Dietary niche partitioning among fossil bovids in late Miocene C₃ habitats: Consilience of functional morphology and stable isotope analysis

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Abstract

Teeth of late Miocene bovids referred to Bovini and “Boselaphini” were subjected to enamel stable carbon and oxygen isotope analysis to test palaeoecological reconstructions based on dental morphology. Teeth of Bovini possess derived characters—including larger size, higher crowns, and increased enamel surface area—that are indicative of feeding on a more fibrous and gritty diet, probably grass. In contrast, teeth of “Boselaphini” reflect the plesiomorphic condition among bovids—being smaller, lower-crowned, and with simple occlusal morphology—and are indicative of a diet with a greater reliance on softer food items such as browse. Late Miocene bovines are also expected to have inhabited drier, more open habitats than did boselaphines. Stable carbon and oxygen isotopic compositions from 30 fossil teeth (18 bovine, 12 boselaphine) from well-dated localities of between 8.3 and 7.9 Ma in age from the Siwalik deposits, Pakistan, were analyzed to test these palaeoecological hypotheses. All δ¹³C values (VPDB) are more negative than −8‰, indicating that both bovines and boselaphines at this time had pure C₃ diets. The mean δ¹³C for bovine teeth (−10.4‰) is more positive than that for boselaphines (−10.9‰), and the differences between these two series are significant (Wilcoxon, p<0.01; t test, p<0.05) while the variances are not. Early bovines thus appear to have exploited more open habitats than did their boselaphine counterparts. Lack of a significant difference between variances suggests that the dietary niche breadth of early bovines was not different from that of boselaphines. Mean δ¹⁸O (SMOW) for bovine teeth (26.3‰) is slightly more negative—as might be expected for grazers—but not statistically significant from the boselaphine δ¹⁸O mean (28.1‰, t test, p=0.066). Overlap in δ¹⁸O values between bovines and boselaphines is high, implying that these two bovid types did not differ greatly in their water intake behaviors. Rather, both fossil bovines and boselaphines probably shared similar obligate drinking habits and dependency on water bodies much as living bovids, bovines, and tragelaphines (clade Bovinae) do today.

Stable isotope analysis results, particularly δ¹³C values, suggest that in the late Miocene neither bovines nor boselaphines inhabited dense forest habitats. And while both bovid taxa may have been mixed feeders to different extents, the δ¹³C values support the hypothesis developed on the basis of dental functional morphology that early bovines evolved inhabiting more open habitats than did contemporaneous boselaphines. The scenario whereby the bovine clade owes its origins to a boselaphine lineage that adapted to drier, more open habitats is supported by the general context of climatic and faunal change in Eurasia in the late Miocene, particularly between 11–8 Ma, when faunal assemblages from many sites exhibit significant turnover events through which open-habitat taxa become present in increasing proportions at the expense of closed-habitat taxa.

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1. Introduction

The earliest representatives of the bovid clade Bovini were recently identified from late Miocene fossil collections from the Indian Subcontinent (Bibi, 2007). The extant crown clade Bovini comprises grazing species such as buffaloes, bison, and cattle. The earliest bovines can be identified by dental remains from the Siwalik deposits, Pakistan, dated at least as far back as 8.9 Ma. These dental remains are distinguished from those of ancestral and contemporaneous boaselaphine bovids primarily by their significantly larger size, higher crowns, larger basal pillars, and more complicated enamel outlines (Fig. 1). Taken together, these adaptations reflect an increased intake of rougher, more fibrous or gritty foods in early bovines, such as grasses, leading to the supposition that early bovines evolved exploiting more open habitats than did ancestral and contemporaneous late Miocene boaselaphine bovids that lacked these dentognathic adaptations (Bibi, 2007). These inferences based on functional morphology are tested here using stable carbon isotope compositions of tooth enamel to examine the feeding characteristics of late Miocene bovines and boaselaphines.

