

Diet of *Theropithecus* from 4 to 1 Ma in Kenya

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***Theropithecus* was a common large-bodied primate that co-occurred with hominins in many Plio-Pleistocene deposits in East and South Africa. Stable isotope analyses of tooth enamel from *T. brumpti* (4.0–2.5 Ma) and *T. oswaldi* (2.0–1.0 Ma) in Kenya show that the earliest *Theropithecus* at 4 Ma had a diet dominated by C₄ resources. Progressively, this genus increased the proportion of C₄-derived resources in its diet and by 1.0 Ma, had a diet that was nearly 100% C₄-derived. It is likely that this diet was comprised of grasses or sedges; stable isotopes cannot, by themselves, give an indication of the relative importance of leaves, seeds, or underground storage organs to the diet of this primate. *Theropithecus* throughout the 4- to 1-Ma time range has a diet that is more C₄-based than contemporaneous hominins of the genera *Australopithecus*, *Kenyanthropus*, and *Homo*; however, *Theropithecus* and *Paranthropus* have similar proportions of C₄-based resources in their respective diets.**

C₃ | East Africa | Koobi Fora | Nachukui | baboon

Today, the Old World monkey genus *Theropithecus* is represented by one species, *T. gelada*, which lives only in the highlands of central Ethiopia. This unusual, grass-eating relict is all that remains of a previously widespread radiation that extended over much of Africa during the Pliocene and Pleistocene. From the period from ~4 to 0.25 Ma, fossils of *Theropithecus* are found in abundance at most of the well-known Plio-Pleistocene hominin fossil localities of Africa (1). The nature and pattern of occurrence of *Theropithecus* fossils attracted the attention of Clifford Jolly early in his career, and his famous 1970 paper (2) on the “seed-eater hypothesis” was one of the first to model early hominin ecology and functional morphology on the characteristics of a nonhuman primate. Most of the *Theropithecus* fossil record is dominated by members of the continuous and geographically widespread *T. darti*–*T. oswaldi* lineage, but during the early and middle Pliocene, the distinct *T. brumpti* lineage was found in the Omo-Lake Turkana Basin (1, 3). The virtual absence of geographic or temporal overlap between the two *Theropithecus* lineages has invited speculation as to their respective habitat preferences and diets (4–7). The association of *T. brumpti* fossils with presumed forest-dwelling bovid fossils and the species’ idiosyncratic pattern of dental wear led some to conclude that the species was a semi-arboreal frugivore (7, 8).

Theropithecus exhibits a distinctive suite of dental, gnathic, and postcranial characteristics related to chewing and food harvesting. These characteristics include an elongated thumb and fore-shortened index finger; this morphology permits precise and efficient plucking and pinching of food items, notably grasses in the case of geladas (9, 10). The combination of features associated with manual grazing along with craniodental specializations facilitating the comminution of high-fiber and/or silica-rich vegetation was highly successful. During the Pliocene, *Theropithecus* was thought to have occupied an ecological niche that is dominated today by ungulates, many of which are ruminants; thus, *Theropithecus* may have shared some of the dietary features of ungulates (such as being capable of chewing and digesting large volumes of low-quality, high-fiber, and/or highly siliceous vegetation), although *Theropithecus* did not have the benefit of hooves or ruminant digestion (11). Modern geladas are able to masticate

grass as effectively as an equid, and they can also ferment cellular material from grass in their hindguts but less effectively than a zebra, which may have aided in this adaptation (6, 12, 13). Even with the richness of the genus’s fossil record and the many paleoecological and functional anatomical studies that have speculated on the respective habitat and dietary preferences of the *T. brumpti* and *T. oswaldi* lineages, many questions remain about their respective dietary specializations and how they may have contributed to the eventual extinction of both lineages.

