Paleogeographic variations of pedogenic carbonate δ¹³C values from Koobi Fora, Kenya: implications for floral compositions of Plio-Pleistocene hominin environments

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Abstract

Plio-Pleistocene East African grassland expansion and faunal macroevolution, including that of our own lineage, are attributed to global climate change. To further understand environmental factors of early hominin evolution, we reconstruct the paleogeographic distribution of vegetation (C₃-C₄ pathways) by stable carbon isotope (δ¹³C) analysis of pedogenic carbonates from the Plio-Pleistocene Koobi Fora region, northeast Lake Turkana Basin, Kenya. We analyzed 202 nodules (530 measurements) from ten paleontological/archaeological collecting areas spanning environments over a 50-km² area. We compared results across subregions in evolving fluviolacustrine depositional environments in the Koobi Fora Formation from 2.0–1.5 Ma, a stratigraphic interval that temporally brackets grassland ascendancy in East Africa. Significant differences in δ¹³C values between subregions are explained by paleogeographic controls on floral composition and distribution. Our results indicate grassland expansion between 2.0 and 1.75 Ma, coincident with major shifts in basin-wide sedimentation and hydrology.

Hypotheses may be correct in linking Plio-Pleistocene hominin evolution to environmental changes from global climate; however, based on our results, we interpret complexity from proximate forces that mitigated basin evolution. An ~2.5 Ma tectonic event in southern Ethiopia and northern Kenya exerted strong effects on paleography in the Turkana Basin from 2.0–1.5 Ma, contributing to the shift from a closed, lacustrine basin to one dominated by open, fluvial conditions. We propose basin transformation decreased residence time for Omo River water and expanded subaerial floodplain landscapes, ultimately leading to reduced proportions of wooded floras and the establishment of habitats suitable for grassland communities.

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Introduction

Global climate is often elected as a catalyst for environmental changes acting as selective pressures on Plio-Pleistocene African hominins (Stanley, 1992; Vrba, 1995, 1999; deMenocal, 2004). Habitat theory of Vrba (1992) and variability selection hypothesis of Potts (1998) credit mammalian evolutionary pattern and process to climate change. Feibel (1999: 276) argues the need for a middle ground, tethering the “global-scale climatic phenomena” to “environmental change, habitat shift, and biotic evolution”, and offers the sedimentary basin as a scale for analysis. Environments within individual basins respond to climate with different sensitivities and thresholds influenced by basin size, topography, depositional and tectonic regime, and water availability (Carroll and Bohacs, 1999; Withjack et al., 2002).

Stable carbon isotope (δ¹³C) records from pedogenic carbonates are interpreted as reflecting the spread of C₄ grasses in East Africa beginning as early as the Miocene (Cerling, 1992). From these data, environmental change and increased...
aridity associated with global climate are temporally correlated with faunal macroevolution including the branching pattern of the hominin lineage and the origins of genus Homo (see review in deMenocal, 2004). Unlike proxies of global climate from the marine realm, pedogenic carbonate isotopes offer direct and local environmental information from the habitats of hominins and other members of the mammalian community. Isotopic studies of pedogenic carbonates in the Turkana Basin have interpreted terrestrial East Africa as responsive to global climate over approximately the last four million years (Cerling et al., 1988; Wynn, 2004). Here we employ stable isotopic values of paleosol carbonates from hominin-bearing sediment in the Koobi Fora region of the basin to examine paleoenvironmental change. We focus on the interval 2.0–1.5 Ma, which brackets a marked shift in aridity (Wynn, 2004) and the appearance of early African Homo erectus in the area (Antón and Swisher, 2004; Wood and Strait, 2004). We enlarge the current database to place our isotopic measures of floral community structure into a paleogeographic framework and integrate climatic and tectonic influences on a basin-wide scale.

Study region

Geographic setting

The Turkana Basin of northern Kenya and southern Ethiopia lies within the eastern branch (or Gregory Rift) of the East African Rift System between the Kenyan and Ethiopian domes (Ebinger et al., 2000). The basin presently contains one of the largest rift lakes, Lake Turkana, with an area of 7,500 km² (Frostick, 1997). Today, the lake is a saline-alkaline and closed-basin lake that receives over 90% of its water from rainfall over the Ethiopian Highlands, via the Omo River (Fig. 1), with minor inputs from the Turkwell and Kerio River systems (Yuretich, 1979). The general climate within this rift bottom setting is arid to semi-arid and receives 250–500 mm of rainfall annually (Nicholson, 1996). Bushland grasslands dominate the landscape, with gallery forests clustered along perennial and ephemeral river channels (Lind and Morrison, 1974).

The Koobi Fora region, situated within the northeast Turkana Basin of Kenya (Fig. 1), is one of the richest fossil and archaeological localities in East Africa (Leakey and Leakey, 1978; Isaac and Isaac, 1997). Plio-Pleistocene sediments exposed in the region are attributed to the Koobi Fora Formation (Brown and Feibel, 1986), which preserves a record of hominin evolution and environmental change for the period ~4.0–1.0 Ma (Feibel et al., 1989, 1991; Brown and Feibel, 1991). Lake Turkana constrains the western margin of the Koobi Fora Formation, while Miocene-Pliocene volcanics to the west define the eastern border (Watkins, 1986). The formation is exposed in geographic subregions of the Koobi Fora region, including Ileret, Il Dura, Karari Ridge, and Koobi Fora Ridge (Fig. 2A), which are segregated into numbered paleontological and archaeological collecting areas (Fig. 1). The extensive geographic exposure of the Koobi Fora Formation, and its well-documented stratigraphy and geochronology, affords reconstruction of a range of habitats across paleolandscape at discrete temporal intervals.

