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Lateral trends in carbon isotope ratios reveal a Miocene vegetation gradient in the Siwaliks of Pakistan

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ABSTRACT

Isotopic analyses of mammalian tooth enamel from a well-defined, laterally extensive 150 k.y. interval (9.15–9.30 Ma) reveal an ecological gradient in vegetation on the late Miocene sub-Himalayan alluvial plain. Two contemporaneous river systems deposited the sediments of this interval, with a mountain-sourced system (herein, Blue-gray) to the southwest interfingering with a foothill-sourced system (Buff) to the northeast. Fossil mammal teeth collected from a 32 km transect across this fluvial gradient are significantly more depleted in ^{13}C from northeastern localities than from southwestern localities. This trend occurs in equids, giraffids, suids, sivapithecine hominoids, and anthracotheres. We propose that the Buff fluvial system provided more equably moist substrate conditions and supported more closed-canopy vegetation than the Blue-gray fluvial system. Herbivores living along the paleovegetation gradient thus acquired different carbon isotopic signatures during the period of tooth enamel formation, resulting from higher $\delta^{13}C$ values in the forage supported by the Blue-gray fluvial system compared with forage associated with the Buff system. The data also imply that many Siwalik mammalian herbivores displayed marked fidelity in juvenile home ranges and habitats.

INTRODUCTION

Stable isotopic analyses of fossil mammalian enamel contribute to reconstructions of past environments and dietary behaviors of taxa (e.g., Morgan et al., 1994; Cerling et al., 1997; Koch et al., 2004; Secord et al., 2008). Most enamel-based studies have focused on interpreting isotopic signals within specific taxa or over a particular interval of time, in order to assess the relative contribution of C_3 versus C_4 plants to diet and to infer vegetation structure. This study examines local habitat variation for a fauna consuming predominantly C_3 vegetation. Intensive sampling of mammalian teeth from a narrow temporal interval (~150 k.y.) extending across a late Miocene fluvial gradient reveals subtle variation corresponding to geographic position along a 32 km transect. This approach offers new insights into the effects of kilometer-scale habitat variation on $\delta^{13}C$ values, vegetation, and mammalian landscape-use patterns.

Neogene vertebrate faunas and sediments of the Potwar Plateau in northern Pakistan have been studied by the Harvard–Geological Survey of Pakistan Research Project since 1973. The >4000 m sequence represents >17 m.y. of deposition that was nearly continuous on the scale of 10^5 yr (Barry et al., 2002). Isotopic analyses of Siwalik paleosols and mammals previously documented a marked change from predominantly C_3 vegetation to C_4 vegetation between 8.5 and 6 Ma, as well as an initial presence of C_4 grasses in the early late Miocene, ca. 10 Ma (Quade et al., 1989; Morgan et al., 1994; Cande and Kent, 1995; Barry et al., 2002; Badgley et al., 2005; Behrensmeyer et al., 2007).

In the late Miocene Dhok Pathan Formation, a stratigraphic marker unit, the blue-gray U sandstone, extends laterally for more than 40 km (Fig. 1). Straddling the U sandstone is a particularly fossiliferous interval, the U-level, 60–90 m thick, that includes 83 localities with >4000 catalogued specimens representing ~60 mammalian species (Barry et al., 2002). The striking sedimentological transition between two adjacent fluvial regimes, the Blue-gray and Buff systems, is documented along the U-level with 19 stratigraphic sections that include a laterally continuous paleomagnetic isochron below the U sandstone (Badgley and Behrensmeyer, 1980; Behrensmeyer and Tauxe, 1982; Tauxe and Badgley, 1984). To the southwest, a thick sequence of multistoried blue-gray sandstones is attributed to a mountain-sourced fluvial system with large-scale channels. To the northeast is a contemporaneous sequence of fine-grained reddish-brown mudstones with single-story, buff-colored ribbon sandstones composing the Buff system, which is attributed to tributary rivers draining local sub-Himalayan foothills. Where these two fluvial systems interfinger, sheet sands associated with the Blue-gray system are more laterally extensive than those of the Buff system and indicate periodic rapid progradation of Blue-gray system sediments over those of the Buff system (Behrensmeyer and Tauxe, 1982). Buff system facies compose an average of 23 ± 10 m of U-level sediments in the southwestern half of the study transect as compared with 50 ± 10 m in the northeastern half of the transect (Fig. 1C). Dominant flow directions in sandstones of the two systems differ significantly, 94° for the blue-gray channels compared with 136° for the buff channels (Behrensmeyer and Tauxe, 1982).