The present study of the stable isotopic composition of the molars of *T. brumpti* and *T. oswaldi* through time was undertaken to shed light on this persistent and vexing set of questions. Stable isotope ratios of ¹³C/¹²C are ideally suited to test this hypothesis because of the difference in isotope ratios between C₃ plants (most dicots) and C₄ plants (grasses and sedges, both of which are monocots) in the tropics; the dietary distinction between C₃ and C₄ plant-derived foods is preserved in the fossil record of Africa for most of the past 10 Ma (14, 15). The δ¹³C values of tooth enamel from modern and fossil browsers are about –12‰ in open forests through grasslands, whereas grazers have δ¹³C values near 2‰, and mixed feeders have intermediate values (16–19). We note that mammals from closed canopy forests are even more depleted in ¹³C than those mammals from open forests (20). Previous studies using isotopes in fossil primates show dietary preferences from pure C₃-derived to predominantly C₄-derived diets (21–27). *Theropithecus* from Southern Africa had a high component of C₄ biomass in the diet during the Plio-Pleistocene (21, 23); however, dating fossils from South African cave deposits is problematic, and a good chronology for the history of dietary evolution in this genus cannot be established.

First, to address the comparison between preadult (during molar formation and maturation) and adult diets (postmolar formation and maturation), we compare diets of modern baboons (*Papio cynocephalus*) using stable isotope ratios of feces from known individuals; baboons were from two groups monitored over a 3-wk period.

We then present stable isotope data for 44 *Theropithecus* specimens from Kenya, principally from the Lake Turkana region but also from Olorgesailie, that range in age from ca. 4 to <1 Ma. For purposes of considering average carbon isotope ratios for the two main *Theropithecus* species under consideration, we included one sample of *T. darti*; this species should be compared with *T. oswaldi*, because it is widely accepted that *T. darti* is the earliest representative of the *T. oswaldi* chronospecies. We discuss *Theropithecus* in the context of C₃- and C₄-derived diet resources and the overall context of isotope ecology in the Turkana Basin. The diet of *Theropithecus* is of interest compared with the diets of early hominins (26, 28) from the same deposits;

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hominins exhibit a change in the use of C₄ resources over this time interval, and thus, these primates were in potential competition for dietary resources.

Results

Preadult Vs. Adult Diet. Isotope ratios measured in tooth enamel are set by the diet of preadults; therefore, to characterize the species as a whole, it is important to establish whether the preadult diet differs from the adult diet. We measured $\delta^{13}\text{C}$ values of fecal matter from two groups of baboons collected over a restricted time period; preadults are not significantly different from adult baboons for each group. Group 1.1 has average $\delta^{13}\text{C}$ values of $-22.0 \pm 1.7\text{‰}$ ($n = 12$) and $-22.6 \pm 1.1\text{‰}$ ($n = 7$) for preadult and adult individuals, respectively; group 1.2 has average $\delta^{13}\text{C}$ values of $-24.2 \pm 1.4\text{‰}$ ($n = 9$) and $-24.3 \pm 1.0\text{‰}$ ($n = 4$) for preadult and adult individuals, respectively (data in Table S1).

Theropithecus Isotope Results. The geological age ranges of the specimens of *T. brumpti* and *T. oswaldi* in this study are ca. 4–2.5 and 2–1 Ma, respectively. Most samples are from the Turkana Basin in northern Kenya, but the later time period includes three specimens from Ologesailie in southern Kenya. The age ranges represented are discontinuous, with an important gap between 2.5 and 2.0 Ma (Fig. 1); additional specimens from this critical time interval in the evolution of *Theropithecus* may be obtained in the future from the Ethiopian National Museum.

The average $\delta^{13}\text{C}$ of *T. brumpti* is $-3.5 \pm 1.5\text{‰}$ (Table S1) ($n = 15$ teeth from 14 individuals), corresponding to an estimated diet that is ca. $65 \pm 10\%$ C₄-based; this result is significantly different (ANOVA; $P < 0.001$) (Fig. 2) than the later *T. oswaldi*, which has an average $\delta^{13}\text{C}$ of $-0.7 \pm 1.5\text{‰}$ (Table S1) ($n = 29$), corresponding to an estimated diet that is ca. $80 \pm 10\%$ C₄-based. The single *T. darti* specimen, which is much older than the related *T. oswaldi*, has a $\delta^{13}\text{C}$ value of -2.5‰ . Thus, the $\delta^{13}\text{C}$ values of tooth enamel from *Theropithecus* increase between 4 and 1 Ma (Fig. 1).