At tropical latitudes today most grasses utilize the C_4 photosynthetic pathway that promotes survival in seasonally arid or heat-stressed regions (Tipple and Pagani, 2007). However, stable carbon isotopic evidence suggests C_4 grasses did not substantially expand in the Siwalik region until after 8.1 Ma, with C_4-dominated habitats first appearing by 7.4 Ma (Barry et al., 2002; Quade and Cerling, 1995; Quade et al., 1989). This suggests that if the earliest bovines evolved by exploiting more open habitats, the terrestrial environment must have been dominated by C_3 floras, potentially C_3 grasslands. Stable carbon isotope analysis distinguishes readily between C_3 and C_4 plants, with C_3 plants displaying bulk organic carbon δ^{13}C values between −35‰ and −22‰ and C_4 plants between −19‰ and −9‰ (Bender, 1971; Cerling and Harris, 1999). Plant δ^{13}C is an inverse function of the ratio of the partial pressure of CO_2 in leaf intercellular spaces (ε) relative to that in the atmosphere (ε_a) (Farquhar et al., 1982a; Farquhar et al., 1982b) and as a result even within either of the C_3 or C_4 ranges there is an observed correlation with increasingly enriched δ^{13}C_{plant} values and increasingly heat- or water-stressed environments (Ehleringer and Cooper, 1988; Farquhar et al., 1989). For example, Medina and Minchin (1980) and van der Merwe and Medina (1991) found that leaves growing in sub-canopy conditions had more depleted δ^{13}C values than those growing at canopy level and in clearings. This phenomenon is ascribed to two factors: (1) the 'canopy effect' whereby δ^{13}C-depleted CO_2 released as a result of decomposition of leaf litter at ground level, is photosynthetically recycled by plants growing nearer to the forest floor (Vogel, 1978); and (2) the observed relationship between plant water-use efficiency and δ^{13}C, whereby unstressed plants growing in shaded/humid/low-salinity conditions will maximize the kinetic (at the stomatal level) and physiological (at the level of the enzyme rubisco) fractionation that discriminates against fixation of the heavier isotope of carbon, 13C (Farquhar et al., 1982a; O’Leary, 1993; van der Merwe and Medina, 1991). Conversely, increases in stressors such as light intensity, salinity, and aridity require plants to combat excessive evaporation by closing leaf stomata (i.e. decreasing stomatal conductance) for longer periods of time, trapping a limited reserve of CO_2 in the leaf and resulting in fixation of a greater proportions of the heavier isotope of carbon than would occur under more optimal conditions (Farquhar et al., 1982a; van der Merwe and Medina, 1991). Studies have shown that decreased shade or water availability can effect δ^{13}C changes of about +1–2‰ in any single plant species (Ehleringer and Cooper, 1988; Michelsen et al., 1996). Changes in the partial pressure as well as the 13C/12C ratio of atmospheric CO_2 can also affect the resulting δ^{13}C value of plant material (and hence herbivore tooth enamel). Given that both the partial pressure and 13C/12C ratio of pre-industrial atmospheric CO_2 do not appear to have changed significantly since the late Miocene (Pagani et al., 1999; Pagani et al., 2005; Passey et al., 2002), δ^{13}C values of fossil teeth examined in this study are interpretable in reference to δ^{13}C endmember values in modern systems.

The δ^{13}C values of plants translate directly to the δ^{13}C values in tissues of the mammalian herbivores that feed on them. Large ruminant enamel bioapatite is enriched in 13C.

Fig. 1. Examples of late Miocene bovine and boaselaphine teeth analyzed in this study. Bovine teeth (left, YPM 19681) are larger, with developed basal pillars, more convoluted enamel ridges, and higher crowns than contemporaneous boaselaphine teeth (right, YPM 19613). Both teeth shown are right upper second molars in mid wear stages. Scale bar equals 1 cm.
by about +14.1±0.5‰ with respect to the plant source (Cerling and Harris, 1999), with living bovines averaging slightly greater values of approximately +14.6±0.3‰ (Cerling and Harris, 1999; Passey et al., 2005). Bovids feeding on pure C3 diets should exhibit ranges between about −21‰ and −8‰, with open-habitat species having more positive values than forest/-canopy species. This is confirmed by studies of living ungulates, such as a study of African bovids (Cerling et al., 2003) which determined that duiker species (Cephalophus spp.), which inhabit rainforests and forests, exhibit much more negative δ13C values than the eland (Tragelaphus oryx), a woodland-savanna species, though both of these bovids are exclusive C3 feeders. Similarly, contrasts between closed and open-habitat bovids in the ancient record can be tested by evaluating tooth enamel δ13C values of specific species. Within a defined age and region, fossil bovids that inhabited more open habitats should exhibit more positive δ13C values than those that inhabited more closed habitats. Analogous studies comparing δ13C values within the C3 range among various fossil ungulates have been performed with relative success on Miocene herbivore communities from Panama (MacFadden and Higgins, 2004), Turkey (Quade et al., 1995), and Florida and California (Feranec and MacFadden, 2006).