Stratigraphy and paleogeography

Although outcrops of the Koobi Fora Formation are discontinuous, stratigraphic control has been determined by radiometrically dated and correlated tuffs, aerially extensive bioclastic lacustrine marker beds, and an established geomagnetic polarity stratigraphy (McDougall, 1985; Brown and Feibel, 1986, 1991; Hillhouse et al., 1986; Feibel et al., 1989; McDougall et al., 1992; Brown et al., 2006; McDougall and Brown, 2006; Fig. 3). Here we focus on the upper Burgi, KBS, and lower Okote Members of the formation, approximately representing the period between 2.0 and 1.5 Ma (McDougall, 1985; Brown and Feibel, 1986, 1991): *Age of Lorenyang Tuff is approximated by sedimentation rate (scaled age).
Fig. 2. Paleogeographic reconstructions of the Koobi Fora Formation between 2.0 and 1.5 Ma (after Feibel, 1988; Feibel et al., 1991; Rogers et al., 1994). A) Modern paleogeography, basemap area equals approximately 50 km² (after Isaac and Behrensmeyer, 1997). B) Paleogeography at 1.7–1.5 Ma. C) Paleogeography at 1.8–1.7 Ma. D) Paleogeography at 1.9–1.8 Ma. E) Paleogeography at 2.0–1.9 Ma.

Sedimentation of these members is inferred to be largely continuous, except for an unconformity (~500,000-year depositional pause) in the upper portion of the Burgi Member (Fig. 4) and the background hiatuses inherent to the sedimentation of the fluviolacustrine environments (Brown and Feibel, 1986; Feibel et al., 1989, 1991).

A large lake formed in the Turkana Basin at about 2.0 Ma, as indicated by the widespread occurrence of lacustrine and associated facies just above the upper Burgi Member unconformity (Brown and Feibel, 1991). This precursor of Lake Turkana, Lake Lorenyang (Fig. 2E), occupied an area of approximately 9,000 km², mainly fed by an ancestor of the modern Omo River (Feibel et al., 1991; Feibel, 1997).

The deposition of the Lorenyang and KBS Tuffs in a deltaic facies (Feibel, 1988) suggests that the ancestral Omo River delta began prograding into the Koobi Fora region by about 1.9 Ma (Brown and Feibel, 1991; Fig. 2D). The river coursed through the region as indicated by fluvial channel and floodplain facies just above the stratigraphic level of the KBS Tuff (White et al., 1981).

Channel and floodplain deposits are more widespread within the upper part of the Olduvai Subchron, suggesting an increase in the prevalence of ancestral Omo River environments at Koobi Fora near 1.8–1.7 Ma (Feibel et al., 1989; Brown and Feibel, 1991; McDougall et al., 1992). Additional channel systems emanated from the highlands along the northeastern basin margin at this time (Feibel et al., 1991). The Omo River and basin margin channels emptied into a shallow lake margin/series of lake margins, over which there were frequent transgressions and regressions (Feibel et al., 1991; Feibel, 1994; Fig. 2C).

After about 1.7 Ma, lake-related depositional environments were virtually absent from the region, except for a few shallow, aerially restricted, and transient examples (Brown and Feibel, 1991; Fig. 2B). For the majority of the period between 1.7 and 1.4 Ma, the main (axial) channels of the ancestral Omo were not readily active in the study area, rather the landscape was occupied by smaller distributaries that either derived from the main channel or from the northeastern margin of the basin (Feibel et al., 1991; Fig. 2B). These distributaries were responsible for the deposition of a series of correlative marker tuffs, referred to as the Okote Tuff Complex, Koobi Fora Tuff Complex, and Ileret Tuff, which have an age near 1.6–1.5 Ma (Brown and Feibel, 1985, 1986; Brown et al., 2006; McDougall and Brown, 2006). Large river channels, attributed to the ancestral Omo, reclaimed the Koobi Fora region near early Chari Member times, ~1.4 Ma (Brown and Feibel, 1991).

East African and Turkana Basin paleoenvironments

Many studies attribute a marked increase in East African aridity and grassland expansion between 2.0 and 1.5 Ma to causes derived from global climate change (reviewed in deMenocal, 2004). Increased terrigenous sediment inputs, ca. 1.7 Ma, from the northern low-latitude areas of continental Africa (deMenocal and Bloemendal, 1995) have been linked with an intensification of Northern Hemisphere Glaciation at ~1.8 Ma (e.g., Shackleton et al., 1990; Shackleton, 1995).

Fig. 3. Composite stratigraphic sections of Koobi Fora Formation by subregions with radiometric ages of tuffs (after Brown and Feibel, 1991; McDougall and Brown, 2006).
Indications of a response to high-latitude glacial conditions are found in marine pollen records from off the coast of northwest Africa, which show wooded savanna to desert vegetation zones appearing around 2.6–2.4 Ma and dominating by 1.8 Ma (Le-roy and Dupont, 1994). East African palynological evidence suggests drier conditions in rift valley lowlands at 2.35 Ma and an intensification of aridity at around 1.8 Ma (Bonnefille, 1995). East and South African mammalian species abundances show a shift to more arid-adapted fauna culminating at 1.8 Ma (e.g., Vrba, 1995; Reed, 1997). Pedogenic carbonate isotope records amassed from several Plio-Pleistocene East African localities also display aridification with increased proportions of C₄ grasses and heightened evaporation of soil water or change in isotopic composition of rainfall (Cerling, 1992; Levin et al., 2004; Wynn, 2004).

Other researchers, however, have found ambiguous or contrasting records of East African paleoenvironments. Kingston and others (1994) found no significant change in vegetation from the Baringo Basin, but a persistent mosaic environment over the last 15 Ma. Plio-Pleistocene vegetation at Olduvai Gorge had a significant amount of wooded vegetation (Sikes, 1994). Trauth et al. (2005, 2007) have suggested the presence of a humid period within the general pattern of East African aridification indicated by the formation of large lakes circa 1.9–1.7 Ma. Suids found in South and East African hominin localities maintain postcranial morphologies for closed and intermediate habitats (Bishop, 1999).