For comparison, the *T. oswaldi* from South Africa have a $\delta^{13}\text{C}$ value of $-2.3 \pm 1.6\text{‰}$ (21, 23) ($n = 11$), which can be distinguished from none of the East African species (Fig. 2).

Comparison with Modern Baboons. Tooth enamel from modern baboons from Africa, including *P. anubis* and *P. hamadryas*, have an average $\delta^{13}\text{C}_{1750}$ value of $-10.2 \pm 2.7\text{‰}$ ($n = 36$; maximum = -2.5‰ ; minimum = -15.5‰) (data in ref. 28), corresponding to a ca. $15 \pm 20\%$ C₄-based diet; the diets of modern baboons are very different from *T. brumpti* or *T. oswaldi* (Fig. 2), with modern baboons having a much a higher dependence on C₃-based diet resources.

Discussion

Preadult Vs. Adult Diet. Tooth enamel forms in baboons in preadults; tooth formation is complete by the time that teeth are

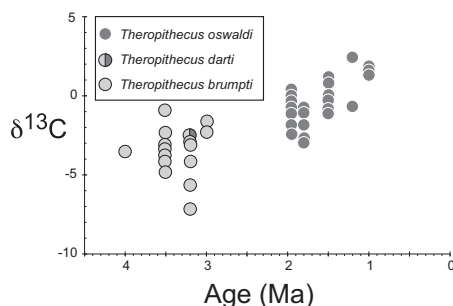


Fig. 1. $\delta^{13}\text{C}$ vs. age for *T. brumpti*, *T. darti*, and *T. oswaldi* from Kenya.

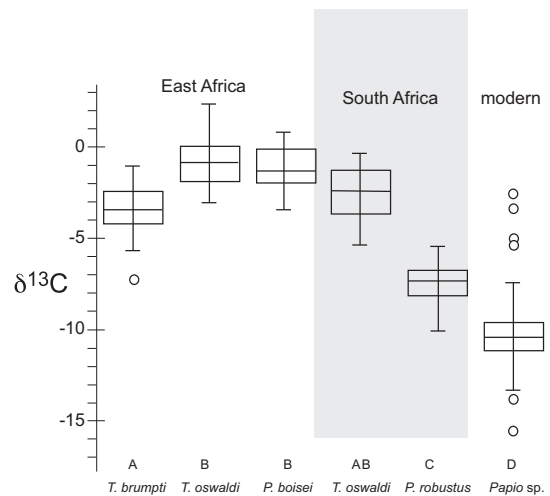


Fig. 2. Box and whisker diagrams showing the $\delta^{13}\text{C}$ ranges for tooth enamel from *Theropithecus* (this study) and *Paranthropus* from the Turkana Basin (26, 28), *Theropithecus* (17, 19) and *Paranthropus* from South Africa (21–23), and baboons from Eastern and Central Africa (28). Letters correspond to statistically different groups based on ANOVA analysis (Tukey posthoc; $P > 0.05$).

erupted, which in *Papio*, is ca. 7 y (29). The results of fecal material collected from two groups of baboons over a short time interval in Amboseli, Kenya, show no significant difference in $\delta^{13}\text{C}$ between preadults and adults, indicating that their respective diets are not distinguished at this level (data in Table S2). Thus, $\delta^{13}\text{C}$ values from the later-formed premolars and molars are representative of long-term diets [i.e., only the earliest permanent teeth (e.g., m1/M1, p4/P4) or deciduous teeth may not fully represent adult diets related to weaning issues]. For this reason, we sampled primarily the second or third molar teeth.

C₃, C₄, and Crassulacean Acid Metabolism Resources in Primate Diets.

Primary dietary components are derived from the base of the food web; in this discussion, we consider terrestrial plants (but see discussion of aquatic food webs below). C₃ and C₄ plants provide a variety of direct dietary resources ranging from low-protein bark and wood to intermediate-protein leaves to high-protein seeds and nuts. Underground storage organs (bulbs, rhizomes, and tubers) also can be important dietary resources.