The oxygen isotope composition of bovid tooth enamel was analyzed in order to test for differing patterns of water intake between bovine and boselaphine fossil bovids. Due to evaporative enrichment, leaf water δ18O values are typically 10–30‰ more positive than the meteoric source (Yakir, 1997). As a result, mammal species that obtain the majority of their water from the plants they eat should exhibit more positive δ18O values than those that are obligate drinkers (e.g. Sponheimer and Lee-Thorp, 1999; Sponheimer and Lee-Thorp, 2001). Sponheimer and Lee-Thorp (1999) found that browsers tend to have slightly more enriched δ18O values than do grazers. On this basis, Miocene fossil boselaphines should be slightly more enriched in 18O than fossil bovines. This expectation is not strong, however, given the water-use habits of the living relatives of these fossils. Living bovines are obligate drinkers with strong affinities to water, exemplified by the water buffalo (Bubalus bubalis), which spends much time fully immersed in water. Among bovine outgroups, the chousings (Tetracerus quadricornis, a boselaphine) and most tragelaphines (Tragelaphus spp.) are water dependent as well (Estes, 1991; Prater, 1965). Given the behavior of these extant species, water intake behaviors of ancient boselaphines and bovines likely depended more on varying local conditions such as water sources (e.g. seasonal waterholes vs. rivers vs. perennial lakes) and climatic variables (e.g. changes in annual precipitation patterns) rather than clade-specific ecological attributes.

This study utilizes stable isotope analysis to test hypotheses and predictions made on the basis of functional morphological differences between teeth of late Miocene bovines and boselaphines from the Siwalik deposits. Primarily, stable isotope are used to test whether dietary intake differed in any significant way between these two bovid groups. Bovines are expected to display more positive δ13C values, indicating that they fed in more open C3 habitats than did boselaphines, and more depleted δ18O values as noted for grazing herbivores that have a greater reliance on meteoric sources for their water needs. Results of the analysis are discussed with implications for the early evolution of Bovini within the context of late Miocene climatic and paleoenvironmental changes.

2. Methods

Thirty fossil specimens were selected for analysis based on their morphology and stratigraphic provenance (Table 1). Eighteen specimens are of early bovines (teeth traditionally referred to Selenoporta or Pachyporta), while twelve are of large non-bovine boselaphine fossils (likely Tragopota) that in this paper will be referred to simply as boselaphines. Sites chosen and their ages are as follows: L008 (8.331±0.04 Ma), L011 (7.926±0.12 Ma), L012 (7.926±0.12 Ma), L056 (7.926±0.12 Ma), L073 (8.018±0.31 Ma), and L074 (8.018±0.31 Ma) (age determinations from Barry et al., 2002).

Enamel was sampled using a Foredom rotary drill at low speeds, fitted with a 33.5-gauge (0.5 mm diameter) inverted cone carbide burr. Between 2000 and 6000 μg of enamel was removed along a single transect from the base to the tip of the crown, typically along either of the buccal ribs (metacone or paracone) on upper teeth or lingual ribs (metaconid or entoconid) on lower teeth, making sure to include no cementum or dentine in the sample. Enamel powder was treated with hydrogen peroxide and acetic acid to remove effects of contaminant organics and inorganic carbonate (Koch et al., 1997). Enamel was treated with 30% H2O2 for between 24 to 48 h, decanted and washed with distilled de-ionized water, then reacted with 0.1 N acetic acid for 4 h, after which samples were decanted and washed. Ethanol was added and samples were dried overnight. The treated enamel was dissolved in 100% phosphoric acid and the resulting CO2 was analyzed with a Gas Bench II coupled to a Thermo Finnigan Delta Plus XP mass spectrometer at the Earth Systems Center for Stable Isotopic Studies, Yale
University. Standards run with the bovid enamel sample included NBS-18, NBS-19, Lincoln Limestone, and the MEme fossil proboscidean standard. For MEme, average run values of −10.37 for δ13C and 25.75 for δ18O were used (L. R. G. DeSantis pers. comm.). Carbon and oxygen isotope values are reported relative to isotopic standards such that

$$\delta^{13}C \text{ or } \delta^{18}O = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where $R_{\text{sample}}$ and $R_{\text{standard}}$ are the $^{13}C/^12C$ or $^{18}O/^16O$ ratios of the sample and standard, respectively. δ13C values are reported relative to the Vienna PeeDee Belemnite (VPDB) standard, while δ18O values are against the Standard Mean Ocean Water (SMOW) standard.

