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Geographic variation in the diet of hypsodont herbivores from the Rancholabrean of Florida

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Abstract

Classifying the diet of ancient animals is important for understanding biological phenomena such as resource partitioning and the evolution of particular environments. Focusing on *Bison*, *Equus*, and *Mammuthus* from three geographical areas of Florida (north, central, and south) during the Rancholabrean, this study uses values of stable carbon isotope composition of tooth enamel carbonate collected from the literature to determine dietary variability, and whether hypsodonty and comparisons with modern analogs accurately represent the scope of forage taxa could utilize. Carbon isotope values show no significant differences in diet between *Bison*, *Equus*, and *Mammuthus* within any of the three designated geographic areas of Florida. The data do show significant differences in diet for *Bison* between north Florida and south Florida, for *Equus* between north Florida and south Florida and between central Florida and south Florida, and for *Mammuthus* between central Florida and south Florida. These results suggest floral differences among the geographic areas of Florida. Mean δ^{13}C values for the taxa suggest that each was an intermediate feeder with a strong preference for grasses and sedges. Comparisons of diet in this study with those based on modern analogs and hypsodonty indicate that both techniques may accurately represent a taxon's average diet. However, the range in δ^{13}C values observed in individuals extended from strict C_4 feeding to strict C_3 feeding and suggests a range in diet from grazing to browsing. This wide range in apparent diet indicates that multiple specimens are required to accurately interpret the feeding strategy of taxa and the relevance of the diet of animals as an indicator of environment in which they lived.

Keywords: Diet; Enamel; Herbivores; Paleoecology; Pleistocene; Stable carbon isotopes

1. Introduction

Accurately classifying the diet of ancient taxa is important for understanding not only the ecology of particular organisms, but also for understanding other biological phenomena, such as resource partitioning or the evolution of particular environments, such as grasslands. Many techniques have been used to interpret ancient diets, including comparisons of fossil taxa to modern analogs, microwear, the use of morphological proxies such as the analysis of hypsodonty index or muzzle width, and the use of geochemical techniques such as stable isotope analyses of hard tissues (Janis and Ehrhardt, 1988; Solounias et al., 1988; Quade et al., 1992; Dompierre and Churcher, 1996; MacFadden

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and Cerling, 1996; Janis et al., 2000). These techniques give an idea of the diet of ancient animals but may not always reflect the total possible diet.

Modern ungulates have been grouped by Hofmann and Stewart (1972) into three main feeding categories. *Concentrate Selectors* (''browsers'') focus feeding on plants other than grasses and sedges. *Bulk and Roughage Feeders* (''grazers'') concentrate feeding on grasses and sedges. *Intermediate Feeders* 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 ancient ungulate diets and used in the interpretation of paleoenvironment when other paleoenvironmental proxies were not analyzed or available (e.g., Janis, 1988; Quade et al., 1992; Solounias et al., 1995; MacFadden and Cerling, 1996; Janis et al., 2000). By using these three categories, the complexity in feeding patterns of ungulates is not addressed. Hofmann and Stewart (1972) suggested further subcategories within the three main categories to reflect some of this complexity. However, these subcategories are seldom used in the paleoecological literature because it is generally difficult to determine the percent of a particular forage type within the diet of an extinct ungulate.

