Dietary change among hominins and cercopithecids in Ethiopia during the early Pliocene

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The incorporation of C_4 resources into hominin diet signifies increased dietary breadth within hominins and divergence from the dietary patterns of other great apes. Morphological evidence indicates that hominin diet became increasingly diverse by 4.2 million years ago but may not have included large proportions of C_4 foods until 800 thousand years later, given the available isotopic evidence. Here we use carbon isotope data from early to mid Pliocene hominin and cercopithecid fossils from Woranso-Mille (central Afar, Ethiopia) to constrain the timing of this dietary change and its ecological context. We show that both hominins and some papionins expanded their diets to include C_4 resources as early as 3.76 Ma. Among hominins, this dietary expansion postdates the major dentognathic morphological changes that distinguish Australopithecus from Ardipithecus, but it occurs amid a continuum of adaptations to diets of tougher, harder foods and to committed terrestrial bipedality. In contrast, carbon isotope data from cercopithecids indicate that C_4-dominated diets of the earliest members of the Theropithecus oswaldi lineage preceded the dental specialization for grazing but occurred after they were fully terrestrial. The combined data indicate that the inclusion of C_4 foods in hominin diet occurred as part of broader ecological changes in African primate communities.

hominins | Woranso-Mille | Theropithecus | carbon isotopes | paleodiet

The Pliocene is a critical time in human evolution when almost all early hominins became committed terrestrial bipeds and expanded their diets to include a wider range of resources than their ancestors. Recent stable isotope studies of *Australopithecus afarensis* teeth indicate that hominins had increased their dietary breadth to include significant amounts of C_4 or crassulacean acid metabolism (CAM) resources by 3.4 Ma (1), which is in contrast to its putative ancestor, *Australopithecus anamensis*, whose diet was limited to predominantly C_3 foods (2). The expansion in hominin diets to include significant amounts of C_4 and CAM resources indicates a transition toward more open-country foods, because C_3 plants include trees, shrubs, forbs, and cool-growing season grasses, whereas C_4 plants are primarily warm-growing season grasses and sedges, and CAM plants include cacti and succulents (3). This dietary expansion may have made it easier for hominins to survive in a greater range of environments or in environments that were more variable. However, we do not know when hominins started to include large proportions of C_4 resources in their diets, nor do we fully understand the ecological context of these changes (1, 4).

We use stable carbon isotope ratios of fossil hominin and cercopithecid teeth from Woranso-Mille in the western part of the central Afar Rift in Ethiopia (Fig. S1) to refine the timing of hominin dietary expansion to include C_4 resources. We also report isotope data from other mammals and soil carbonates to evaluate the environmental context and the diagenetic integrity of the isotope data. We use stable carbon isotope ratios, or $\delta^{13}C$ values, of fossil teeth to evaluate the dietary proportion of plants that use the C_3 vs. C_4 photosynthetic pathway, based on the premise that C_3 and C_4 plants have distinct carbon isotope signatures and that the $\delta^{13}C$ value of tooth enamel reflects the

carbon isotope composition of an animal's diet (5). Fossil teeth from the Woranso-Mille paleontological study area are well-suited to fill the temporal gap in the isotopic record of hominin diet because they are part of a record of Pliocene mammalian fossils that spans 3.76–3.2 Ma (6–11). The hominin fossils from Woranso-Mille include those that are morphologically intermediate between *Au. anamensis* and *Au. afarensis*, some that are definitively *Au. afarensis*, and others that represent additional species (7–9, 12). The cercopithecids include multiple species of colobines and at least two papionins (10). *Theropithecus oswaldi* cf. *darti* is the most common cercopithecid in the assemblages (>90% of identifiable cercopithecid specimens; 40% of the total identifiable mammal specimens) (6, 10); it represents the oldest and most primitive representative of the long-lasting *T. oswaldi* lineage whose morphology became increasingly specialized for grazing throughout the Pliocene and into the Pleistocene (13). The carbon isotope data from cercopithecids sympatric to hominins at Woranso-Mille make it possible to evaluate the ecological context for dietary changes in hominins.

Results

We report carbon and oxygen stable isotope data from 152 fossil teeth of hominins, cercopithecids, bovids, giraffids, hippopotamids, suids, rhinoceratids, and proboscidea from three time intervals at Woranso-Mille (3.76–3.57 Ma, 3.57–3.47 Ma, and 3.47–3.2 Ma; see *Supporting Information* for additional context). Among these teeth, $\delta^{13}C$ values range from −14.0 to +1.1‰ and represent the full spectrum of $\delta^{13}C$ values expected for tooth enamel from mammals with diets of exclusively C_3 and exclusively C_4 resources (Fig. 1 and Dataset S1). Presumed browsers such as giraffids and colobines yield $\delta^{13}C$ values at the lower end