Within the Turkana Basin, contrasting and complex proxy records also confound environmental interpretations. Mammalian species abundances show a gradual shift to more arid-adapted fauna from 2.5 to 1.8 Ma rather than a “turnover pulse” coinciding with glacial intensification (Behrensmeyer et al., 1997). Additional studies on the same dataset proposed a series of pulses occurring at periods of 100,000 years (Bobe and Behrensmeyer, 2004). Palynological evidence indicates that grass species dominated from lake and delta environments at 2.0 Ma (Bonnefille and Vincens, 1985); however, cooler and more humid conditions have been interpreted in areas of the basin by the presence of highland and riverine pollen species (Bonnefille, 1976). Cerling and others (1988) and Wynn (2000) demonstrated tropical grass expansion in the Turkana Basin over the last 4.3 Ma, with marked aridity events during the intervals between 3.58–3.35, 2.52–2.00, and 1.81–1.58 Ma. However, Wynn’s (2004: his figure 2B) compilation illustrated a mean value trending toward wooded vegetation between 1.8–1.5 Ma. Wynn (2004) also reported a general aridification trend with increasingly shallower calcic horizon depths in Turkana Basin paleosols, although he found an excursion to a humid period between 1.9 and 1.8 Ma with depth to calcic horizon estimates.

Materials and methods

Stable carbon isotopes ($\delta^{13}C$) of pedogenic carbonates

The C₃ (Calvin-Benson) and C₄ (Hatch-Slack) photosynthetic pathways have distinct differences in the fractionation of carbon isotopes (see Ehleringer, 1989). Woodland vegetation (trees, shrubs, temperate grasses) utilizing the C₃ pathway discriminate against the heavier and kinetically slower isotope of carbon, $^{13}$C; whereas tropical grasses using the C₄ pathway also discriminate but allow the inclusion of more $^{13}$C into tissues than do C₃ flora. Since most low-latitude grasses use the C₄ pathway, East African vegetation shows a clear separation in $\delta^{13}C$ values (C₃: −31.4 to −24.6‰, C₄: −14.1 to −11.5‰; Cerling et al., 2003).

Following soil gas diffusion models of Cerling (1984) and Cerling and Quade (1993) and the conditions of respiration rates developed by Quade et al. (1989), pedogenic carbonates at depths greater than 30 cm in soils with relatively high
respiration rates incorporate CO₂ of decaying organic matter derived from surface vegetation during soil development. δ¹³C values of pedogenic carbonates from the savanna biome are intermediate between the C₃-C₄ end members and reflect the percentage of grasses versus woody vegetation present on the land surface with an isotopic fractionation between 13.5—16.6‰ (Cerling and Quade, 1993). Pedogenic carbonates form under a negative water budget in regions with rainfall below 100 cm/yr during periods averaging hundreds to thousands of years (Jenny, 1941, 1980; Birkeland, 1984; Srivastava, 2001). Fossil soils preserved in the Plio-Pleistocene Koobi Fora Formation are dominated by paleovertisol, formed under a dry season of four or more months and 250—1,000 mm of annual moisture (Feibel, 1988; Wynn, 2000, 2004).

**Soil carbonate sampling strategy and analysis**

We examined pedogenic carbonate isotope (δ¹³C) values from paleosols to reconstruct geographic distribution of vegetation (C₃-C₄ pathways) through time to assess the nature, timing, and controls on paleoenvironmental change in hominin-associated habitats of Koobi Fora. We compared lake-margin, river floodplain, and distributary channel floodplain depositional landscapes for the period of ~2.0—1.5 Ma that temporally brackets grassland ascendancy in East Africa as documented in Wynn’s (2004) third C₄ expansion event. We enhanced the previous isotopic studies of pedogenic carbonates from the Turkana Basin (Cerling et al., 1988; Wynn, 2004) for the 2.0—1.5 Ma time interval by: 1) increasing the sample size (nODULES, n = 202; analyses, n = 530), and 2) conducting widespread sampling of synchronous lateral horizons in the Koobi Fora Formation. This lateral sampling approach has been suggested for attaining ecotonal variability and habitat gradient (e.g., Kingston et al., 1994; Levin et al., 2004; Wynn, 2004). With attention to paleohydrology (after Levin et al., 2004), we partitioned the northeast Turkana Basin as subregions by proximity to precursors of Lake Turkana and to the ancestral Omo River system, which was the main control of basin-wide hydrology and deposition during the Plio-Pleistocene (e.g., Feibel et al., 1991).

Our study interval begins with the upper Burgi Member (2.0 to 1.9 Ma), spans the entire KBS Member (1.9 to 1.6—1.5 Ma), and ends with the lower portion of the Okote Member (1.6—1.5 Ma (e.g., Brown and Feibel, 1986, 1991; McDougall and Brown, 2006)). We sampled exposures from collecting area 1a in the Ileret subregion, area 41 in the II Dura subregion, areas 101, 102, 103, and 104 along the Koobi Fora Ridge, and areas 105, 130, 131, and 133 on the Karari Ridge (Fig. 1). Our study covers approximately 50 km² in total area of exposure and examines evolving paleolandsapes along lake-margin areas and floodplain areas. The Koobi Fora Ridge and Karari Ridge span three and four of the environments through time, respectively, whereas the II Dura and Ileret subregions only record one depositional regime (Fig. 2B–E).

Age control of pedogenic carbonates was determined with the established chronostratigraphic framework and scaled with sedimentation rates for each subregion. For example, with the KBS Tuff dated to 1.87 Ma (McDougall and Brown, 2006) and an average sedimentation rate of the Karari Escarpment determined as 6.2 cm/kyr (Feibel, 1988), we calculated a fossil soil located five meters above the KBS Tuff in collecting Area 105 to be approximately 1.79 Ma. All ages are expected to have an error of 0.03—0.05 Ma (e.g., Feibel et al., 1989).

In addition to the sedimentological indicators of paleogeography, we used paleopedology to interpret environmental context of the isotopic results. At the outcrop, we identified pedogenic carbonate and paleosols by criteria set forth in Retallack (2001) and refined for the Turkana Basin by Wynn (2000, 2001, 2004). We sampled pedogenic carbonates in the preserved calcic horizon of the paleosol at a minimum of 30 cm below the contact with the overlying stratum, as suggested by Quade and others (1989), and excavated back from the vertically exposed surface by approximately 50 cm (e.g., Sikles, 1994). Calcite nodules were extracted from within individual peds. Since most Turkana fossil soils are paleovertisols, they show vertic features and slickensided surfaces; we chose calcite nodules that exhibited slickensides and/or were adjacent to slickensided surfaces. Although abundant in the formation deposits, we did not include calcareous rhizoliths in this study due to isotopic alteration by shallow cementation (Driese and Mora, 1993) and groundwater (Liutkus et al., 2005).