A concern when placing taxa into discrete feeding categories, especially when using modern analogs or proxies based on modern analogs, is understanding whether extant taxa are utilizing the entire range of potential diet, or if the taxa are confined to using only a portion of potential diet. At question is whether the realized dietary niche of extant taxa adequately represents their fundamental dietary niche. Although modern analogs demonstrate what type of diet is possible in a particular taxon, other ecological influences on diet need to be considered. As a hypothetical example, ancient ungulate taxa are compared to their extant counterparts. The modern ungulate taxa being compared to the ancient taxa have all been shown to be strict grazers in the environments where they occur. Because the ancient taxa have similar morphologies to these extant taxa, they too are suggested to be grazers. Because other indicators of paleoenvironment have yet to be explored, the environment in which the ancient taxa were found is interpreted as having been an open grassland. However, the modern comparative taxa are using only a portion of their potential diet and might be currently grazing because of a preference for grass, because competition makes browsing less available to them, or because grass is the only available resource. The realized dietary niche of the modern taxa is not representative of their fundamental dietary niche, and the modern taxa could survive, and be just as fit, on a variety of forage such as trees, shrubs, and grasses. In this example, if the dietary range was known for the ancient taxa, the interpretation of the available forage, and possibly the paleoenvironment itself, may have been different, as being more indicative of a closed or mixed environment rather than an open grassland. Therefore, it is important to determine the total variation possible in the diets of taxa. If taxa themselves are to be used as indicators of paleoenvironment, their realized niche must be examined as to whether it adequately represents their fundamental niche. To accomplish this, the variability of ecological traits, such as diet and/or habitat occupation, in taxa should be examined geographically and temporally in order to determine the total amount of variation possible.

This study examines the variability in diet of the three hypsodont herbivore taxa, *Bison*, *Equus*, and *Mammuthus*, from the Rancholabrean Land Mammal Age (330 to 10 ka) of Florida. Where 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 proportion of particular forage in the diet and ultimately the range in diet utilized. This proxy can be used to distinguish browsers, grazers, intermediate feeders with a preference for grasses and sedges, and intermediate feeders with a preference for browse on a continuous scale rather than pigeon-holing them into discrete dietary categories. This study also examines whether hypsodonty, the condition of having high-crowned teeth, and a comparison to modern analogs accurately reflect the forage upon which these ancient taxa could survive.

2. Background and methods

2.1. Carbon isotopes and diet

The carbon isotope values of fossil teeth are useful in paleodiet studies because the three different photosynthetic pathways, C_3, C_4, and Crassulacean Acid Metabolism (CAM) impart different ratios of

$^{13}C/^{12}C$ in different kinds of plants, which are ultimately reflected in the animals that forage on them. 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 on different kinds of plants will reflect the isotope ratio ingested ($^{13}C/^{12}C$; DeNiro and Epstein, 1978; Quade et al., 1992). The $^{13}C/^{12}C$ ratio of tooth enamel is further enriched by $+14.1 \pm 0.5‰$, expressed in the standard delta notation[1], 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 has been shown to be resistant to diagenesis, and thus reliably reflects stable isotope values derived from feeding (Quade et al., 1992; Wang and Cerling, 1994; Koch et al., 1997). In general, grazers are predominantly C_4 feeders, browsers are predominantly C_3 foragers, and intermediate feeders utilize both C_3 and C_4 plants. Caution must be used when interpreting carbon isotope values from 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). CAM photosynthesis is found in succulents, such as cacti, and predominates in xeric habitats (Ehleringer et al., 1991). It is assumed that *Bison*, *Equus*, and *Mammuthus* did not make succulents a significant proportion of their diet, and the isotopic effects of CAM photosynthesis are not considered to factor into this study.

2.2. Interpreting carbon isotope values in paleoecology

As noted above, herbivores will reflect the carbon isotope values of plants ingested. Modern C_3 plants, trees and shrubs, and high latitude grasses, have a mean carbon isotope value of $-27.0‰$, and generally range from $-24.0‰$ to $-30.0‰$, while modern C_4 plants, tropical sedges and grasses, have a mean isotopic value of $-13.0‰$, and generally range from $-11.0‰$ to $-15.0‰$ (O'Leary, 1988; Quade et al., 1992; Koch et al., 1998). Using a $+14.0‰$ 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 $-10.0‰$, while 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 CO_2 in the modern atmosphere, which has decreased from about $-6.5‰$ to about $-8.0‰$ due to fossil fuel burning over the last 200 years (Friedli et al., 1986; Marino and McElroy, 1991; Marino et al., 1992). For this reason, enamel isotope values from Pleistocene specimens are about 0.5‰ to 1.3‰ more positive than the modern taxa due to pre-industrial $\delta^{13}C$ differences compared to the modern (Koch et al., 1998). Based on the above, herbivore enamel resulting from a diet of pure C_3 plants would not have an isotopic value more positive than $-8.7‰$, while enamel resulting from 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 (defined herein as $< 10\%$ C_4 diet), values more positive than $-1.3‰$ are interpreted to signal primarily grazing (here defined as $< 10\%$ C_3 diet), and values between $-7.9‰$ and $-1.3‰$ result from intermediate feeding strategies (defined as $10\% < C_4 < 90\%$).

