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Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana, Kenya: evidence from mammalian herbivore enamel stable isotopes

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Abstract

Carbon (^{13}C:^{12}C) and oxygen (^{18}O:^{16}O) stable isotope ratio analysis was performed on well-preserved tooth enamel carbonate from fossil fauna recovered from a single excavation at the early hominid site of Allia Bay, East Turkana, Kenya. These data show greater enrichment in both ^{12}C and in ^{16}O than expected, based on the oxygen isotope composition of the middle Pliocene ocean, and on today's ecology. The pattern of these data argues against a diagenetic explanation for the enrichment. The carbon stable isotope data of known browsers suggest a more extensive canopy cover during the middle Pliocene than today's environments. The presence of browsing pig genera, hippo genera, deinotheres, and giraffes with δ^{13}C values more negative than today's all argue for woodland habitats. The presence of several grazing genera point to the presence of grasslands as well. The oxygen stable isotope ratios indicate that the site was better-watered than today, although the source, seasonal pattern, and actual amount of water cannot be determined from these data. The overall mosaic of environments suggested by these data, in combination with reports of exotic trees recovered in nearby deposits, indicate that woodlands were present in the region 3.9 my, unlike today. Such a setting matches expectations for the selective advantages of nut-eating, bipedal hominids over other hominoids.

Keywords: Human evolution; East Africa; Allia Bay; Australopithecus anamensis; Pliocene; Paleoecology; Paleodiet; Tooth enamel; Carbon isotopes; Oxygen isotopes

Introduction

The Primate family Hominidae is defined largely by our diagnostic mode of locomotion, bipedalism; yet it is far from clear when (Brunet et al., 2002; White et al., 1994) or why (Isbell and Young, 1996; Steudel, 1996; Wheeler, 1984) bipedality first appeared. Further, bipedalism may have originated more than once (Leakey et al., 2001; also see White, 2003), although morphologically there exists a general similarity across hominid taxa in relation to that of the other hominoids (McHenry and Coffing, 2000). Ecological information on early hominid sites is therefore critical for understanding the circumstances under which bipedalism was adaptively advantageous for early hominid species. Associated faunal compositions suggest the earliest hominids lived in woodlands (e.g., WoldeGabriel et al., 1994); but various lines of evidence indicate that middle Pliocene hominids occupied more open, mixed environments (Kappelman et al., 1997; Kingston et al., 1994; Reed, 1997). Inferring how bipedalism functioned in each individual hominid species requires extensive knowledge of habitat and ecology for each site containing hominid remains. Toward that end, the present paper presents one line of evidence, i.e., stable isotope ratios of carbon and oxygen in mammalian tooth enamel, for an early

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hominid site, Area 2611 (Fig. 1), Allia Bay, East Lake Turkana, in northern Kenya (Leakey and Walker, 1985). The site, dated repeatedly to 3.9 my, produced a bipedal hominid, *Australopithecus anamensis* (Coffing et al., 1994; Leakey et al., 1995), and the data presented here complement those published previously on pedogenic carbonates from the site of Kanapoi on the west side of Lake Turkana, which produced the same species (Wynn, 2000).

The area surrounding Allia Bay today is situated near the eastern shore of Lake Turkana and is quite arid. There are several ephemeral streams that might last days or remain completely dry in some years and a limited number of waterholes, but the main source of permanent water is the lake itself. The vegetation is arid and subarid scrub with large expanses of C_4 grassland supported by a strongly seasonal moisture pattern (Brown and Feibel, 1991). Stable isotope data on soil organics and soil carbonate indicates that 60–80% of the vegetation is C_4 grasses and euphorbs with only 20–40% trees and shrubs (Cerling et al., 1988). Nonhuman primates, baboons (*Papio* sp.), and vervet monkeys (*Cercopithecus aethiops*), are found near the limited waterholes and many associated mammalian species are drought-adapted representatives of their particular genera (Feibel et al., 1991).

