 15:795–805.

Stowe, L. G., and J. A. Teeri. 1978. The geographic distribution of C_4 species of the Dicotyledonae in relation to climate. American Naturalist 112:609–623.

Strömberg, C. A. E. 2002. The origin and spread of grass-dominated ecosystems in the late Tertiary of North America: preliminary results concerning the evolution of hypsodonty. Palaeogeography, Palaeoclimatology, Palaeoecology 177:59–75.

Strömberg, C. A. E., H. E. LaGarry, and L. A. LaGarry. 2000. New paleobotanical records from the late Tertiary of Nebraska. Geological Society of America Abstracts with Programs 32:A-221.

Teeri, J. A., and L. G. Stowe. 1976. Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23:1–12.

Teeri, J. A., L. G. Stowe, and D. A. Livingstone. 1980. The distribution of C_4 species of the Cyperaceae in North America in relation to climate. Oecologia 47:307–310.

Tieszen, L. L., B. C. Bradley, N. B. Bliss, B. K. Wylie, and D. D. Dejong. 1997. NDVI, C3 and C4 production, and distributions in Great Plains grassland land cover classes. Ecological Applications 7:59–78.

Wang, Y., and T. E. Cerling. 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology 107:281–289.

Webb, S. D. 1974. Pleistocene mammals of Florida. University Presses of Florida, Gainesville.

———. 1991. Historical Biogeography. Pp. 70–100 *in* R. L. Myers and J. J. Ewel, eds. Ecosystems of Florida. University of Central Florida Press, Orlando.

Webb, S. D., and F. G. Stehli. 1995. Selenodont Artiodactyla (Camelidae and Cervidae) from the Leisey Shell Pits, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37:621–643.

Witmer, L. M. 1995. The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils. Pp. 19–33 *in* J. J. Thomason, ed. Functional morphology in vertebrate paleontology. Cambridge University Press, New York.

Woodburne, M. O. 1987. Cenozoic mammals of North America: geochronology and biostratigraphy. University of California Press, Berkeley.

Appendix 1

Sample number, species, UF catalog number, element sampled, locality, NALMA, and δ^{13}C value from *Hemiauchenia* specimens. ? in species column refers to suspected species based on the locality in which the element was found or age of the element. In element abbreviations, upper case denotes upper tooth; lower case denotes lower tooth; ''fragment'' means that only a partial piece of the tooth was available and sampled. L = left side; R = right side; M = molar; P = premolar. Sample numbers beginning with F&MCF and MCF&C refer to the previously published data of Feranec and MacFadden (2000) and MacFadden and Cerling (1996), respectively.