2.3. Study area: Florida during the Rancholabrean

Florida is ideal for this study for two main reasons. First, the taxa of concern, *Bison*, *Equus*, and *Mammuthus*, are abundant during the Rancholabrean Land Mammal Age throughout the entire state. Second, the flora removes many of the ambiguities that can occur when interpreting plant type from isotopic values.

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[1] Isotope ratios are represented using standard δ-notation compared to the PDB: $\delta^{13}C_{pdb} = [(R_{sample}/R_{standard}) - 1] \times 1000$; where $R = {}^{13}C/{}^{12}C$.

This is because nearly all present-day browse in Florida is C_3 (>97%; Stowe and Teeri, 1978), while most of the grasses and many 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). Studies of modern floral composition on sites near fossil localities within this study show that C_3 grasses and sedges may be present and represent up to 40% of the species richness, but are generally confined to wetter areas and are not widespread on the landscape (Easley and Judd, 1990; Huffman and Judd, 1998).

Vegetation models and proxy data suggest that glacial periods were drier than present with decreasing CO_2 levels, conditions that favor the spread of open vegetation and C_4 photosynthesis (Webb, 1991; Ehleringer et al., 1997; Cowling, 1999; Jackson et al., 2000; Huang et al., 2001). Thus, it is unlikely that the percentage of C_3 photosynthesis was greater in the past. It is important to note that climate and vegetation distributions varied during glacial–interglacial cycling. For example, analysis of pollen from lake cores in Florida have shown that the landscape fluctuated between a drier, *Quercus*-dominated flora to a wetter, *Pinus*-dominated flora similar to that present today (Grimm et al., 1993). This pattern was probably not unique for the latest part of the Pleistocene of Florida, but likely typical for the time period covered by this study.

2.4. Hypsodonty and modern ungulate diets

Hypsodonty, or the condition of having high-crowned teeth, is generally measured by dividing tooth crown height by the anteroposterior length of the same tooth. This hypsodonty index (HI) of herbivores has been shown to be positively correlated to the percentage of grass included in the diet and/or the openness of an ecosystem (Janis, 1995). Modern hypsodont animals are generally grazers and live in open habitats. *Bison*, *Equus*, and *Mammuthus* from the Rancholabrean of Florida are all known to be hypsodont, and because of this each would generally be considered to graze and inhabit open habitats (MacFadden and Cerling, 1996).

Because *Bison* and *Equus* have extant counterparts, their modern diets might give some insight into the ancient diets. North American bison (*Bison bison*) are known to feed predominantly on grasses (Meagher, 1986; Nowak, 1999). Meagher (1986) notes that North American bison graze in every season and include up to 96% grass in their diet. Meagher (1986) also suggested that North American bison restrict their use of forests to special purposes such as an escape from severe winter storms. However, Nowak (1999) notes that the European bison (*B. bonasus*) forage mainly on twigs, bark, and leaves of trees. The modern analog of North American *Equus* would be feral individuals of *Equus caballus*. Studies on feral populations of *E. caballus* show that grass is the main food source utilized (generally $\geq 90\%$), but browse can make up a significant portion (up to 50%) of the diet (Hansen, 1976; McInnis and Vavra, 1987; Smith et al., 1998; Bennett and Hoffman, 1999). For the non-North American *Equus* species, *E. burchelli*, *E. grevyi*, *E. quagga*, and *E. zebra*, a similar pattern of grazing with some browsing was noted, but generally >90% grass was ingested (Kingdon, 1979; Grubb, 1981; Penzhorn, 1988; Churcher, 1993). Comparing these taxa to modern analogs, and focusing on the North American forms, fossil *Bison* and *Equus* in this study are expected to forage predominantly on grasses and sedges but include some browse in their diets.