In the laboratory, we sectioned pedogenic nodules and sampled micritic portions with a 0.5 mm carbide drill bit (Foredom Series), avoiding surface and sparry calcite. We subsampled nodules 2—6 times depending on size in order to test for internal nodular variability and averaged the subsample values. Approximately 5% of the samples were analyzed by cathodoluminescence (CL) to test for groundwater contribution (Marshall, 1988; Wynn, 2004). All isotopic analyses were conducted at the Stable Isotope Laboratory at Rutgers University on a Micro mass Optima Mass Spectrometer with an attached Multi-Prep device. Samples were reacted in 100% phosphoric acid at 90 °C for 13 minutes. δ¹³C values are reported versus the Pee Dee Belemnite reference standard (V-PDB) through analysis of the laboratory standard (NBS-19) with values of 1.95‰ for δ¹³C (Coplen et al., 1983).

We used Wynn’s (2000, 2001) savanna environment categories to interpret the δ¹³C values as they reflect floral community structure and composition. We acknowledge the fluidity of ecotonal boundaries, but attempt to explain floral community change with statistically significant shifts in δ¹³C values. As widespread sampling of fossil soils at one interval potentially yields a wide range of isotopic ratios spanning the values of C₃-C₄ communities, we approached the question of significant change in vegetation across space and through time in the following ways. In order to gauge change in vegetation across space, we compared results by subregion, due to position within the basin (e.g., proximal to the basin margin, proximal to the lake shore). For change in vegetation through time, we delineated brackets of time that witnessed major changes in paleogeography. Paleogeographic interpretations are based on sedimentary evidence and provide the context for our isotopic results. We present our results in 100-kyr...
intervals that confine major changes of paleogeography and deposition: 2.0–1.9 Ma, 1.9–1.8 Ma, 1.8–1.7 Ma, 1.7–1.6 Ma, and 1.6–1.5 Ma. The last two intervals record the same depositional environment. We also examined the results by subregion and by subregion within 100-kyr intervals. In all approaches, we treated our groups as populations and compared means and variances between groups with one-way ANOVA, Tukey’s all pairs comparison, and Kruskal-Wallis rank sum tests. We also interpolated change through time amongst all datapoints with a 10% weighted smooth curve fit after Stineman (1980). All summary statistics and statistical analyses were conducted with Kaleidagraph® Software.

Results and interpretation

$\delta^{13}$C values of pedogenic carbonates

$\delta^{13}$C values of all pedogenic carbonates from Koobi Fora yielded a mean of $-5.5^{\%}$ and standard deviation of 1.6 (Table 1). Summary statistics are shown by formation and subregions (Table 1) and by 100-kyr intervals (Table 2). Estimated with a 10% weighted smooth curve fit, the formation shows a 3% depletion in $^{13}$C from 2.0 to 1.75 Ma. After 1.75 Ma, the curve fluctuates within 1% (Fig. 5). Results from 100-kyr intervals representing different depositional environments show that all are not likely drawn from one population ($p < 0.001$). One-way ANOVA and Tukey’s all pairs comparison results are shown in Tables 3 and 5. Four of ten paired comparisons show significant differences between groups ($p < 0.001$); the first two 100-kyr intervals (2.0–1.9 Ma, 1.9–1.8 Ma) vary significantly from the next two 100-kyr intervals (1.8–1.7 Ma, 1.7–1.6 Ma) (Table 2; Fig. 6). Kruskal-Wallis rank sum test corroborates the results of the one-way ANOVA (Table 3).

Results by subregion for all time intervals also show meaningful differences between groups. One-way ANOVA and Tukey’s all pairs comparison results are shown in Tables 4 and 6. Kruskal-Wallis rank sum test yielded similar results (Table 4). The data from the Karari Ridge and Il Dura are significantly different from those of the Koobi Fora Ridge and Ileret (p < 0.001; Fig. 7). Furthermore, comparing the subregions within individual 100-kyr intervals yields significant differences between groups (Fig. 8). In the 1.9–1.8 Ma interval, data from the Karari Ridge, Il Dura, and Koobi Fora Ridge do not vary significantly from one another. Results from the one-way ANOVA and Kruskal-Wallis rank sum test indicate that the samples are likely from the same distribution. However, results from the following three 100-kyr intervals show that the subregions reflect different populations (Fig. 8); results from the one-way ANOVA and Kruskal-Wallis rank sum test corroborate the smooth curve fits ($p < 0.001$). In each of the 1.8–1.7 Ma, 1.7–1.6 Ma, and 1.6–1.5 Ma intervals, data from the Karari subregion significantly vary from those of the Koobi Fora Ridge and Ileret subregions ($p < 0.001$).

Table 1
Summary statistics by subregions

<table>
<thead>
<tr>
<th></th>
<th>All subregions</th>
<th>Koobi Fora Ridge</th>
<th>Karari Ridge</th>
<th>Ileret</th>
<th>Il Dura</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample size</td>
<td>202</td>
<td>71</td>
<td>85</td>
<td>39</td>
<td>7</td>
</tr>
<tr>
<td>Mean $\delta^{13}$C value</td>
<td>$-5.47$</td>
<td>$-4.73$</td>
<td>$-6.27$</td>
<td>$-4.76$</td>
<td>$-7.05$</td>
</tr>
<tr>
<td>Median $\delta^{13}$C value</td>
<td>$-5.46$</td>
<td>$-4.69$</td>
<td>$-6.35$</td>
<td>$-4.60$</td>
<td>$-6.31$</td>
</tr>
<tr>
<td>Minimum $\delta^{13}$C value</td>
<td>$-10.43$</td>
<td>$-10.43$</td>
<td>$-9.07$</td>
<td>$-6.74$</td>
<td>$-9.53$</td>
</tr>
<tr>
<td>Maximum $\delta^{13}$C value</td>
<td>$0.43$</td>
<td>$0.43$</td>
<td>$-3.30$</td>
<td>$-3.38$</td>
<td>$-5.79$</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>1.63</td>
<td>1.85</td>
<td>1.19</td>
<td>0.87</td>
<td>1.59</td>
</tr>
<tr>
<td>Standard error</td>
<td>0.11</td>
<td>0.22</td>
<td>0.13</td>
<td>0.14</td>
<td>0.60</td>
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<tr>
<td>Variance</td>
<td>2.65</td>
<td>3.40</td>
<td>1.42</td>
<td>0.77</td>
<td>2.52</td>
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<tr>
<td>Skewness</td>
<td>$-0.04$</td>
<td>$-0.47$</td>
<td>0.06</td>
<td>$-0.52$</td>
<td>$-0.89$</td>
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<tr>
<td>Kurtosis</td>
<td>1.31</td>
<td>2.31</td>
<td>$-0.18$</td>
<td>$-0.63$</td>
<td>$-1.08$</td>
</tr>
</tbody>
</table>