Most dicots in East Africa use the C₃ pathway. Thus, most trees, shrubs, and bushes are C₃ along with many of the herbaceous dicots (including many legumes, melons, fruits, and vegetables). Most C₃ plants in Africa have $\delta^{13}\text{C}_{1750}$ values ranging from ca. -25‰ to -28‰ (14, 17, 18); values more positive (to -23‰) are found in xeric regions, and closed canopy forests have $\delta^{13}\text{C}$ values between ca. -30‰ and -35‰ (20). Primary forest resources are almost entirely C₃; soil carbon isotopes (30) show that few, if any, C₄ plants are present in forests (>80% canopy cover). Even open grasslands in Africa can have an important abundance of nonwoody C₃ forbs and herbs present (30).

C₄ plants are primarily tropical grasses and sedges, both of which are monocots. C₄ plants in East Africa have $\delta^{13}\text{C}$ values between ca. -10‰ and -15‰ (14, 17, 18). Tropical grasses make up >30% of the photosynthetic primary productivity (NPP) in the tropics (31, 32), and thus, tropical grasses and sedges are the most likely candidates as significant dietary resources of primates. Leaves, seeds, and underground storage organs are potential diet resources for grasses and sedges. It is important to note that a few dicots use the C₄ pathway, including some known to be food resources for modern humans (33); these dicots include members of the Acanthaceae, Amananthaceae, and Boraginaceae families as well as others. Today, C₄ dicots in Africa are minor parts of the regional ecosystem in

terms of their contribution to total photosynthetic productivity, although C_4 dicot plants may be important on a local scale.

Crassulacean Acid Metabolism (CAM) plants have $\delta^{13}C$ values similar to the $\delta^{13}C$ values of C_4 plants, especially in Africa (34). CAM plants in Africa include many succulents and are represented in a number of families, including Agavaceae (e.g., *Sansevieria*), Aizoaceae, Chenopodiaceae (e.g., *Salsola*), Crassulaceae, Euphorbiaceae (e.g., *Euphorbia*), and Liliaceae (e.g., *Aloe*). However, none of these plants are known to be important dietary resources for primates, and CAM plants are unlikely to have been important diet resources for fossil primates.

Secondary diet components are important for omnivores and carnivores; the C_3 or C_4 primary isotope signal can be inherited through a diet comprised of animals that themselves consumed C_3 or C_4 resources (35). There is little indication in the morphology of *Theropithecus* that omnivory or carnivory was important in dietary considerations, and we do not consider either omnivory or carnivory to be a major potential source of C_4 resources for *Theropithecus*. One of the remarkable aspects of the ecology of the modern gelada is its near-exclusive and year-round reliance on grasses (36, 37). Plio-Pleistocene theropithecids had a more varied diet than the diet of the gelada, but there are no dental indicators of carnivory (7).

Aquatic food webs are based primarily on the primary production of algae, which primarily uses the C_3 pathway; because of CO_2 limitations in aquatic ecosystems, algae sometimes use bicarbonate rather than CO_2 for carbon assimilation, which gives them higher $\delta^{13}C$ values than are typical for C_3 photosynthesis (38, 39). Thus, some aquatic ecosystems could have an apparent C_4 component because of this effect, which would be passed along the food web to secondary consumers, such as fish. We do not consider aquatic resources as an important dietary component for *Theropithecus* in the discussion below.