In this study, Florida was divided into north (N, above 29°N), central (C, between 27°N and 29°N), and south (S, below 27°N) geographic areas to get a better picture of dietary potential across a range in latitude. This grouping of localities (Fig. 1) into geographic areas was done because in many cases the scant number of specimens from any one locality is too few to adequately represent total variation of diet. The geographic areas used within this study roughly correspond to three different modern ecoregions recognized within Florida (Ricketts et al., 1999). The area designated as N in this study corresponds to the modern Southeastern Conifer Forest ecoregion. The area designated as C corresponds to a mixed Southeastern Conifer Forest ecoregion and Florida Sand Pine Scrub ecoregion. The area designated as S corresponds to the Everglades ecoregion (Ricketts et al., 1999). The N and C areas would be expected to be more similar to each other than either would be to the S area, based on the modern ecoregions (Ricketts et al., 1999). The modern ecoregions provide a guide in this study to establish whether there is a geographic difference in potential diet in order to

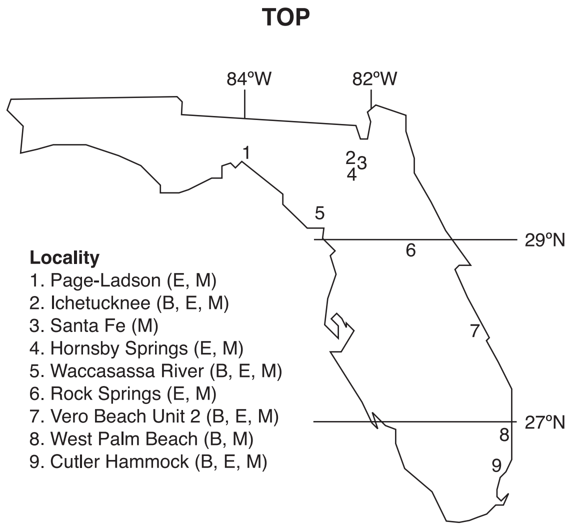

Fig. 1. Position of localities from which specimens derive. B—*Bison*; E—*Equus*; M—*Mammuthus*.

ultimately determine the total variation in diet. These ecoregions are not presumed to have persisted, as they are currently recognized, over the past 330 ky.

Stable carbon isotope data for *Bison*, *Equus*, and *Mammuthus* from the Rancholabrean of Florida was gathered from the literature (MacFadden and Cerling, 1996; Koch et al., 1998; Feranec and MacFadden, 2000). There were 69 specimens included in this study, 19 of *Bison* (11N: 2C: 6S), 23 of *Equus* (15N: 4C: 4S), and 27 of *Mammuthus* (11N: 8C: 8S). Three comparisons were made in this study, (1) between genera within geographic areas (e.g., north Florida *Bison* vs. *Equus* vs. *Mammuthus*), (2) between geographic areas for one particular genus (e.g., north *Bison* vs. central *Bison* vs. south *Bison*), and (3) between geographic areas combining individuals of all three genera (e.g., north Florida vs. central Florida vs. south Florida). Mean differences were compared by ANOVA and post hoc LSD tests. The post hoc LSD tests are similar to *t*-tests but take into consideration multiple comparisons. Temporally finer scale analyses would have been preferred but due to the preservation of the assemblages, and current knowledge of the ages of localities, these were impossible. Statistical analyses were run on Microsoft Excel 2000 and SPSS Student Version 8.0 for Windows, with significance set at $p < 0.05$. The precision for each sample is reported as ≤0.2‰ in all three studies.