Fig. 5. $\delta^{13}$C ($^{\%}$) vs. age (Ma). Pedogenic carbonate $\delta^{13}$C values from paleosols in the Koobi Fora Formation between 2.0 and 1.5 Ma. Black line represents 10% weighted smooth curve fit of all data points (○). Savanna categories are taken from Wynn (2000, 2001).
Interpretation of floral compositions

The Koobi Fora Formation preserves a range of habitats from forest (minimum \( \delta^{13}C: -10.4\%_{oo} \)) to savanna grassland (maximum \( \delta^{13}C: 0.4\%_{oo} \)) with the majority of environments falling in the mosaic compositions including savanna woodland, thicket and scrub, and low-tree shrub savanna (mean \( \delta^{13}C: -5.5\%_{oo}; \) interpreted after Wynn, 2000, 2001). Based on Cerling’s (1984) model of C4 contribution to soil CO2, tropical grasses comprised 46% of the average landscape and ranged from 11\% to 89%. Floral compositions by subregion are presented below (Table 1; Figs. 7 and 8).

Il Dura. Sampled paleosols are moderately to well-developed clay vertisols, based on thickness, ped structure, and large dish-shaped slickensides (e.g., Aberegaiya variant after Wynn, 2000), with a soil moisture estimate of >1000 mm/yr by calcic horizon at depth of approximately 600–800 cm (Wynn, 2000, 2004). We observe low \( \delta^{13}C \) values prior to 1.8 Ma, with grasses comprising 35\% (range: 18\%–44\%) of the flora. We interpret woodland savanna and/or thicket and scrub environments in this subregion.

Ileret. The sampled Ileret soils are thin (40–60 cm), immature vertisols similar to Dite paleosols (Wynn, 2000) based on their crumb ped structures, shallow calcic horizons, and their stratigraphic positions between channelized tuffs. Samples are from one depositional environment and fluctuate in \( \delta^{13}C \) values between \(-6\%_{oo}\) and \(-4\%_{oo}\) (Fig. 8), constituting approximately 40–60\% of grassy vegetation. We interpret the savanna category based on isotopic results primarily as low-tree shrub, with few woodland, and thicket and scrub environments.

Koobi Fora Ridge. Paleosols from the Koobi Fora Ridge vary markedly in morphology but generally show a high clastic content likely due to proximity to a fluctuating lake margin (Feibel, 1988). One soil in particular, the Lorenyang pedotype (after Wynn, 2004), is present at and after 1.8 Ma, and shows distinct sand-filled surface cracks and a thick calcic horizon. This fossil soil has been interpreted to support seasonally sparse savanna grassland with little time for development due to quick burial (Wynn, 2004). \( \delta^{13}C \) results from this subregion corroborate the previous interpretations of expansion of C4 grasses after 1.8 Ma (Cerling et al., 1988; Wynn, 2004). The weighted smooth curve of \( \delta^{13}C \) values at 1.9–1.8 Ma increases from \(-6\%_{oo}\) to \(-4\%_{oo}\) (40–60\% grasses), placing the area within the low-tree shrub category. After 1.8 Ma, the curve shifts to more open savanna grassland environments and then returns to the low-tree shrub category at 1.65 Ma (Fig. 8).

Karari Ridge. The Karari paleosols show morphological diversity. Below the KBS Tuff, the Karari shares the Aberegaiya paleosol with the Il Dura subregion. Directly underlying the Okote Tuff Complex (∼1.6–1.5 Ma), the Kimere pedotype

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### Table 3
Results of one-way ANOVA and Kruskal-Wallis rank sum test of 100-kyr interval groups

<table>
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<tr>
<th>One-way ANOVA</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
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<tr>
<td>Total</td>
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<td>531.91</td>
<td>2.65</td>
<td>10.51</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>A</td>
<td>4</td>
<td>93.55</td>
<td>23.39</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>197</td>
<td>438.35</td>
<td>2.23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kruskal-Wallis</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>rank sum test</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K-W statistic</td>
<td></td>
<td>37.02</td>
<td></td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

### Table 4
Results of one-way ANOVA and Kruskal-Wallis rank sum test of subregion groups

<table>
<thead>
<tr>
<th>One-way ANOVA</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>201</td>
<td>532.00</td>
<td>2.65</td>
<td>21.47</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>A</td>
<td>3</td>
<td>130.58</td>
<td>43.53</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>198</td>
<td>401.42</td>
<td>2.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kruskal-Wallis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>rank sum test</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K-W statistic</td>
<td></td>
<td>63.20</td>
<td></td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