Diet of *Theropithecus* in East Africa from 4 to 1 Ma. The diet of the earliest *Theropithecus*, *T. brumpti*, in the Turkana Basin has a high component of C_4 -based resources. On average, this diet was between ca. 55% and 75% C_4 -based; even the most ^{13}C -depleted specimen (KNM-ER 1566) has a $\delta^{13}C$ value of -7.2‰ , corresponding to a diet that is ca. 35–40% C_4 -based. Paleosol evidence from the Koobi Fora and Nachukui Formations from this time interval suggests a habitat that had 40–60% woody cover (30, 40). Stable isotope studies of modern soils in East Africa show that closed riparian forests [$>80\%$ woody cover; e.g., Tana River (30)] have negligible C_4 biomass in the understory but that C_4 plants are found in riparian woodlands [$<80\%$ woody cover (30)]. Paleogeographic reconstructions for this time interval (41) show that the proto-Omo River flowed through the region, and this river was likely accompanied by a narrow (hundreds of meters wide) riparian forest corridor but with grassy woodland (i.e., $>40\%$ woody cover) (definition in ref. 42) outside of the corridor. Thus, *T. brumpti* had a diet that was strongly skewed to C_4 -based resources, and *Theropithecus* could not have been restricted to riparian forests. Using mixing lines and mass balance relationships based on the relationship between soil carbon and woody cover (30), 60% woody cover would have soil $\delta^{13}C$ contributions from C_3 woody cover, C_3 forbs and herbs, and C_4 grasses or sedges of ca. 60%, 15%, and 25%, respectively. In a riparian forest, for which there is no paleosol evidence of $>1\%$ areal coverage on the timescales of paleosol formation (ca. 1,000 y for a single locality), 80% woody cover would correspond to soil $\delta^{13}C$ contributions from C_3 woody cover, C_3 forbs and herbs, and C_4 grasses or sedges of ca. 80%, 10%, and 10%, respectively (30). Thus, a true forest would have little of the dietary resources used by *T. brumpti*, and therefore, *T. brumpti* would have obtained its dietary resources from outside any narrow riparian forest corridor.

The later (ca. 2- to 1-Ma time interval) *T. oswaldi* had increasingly higher contributions of C_4 -based diet between 2 and 1 Ma and by 1 Ma, had a diet that was comprised essentially of 100% C_4 resources. At 1 Ma, three specimens from Olorgesailie have an average $\delta^{13}C$ value of $+1.6\text{‰}$; for comparison, modern warthogs (*Phacochoerus aethiopicus*) from Kenya have an average $\delta^{13}C_{1750}$ value of $0.8 \pm 1.2\text{‰}$ ($n = 41$; values from ref. 43 corrected to 1750 as described in *Methods*). This difference of ca.



Fig. 3. (A) Example of C_4 grass (*Cynodon* sp.) with seeds that are used seasonally by primates (vervet monkeys and baboons) in Samburu Reserve, Kenya. (Left) Before handling. (Right) After seeds have been stripped. (B) Common baboons (*P. anubis*) digging C_4 grass rhizomes in Samburu Reserve, Kenya. (C) *T. gelada* in C_3 grassland of the Simien Mountains, Ethiopia. Photograph by George Chaplin.

‰ could be because of a difference in the isotope enrichment between the primate and suid species (i.e., a physiological difference in digestion processes), or it could be because of a real, but slight, dietary difference. The habitat in the upper part of the Koobi Fora and Nachukui Formations [Upper Burgi, Kay Behrensmeier Site (KBS), and Okote Members] had less woody cover than the early periods: paleosol evidence suggests a woody cover between 20% and 40% for this time interval, which would be a wooded grassland using the United Nations Educational, Scientific, and Cultural Organization terminology for African vegetation (42). Using mixing lines and mass balance relationships (30), 20% woody cover would have soil $\delta^{13}\text{C}$ contributions from C_3 woody cover, C_3 forbs and herbs, and C_4 grasses or sedges of 20%, 30%, and 50%, respectively.

Overall, the environment throughout the 4- to 1-Ma time interval shows that the habitat became increasingly open: from grassy woodlands or shrublands to wooded grasslands or bushed grasslands. Throughout the 4- to 1-Ma period, most of the diet resources of both *T. brumpti* and *T. oswaldi* were predominantly C_4 -based, with average C_4 -based contributions of ca. 60% and 80%, respectively. The fraction of C_4 -based diet resources for *T. brumpti* is higher than previous interpretations, which implied a predominantly C_3 -based browsing diet for this species (5–7). The composition of the diet of *T. brumpti* has been a subject of speculation for decades, because the masticatory apparatus of the species is highly specialized for the ingestion of large objects and the requirements of a wide gape, especially in males (6). Underground storage organs of C_4 -based bulbous grasses and sedges (i.e., corms, rhizomes) may have been important to the species' diet, which has been speculated for some contemporaneous hominins (44, 45). However, *Theropithecus* has higher $\delta^{13}\text{C}$ values than modern African mole rats that feed extensively on underground storage organs (46), suggesting that underground storage organs alone were not sufficient for the extent of C_4 use by *Theropithecus*.