3. Results

3.1. Stable carbon isotope values

In north Florida (Table 1, Fig. 2), *Bison* had a mean $\delta^{13}C$ value of −3.4‰ and a standard deviation of 2.2‰, with a range from −8.7‰ to −0.5‰. *Equus* had a mean $\delta^{13}C$ value of −4.2‰ and a standard deviation of 2.4‰, with a range from −9.4‰ to 0.6‰. *Mammuthus* had a mean $\delta^{13}C$ value of −2.6‰ and a standard deviation of 2.3‰, with a range from −7.2‰ to 0.5‰. The mean for all specimens of the three genera in the north section of Florida was −3.5‰ with a standard deviation of 2.4‰.

In central Florida, *Bison* had a mean $\delta^{13}C$ value of −2.2‰ and a standard deviation of 3.9‰, with a range from −4.9‰ to −0.6‰. *Equus* had a mean $\delta^{13}C$ value of −4.8‰ and a standard deviation of 3.8‰, with a range from −10.5‰ to −2.4‰. *Mammuthus* had a mean $\delta^{13}C$ value of −2.8‰ and a standard deviation of 2.0‰, with a range from −7.4‰ to −1.1‰. The mean for all specimens of the three genera in the north section of Florida was −3.3‰ with a standard deviation of 2.8‰.

In south Florida, *Bison* had a mean $\delta^{13}C$ value of 0.3‰ and a standard deviation of 0.9‰, with a range from −4.4‰ to 1.9‰. *Equus* had a mean $\delta^{13}C$ value of −0.3‰ and a standard deviation of 0.4‰, with a

Table 1
Mean carbon isotope values and standard deviations for *Bison*, *Equus*, and *Mammuthus* in three latitudinal sections in Florida[a]

Genus	North	Central	South
Bison (N–S)	−3.4‰ ± 2.2‰	−2.2‰ ± 3.9‰	0.3‰ ± 0.9‰
Equus (N–S; C–S)	−4.2‰ ± 2.4‰	−4.8‰ ± 3.8‰	−0.3‰ ± 0.4‰
Mammuthus (C–S)	−2.6‰ ± 2.3‰	−2.8‰ ± 2.0‰	−0.8‰ ± 1.0‰

[a] Carbon isotope values are given relative to the V-PDB. There were no significant differences between genera within a particular geographic section. Significant differences within a genus between geographic sections are given in parentheses. Abbreviations: N, north; C, central; S, south.