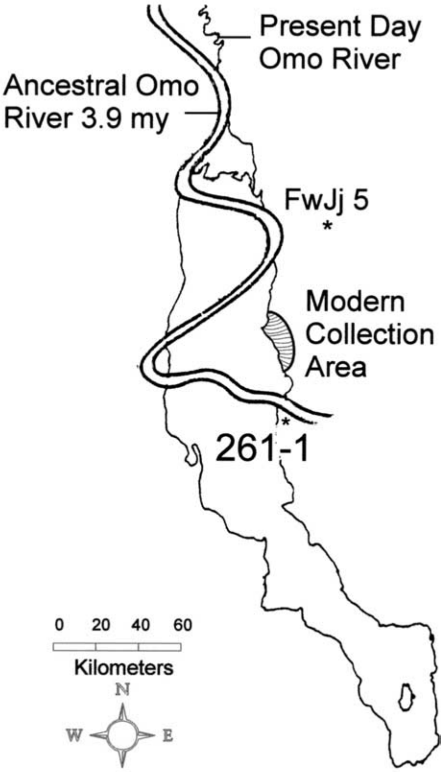

Fig. 1. Map of today's Lake Turkana, which is located in northernmost Kenya, showing the region of modern sample collection as well as the fossil collection site. The placement of the fossil Omo River at 3.9 my, when *Australopithecus anamensis* lived in the region, is based on Feibel et al. (1991).

In many aspects, the region was the same in the Pliocene with the same overall basin shape and with the ancestor of today's Omo River as its main source of water (Feibel et al., 1991). Today's lake receives approximately 80% of its water from the Omo River that, in turn, receives its water from the Ethiopian highlands. This relationship has been in place for at least 5 my. At the time that the Allia Bay site was deposited, a perennial river, the ancestral Omo, existed in the basin and the hominid-bearing site was located on its shores (Coffing et al., 1994; Fig. 1). The river's presence may be due to tectonic events that opened an outlet to the Indian Ocean (Feibel et al., 1991), but there may also have been more water flowing through the basin that forced an outlet. Sea level was at least 25 m higher in the middle Pliocene than it is today (Dowsett et al., 1994); higher sea-surface temperatures in the higher latitudes (Thompson and Fleming, 1996) melted large portions of the ice sheets. Temperatures in the tropical latitudes were probably similar to today (Dowsett et al., 1996) but overall moisture levels may have been higher as they were in the middle latitudes (Thompson and Fleming, 1996).

The effect on tropical plant communities is not as clear as on higher latitude communities where moister conditions resulted in greater expanses of forest than exist today (Thompson and Fleming, 1996). There is a paucity of plant remains from Pliocene Allia Bay and indirect indicators provide somewhat conflicting data. Carbon isotope ratios in marine organic matter (Raymo et al., 1996) and modeling of atmospheric carbon dioxide concentrations (Crowley, 1996) suggest an atmosphere similar to that of today. This supports the interpretation that the plant composition of the basin was roughly similar to that of today with a mix of C_3 trees and shrubs with C_4 grasses in open areas. Faunal preservation concurs in that many of the fossils appear to be secondarily deposited as if they washed into the river from a surrounding floodplain (Feibel et al., 1991). In addition, the fossil fauna contains genera that could inhabit open floodplain regions, gallery forest, and dry bushland (Coffing et al., 1994; Feibel et al., 1991). In contrast, the carbon isotope data from paleosol carbonates suggest a predominance of C_3 flora 4–1.8 my with only 20–40% C_4 flora during the Lonyumun Member, which contains the Allia Bay site (Cerling et al., 1988). An attempt to combine both sets of data suggests that riparian woodland and gallery forests, more extensive than today, dominated the basin, masking the presence of C_4 grasses on floodplains and along seasonally flowing streams (Feibel et al., 1991).

More recent analysis of pedogenic carbonates from several strata dated to ca. 4 my at Kanapoi indicates that *Australopithecus anamensis*, in that area, inhabited a savanna region dominated by low trees and shrubs (Wynn, 2000).

A river basin dominated by C_3 trees and shrubs provides very different food options for a bipedal hominid than does the present Turkana basin where a depauperate primate fauna exists today (Sept, 2001). An expansion of gallery forest and riparian woodland would also provide trees that could be used for sleeping (Sept, 1998), in addition to a wider variety of food items. Although Feibel and colleagues conclude that the main plant composition was similar to today, they note the presence of exotic trees, including *Brachystegia*, from other deposits which had better preserved plant material (Deschamps and Maes, 1985 as cited in Feibel et al., 1991, p. 326). Thus, it seems possible that such exotics were present during the middle Pliocene in the Lake Turkana basin if soil and rainfall conditions were adequate to support such plants. The goal of the present project is to obtain additional evidence about the environments surrounding the site by analyzing carbon and oxygen isotope ratios from tooth enamel in the fragmentary fauna recovered from the site.