Shapiro–Wilks tests were performed on all sample series values to determine whether distributions were normal or not. For all samples, $F$ tests and Student’s $t$ test assuming equal variances were used. For non-normal distributions, the non-parametric Wilcoxon two-sample test (equivalent to Mann–Whitney $U$ test) was used in addition. Statistical tests were performed using JMP 6.0 software. Significance was set to $\alpha=0.05$.

3. Results

3.1. Carbon isotope ratios

The total range of variation for all values is just under 3‰, ranging from $-12.2\%$ to $-9.6\%$ (Fig. 2, Table 1). The mean δ13C value for all 18 bovine samples is $-10.4\%$ (range $-12.2\%$ to $-9.6\%$) while for the 12 boselaphine samples the mean is $-10.9\%$ (range $-11.6\%$ to $-9.8\%$). Shapiro–Wilks tests reveal that while boselaphine δ13C values are normally distributed ($p>0.05$), bovine δ13C values are not ($p=0.0058$), and so a Wilcoxon test was performed along with the $t$ test. An $F$ test determined that variances between bovine and boselaphine δ13C values were not significantly different. Both the Wilcoxon and $t$ test indicate that bovine and
boselaphine $\delta^{13}C$ values are significantly different (two-sample Wilcoxon, $p<0.01$; $t$ test, $p=0.0316$). The $\delta^{13}C$ values of bovine and large boselaphine teeth separate at $-10.7\%$ although two bovine samples display $\delta^{13}C$ values more negative than $-10.7\%$, these in fact being the two most negative values recorded among all thirty samples analyzed. Likewise, among the boselaphine samples, two exhibit $\delta^{13}C$ values more positive than $-10.7\%$ though both these samples remain more negative than the most enriched bovine samples (Fig. 2).

3.2. Oxygen isotope ratios

The $\delta^{18}O$ values for all samples range between 32.6‰ and 22.4‰. Means for the 18 bovine and 12 boselaphine samples are 26.3‰ and 28.1‰, respectively. Shapiro–Wilk tests reveal that boselaphine and bovine $\delta^{18}O$ values are each normally distributed ($p>0.05$), a two-sided $F$ test between bovine and boselaphine $\delta^{18}O$ values indicate that sample variances are not significantly different, and a two-tailed $t$ test finds that the difference between the means is not significant ($p=0.066$).

4. Discussion

4.1. Carbon isotope ratios—paleodiets

In general, ranges of carbon isotope values follow the relationships predicted on the basis of functional mor-
Increases in crown height are an adaptation to increased rates of wear, and it is known that the consumption of grasses by herbivores produces greater tooth wear than would occur with strict adherence to a diet of leaves primarily because grasses are closer to ground level and so naturally result in greater intake of hard soil particles by the grazer (Mainland, 2003; Sanson et al., 2007). In contrast, teeth of fossil bovinae, both ancestral to and contemporaneous with Bovini, lack these advanced characters and remain quite primitive in overall morphology. Among living bovinae, tragelaphines, species of which are primarily browsers (Tragelaphus spp.), retain the primitive dental morphological condition least changed from that of the common ancestor of all the Bovinae (Bovini+Boselaphini+Tragelaphini).

Though early bovinae appear to have evolved to handle a diet composed of more abrasive foods, they did so in the early late Miocene (by at least 8.9 Ma, Bibi, 2007), well before the expansion and dominance of grasslands by heat-tolerant C4 grasses which took place at 7.4 Ma in the Siwaliks sequence (Barry et al., 2002). As such, it is most likely that early bovines evolved feeding increasingly on C3 grasses and inhabiting more open C3 grassland environments. The fact that all of the samples analyzed here presented δ13C values more negative than −8.0‰ establishes that bovine diets in the Siwaliks at around 8 Ma were purely C3-dominated, including no significant component of C4 plants.