We present isotopic data from mammalian teeth that document a statistically significant $\delta^{13}C$ gradient within the U-level from the southwest to the northeast over 32 km. We propose that the isotopic gradient largely results from variation in the $\delta^{13}C$ of plants, which in turn tracks levels of plant moisture stress related to groundwater availability in the Blue-gray versus the Buff fluvial systems.

METHODS

Isotopic samples include 100 molars and premolars from five mammalian orders collected from surface fossils at 26 localities primarily in Buff system deposits (GSA Data Repository Table DR1[1]). Several milligrams of drilled enamel were treated successively for 15 min each with 3% H_2O_2 and 0.1 M CH_3COOH and ~0.5 mg reacted with 100% H_3PO_4 at 90 °C on an automated carbonate device connected to a Finnigan MAT 252 mass spectrometer at the University of Utah. Four ~50 mg powdered

[1]GSA Data Repository item 2009030, Table DR1 (Siwalik U-level mammalian isotopic and locality data) and Table DR2 (specimen counts for large herbivore taxa from the U-level), is available online at www.geosociety.org/pubs/ft2009.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

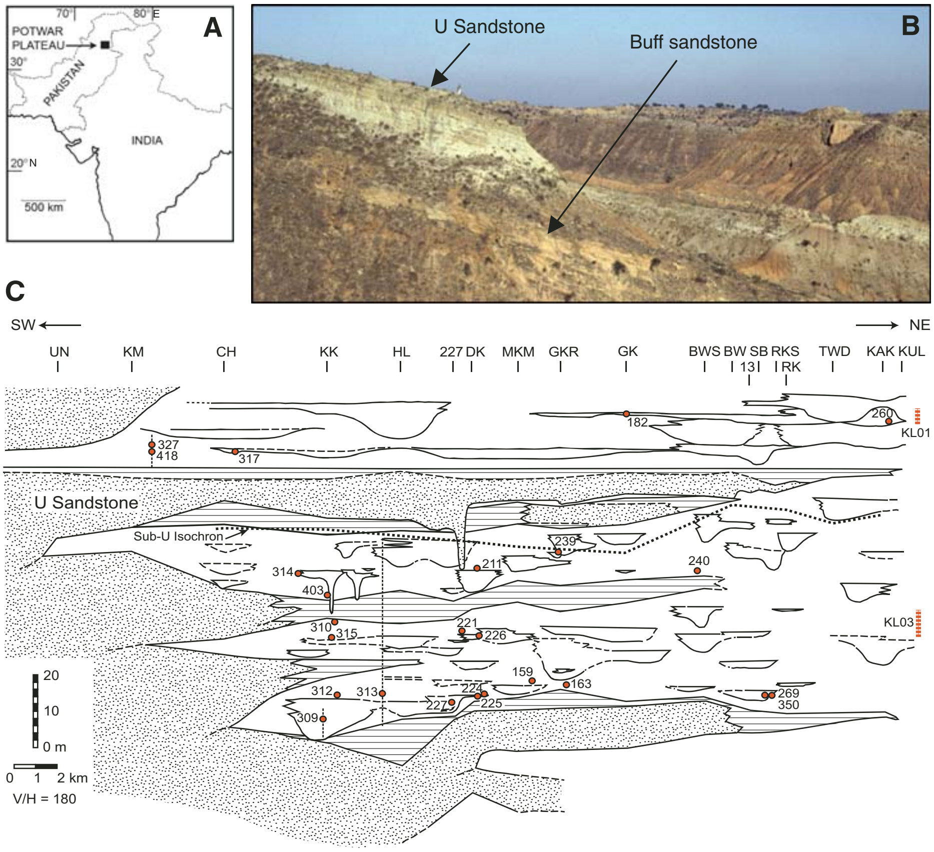

Figure 1. A: Map of Indian subcontinent highlighting Potwar Plateau. B: Photo of interfingering lithofacies of the two fluvial systems, the Blue-gray (U sandstone and gray silts and clays) and Buff (sandstones with associated brown, red and orange silts and clays), near Ganda Kas (GK). C: Panel diagram of U-level with placement of 26 fossil localities included in this study and location of 19 