Background: stable isotope analysis

Carbon

The distribution of $\delta^{13}C$ values across all plant species is bimodal, and animals eating plants record the signal in their tissues. At this level, we used carbon stable isotope analyses to evaluate the presence of C_4 grazers and C_3 browsers in the Allia Bay fauna because at lower altitudes across East Africa today all grasses are C_4 and all trees and shrubs are C_3. The carbon isotope signal of tooth enamel faithfully records feeding patterns in modern ruminants (Cerling and Harris, 1999), and finer discriminations can be made from the stable isotope data. The $\delta^{13}C$ values in hair samples from extant primates living in varying ecological habitats recorded the extent of canopy cover. Primates from closed-canopy forests have significantly lower values than those from more open habitats (Schoeninger et al., 1997), and values from open habitats are significantly lower than those from a drought-afflicted habitat (Schoeninger et al., 1998). Tooth enamel $\delta^{13}C$ values in ruminants from closed-canopy habitats also differ from those in more open habitats (Cerling and Harris, 1999), suggesting that finer discriminations of ecological variation are probably recorded in tooth enamel $\delta^{13}C$ values of the fauna from the Allia Bay site. We analyzed fossil specimens and, when possible, compared them with their modern equivalents to determine if Pliocene Allia Bay experienced the same amount of canopy cover as today, more than today, or less than today.

Oxygen

The oxygen isotope ratios in various minerals, including the carbonate in tooth enamel apatite, depend on two variables: the temperature of formation (body temperature in mammals) and the oxygen isotopic ratio in the animal's source water (Longinelli, 1984; Urey, 1947). In general, the $\delta^{18}O$ values in lake waters and in rain vary predictably along latitudinal and temperature gradients, but there is a large amount of variation (Dansgaard, 1964). Animal $\delta^{18}O$ values also vary due to body size effects, differential cooling mechanisms, differential means of obtaining body water, and other variables (Bryant and Froelich, 1995; Kohn et al., 1996). For these reasons, we did not attempt to use animal $\delta^{18}O$ values to calculate temperatures, source water values, or metabolic adaptations across mammal species.

On the other hand, as mentioned above, sea level was about 25 m higher in the middle Pliocene than it is today (Dowsett et al., 1994). Benthic foraminifera from the early to middle Pliocene have $\delta^{18}O$ values that are 2–4‰ less positive than today's foraminifera (Hoefs, 1997, Fig. 66), indicating a lack of ice-sheets at the poles since these preferentially remove ^{16}O. The ocean composition at the time must also have been ca. 2–4‰ less positive than today. Thus, the Allia Bay fossil enamel carbonates should be about 2–4‰ lower than modern enamels if a change in source water (ultimately the ocean) was the only process active.

Diagenesis and its assessment

It is commonly assumed that fossil enamel is not subject to diagenetic alteration, although several recent studies have called this into question (Bryant et al., 1993; Kohn et al., 1999; Lee-Thorp, 2000; Sponheimer and Lee-Thorp, 1999a). In a previous study, we assessed 31 fossil fragments from Allia Bay using cathodoluminescence spectroscopy coupled with electron microprobe analysis and powder X-ray diffraction analysis (Reeser et al., submitted; see Schoeninger et al., 2003 for an abstracted version). One of the fragments was completely altered, five had variable levels of diagenetic elements in all areas analyzed, and 25 showed surface alteration with minimal alteration on the interiors. Stable isotope analysis of carbonates from the exteriors and interiors of a subset supported this interpretation (Schoeninger et al., 2003), and we limited isotopic analyses for the present study to samples taken from enamel interiors.

Materials and methods

Fossil fragments from a single excavation site (261-1), which lies just beneath the Moiti Tuff were available for analysis. Due to their fragmentary nature, most of the fauna could be identified to genus level only, but the fact that none of the samples came from the surface and all came from a single excavation locale offset this drawback. Of the complete fossil set, only hippos, elephants, giraffes, suids, and deinotheres are environmental indicators because the remaining taxa (mostly bovids from indeterminate genera) have feeding habits that vary widely across genera. Modern mammal teeth and bones, recovered by MS during surface survey in 1984 and 1993, serve as comparisons for the fossil set. The fossil tooth fragments were analyzed after removal of at least the outer 0.25 mm of enamel; whenever possible 0.5 mm of enamel was removed.