Even within the C3 range, significant differences do exist between δ13C values of bovine and boselaphine fossil enamel, with bovine teeth having slightly higher δ13C. Such enrichment is only to be expected if the bovines were feeding on plants that themselves were slightly enriched in 13C. It has been shown that C3 plant δ13C values become progressively more positive with a change from a sub-canopy mesic to open xeric environments, due to the canopy effect (Medina and Minchin, 1980; van der Merwe and Medina, 1991; Vogel, 1978) and plant water-use efficiency responses to increased heat stresses in open environments (Farquhar et al., 1982a; O’Leary, 1993; van der Merwe and Medina, 1991). As a consequence, the differences in δ13C values between bovine and boselaphine fossil bovids presented in this study indicate that early bovines evolved exploiting more open environments than did boselaphines. The fact that the means of these two series differ by less than 1‰ suggests that the environmental/dietary differences between late Miocene bovines and boselaphines, though distinctive, were not extreme. For example, in a study of mammals from the Ituri Forest (Cerling et al., 2004), sub-canopy dwellers including the dwarf antelope (Neotragus batesi) exhibited an average δ13C value of −22.8‰, more than 5‰ lighter than that of gap-clearing inhabitants including sitatunga (Tragelaphus spekei). In contrast, the less than 1‰ separation between δ13C means of late Miocene bovine and boselaphine teeth is comparable to the differences in mean values recorded for species inhabiting similar environments such as lesser kudu (Tragelaphus imberbis) and greater kudu (Tragelaphus strepsiceros) from modern xeric bushlands in Kenya (Cerling et al., 2003), both species being C3 feeders in thicket or riverine forest habitats in arid environments. The actual diets of the fossil bovines and boselaphines and those of these living tragelaphines are not comparable, however, as the fossil taxa may have included significant quantities of C3 grasses in their diets while living tragelaphines feeding on a substantial amount of grass would display δ13C values more positive than −8‰ given that tropical grasses are predominantly C4 plants.

It is likely that both the early bovines as well as the fossil boselaphines sampled inhabited some form of open C3 habitat, perhaps open forest or mosaic woodland-grassland environments where the boselaphines would more selectively feed on browse and fresh grass shoots while the early bovines would have an expanded diet that overlapped with the boselaphines but included also more of the tougher grasses. The reconstruction of mixed diets for both these taxa but with relatively greater dietary roughage in Bovini is in concordance also with the results of tooth cusp mesowear analysis (Bibi, 2007; Fortelius and Solounias, 2000). Dietary separation between these two bovid groups may have only been seasonal. Many studies (Bell, 1969; Dekker et al., 1996; Schuette et al., 1998; Traill, 2004) have shown that dietary behaviors among different sympatric African bovids can be remarkably similar during the wet season—when resources are not limiting—but can come to differ greatly with the first onset of the dry season when the food items that were every species’ favored food items become scarce or altogether depleted. Bell’s (1969) study of feeding behaviors among gazelle (Gazella thomsoni), topi (Damaliscus korrigum), wildebeest (Connochaetes taurinus), zebra (Equus burchelli), and savanna buffalo (Syncerus caffer) found that the larger species were able to include greater quantities of the medium to tall grasses that are less nutritious but more plentiful during the dry season than the more protein-rich short grasses that all these herbivores favored during the wet season. This is largely explained by the fact that larger animals have relatively lower metabolic requirements than smaller ones (Hungate et al., 1959; Bell, 1969). The observation that herbivore
body size is inversely correlated with the nutrient content of their food (protein to fiber ratio) has been dubbed the Jarman–Bell principle (Bell, 1971; Codron et al., 2007; Geist, 1974; Jarman, 1974) and has been used to relate body size, population structure and biomass, and habitat preferences in a variety of ungulates. Using these same principles, one can reconstruct the ecological context of late Miocene boiselaphines and bovines. With the evolution of added chewing surfaces, increased crown height, and larger size (Fig. 1), early bovines were adapting to pressures selecting for the ability to incorporate more fibrous and less nutritious food items in their diet.