stratigraphic sections. Blue-gray system is shaded with stipples (sand) and horizontal lines (gray silts and clays); thicknesses are plotted relative to gray horizontally bedded silts at top of U sandstone. Vertical dashed lines indicate uncertainty in precise stratigraphic placement of localities; heavy dotted broken line marks sub-U paleomagnetic isochron. Modified from Behrensmeyer and Tauxe (1982).

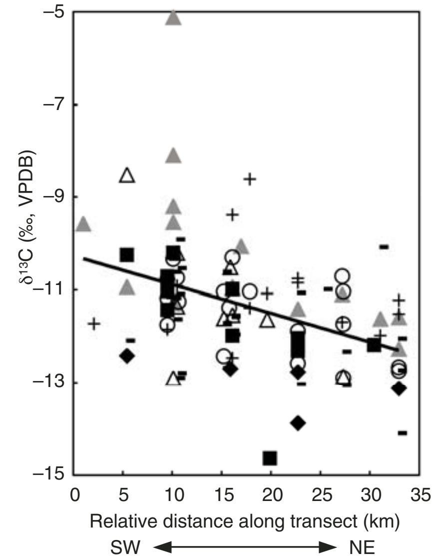

Figure 2. Stable carbon isotope data from U-level mammals (n = 100), including *Sivapithecus sivalensis* (◆), Hipparionines (▲), *Propotamochoerus hysudricus* (O), *Hippopotamodon sivalense* (+), *Merycopotamus medioximus* (△), *Bramatherium megacephalum* (■), and all other specimens (–) which include bovids, tragulids, and proboscideans (Table DR1 [see footnote 1]). Line represents standard least squares regression model (Table 1, a). Spatial position of fossil localities is defined relative to locality Y0418. VPDB—Vienna Peedee belemnite.

samples were pretreated successively with 5% NaOCl and 1 M CH_3COOH for 16 h, and reacted with 100% H_3PO_4 at 90 °C for 24 h. The evolved CO_2 was collected by cryogenic separation and analyzed on a VG prism mass spectrometer at Harvard University. Precision for replicate samples was ±0.3‰ (n = 11) and for four standards was <±0.2‰ (n = 154) for $\delta^{13}C$ and $\delta^{18}O$.

Depositional environments of fossil localities were assigned according to the schema of Behrensmeyer et al. (2005). The geographic position of each fossil locality was determined from grid coordinates on field maps and is accurate to within ~91 m² (100 yd²).