---

### Table 5
Results of Tukey’s all pairs comparison by 100-kyr interval groups

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Mean difference</th>
<th></th>
<th>P</th>
<th>95% CL</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1.7-1.6) vs. (2.0-1.9)</td>
<td>2.25</td>
<td>6.52</td>
<td>&lt;0.0001</td>
<td>0.91–3.59</td>
</tr>
<tr>
<td>(1.7-1.6) vs. (1.9-1.8)</td>
<td>1.37</td>
<td>6.97</td>
<td>&lt;0.0001</td>
<td>0.60–2.13</td>
</tr>
<tr>
<td>(1.7-1.6) vs. (1.6-1.5)</td>
<td>0.63</td>
<td>2.74</td>
<td>0.2998</td>
<td>0.26–1.52</td>
</tr>
<tr>
<td>(1.7-1.6) vs. (1.8-1.7)</td>
<td>0.13</td>
<td>0.63</td>
<td>0.9916</td>
<td>0.68–0.95</td>
</tr>
<tr>
<td>(1.8-1.7) vs. (2.0-1.9)</td>
<td>2.12</td>
<td>5.94</td>
<td>0.0004</td>
<td>0.73–3.50</td>
</tr>
<tr>
<td>(1.8-1.7) vs. (1.9-1.8)</td>
<td>1.24</td>
<td>5.74</td>
<td>0.0007</td>
<td>0.40–2.08</td>
</tr>
<tr>
<td>(1.6-1.5) vs. (2.0-1.9)</td>
<td>0.50</td>
<td>2.02</td>
<td>0.6105</td>
<td>0.46–1.46</td>
</tr>
<tr>
<td>(1.6-1.5) vs. (1.9-1.8)</td>
<td>1.62</td>
<td>4.39</td>
<td>0.0183</td>
<td>0.18–3.06</td>
</tr>
<tr>
<td>(1.9-1.8) vs. (2.0-1.9)</td>
<td>0.74</td>
<td>3.14</td>
<td>0.1762</td>
<td>0.18–1.66</td>
</tr>
</tbody>
</table>

---

Fig. 6. Nonparametric box and whisker plots of \( \delta^{13}C \) values (\( \%_{oo} \)) by 100-kyr interval groups.
shows the presence of thick (~0.5 m) columnar and slickensided carbonate horizon, suggesting a stable land surface and pedogenesis for a substantial period of time (e.g., Wynn and Feibel, 1995). Within the Okote Tuff Complex, soils are poorly developed and characterized as Dite paleosols similar to those found in the Ileret subregion. δ13C values from morphologically different pedotypes preserved on the Karari Ridge do not show the grassland expansion trend. Before 1.9 Ma, the smooth curve fit of δ13C values fluctuates between −8 and −6‰ (30–40% grasses), placing the subregion within the savanna woodland and thicket and scrub categories (Fig. 8). We observe a 1‰ increase after 1.8 Ma showing an excursion to the low-tree shrub category. By 1.75 Ma environments have returned to the woodland and thicket savannas.

**Controls on δ13C values and floral compositions**

Paleogeographical, sedimentological, and paleohydrological changes related to the precursors of Lake Turkana and the Omo River influenced floral compositions and distributions through time. We suggest that differences in the isotopic ratios of paleosol carbonates were controlled by the context of paleosols in relation to the inherent array of moisture and depositional conditions found in fluviolacustrine systems. We discuss four paleogeographic factors: water availability, sediment accumulation rates, ratios of subaqueous:subaerial land, and open and closed basin conditions. We also view tectonics (subsidence rates) as an important force on paleogeographic change that can lead to differential distributions of the isotopic data. As compared with paleoclimate, these tectonic-subsubsidence controls on paleogeographic change may have exerted an equal or greater influence on the observed floral patterns.

**Paleogeographic controls on subregional δ13C values**

We assume simple forcing relationships between paleogeographic changes and floral distribution. Wooded vegetation typifies gallery forests clustered along channel banks of the modern Omo River. Tropical grasses are found in the lateral floodplain environments. Mixed communities are generally between the two areas in overbank environments with small channels dispersed within a flood basin (Carr, 1976). Results of C3-C4 patterns by subregion illustrate these predictions.

Our results of the II Dura subregion agree with the paleogeographic location near the axial meandering proto-Omo River, where a higher proportion of C3 vegetation is expected. Ileret paleosols are poorly developed and interpreted as indicative of floodplain areas laden with small distributary channels of the ancestral Omo River, supporting low-tree shrubs and grasses. Our section from the Koobi Fora Ridge begins just after 1.9 Ma, when a deltaic system begins to form along northern margins of Lake Lorenyang. Oscillations of lake-level after 1.9 Ma, coupled with high rates of clastic input from deltaic sedimentation, may have reduced suitable lake-margin habitats for woodland floral communities, thus increasing the proportion of grasses. As compared with other subregions, the unique proximity to basin margin channel systems and paleogeographic history of the Karari Ridge may indicate a different water availability regime and explain the exceptionally low δ13C values. Marginal systems likely provided a consistent supply of water to C3 floral communities, buffering against variations spurred by paleogeographic shifts from lacustrine-related environments at ~1.9–1.8 Ma to fluvial channel and floodplains after 1.8 Ma.

Observed paleogeographic patterns influenced preservation of the soil carbonate and the manner in which vegetation is recorded in isotopic values. Pedogenic carbonate formation is inhibited near channel and lake-margin areas with high water tables and sedimentation rates (van Breemen and Buurman, 2002). As a result, our ability to reconstruct vegetation is limited to the drier subaerial portions of the landscape with carbonate precipitation. Sampling strategies for isotopic records from paleosol carbonates may be biased to strata of floodplain environments—the preferred habitats for tropical grasses. Landscapes with a high proportion of floodplains to channels may skew paleosol isotopic records toward a C4 signal. Consequently,
carbonate isotopic values will not capture the pure C3 values in the savanna environment, but rather combine values from fluctuating floral compositions as the meander belt avulses (Levin et al., 2004). For comparison, lacustrine systems have a comparatively high proportion of subaqueous to subaerial landscapes, suggesting a low amount of suitable substrate for paleosol and pedogenic carbonate formation. These systems often have relatively faster sedimentation rates, which are not conducive for the prolonged development of soils (Jenny, 1980; Retallack, 2001, van Breemen and Buurman, 2002). At 1.8 Ma, river avulsion from the eastern basin (e.g., Brown and Feibel, 1991; Feibel et al., 1991) may have dampened C3 contributions to soil carbonate isotopic values. Subsequent emplacement of smaller fluvial-distributary systems and expanded floodplain environments (Fig. 2) may have further reduced the signal of wooded vegetation.