Comparison with South African *Theropithecus*. *Theropithecus* from East Africa has similar $\delta^{13}\text{C}$ values to values previously reported for *Theropithecus* from South Africa (Fig. 2). Although *T. brumpti* does not occur outside of the Turkana Basin, members of the *T. darti*–*T. oswaldi* are represented at the South African Plio-Pleistocene cave sites of Makapansgat (*T. darti*), Swartkrans (*T. oswaldi*), and Gladysvale (*T. oswaldi*). *Theropithecus* co-occurs with diverse cercopithecoids—including several *Parapapio* species—and *Australopithecus africanus* (Makapansgat and Gladysvale), *Paranthropus robustus* (Swartkrans), and early *Homo* (Swartkrans and Gladysvale) (1, 47). *Theropithecus* consistently exhibits stable isotopic profiles—indicating a strongly C_4 -based diet composed mostly of grasses—whereas other cercopithecoids concentrated on a wide variety of C_3 plant foods (21, 23, 47).

Comparison with East African Contemporary Hominins. The earliest *Theropithecus* analyzed is a single M-fragment (KNM-ER 20441) that is ca. 4 Ma, and it is from the same site where *Australopithecus anamensis* is found. The four individual *Au. anamensis* have $\delta^{13}\text{C}$ values that range from -10.0‰ to -11.6‰ (27), which represents a pure or nearly pure C_3 -derived diet. In contrast, this single *Theropithecus* individual has a $\delta^{13}\text{C}$ value of -3.5‰ , which indicates a high (>60%) reliance on C_4 resources.

The later *Au. afarensis* and *Kenyanthropus platyops*, with ages between ca. 3.0 and 3.5 Ma, have a mixed C_3/C_4 diet, with tooth enamel $\delta^{13}\text{C}$ values ranging from ca. -3‰ to -13‰ and averaging $-7.5 \pm 2.6\text{‰}$ ($n = 20$) and $-6.2 \pm 2.7\text{‰}$ ($n = 20$), respectively (26, 48). In contrast, the contemporaneous *T. brumpti* has a $\delta^{13}\text{C}$ range of ca. -1‰ to -7‰ , with an average of $-3.5 \pm 1.6\text{‰}$ ($n = 14$), indicating a diet using a much higher fraction of C_4 resources than the hominins of this age range.

P. boisei was contemporary to *T. oswaldi*. Both of these primates had $\delta^{13}\text{C}$ values indicating that C_4 -based resources (26) were predominant in their respective diets: both had a ca. 25/75 ratio for C_3 - to C_4 -based diet resources. From the perspective of stable isotope analysis, *P. boisei* and *T. oswaldi* have similar diets (Fig. 2) and could have been competing for similar resources.

Several species of *Homo* overlap in time with *T. oswaldi*. The diet of *Homo* was consistently depleted in ^{13}C compared with *Theropithecus* (26), with little overlap in the range of $\delta^{13}\text{C}$ values. Although *Homo* consumed a mixed C_3 – C_4 diet, its reliance on C_4 resources was considerably less than *Theropithecus*.

In the several million years of overlap in time with hominins, *Theropithecus* consistently had the most positive $\delta^{13}\text{C}$ values of any primate in East Africa except *Paranthropus*, where it has indistinguishable values. The earliest hominin to be compared, *Au. anamensis* at ca. 4 Ma, had a diet that was solely or almost solely based on C_3 resources, whereas the contemporaneous *Theropithecus* had a C_4 -dominated diet. Of the hominins, only *P. boisei* had a diet with a reliance on C_4 resources as high as a contemporaneous *Theropithecus* species.