RESULTS

The isotopic data indicate a predominantly C_3 open-canopy ecosystem between 9.15 and 9.30 Ma (Fig. 2), consistent with previous results derived from paleosols (Quade et al., 1989). Within this ecosystem, however, a significant isotopic gradient in carbon is recorded in fossil mammal teeth along the 32 km U-level transect (R^2 = 0.164, p < 0.0001; Table 1, a). Most specimens yielded $\delta^{13}C$ values between −10‰ and −13‰ (n = 85). All isotopic values <−13‰ (n = 6) are from specimens in the northeastern portion of the transect, while all isotopic values >−10‰ (n = 9) are from specimens in the southwestern portion (Fig. 2). Over 32 km, the net isotopic change is 2‰, from −10.3‰ to −12.3‰ (Fig. 2; Table 1, a). The sample subset from the southwestern half of the transect is significantly more enriched in ^{13}C than that from the northeastern half of the transect (Wilcoxon 2-sample test, W = 2430; p < 0.0001). This pattern tracks the sedimentological transition from the Blue-gray, sand-dominated fluvial system in the southwest to the Buff mudstone-dominated fluvial system in the northeast (Fig. 1).

There is no parallel isotopic gradient in $\delta^{18}O$ across the U-level transect (Fig. 3). Rather, the two probable canopy feeders, the hominoid *Sivapithecus sivalensis* and the giraffid *Bramatherium megacephalum*, are significantly more enriched in ^{18}O than the highly water-dependent anthracothere *Merycopotamus medioximus* (Lihoreau et al., 2004) and the suid *Propotamochoerus hysudricus* (t-test, p < 0.0001, df = 42).

TABLE 1. STANDARD LEAST SQUARES REGRESSIONS OF $\delta^{13}C$ VALUES ON DISTANCE ALONG THE U-LEVEL TRANSECT

Isotopic samples	Slope	Intercept	R^2	p
a: All samples (n = 100)	–0.061	–10.271	0.164	<0.0001
b: Fossils from floodplain channel localities (n = 51)	–0.055	–10.534	0.104	0.0213
c: Fossils from other depositional contexts* (n = 34)	–0.055	–10.422	0.389	<0.0001
d: U2 level fossils (n = 38)	–0.096	–9.636	0.147	0.0173
e: U9 level fossils (n = 32)	–0.048	–10.690	0.199	0.0104
f: *Bramatherium megacephalum* (n = 11)	–0.106	–9.947	0.418	0.0317
g: Hipparionines (n = 15)	–0.099	–8.579	0.315	0.0295
h: *Propotamochoerus hysudricus* (n = 19)	–0.058	–10.375	0.331	0.0099
i: *Sivapithecus sivalensis* (n = 5)	–0.032	–12.342	0.322	0.3181
j: *Merycopotamus medioximus* (n = 9)	–0.133	–9.299	0.390	0.0722
k: *Hippopotamodon sivalense* (n = 14)	–0.010	–10.893	0.009	0.7457

*Excludes categories FC? (possible floodplain channel) and unknown (Table DR1; see footnote 1).

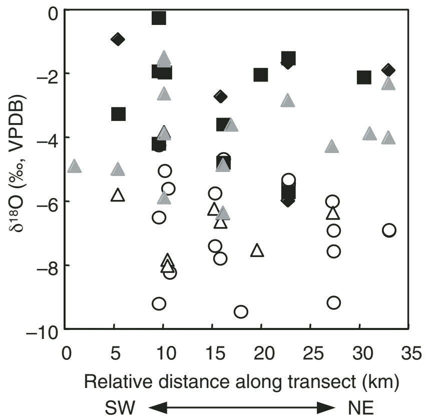

Figure 3. Stable oxygen isotope data (n = 57) showing separation between canopy feeders (dark symbols) and less evaporative habitat foragers (open symbols). Equids (gray) show intermediate values. Symbols and abbreviations as in Figure 2.

The $\delta^{13}C$ isotopic gradient is not explained by the lateral distribution of depositional environments, taxonomic representation of collected fossils, or stratigraphic position of localities within the U-level (Table DR1). The lateral isotopic trend is significant for samples from the most common depositional setting for fossil localities, floodplain channel, as well as for samples from the remaining localities (Table 1, b and c). The majority of samples derive from the oldest and youngest portions of the U-level (U2 and U9), and both subsets produce the same significant trend (Table 1, d and e). The isotopic trend is significant within three of the four best-sampled taxa—*Bramatherium megacephalum*, hipparionine equids, and *Propotamochoerus hysudricus* (Table 1, f–h), and present within *Sivapithecus sivalensis* and *Merycopotamus medioximus* (Table 1, i and j). The trend is not observed in the well-sampled large suid *Hippopotamodon sivalense* (Table 1, k).