Following Koch (Koch et al., 1997) and Lee-Thorp (Lee Thorp et al., 1989), samples were cleaned of matrix, and enamel was separated from dentine and cementum using a hand-held Dremel drill. Samples were reduced in a Spex mill and pretreated with sodium hypochlorite (bleach) and acetic acid (3% buffered 1:1 with calcium acetate). Carbon dioxide was produced by hydrolysis in 100% phosphoric acid at 25 °C (see McCrea, 1950), collected cryogenically, and analyzed on a VG 602E Micromass isotope ratio mass spectrometer. Data are reported in the standard delta (δ) notation relative to the PeeDee Belemnite standard. Precision based on standard replicates of NBS 19 is 0.05‰ for $\delta^{13}C$ $(n = 19)$ and 0.2‰ for $\delta^{18}O$ $(n = 19)$ and of homogenized goat tooth enamel (modern) is 0.09‰ for $\delta^{13}C$ $(n = 22)$ and 0.4‰ for $\delta^{18}O$ $(n = 17)$.

Results

The pattern of $\delta^{18}O$ values of the fossil samples differs from that of the modern samples as plotted in Figs. 2 and 3. Modern taxa sampled show expected high $\delta^{18}O$ values for animals with C_3 diets and low $\delta^{18}O$ values in those with C_4 diets and low $\delta^{18}O$ values (see Kohn et al., 1998, for a discussion), since C_3 feeders obtain their body water from ^{18}O enriched plant material while C_4 feeders obtain their body water from ^{18}O depleted surface water. The fossil taxa, however, do not conform to these expectations. In addition, many of the values are similar to those previously reported for the immediately overlying Moiti Tuff paleosol carbonates ($\delta^{18}O$ between −1.5‰ and +0.5‰ reported in Cerling et al., 1988). This suggests that some alteration and concomitant smoothing of $\delta^{18}O$ values has occurred. We are beginning to test this by analyzing multiple micro-samples from individual tooth fragments to determine if the seasonal variation in $\delta^{18}O$ values (Bryant et al., 1996;

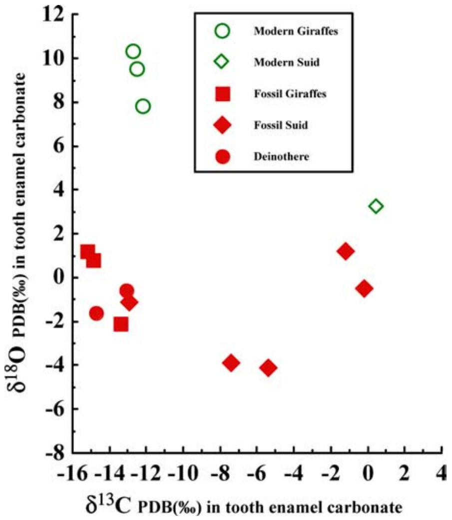

Fig. 2. Plot of stable isotope values for carbon and oxygen in fossil giraffes, pigs (suids) and deinotheres from Allia Bay site 261-1 compared with modern equivalents from the region. The fossil giraffes have more negative $\delta^{13}C$ values than their modern counterparts. The deinotheres and some of the fossil suids also have more negative $\delta^{13}C$ values than modern browsers in the region today. The presence of these genera and the stable isotope data suggest greater representation of woodlands in the middle Pliocene Turkana basin than today.

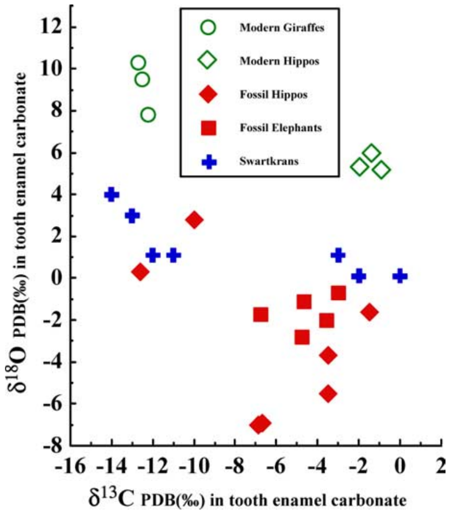

Fig. 3. Plot of stable isotope values for carbon and oxygen in fossil hippos and elephants from Allia Bay site 261-1 compared with modern equivalents from the region. Some of the fossil hippos and fossil elephants show a grazing signal in their stable carbon isotope ratios thereby indicating the presence of grasslands in the middle Pliocene Turkana basin. The presence of browsing hippos and of mixed feeding hippos and elephants further supports our proposed reconstruction of the Allia Bay site as a woodland savanna. For discussion of the Swartkrans data see text; data from Swartkrans are from Sponheimer and Lee-Thorp (1999b).