Sample number	Species	UF number	Element	Location	Age	δ^{13}C
RSF0029	*vera*?	23946	rp4	Bone Valley	Hemphillian	−5.6
F&MCF, 2000(RSF-60)	*blancoensis*?	uncataloged	M fragment	Santa Fe River	Blancan	−10.7
F&MCF, 2000(RSF-61)	*blancoensis*?	uncataloged	M fragment	Santa Fe River	Blancan	−13.1
F&MCF, 2000(RSF-62)	*blancoensis*?	17693	m3	Santa Fe River	Blancan	−13.4
F&MCF, 2000(RSF-63)	*blancoensis*?	uncataloged	M fragment	Santa Fe River	Blancan	−12.9
MCF&C, 1996–72	*blancoensis*?	uncataloged	M/P	Santa Fe River	Blancan	−14.7
RSF0035	*blancoensis*	104500	rm3	Macasphalt 1A	Blancan	−8.7
RSF0043	*blancoensis*?	100096	M fragment	Macasphalt 1A	Blancan	−12.0
RSF0048	*blancoensis*	V-5107	m3	Santa Fe River	Blancan	−9.7
RSF0053a	*blancoensis*?	uncataloged	RM1	Lehigh Acres	Blancan	−9.3
RSF0053b	*blancoensis*?	uncataloged	RM1	Lehigh Acres	Blancan	−8.1
RSF0030	*macrocephala*	17518	LP4	Inglis 1A	Irvingtonian	−10.2
RSF0031	*macrocephala*	45284	lm3	Inglis 1A	Irvingtonian	−11.2
RSF0032	*macrocephala*	18223	lm3	Inglis 1A	Irvingtonian	−11.3
RSF0033	*macrocephala*	17522	rm3	Inglis 1A	Irvingtonian	−12.4
RSF0034	*macrocephala*?	uncataloged	LM3	Inglis 1A	Irvingtonian	−10.8
F&MCF, 2000(RSF-19)	*seymourensis*	64219	lm3	Leisey 1A	Irvingtonian	−8.0
F&MCF, 2000(RSF-20)	*seymourensis*	80053	rm3	Leisey 1A	Irvingtonian	−8.3
F&MCF, 2000(RSF-21)	*seymourensis*	142321	lm3	Leisey 1A	Irvingtonian	−5.6
F&MCF, 2000(RSF-22)	*seymourensis*	64315	LP4	Leisey 1A	Irvingtonian	−8.3
F&MCF, 2000(RSF-23)	*seymourensis*	83964	RP4	Leisey 1A	Irvingtonian	−3.6
RSF0036	*seymourensis*	132000	rm3	Leisey 1A	Irvingtonian	−3.2
RSF0037	*seymourensis*	84239	LP3	Leisey 1A	Irvingtonian	−4.0
RSF0038	*seymourensis*	85085	RM	Leisey 1A	Irvingtonian	−8.7
RSF0039	*seymourensis*	80737	RP4	Leisey 1A	Irvingtonian	−8.2
RSF0040	*seymourensis*	83965	RM3	Leisey 1A	Irvingtonian	−6.2
RSF0045	*macrocephala*?	56589	M	Haile 8A	Rancholabrean	−10.3
MCF&C, 1996–97	*macrocephala*?	uncataloged	rp4	Cutler Hammock	Rancholabrean	0.4
RSF0023	*macrocephala*?	uncataloged	lp4	Cutler Hammock	Rancholabrean	−0.1
RSF0024	*macrocephala*?	uncataloged	rp3	Cutler Hammock	Rancholabrean	−0.5
F&MCF, 2000(RSF-43)	*macrocephala*?	47443	m3	Waccasassa River	Rancholabrean	−8.6
F&MCF, 2000(RSF-44)	*macrocephala*?	47442	m3 fragment	Waccasassa River	Rancholabrean	−4.6
F&MCF, 2000(RSF-45)	*macrocephala*?	47445	m3	Waccasassa River	Rancholabrean	−11.8
F&MCF, 2000(RSF-46)	*macrocephala*?	47443	m3	Waccasassa River	Rancholabrean	−12.1
F&MCF, 2000(RSF-47)	*macrocephala*?	47544	P4	Waccasassa River	Rancholabrean	−5.7
F&MCF, 2000(RSF-101)	*macrocephala*?	47543	M	Waccasassa River	Rancholabrean	−10.0
F&MCF, 2000(RSF-102)	*macrocephala*?	47542	M	Waccasassa River	Rancholabrean	−13.7
F&MCF, 2000(RSF-103)	*macrocephala*?	47545	M	Waccasassa River	Rancholabrean	−12.6

Appendix 1. Continued.

Sample number	Species	UF number	Element	Location	Age	δ^{13}C
RSF0025	*macrocephala*?	uncataloged	m3	Reddick 1	Rancholabrean	−11.7
RSF0026	*macrocephala*	2855	M	Reddick 1	Rancholabrean	−14.0
RSF0027	*macrocephala*	8902	RM3	Reddick 1	Rancholabrean	−9.2
RSF0049	*macrocephala*?	47502	M fragment	Waccasassa River	Rancholabrean	−13.5
RSF0050	*macrocephala*?	47440	m3	Waccasassa River	Rancholabrean	−10.7
RSF0051	*macrocephala*?	47503	M	Waccasassa River	Rancholabrean	−9.8
RSF0052	*macrocephala*?	47501	M fragment	Waccasassa River	Rancholabrean	−7.7
RSF0041	*macrocephala*?	46828	fragment	Withlacoochee River	Rancholabrean	−2.2
RSF0042	*macrocephala*?	46827	M	Withlacoochee River	Rancholabrean	−9.2
RSF0044	*macrocephala*?	18028	RM3	Withlacoochee River 7A	Rancholabrean	−7.9
RSF0046	*macrocephala*?	18334	M	Paines Prairie Dredge	Rancholabrean	−9.0
RSF0047	*macrocephala*?	11503	M	Sarasota Intercoastal Waterway	Rancholabrean	−5.0