**Basin scale paleogeographic and tectonic factors**

Basin scale factors of paleogeographic change also influenced the character of paleosol and carbonate formation and associated floral compositions. Tectonism was a strong driver of paleogeographic changes in the Koobi Fora region during the Plio-Pleistocene (Brown and Feibel, 1991; Feibel et al., 1991). We propose an integrative explanation of paleogeographic evolution that incorporates climate and tectonics after Carroll and Bohacs (1999) and Withjack and colleagues (2002). These authors suggest that diachronic changes in the aerial distributions, facies, and environments of lake basins result from the combined effects of tectonic subsidence and climate and their control on the rate of potential accommodation space (mostly tectonic subsidence) and the delivery of water and sediment to a basin (mostly climate). Volcano-tectonic events at \( \sim 2.5 \) Ma changed subsidence and basin accommodation rates and contributed to the transformation of the Turkana Basin from a hydrologically closed lacustrine-dominated basin to an open fluvial one over 2.0–1.5 Ma. We suggest that moisture and floral patterns are explained by resultant shifts in paleogeography, proportions of subaqueous landscapes relative to subaerial landscapes, and hydrologically open or closed basin conditions. Plio-Pleistocene grassland expansion at Koobi Fora is linked with expanded subaerial floodplains and expedient basin water loss from the through-flowing ancestral Omo River, ultimately generated by tectonic-subsidence factors.

According to the models of Carroll and Bohacs (1999) and Withjack and others (2002), a basin—which is underfilled with water and sediment (subidence-accommodation > sediment-water input)—contains a closed lake system with inputs from rivers, runoff, and precipitation but outputs only by means of evaporation. A balance-filled basin (subidence-accommodation = sediment-water input) commonly contains an open lake system with relatively equal amounts of sediment and water input and output via rivers. An overfilled basin (subidence-accommodation < sediment-water input) is characterized by more water and sediment than the basin can accommodate and, consequently, is easily transformed into a through-flowing fluvial system.

The presence of major unconformities in the Koobi Fora Formation (Fig. 4) is associated with volcano-tectonic down-warping of the Turkana Basin and associated uplift of the Ethiopian Plateau in southern Ethiopia (Brown and Feibel, 1991; Feibel et al., 1991). Our stratigraphic study interval begins just above the level of the upper Burgi unconformity (\( \sim 2.5–2.0 \) Ma). This hiatus was generated by tectonic disruption in the basin evident by the Stephanie Uplift to the northeast and gentle tilting of the strata in the Koobi Fora region associated with an interval of synsedimentary basin conditions. Our interpretation of the Koobi Fora region as an underfilled basin with a large degree of potential accommodation space at \( \sim 2.5–2.0 \) Ma is supported by the plot of sedimentation rates for the entire Koobi Fora Formation (Fig. 4), which suggests an exponential and positive increase in sediment accumulation beginning just after 1.9 Ma and ending around 1.7 Ma. Structural movements at about 2.5 Ma resulted in increased subsidence rates and
ample space to accommodate a large influx of sediment into the basin between 1.9—1.7 Ma.

Prior to about 1.9 Ma, the Turkana Basin had a fluvial outlet to the southeast but was occupied by a relatively deep and broad lake, Lake Lorenyang (Feibel, 1994). The sedimentation rate curve (Fig. 4) may indicate that there were relatively few sediments accumulating under a low proportion of sediment supply relative to accommodation rate; sedimentation was outpaced by the rate of subsidence generation. Evidence from paleogeography and sedimentation rates suggests that the basin was balanced-filled or underfilled with sediment and overfilled with water (cf., Carroll and Bohacs, 1999; Withjack et al., 2002).

The period between 1.9 and 1.7 Ma was a highly variable time in the basin with respect to depositional environments; lake waters became shallower, lake level frequently oscillated, and deltaic and fluvial environments were active during this interval (Fig. 2). Beginning at 1.9 Ma and continuing to 1.7 Ma, the sedimentation rate curve shows a shift to a near vertical trend that crosses to above the extrapolated mean sedimentation rate line (Fig. 4). These patterns may indicate an “instantaneous” rate of sediment accumulation under conditions of a more equal or lower proportion of accommodation rates relative to sediment supply rates as compared to earlier times; sedimentation kept pace with or exceeded subsidence. The sedimentation rate curve and paleogeography support the interpretation that after 1.7 Ma the basin was progressing toward an infilled status, overfilled after the models of Carroll and Bohacs (1999) and Withjack and others (2002).

After 1.7 Ma, the sedimentation rate curve takes a sharp turn back towards the mean sedimentation rate line (increase in the rate of sediment accumulation), which may suggest a lower proportion of accommodation relative to sediment supply rates as compared with the 1.9—1.7 Ma period; sedimentation outpaced subsidence. Brown and Feibel (1991) suggest that during 1.7—1.4 Ma the Turkana Basin had very few landscapes with lacustrine-related sedimentary environments, but there was a preponderance of fluvial channel and floodplain environments. The protracted transformation of the basin from a lacustrine-dominated setting to one with a through-flowing river suggests infilling under a regime of progressively less tectonic subsidence (Carroll and Bohacs, 1999; Withjack et al., 2002).

Our examined stratigraphic interval brackets at least four successive times of differential sedimentation in the Plio-Pleistocene Turkana Basin, including periods of lacustrine, deltaic, shallow/fluctuating lacustrine, and fluvial channel and floodplain deposition (Fig. 2B—E). Previous research demonstrates that these periods are tracking the transformation of the basin from a hydrologically closed lake basin to one that is open with a through-flowing ancestral Omo River (Brown and Feibel, 1991). Shifts in isotopic ratios and inferred floral patterns are coeval with these periods (Figs. 5 and 6). We interpret these data as indicating relatively wet conditions during lacustrine and deltaic intervals and dry conditions during shallow/fluctuating lacustrine and fluvial intervals. We suggest moisture and floral patterns are controlled by paleogeography, proportion of subaqueous relative to subaerial landscapes, and hydrologically open or closed basin conditions. In half-graben basins with lakes, there are high proportions of subaqueous landscapes relative to subaerial settings (cf., Gawthorpe et al., 1994; Leeder et al., 1998; Gawthorpe and Leeder, 2000). Our findings of more closed savanna environments are associated with the lake basin pooling water and a lack of suitable subaerial substrate for well-developed pedogenic carbonates and grassland communities on which to form. In comparison, we associate through-flowing fluvial intervals with lower proportions of subaqueous to subaerial landscapes and hydrologically open conditions (Gawthorpe et al., 1994; Leeder et al., 1998; Gawthorpe and Leeder, 2000). Indications of grassland expansion during these intervals may stem from pronounced water loss in the basin under an open hydrology. The fluvial intervals are coeval with isotopic evidence of grassland expansion and, by inference, increased aridity. We interpret this finding as a result of a very low proportion of subaqueous relative to subaerial landscapes coupled with expedient basin water loss from the through-flowing ancestral Omo River. The rise of the subaerial fluvial landscapes resulted in expansion of preferred floodplain habitats for C₄ vegetation.