Fricke et al., 1998; Kohn et al., 1998), indicated by the pedogenic carbonates at Kanapoi (Wynn, 2000), is retained.

Although the overall range of variation in $\delta^{18}O$ values may be curtailed, the fossil samples show a range of −8‰ to +3‰, which overlaps the Moiti Tuff carbonates. In contrast, the modern samples show a range of +4‰ to +13‰. The consistent pattern of the offset and the large size of the samples we analyzed, argues against normal seasonal variation in $\delta^{18}O$ as an explanation for this difference. Further, the difference between these two distributions is at least 7‰ greater than is expected based solely on the difference in $\delta^{18}O$ value of the modern ocean versus that of the Pliocene ocean. This suggests another parameter is relevant. One likely possibility is the "amount effect" first discussed in terms of the negative correlation between $\delta^{18}O$ values and the amount of rainfall in a month (Dansgaard, 1964). Higher rainfall levels during the time of enamel formation in these fossil mammals can account for the lower $\delta^{18}O$ values we report for these samples. This rainfall could have been limited to the Ethiopian highlands and contributed to lower $\delta^{18}O$ values in the Omo River; but there may have been higher rainfall levels within the Turkana basin itself. In both cases, groundwater levels should have been higher and the basin, overall, should have provided greater amounts of water for plant growth and for the animals living on those plants.

In contrast to the $\delta^{18}O$ values, the overall pattern of $\delta^{13}C$ values in the fossil samples from Allia Bay is similar to that of modern samples from the same region although there are some differences (Fig. 2). First, the C_3 end of the distribution is about 1‰ more negative than in the modern samples. Given the ^{12}C enrichment in today's atmosphere compared with that of the middle Pliocene (Cerling et al., 1997), this minimal difference probably translates to a greater difference in reality. Second, the C_4 end of the distribution is not as positive in the fossil specimens as it is in the modern specimens, although sampling error due to small sample sizes may account for this.

A consideration of individual taxa suggests that the distribution of $\delta^{13}C$ values, in concert with the $\delta^{18}O$ values, indicate that the environment was better watered during the middle Pliocene than today. For example, the warthog (*Phacochoerus*, a grazer) is the only suid genus present today in the region, but a browser/mixed feeding genus (*Nyanzachoerus*) is present in the 261-1 assemblage (Feibel et al., 1991). The $\delta^{13}C$ values across the fossil suids (diamonds in Fig. 2) also show that grazing, browsing, and mixed feeding genera were all present. The presence of browsers (−13‰) suggests the presence of more closed environments during the middle Pliocene than exist today. Supporting this interpretation is the presence of deinotheres (circles in Fig. 2) with a pure C_3 signal (browse), as previously suggested on the basis of tooth morphology (Harris, 1983), and reported for deinotheres in other areas (Cerling et al., 1997). It is worth noting that the two samples are up to 3‰ more negative than modern giraffes (pure browsers) and that the fossil giraffes (squares in Fig. 2) also have $\delta^{13}C$ values that are 1–3‰ more negative. These more negative values suggest that the Turkana basin of the middle Pliocene had regions of greater canopy cover than today.