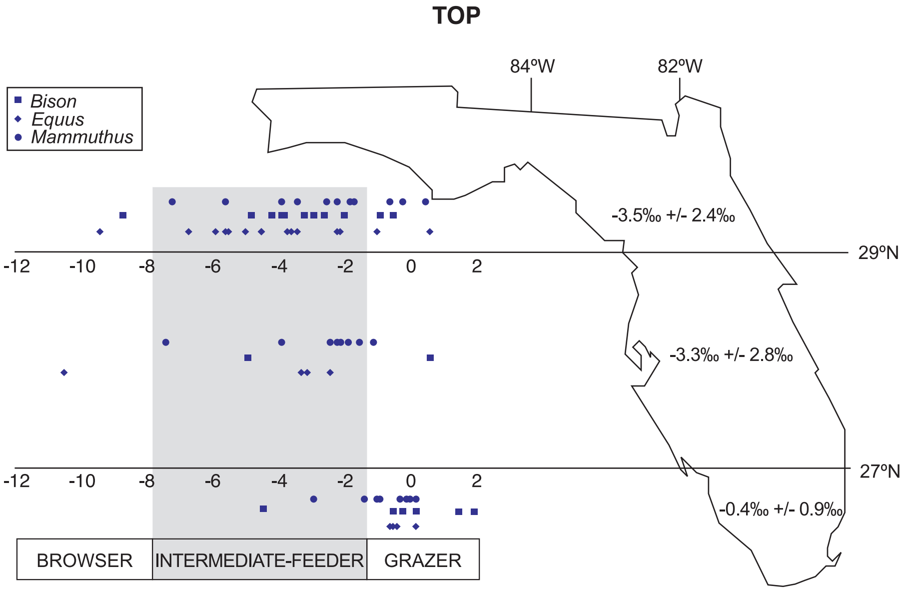

Fig. 2. Carbon isotope values for *Bison*, *Equus*, and *Mammuthus* in the three geographic areas of Florida. Mean δ^{13}C value and standard deviations for each area are provided in the map. ■—*Bison*; ◆—*Equus*; ●—*Mammuthus*.

range from − 0.6‰ to 0.2‰. *Mammuthus* had a mean δ^{13}C value of − 0.8‰ and a standard deviation of 1.0‰, with a range from − 2.9‰ to 0.2‰. The mean for all specimens of the three genera in the south section of Florida was − 0.4‰ with a standard deviation of 0.9‰.

3.2. Statistical analysis of herbivores

No significant differences in δ^{13}C values between the three herbivore genera, *Bison*, *Equus*, and *Mammuthus* exist within any of the geographic areas of Florida. In the second comparison, a significant difference in δ^{13}C values ($p < 0.018$) was observed for *Bison* between north Florida and south Florida. There were no significant differences observed for *Bison* between central Florida and either the north or south geographic regions of Florida. For *Equus*, significant differences were observed in δ^{13}C values between north Florida and south Florida ($p < 0.015$), and between central Florida and south Florida ($p < 0.021$). No significant difference was observed for *Equus* between north Florida and central Florida. For *Mammuthus*, a significant difference was observed in δ^{13}C values between central Florida and south Florida ($p < 0.049$). Results were not significant between north Florida and central Florida, and were marginally insignificant between north Florida and south Florida ($p < 0.057$) for *Mammuthus*. In the third comparison, significant differences were observed in δ^{13}C values combining all genera, between north Florida and south Florida ($p < 0.001$), and between central Florida and south Florida ($p < 0.002$). No significant differences were observed between north Florida and central Florida.

4. Discussion

The mean δ^{13}C values for each taxon suggest that all were intermediate feeders with a strong preference for grasses and sedges. This finding is what is expected using a modern analog or hypsodonty (morphological proxies) as indicators of diet. However, placing *Bison*, *Equus*, and *Mammuthus* into discrete categories obscures information about the range in diet or range in habitat, which could ultimately confound our interpretation of paleoecosystems. This is exemplified by the similarity in forage observed between taxa within a particular geographic area, in contrast to significant differences observed in forage intake between the geographic areas. There appears to be a significant floral difference between north Florida and south Florida, and between central Florida and south Florida. This difference may be explained by a higher percentage of C_4 forage available in south Florida. Without knowing the range in diet possible, and without any other paleoenvironmental information, the three geographical areas of Florida might have been interpreted as having similar ecosystems/floral compositions. However, it appears that many different types of environment can support these animals, and the taxa are capable of feeding on a wide range of food. Each taxon showed the ability to forage on significant quantities of C_3 and C_4 plants suggesting a range in dietary scope of browsing to grazing. Therefore, caution must be taken when interpreting environment from proxies not directly related to the flora, or when diet is incompletely known.

5. Conclusions

This study has shown no significant differences in diet between *Bison*, *Equus*, and *Mammuthus* within any one of the three geographic areas of Florida. The data do show significant differences in diet for *Bison* between north Florida and south Florida, for *Equus* between north Florida and south Florida and between central Florida and south Florida, and for *Mammuthus* between central Florida and south Florida. These data suggest a floral difference between south Florida and the rest of the Florida peninsula during the latest Pleistocene. Mean $\delta^{13}C$ values suggest that each taxon was an intermediate feeder with a strong preference for grasses and sedges. However, the range in $\delta^{13}C$ values of individuals of all three taxa extended from C_4 feeding to C_3 feeding, suggesting a range in diet from grazing to browsing. These data also suggest that the use of modern analogs and morphological proxies, such as the HI, may give an accurate representation of the average diet of a taxon. Unfortunately, modern analogs and morphological proxies are not able to capture the ability of animals to adjust to their surroundings, especially under survival pressure, and may thus result in a misinterpretation of paleoenvironment.