DISCUSSION

The observed isotopic gradient could result from: (1) stochastic variability in $\delta^{13}C$ values, (2) a spatial diagenetic gradient that altered $\delta^{13}C$ values during fossilization, (3) the presence of more C_4 grasses toward the southwestern end of the sampled transect, or (4) an original ecological gradient influencing $\delta^{13}C$ values of the dominant C_3 vegetation. Temperature and solar radiation levels can also exert measurable differences on $\delta^{13}C$ plant values (O'Leary, 1988; Farquhar et al., 1989; Tieszen, 1991; Heaton, 1999), but are unlikely to have varied directionally across the original U-level landscape at the scale of this study.

Stochastic variation in $\delta^{13}C$ values could arise from small sample sizes. However, it is statistically very unlikely that the same spatial gradient, as expressed in the slopes of regression models, would be evident when the fossil sample is partitioned by depositional environment (Table 1, b and c), by stratigraphic level (Table 1, d and e), and by taxa (Table 1, f–h) if the actual distribution of $\delta^{13}C$ values were independent of their position along the transect.

Although many factors influence $\delta^{18}O$ values of herbivores, taxa feeding on upper-canopy and open-habitat vegetation tend to be more enriched in ^{18}O than taxa feeding on vegetation from less evaporative habitats (e.g., Levin et al., 2006; Nelson, 2007). Consistent separation in $\delta^{18}O$ values of five well-sampled taxa across the U-level argues against systematic diagenetic alteration of enamel carbonate from exchange with groundwater prior to fossilization (Fig. 3).

According to the third hypothesis, C_4 grasses could have composed a higher proportion of the vegetation toward the southwestern end of the U-level transect. The presence of the isotopic gradient in both grazing and browsing taxa (Fig. 2), however, implies that varying amounts of C_4 vegetation are not the primary cause of the isotopic pattern. Paleosol carbonate data from three sections in the northeastern half of the transect (DK, GK, and KAK in Fig. 1) indicate C_3 vegetation ($\delta^{13}C$ averages −10.3‰ ± 1.1‰, n = 25); U-level paleosol data from farther southwest are currently unobtainable. In addition, the taxonomic composition of fossil mammals does not indicate any increase in grazing species toward the southwest, which would be expected if southwestern habitats included more grass (Table DR2). Minor observed variation in taxonomic composition, abundance, or co-occurrence along the 32 km transect can be explained by differences in fossil locality productivity.

The isotopic trend along the U-level transect in equids, giraffids, and the suid *Propotamochoerus hysudricus*, along with a similar pattern in anthracotheres and hominoids, supports the fourth hypothesis, i.e., variations in $\delta^{13}C$ values of C_3 vegetation on the original Miocene landscape that were incorporated into the tooth enamel of herbivores foraging over different proportions of Blue-gray versus Buff system substrates. The ubiquity of giraffids and hipparionines, taxa independently assessed as primarily browsers and grazers, respectively (Morgan et al., 1994; Belmaker et al. 2007), indicates a continuous mix of both browse and graze. This hypothesis also implies high local habitat fidelity of juvenile and adolescent large herbivorous mammals, because the enamel isotopic signature is set during crown development. Home range sizes of <1–5 km^2 are reported for many medium- and large-bodied African ungulates in their preferred habitats (Estes, 1991). Taphonomic analysis indicates that most fossil remains were not significantly transported with respect to the life habitats of the mammals (Badgley, 1986).