Comparison with Modern *Theropithecus* and *Papio*. Modern baboons and gelada monkeys are the closest relatives to the fossil *T. brumpti* and *T. oswaldi*. Today, a single species of *Theropithecus* is restricted to montane regions in Ethiopia; *Papio* is found throughout most of Africa. Modern baboons in Africa have $\delta^{13}\text{C}_{1750}$ values that indicate a diet dominated by C_3 diet resources (Fig. 2), but some baboons show a component of C_4 -based resources in their diets. Modern primates often have a small C_4 component to their diet, which can be obtained from stripping of seeds from mature grasses or digging for grass rhizomes (Fig. 3). Modern *T. gelada*, now living only in the Ethiopian Highlands above ca. 3 km elevation, has an almost exclusive C_3 grass diet (49, 50); C_4 grasses are rarely present above 3 km elevation (51) because of the cooler temperatures. Thus, modern geladas are grazers, but their diets are very distinct from their fossil relatives: modern *Theropithecus* has a C_3 grass diet, whereas fossil *Theropithecus* had a C_4 -derived diet, likely C_4 grasses. There are significant anatomical differences between C_3 and C_4 grasses (e.g., proteins are protected by the bundle sheath cells in C_4 grasses) (52), but it is not known

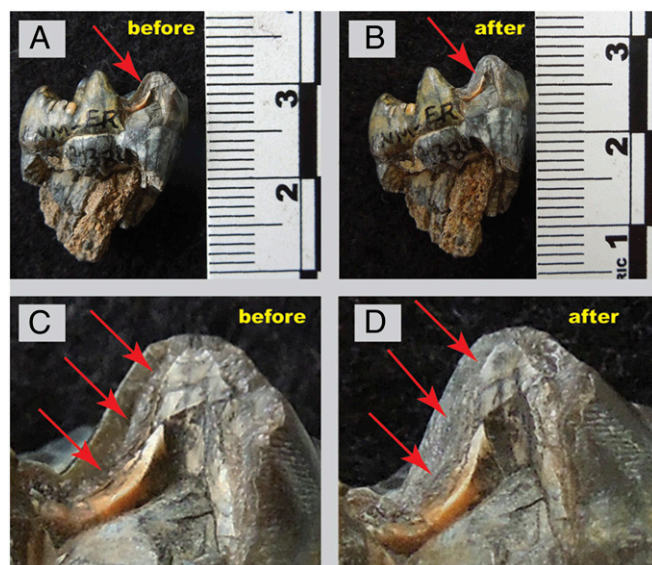


Fig. 4. Example of sampling of KNM-ER 30384. (A) Before sampling (arrow shows region to be sampled). (B) Same view as A but after the sample was collected. (C) Enlargement of A with enamel to be sampled (arrows show region to be sampled). (D) Same view as C but after the sample was collected.

if this feature makes a significant difference in digestibility of grasses by mammals.

Paleoenvironmental Considerations. Paleotemperature reconstructions of the fossil habitat of *Theropithecus* in the Turkana basin are based on the Δ_{47} -clumped thermometer (53); the results of that study suggest that soil temperatures and therefore, mean annual temperatures in the Turkana Basin from 4 to 1 Ma were similar to the analogous temperatures of today. The modern mean annual temperature is ca. 30 °C, which is at the hot extreme of global mean annual temperatures.