Caveats discussed in this paper resonate even more strongly further back in time as modern analogs become scarce or tenuous. A more ancient example where further caution may be warranted in interpreting ancient diets and dietary influence on determining paleoenvironment is with the suggested spread of C_3 grasslands at the beginning of the Miocene (ca. 18 Ma) and the subsequent decline in primary productivity in the plains of North America through the Miocene (Janis, 1989; McNaughton, 1991; MacFadden, 1997; Janis et al., 2000), as inferred from the decrease in diversity of taxa having low-crowned teeth and increase in proportion of taxa having hypsodont dentitions (Janis et al., 2000, 2002, 2004). The range in diet of the brachyodont taxa and hypsodont taxa currently is not known. Whereas the early Miocene hypsodont taxa were probably, on average, the first to include significant proportions of grass in their diet, and the low-crowned taxa most likely were *Concentrate Selectors*, it cannot be known what portion of the range in diet was being used at a particular locality. Therefore, it also cannot be known without additional paleoenvironmental information whether the habitats, where these taxa occurred, were open or closed or how productive were the environments. Determining the scope of diet and the variety of plants on which taxa survived needs to be a priority especially if the diet of fossil taxa is going to be used as a proxy for the flora present and available in an ancient ecosystem.

Placing ancient animals into discrete feeding categories through the use of morphological proxies and modern analogs provides for a basic understanding of the diets in extinct taxa. When used in conjunction with other proxies, these diets may even provide insights into the environments where the fossils were located. However, this study has shown that fossil taxa have a range in diet that transcends the discrete feeding categories that might be indicated by morphological data alone.

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Appendix A

UF catalog number, genus, geographic location, locality, δ^{13}C value, and reference from the publication where data was taken[2]

UF catalog #	Genus	Geographic section	Locality	δ^{13}C	Reference
19,376	*Bison*	north	Ichetucknee	–3.9	MCF
47,702	*Bison*	north	Waccasassa River	–0.9	RSF
47,704	*Bison*	north	Waccasassa River	–3.8	RSF
47,716	*Bison*	north	Waccasassa River	–3.2	RSF
47,717	*Bison*	north	Waccasassa River	–4.2	RSF
47,721	*Bison*	north	Waccasassa River	–2.9	RSF
47,722	*Bison*	north	Waccasassa River	–0.5	RSF
47,753	*Bison*	north	Waccasassa River	–4.8	RSF
47,817	*Bison*	north	Waccasassa River	–2.0	RSF
47,818	*Bison*	north	Waccasassa River	–8.7	RSF
48,893	*Bison*	north	Waccasassa River	–2.6	RSF
8633	*Bison*	central	Vero Beach Unit 2	–4.9	Koch
8635b	*Bison*	central	Vero Beach Unit 2	0.6	Koch
Unc. 96–99	*Bison*	south	Cutler Hammock	–0.5	MCF
Unc. 96–98	*Bison*	south	Cutler Hammock	1.5	MCF
14,685	*Bison*	south	Cutler Hammock	–4.4	Koch
14,686	*Bison*	south	Cutler Hammock	1.9	Koch
17,063	*Bison*	south	West Palm Beach	0.2	Koch
51,151	*Bison*	south	West Palm Beach	–0.2	Koch
V4066a	*Equus*	north	Ichetucknee	–6.7	MCF
4024	*Equus*	north	Hornsby Springs	–4.5	Koch
14,641	*Equus*	north	Waccasassa River	–3.7	RSF
14,645	*Equus*	north	Waccasassa River	–4.5	RSF
14,650	*Equus*	north	Waccasassa River	–3.4	RSF
14,656	*Equus*	north	Waccasassa River	–1.0	RSF
14,661	*Equus*	north	Waccasassa River	–5.0	RSF
14,671	*Equus*	north	Waccasassa River	–5.6	RSF
14,690	*Equus*	north	Waccasassa River	–3.6	RSF
14,702	*Equus*	north	Waccasassa River	–5.5	RSF
14,721	*Equus*	north	Waccasassa River	0.6	RSF
27,529	*Equus*	north	Hornsby Springs	–9.4	Koch
27,534	*Equus*	north	Ichetucknee	–2.2	MCF
48,328	*Equus*	north	Waccasassa River	–2.1	RSF
148,670	*Equus*	north	Page-Ladson	–5.9	Koch
8099	*Equus*	central	Vero Beach Unit 2	–3.3	Koch
8100	*Equus*	central	Vero Beach Unit 2	–3.1	Koch
48,974	*Equus*	central	Rock Springs	–10.5	Koch
48,975	*Equus*	central	Rock Springs	–2.4	Koch
Unc. 96–104	*Equus*	south	Cutler Hammock	–0.6	MCF
Unc. 96–103	*Equus*	south	Cutler Hammock	–0.5	MCF