4.2.Paleoclimate and evolution

The selective pressures that drove the evolution of grazing morphologies were likely a consequence of physical environmental changes that resulted in the creation of more open habitats at the expense of more closed ones. Numerous studies point to exactly this type of mesic–xeric environmental change during the early late Miocene, between about 11.8 Ma, in the Siwaliks region but also in Eurasia as a whole (Damuth et al., 2002; Fortelius et al., 2002; Fortelius et al., 2006; Franzen and Storch, 1999; Quade and Cerling, 1995). The late Miocene evolution of Bovini within the context of ecological change is consistent within the general picture of faunal turnover in the Siwaliks at the same time. Isotopic evidence suggests shifts towards drier, more seasonal environments at around 9.2 Ma, with C4 grasses beginning to establish by 8.1 Ma, and the first C4-dominated habitats (paleosol carbonate δ13C values greater than −4‰) appearing at 7.4 Ma (Barry et al., 2002; Quade et al., 1989). Barry et al. (2002) note that two of these major episodes of faunal turnover take place around this time, in the period between 8 and 7 Ma. The nature of the faunal changes during this time appear also to be consistent with the isotopic vegetational reconstructions, with increasing proportions of open-habitat taxa at the expense of closed-habitat taxa (Barry et al., 2002). The primary physical climatic change that produced these environmental changes appears to have been increased seasonality (Quade et al., 1989), with stronger precipitation contrasts between wet and dry seasons occurring during this time. In particular, the significance of seasonal intensification in terms of a drier or prolonged dry season that could no longer support the previously greater extent of forested habitats should be emphasized. In concert with increasing aridity, new annual fire regimes may have played an important role in the development of late Miocene open habitats (Bond and Keeley, 2005; Keeley and Rundel, 2005). The evolution of Bovini in the Siwaliks region in the late Miocene then appears to have been part of a greater wave of faunal and environmental change and adaptation in response to the development of drier, more seasonal, open habitats.

Unlike early bovines, late Miocene boiselaphines appear to have responded to these climatic and environmental changes with less ‘drastic’ measures, maintaining what is essentially primitive dentognathic morphology. These fossil boiselaphines may have been ecologically analogous to living tragelaphines (such as the greater and lesser kudus mentioned above) that restrict themselves to forested micro-habitats within generally more arid and open environments, thus ensuring a perennial, though spatially restricted, supply of browse-based foods such as leaves, herbs, and fruits.

4.3. Morphological innovation and niche breadth

It has been suggested (Bibi, 2007) that the morphological novelties characterizing the earliest Bovini probably resulted in the ability of these bovids to expand their dietary spectrum rather than to simply shift it over, a phenomenon that has been observed in other graze-adapted fossil mammals (Feranec, 2003; Feranec, 2004; Feranec, 2007). To use Hutchinson’s (1957) terminology, early bovines, in evolving new morphologies, might have expanded their fundamental niche, though not necessarily their realized niche. The results of the current study in fact provide no good evidence for either a broadening or a narrowing of the fundamental niche: while the fossil bovines do show a greater absolute range of δ13C values than do the boiselaphines (Fig. 2), the variances themselves are not statistically significant, implying that these groups maintained essentially similar dietary niche breadths (Feranec, 2007). Therefore, the fundamental niche of early bovines appears simply to have shifted over (indicated by more positive δ13C values) relative to that of boiselaphines, without evidence for any broadening. However, the fact that the entirety of the measured values lie ‘crowded’ at the most positive end of the possible C3 range may confound the ability to perceive broadened niches using δ13C analysis. There is also the possibility that early bovines retained the ability to feed in more closed habitats but only did so rarely, erratically, and when forced to. With regard to living bovines, this may be illustrated in the example of the African savanna buffalo (Syncerus caffer), which throughout the year prefers grazing in grasslands but will move to forest browsing if their preferred riverine grassland habitats are occupied by
wildebeest (*Connochaetes taurinus*) during the dry season when resources are limiting (Sinclair, 1977). Further work, such as serial sampling for determination of within-specimen isotopic variability (amplitude of seasonal signals), may better address this hypothesis (e.g. Cerling et al., 2006; Nelson, 2005). Such work would include preferably specimens identified to the level of species and from a wider chronological range extending into times when C₄ became a prominent dietary component.