**Climatic factors**

Overall, our results show a shift from C₃ vegetation and decreased evaporation to higher C₄ proportions and evaporation increase during 2.0—1.5 Ma, which we can ultimately link to tectonic-subsidence, accommodation space, basin infilling, and their control on paleohydrology. However, the establishment of grasslands recorded in the entire basin and East Africa after 1.8 Ma, initially proposed by Cerling (1992), suggests an overprint of a large-scale influence often attributed to global climate change. Changes in the isotopic character of water and vegetation in the Koobi Fora region during our study interval has been shown as a response to global climate change due to glacial activity in the Northern Hemisphere (see deMenocal, 2004 for a recent review), and as a result, may explain our observed shift in δ¹³C values from 2.0 to 1.75 Ma. Based on the climate forcing model for the Turkana Basin proposed by Lepre et al. (2007), we would expect to observe cycles in water availability and, therefore, fluctuations in floral communities coinciding with orbital periodicities. We do not observe periodicities in our isotopic results. This is in part due to the preservation of soils though time (i.e., there are large gaps in the stratigraphic record hindering continuous isotopic records). If climate is producing recurring sedimentary packages (e.g., deep lake, shallow lake, beach, paleosol), soil carbonates are recording only one segment of the orbital cycle. Moreover, soil carbonate isotopes are sensitive to local vegetation change, which potentially masks floral changes on orbital timescales. Additional work with complementary isotopic proxy records of environmental change (e.g., lacustrine invertebrates) may increase our understanding of climate’s role on the Turkana Basin.
Our $\delta^{13}C$ values indicate grassland expansion from 2.0 to 1.75 Ma, trending from more closed savanna woodlands to more open low-tree shrub savannas. Environments fluctuated within the low-tree shrub savanna category from 1.75 to 1.5 Ma. We propose that habitat fragmentation increased; that is, wooded environments are maintained, and the mosaic and grassland pieces are expanded. Behrensmeyer and others (1997) interpreted faunal turnover as a slow process in the Turkana Basin between 2.5 and 1.8 Ma rather than a short-term pulse coinciding with the onset of Northern Hemisphere Glaciation between 2.8 and 2.5 Ma. Our change in average floral composition between 2.0 and 1.75 Ma coincides with one of the highest faunal turnover pulses in the Turkana Basin (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004). Based on our interpretation of paleogeographic controls on floral distribution, the timing of faunal turnover is coeval with the transformation of the basin from a closed lacustrine-dominated basin to an open fluvial setting.

We interpret our results to reflect habitat partitioning by subregion possibly due to differential water supply. Along the Karari Ridge, the axial system and possibly marginal rivers sustained wooded environments when other subregions in the basin were beginning to show grassland spread. Higher frequencies of archaeological evidence in the KBS and Okote Members along the Karari Ridge have been suggested as indicators of home range expansion and excursions into marginal and drier habitats by early African Homo erectus (Rogers et al., 1994). If preservational differences are negligible amongst the subregions, the Karari Ridge as reconstructed by $\delta^{13}C$ values of pedogenic carbonates was a wetter and more wooded environment from 2.0 to 1.5 Ma. Rather than the hominins venturing into marginal and drier habitats, the abundance of archaeological sites and hominin paleontological material may attest to habitat preference in well-watered areas with woodland savanna and low tree-shrub grassland compositions. Habitat partitioning by subregion may have created additional niche spaces for sympatric Homo and Paranthropus (Bromage and Schrenk, 1995; Wood and Strait, 2004) and possibly higher percentage of ecotonal boundaries between wooded and grassland environments, which may have afforded early Homo increased scavenging opportunities (after Blumenschine, 1987). Scavenging or other behaviors that resulted in greater dietary reliance on animal meat and marrow may have resulted in home range expansion (Leonard and Robertson, 2000), facilitating dispersal (Shipman and Walker, 1989; Antón et al., 2002).

Conclusions

We conclude that the paleogeographic distribution of $\delta^{13}C$ values from soil carbonate from 2.0–1.5 Ma coincided with the path and character of the ancestral Omo River and precursors of Lake Turkana. Overall, the basin shifted from closed to more open savannas from 2.0–1.75 Ma, after which time mosaic conditions persist. Paleoenvironmental change at Koobi Fora from 2.0–1.5 Ma was ultimately related to volcanic-tectonic events at $\sim$2.5 Ma in the northern portion of the eastern branch of the East African Rift. Down-warping of the Turkana Basin and the associated uplift of the Ethiopian Plateau, the subsequent changes in subsidence and accommodation, and basin infilling gradually transformed the basin from a lake system to a flow-through fluvial system between 2.0 to 1.5 Ma. As a result, there was a through-time decrease in the residence time of Omo River water in the basin and an expansion of subaerial landscapes. Climate may have served to modify or exaggerate the effects of tectonic perturbations by altering rainfall quantities delivered to the catchment areas of the ancestral Omo River. The combined effects of these phenomena caused a decrease in wooded habitats by increasing basin water loss and expanding subaerial floodplain habitats suitable for grassland communities. Habitat fragmentation resulting from basin-wide evolution may have created additional niche spaces and scavenging opportunities for sympatric hominins. Based on our subregion environmental reconstructions and the distribution of archaeological traces at Koobi Fora, we interpret that tool-using hominins preferred relatively more closed and well-watered environments.

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