Conclusions

Theropithecus was a common and ecologically significant large-bodied primate in East Africa from 4 to 1 Ma. Stable isotope evidence shows that the early *T. brumpti* had a diet that was dominated by C_4 plants, presumably grasses or sedges, which made up ca. 65% of its diet between 4 and 2.5 Ma. This interpretation contrasts with earlier reconstructions of *T. brumpti* as a forest-dwelling creature that derived all, or most, of its resources from the forest. The later *T. oswaldi* had an even higher percentage of C_4 -derived resources, comprising virtually 100% C_4 by 1 Ma. The overall diet trend of *T. brumpti* to *T. oswaldi* is from an earlier diet, where C_4 resources were dominant, to the later diet, which was comprised almost exclusively of C_4 -derived resources. *Theropithecus* is ecologically and evolutionarily significant, because it is the only primate genus to have occupied a grass-eating niche throughout its history. During the Pliocene, *Theropithecus* species competed successfully with ungulates in environments increasingly dominated by C_4 grasses. It is likely that several factors may have contributed to the eventual extinction of *T. oswaldi* (54, 55); the most fundamental of these factors was the species' inability to survive amid hooved ruminant competitors in the grasslands of the Pleistocene (28) while competing for forage resources with highly variable nutritional qualities through the seasonal cycle. C_4 grasses have undergone major expansion in tropical ecosystems over the past 10 million y (14), beginning at ca. <1% NPP and now contributing >60% NPP in tropical savannas (31, 32). The C_4 clades of grasses underwent significant evolution during this time (56), although there is almost no macrofossil record of C_4 grasses or their evolution. During these millions of years of evolution, C_4 plants evolved defenses, and likewise, their primary consumers evolved strategies to overcome these defenses. The competition between the various ungulates and between ungulates and other grazers, such as *Theropithecus*, is part of that evolutionary story.

Methods

Samples were obtained from the National Museums of Kenya; 41 specimens were from the Koobi Fora and Nachukui Formations in northern Kenya, and 3 specimens were from the Olorgesailie Formation in southern Kenya. Of these specimens, two teeth were sampled from one of the specimens (KNM-ER 3775). *Theropithecus* enamel from broken tooth surfaces was sampled, and therefore, information concerning microwear was not compromised (Fig. 4); approximately 1–5 mg powder were obtained using a high-speed rotary drill. Powdered samples were treated with 0.1 M buffered acetic acid for 30 min to remove secondary carbonates; this process leads to a significant sample loss (ca. 0.5 to >1 mg per sample) but is needed to remove contamination (26).

Samples (200–500 μ g) were reacted with phosphoric acid (57) at 90 °C in silver capsules and analyzed on an isotope ratio mass spectrometer after cryogenic separation of CO_2 ; results are reported using the standard permil (‰) notation, with Vienna–Pee Dee Belemnite as the standard for both oxygen and carbon isotope measurements. Corrections for temperature-dependent isotope fractionation in oxygen were made using modern and fossil internal reference materials that had been reacted at 25 °C and 90 °C (58). For comparative purposes, modern mammals have had their $\delta^{13}C$ values adjusted to compensate for recent changes in atmospheric $\delta^{13}C$ values (17, 59, 60); such $\delta^{13}C$ values are reported as $\delta^{13}C_{1750}$.

Baboon fecal material was used to compare diets of preadult and adult primates; these data can evaluate the issue of diet recorded in tooth enamel, which forms in preadults. Final tooth eruption in baboons occurs at about 7 y (29); therefore, we compare diets of preadults (>2 and <7 y) with adult (>7 y) diet. Samples were collected over a ca. 3-wk period from two distinct baboon groups as part of the long-running Amboseli Baboon Research Project. Samples were dried at 105 °C and analyzed for $\delta^{13}C$ after combustion in an elemental analyzer in series with an isotope ratio mass spectrometer operating in continuous-flow mode. $\delta^{13}C$ values are reported relative to Vienna–Pee Dee Belemnite.

We use the $\delta^{13}C$ value of –26‰ for a pure C_3 diet and the $\delta^{13}C$ value of –12‰ for a pure C_4 -based diet to estimate the nominal fraction of the C_4 component to the diet of these primates. The isotope enrichment for diet-enamel in primates has not been established but is likely between 12‰ and 15‰ based on comparison with other large mammals (17, 61); using an isotope enrichment of 14‰, these nominal values for C_3 and C_4 plants give enamel values of –12.4‰ and + 1.8‰ for pure C_3 - and pure C_4 -based diets. These values are compatible with $\delta^{13}C$ values of sympatric browsers (deinotheres and giraffes) and grazers (equids and suids) from the fossil record in the Turkana Basin and the atmosphere-corrected $\delta^{13}C$ values of modern browsers (bovids and giraffes) and grazers (bovids, equids, and suids) from eastern Africa (17–19, 26, 43, 62).

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