4.4. Oxygen isotope ratios—water intake behaviors

Oxygen isotope ratios in the fossil bovine and boselaphine teeth display means that are different but not significantly so. Spörheimer and Lee-Thorp (1999) found that browsers tend to exhibit slightly more enriched δ¹⁸O values than grazers, the interpretation being that browsers derive a greater ratio of their water directly from their food than do grazers. The fact that the fossil boselaphine teeth are on the average more enriched in δ¹⁸O than the fossil bovine teeth would support the hypothesis that these Miocene boselaphines browsed more and drank less while the fossil bovines grazed more and as a consequence also drank more. However, this argument is tenuous based on the current data. The most enriched δ¹⁸O values are those of boselaphines while the single most depleted value is from a bovine specimen (Fig. 2A). Tooth enamel δ¹⁸O values show no consistent relationship either to morphology or to locality. Rather, the variation in δ¹⁸O values probably reflects behavioral differences in water intake at the level of the different individuals sampled. Living Bovini, Boselaphini, and Tragelaphini are obligate drinkers more or less tied to water sources, though much of their water intake must derive also from the plant matter they ingest, and this may have been the situation for their late Miocene fossil relatives as well. Variations in enamel δ¹⁸O values can be the result of any number and combination of water intake behaviors such as feeding from canopy tops (enriched) vs. understory (depleted), or drinking from evaporating waterholes (enriched) vs. rivers (depleted). These behaviors are likely to have been highly variable even within individual bovid from place to place and season to season. Thus, the late Miocene bovines and boselaphines sampled appear to have been opportunistic rather than restricted in their water intake behaviors.

5. Conclusions

Thirty fossil dental specimens attributable to late Miocene (~8 Ma) bovines and boselaphines were sampled for bioapatite carbon and oxygen isotope ratios. The results provide support for fine-scale niche-partitioning between these two bovid phylogenetic/functional groups along a dietary axis reconstructed using δ¹³C carbon isotope ratios. All values are clustered between −9‰ and −13‰, indicating that both bovines and boselaphines lived in pure C₃-dominated environments. In accordance with predictions made on the basis of the functional morphological differences between fossil bovine and boselaphine teeth (Bibi, 2007), fossil bovine dental enamel on the whole exhibits significantly more positive δ¹³C values while fossil boselaphine teeth have more negative δ¹³C values. Enrichment of the heavier isotope of carbon (more positive δ¹³C values) in bovine teeth is indicative of feeding on C₃ plants growing in more open environments—such as canopy gap clearings or grasses in open C₃ grasslands—than inhabited by boselaphines which exhibited more negative values signifying feeding in more closed habitats. Outlier specimens within both the bovine and boselaphine series indicate that while diets were on the whole different, important dietary variations at the individual level were often significant, resulting in some more depleted and more enriched δ¹³C values than expected in bovines and boselaphines, respectively. Niche breadth, estimated as the variance of bovine and boselaphine δ¹³C values about their respective means, does not differ significantly between these two bovid groups. There is thus no evidence here that the evolution of novel morphological features associated with increased grazing permitted a broadening of the fundamental niche in early bovines. However, the fact that all specimen δ¹³C values in this study are clumped at the most positive end of the C₃ feeding range gives reason to consider whether the absence of a C₄ component may preclude detection of expanded niche breadth in this case. Further studies including younger specimens (<7.4 Ma) and the C₄ dietary spectrum may better address the question of fundamental niche broadening.

Oxygen isotope δ¹⁸O values are not significantly different between late Miocene bovines and boselaphines. Living representative of Bovinae (Bovini + Boselaphini + Tragelaphini) are all obligate drinkers more or less dependent on proximity to water bodies, and it is likely that this was the case for both the fossil bovines and boselaphines sampled in the study.

This study has utilized stable isotopes to test ecological hypotheses developed on the basis of functional analysis of dental occlusal morphology (Bibi, 2007). The result is a high-resolution analysis that discriminates between more closed- and more open-environment resource use within a narrow range of isotopic values
In tracing the morphological and ecological origins and evolution of a single herbivorous clade (Bovini), this study contributes to ongoing and wide-ranging efforts to reconstruct and explain the emergence of proto-modern climate systems, biotas, community structures, and taxa in late Miocene times, between about 10 and 5 Ma.

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