The basin also supported regions of grassland savanna. The $\delta^{13}C$ values demonstrate that there was a purely grazing suid, and samples attributed to Elephantidae indet. and *Elephas* sp. (Coffing et al., 1994) also show purely grazing $\delta^{13}C$ values (see Fig. 3). Today all species of *Elephas* are limited to the subcontinent of India and are considered mainly grazers, whereas the African proboscidean (genus *Loxondonta*) varies between browsing and grazing depending on the environment (see overview in Cerling et al., 1999). The proboscidean genera at Allia Bay are clearly grazers, although some individual samples show evidence of mixed feeding. Their $\delta^{13}C$ values partially overlap those reported previously for *Loxondonta* (Cerling et al., 1999) but many of the individuals show an almost pure C_4 diet. This suggests that a significant portion of the Turkana basin supported C_4 grasses, perhaps in a wooded savanna setting. The same argument can be made based on the fossil hippo samples. Several samples of fossil hippo were analyzed, although no identifications were available. The samples show $\delta^{13}C$ values indicative of pure browse (−13‰ and −10‰), of pure graze (−2‰ to −4‰), and of mixed feeding (−7‰). This suggests that fossil pygmy hippos are present in the collection, which may have "exploited fluvial habitats" (Feibel et al., 1991, p. 330) such as that surrounding the fossil Omo River.

Discussion and conclusions

In combination, these stable isotope data support and strengthen the faunal composition data in suggesting areas with woodland canopies that were more closed than are found surrounding Lake Turkana today. When compared with data on browsing and grazing fauna recovered from Member 2 at Swartkrans (Sponheimer and Lee-Thorp, 1999b; Fig. 3), the $\delta^{18}O$ values from the middle Pliocene site at Allia Bay suggest the presence of wetter environments than in the much younger site in South Africa. The $\delta^{13}C$ values and the faunal composition at the Allia Bay site in northern Kenya suggest environments with more woodlands in the middle Pliocene than in the late Pliocene/early Pleistocene site of Swartkrans in South Africa. Swartkrans lacks the deinotheres, giraffes, and browsing suids that show such negative values at Allia Bay. Swartkrans is thought to be surrounded by "a mosaic of grassland and tree cover which was probably denser alongside the ancient Blaaubank stream" (Sponheimer and Lee-Thorp, 1999b, p. 724). Our data from Allia Bay suggest a mosaic of woodlands with its greatest density along the ancestral Omo River and with more open savanna in the basin margins or uplands. Wynn (2000) emphasizes the low tree and shrub habitat indicated by his analysis of paleosol carbonates from Kanapoi but his stable isotope data and the range of carbonate types from hominid-bearing layers overlap with those of woodland savanna as well (see Wynn, 2000, Fig. 7). The environments surrounding Lake Turkana must have consisted of a mosaic of habitats similar to those documented for the nearby Tugen Hills sequence (Kingston, 1999); but overall the region was more heavily wooded than today.

The specific composition of the plant community in the Turkana basin cannot be determined from our stable isotope data even though the amount of woodland cover can be estimated very crudely. If, as suggested previously, the principal trees of the forest sections have changed over time, and if trees recovered from nearby deposits (Feibel et al., 1991), are representative of species widely spread in the middle Pliocene, then some nut/seed-bearing trees may have been present at Allia Bay. *Brachystegia*, a leguminous seed-bearing tree, has been recovered from the Middle and upper Member G of the Shungura Formation, which is equivalent in time to part of the Koobi Fora Formation. *Brachystegia* is largely restricted to more southern portions of the continent today but it is found along the Kenyan coast. If a fluvial corridor connected the Lake Turkana basin with the coast during the middle Pliocene as suggested (Feibel et al., 1991), the wetter conditions in the basin could well have supported a miombo-type of woodland. Arid country chimpanzees live in such regions today and Allia Bay middle Pliocene environments may have been attractive to early hominids for similar reasons (McGrew, 1992; Moore, 1992). More work is necessary to test this and other scenarios, and there are many other types of woodland savanna that would provide nut- and seed-bearing trees for early hominid exploitation. Today, baobab trees provide significant calories and protein for Hadza foragers in their woodland environment in northern Tanzania (Schoeninger et al., 2001).

Australopithecus anamensis had tooth enamel thicker than in chimpanzees and gorillas (Ward et al., 1999). As such, they should have been successful in feeding competition with ancestral hominoid species when seeds ripened and were more difficult to process in the mouth (Kingston et al., 1994; Schoeninger et al., 2001). The bipedality reported in these early hominids would also have given a competitive edge for traveling between stands of trees with ripe seeds (Isbell and Young, 1996). It would take only a slight increase in rainfall to provide enough to support a woodland savanna. The stable isotope data support interpretations of such an increase and the nearby deposits support interpretations of plant availability for providing a nutrient-dense food (high in lipid and protein) that were not available to other hominoid species (Schoeninger et al., 2001).

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