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[2] Abbreviations: Koch—Koch et al. (1998); MCF—MacFadden and Cerling (1996); RSF—Feranec and MacFadden (2000).

Appendix A (*continued*)

UF catalog #	Genus	Geographic section	Locality	$\delta^{13}C$	Reference
Unc. 96–102	*Equus*	south	Cutler Hammock	– 0.4	MCF
Unc. 96–101	*Equus*	south	Cutler Hammock	0.2	MCF
V4086	*Mammuthus*	north	Ichetucknee	– 0.6	MCF
987	*Mammuthus*	north	Hornsby Springs	– 5.6	Koch
10,533	*Mammuthus*	north	Santa Fe	– 7.2	MCF
10,534	*Mammuthus*	north	Santa Fe	– 3.4	MCF
14,779	*Mammuthus*	north	Page-Ladson	– 0.2	Koch
14,780	*Mammuthus*	north	Page-Ladson	0.5	Koch
16,606	*Mammuthus*	north	Waccasassa River	– 2.2	RSF
48,899	*Mammuthus*	north	Waccasassa River	– 1.7	RSF
48,901	*Mammuthus*	north	Waccasassa River	– 1.8	RSF
48,904	*Mammuthus*	north	Waccasassa River	– 2.5	RSF
48,928	*Mammuthus*	north	Waccasassa River	– 3.9	RSF
4383	*Mammuthus*	central	Rock Springs	– 3.9	Koch
4473	*Mammuthus*	central	Rock Springs	– 7.4	Koch
8620	*Mammuthus*	central	Vero Beach Unit 2	– 1.5	Koch
8636	*Mammuthus*	central	Vero Beach Unit 2	– 2.2	Koch
8637	*Mammuthus*	central	Vero Beach Unit 2	– 2.1	Koch
8638	*Mammuthus*	central	Vero Beach Unit 2	– 1.9	Koch
48,987	*Mammuthus*	central	Rock Springs	– 1.1	Koch
119,828	*Mammuthus*	central	Rock Springs	– 2.4	Koch
51,197	*Mammuthus*	south	West Palm Beach	– 0.1	Koch
148,672	*Mammuthus*	south	West Palm Beach	– 1.0	Koch
148,679	*Mammuthus*	south	Cutler Hammock	– 2.9	Koch
148,680	*Mammuthus*	south	Cutler Hammock	0.2	Koch
148,681	*Mammuthus*	south	Cutler Hammock	0.0	Koch
148,682	*Mammuthus*	south	Cutler Hammock	– 0.9	Koch
148,683	*Mammuthus*	south	Cutler Hammock	– 0.3	Koch
148,684	*Mammuthus*	south	Cutler Hammock	– 1.4	Koch

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