In modern ecosystems, modest variation in groundwater levels, location of permanent water sources, and topography can produce isotopic gradients within C_3 plant taxa over a few kilometers, similar to those observed across the U-level transect. Higher groundwater tables, greater proximity of perennial water sources, and lower elevation are correlated with decreases of 1‰–2‰ in C_3 plant $\delta^{13}C$ values due to increased water availability within modern ecosystems (Ehleringer and Cooper, 1988; Garten and Taylor, 1992; Horton et al., 2001; Codron et al., 2005). Despite similar annual rainfall and vegetation type, groundwater availability resulted in differences of >3‰ in soil organic $\delta^{13}C$ from a series of soil cores over ~50 km in the Okavango Delta region in Botswana (Bird et al., 2004).

Although it might be expected that $\delta^{18}O$ values of the U-level mammals sampled would covary with the $\delta^{13}C$ values, this covariation does not occur (cf. Figs. 2 and 3). However, the lack of parallel isotopic gradients in $\delta^{13}C$ and $\delta^{18}O$ in the mammals is consistent with isotopic data from a series of laterally sampled Neogene paleosols in another area of the Potwar Plateau. Soil carbonate $\delta^{18}O$ values do not closely track $\delta^{13}C$ values within most of these paleosols and instead are correlated with long-term trends in rainfall (Behrensmeyer et al., 2007).

Observed variations in channel frequency and topography along the U-level signify lateral variations in water availability. Reconstructions of the fluvial architecture suggest that the elevation of the composite alluvial plain was higher to the southwest during episodes of rapid aggradation and eastward excursions of the Blue-gray system relative to the Buff system (Behrensmeyer and Tauxe, 1982). Higher elevation and more porous substrates under a strongly seasonal climate regime would result in a lower dry-season water table. Thus, vegetation growing in the channel belt of the Blue-gray river system would have experienced greater seasonal water stress than in the mudstone-dominated substrates of the Buff system. The modern Sun Kosi River, originating in the Nepal Himalaya, provides a reasonable modern analogue for the mountain-sourced, flood-prone, sand-dominated Blue-gray fluvial system, with the alluvial plain to its east characterized by parallel foothill-sourced drainages similar in scale to the channels of the Buff fluvial system (Gole and Chitale, 1966).

CONCLUSIONS

Siwalik U-level mammalian herbivores, dated to 9.15–9.30 Ma, exhibit spatial variation in $\delta^{13}C$ values that tracks a lateral change in fluvial regime over more than 30 km. We propose that the mud-rich sediments of the foothill-sourced Buff fluvial system to the northeast maintained higher levels of soil moisture and seasonal moisture equability for the vegetation and herbivorous fauna, leading to lower $\delta^{13}C$ values in their enamel relative to values associated with the mountain-sourced Blue-gray, sand-dominated fluvial system to the southwest. Our interpretation is that the animals in life foraged over substrates consisting of different proportions of the Buff and Blue-gray systems, thereby acquiring differing carbon isotope signatures in their teeth. Alternative hypotheses to explain the observed gradient (stochastic variation, diagenesis, and a mixture of C_4 and C_3 vegetation) are not supported by the data.

The isotopic gradient also implies local habitat fidelity on a scale of ~1–10 km, on a yearly or seasonal basis, for primate and ungulate taxa. Spatially varying isotopic composition of ingested vegetation could only be detected if these mammals were preserved in proximity to their places of early maturation. The observed ecological gradient appears to have persisted through the time span of the U interval, 150 k.y. Our interpretation that the gradient was caused by varying substrate moisture regimes across the aggrading Blue-gray versus Buff fluvial systems suggests overall ecological stability in the late Miocene ecosystem during the U-level time interval.

This study of one temporally constrained stratigraphic interval highlights the potential of paleoecological analyses to detect kilometer-scale habitat variation in the geological past. Both detailed lateral and vertical sampling are recommended to distinguish spatial variation in ecological trends at a given time from those reflecting change over time. Our results also indicate that ecological signals well beyond the scale of the burial environment can be captured in multi-locality samples of vertebrate remains.

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