Significance

Dietary change among hominins is a critical aspect of human evolution. Here we use carbon isotope data from fossil teeth of hominins, monkeys, and other mammals from Ethiopia to document C_4 food consumption by both hominins and the baboon, *Theropithecus oswaldi*, during the early Pliocene. The expansion of hominin diet and the appearance of the *Theropithecus oswaldi* lineage as early as 3.76 Ma mark a major ecological change within African primate communities. The ability to eat a range of C_3 and C_4 foods indicates that early Pliocene hominins were likely generalists who could thrive in different and perhaps varying environments.
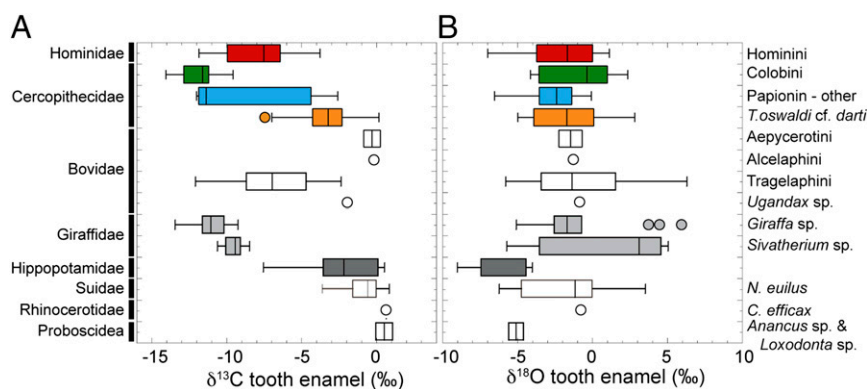
Fig. 1. Box and whisker plots of $\delta^{13}C$ (*A*) and $\delta^{18}O$ (*B*) values for the fossil tooth enamel data from Woranso-Mille. Median values are marked by a vertical line within the box, the edges of the boxes represent quartile values, the horizontal lines indicate the range, and outliers are plotted as circles.

of this range, whereas $\delta^{13}C$ values of presumed grazers including alcelaphini, *Loxodonta*, *Anancus*, and *Notochoerus euilus* are at the high end of this range. These distributions suggest that the carbon isotope data from the fossil teeth at Woranso-Mille preserve dietary information and are not products of diagenesis. There are no significant differences in $\delta^{13}C$ values among any of the mammalian taxa from the different time intervals sampled at Woranso-Mille ($P > 0.05$), such that we consider the fossil $\delta^{13}C$ data from all of the time intervals together.

Hominins. Sampling was limited to fragmentary hominin teeth whose genus and species cannot be determined with certainty; the sample may include intermediate forms of the *Au. anamensis–Au. afarensis* lineage, *Au. afarensis*, *Australopithecus deyiremeda*, and a yet unnamed species represented by the BRT-VP-2/73 foot (9, 12). The Woranso-Mille hominin teeth yield a mean $\delta^{13}C$ of $-7.9 \pm 2.5‰$ (1σ) and range from -11.8 to $-3.8‰$ ($n = 16$, median $-7.5‰$). The $\delta^{13}C$ values of hominin teeth from Woranso-Mille are indistinguishable from that of non-*Theropithecus* papionins, *Tragelaphus*, sivatheres, and hippopatimds ($P > 0.1$), but distinct from the $\delta^{13}C$ values of all other taxonomic groups sampled ($P < 0.001$). Notably, $\delta^{13}C$ values of hominins at Woranso-Mille are significantly higher than $\delta^{13}C$ values of sympatric colobines and lower than $\delta^{13}C$ values of sympatric *Theropithecus* individuals (Fig. 1). The range in $\delta^{13}C$ values among hominins at Woranso-Mille indicates that some individuals had diets dominated by C_3 foods, whereas other individuals had a significant component of C_4 resources in their diet. The observed variation in $\delta^{13}C$ values among hominins at Woranso-Mille may reflect dietary differences among hominin species; however, the fragmentary nature of the sampled teeth precludes us from connecting the stable isotope results to specific hominin taxa.

The range in $\delta^{13}C$ values of the Woranso-Mille hominins overlaps with those from older hominins, such as *Ardipithecus ramidus* (median $-10.3‰$, range $-11.2‰$ to $-8.5‰$, $n = 5$) (14) and *Au. anamensis* (median $-11.2‰$, $-12.0‰$ to $-9.5‰$, $n = 12$) (2) (Fig. 2 and Dataset S2). The distribution of $\delta^{13}C$ values of the Woranso-Mille hominins are significantly more positive than $\delta^{13}C$ values of *Au. anamensis* ($P = 0.002$). The $\delta^{13}C$ values of the Woranso-Mille hominins are indistinct from the majority of younger Pliocene hominins, including *Au. afarensis* (1), *Australopithecus africanus* (4, 15–18), and *Kenyanthropus platyops* (2), with the exception of two individuals of *Australopithecus bahrelghazali* that incorporated significantly more C_4 resources in their diet (19) and *Australopithecus sediba*, whose diet was restricted to C_3 foods (20). The Woranso-Mille hominins also have substantially more C_4 foods in their diets than the extant primates for which carbon isotope data from tooth enamel

are available (Dataset S3), but we note that these data have mostly been generated from animals living in forests and do not represent the full spectrum of environments in Africa today. In summary, the $\delta^{13}C$ values from the Woranso-Mille hominins indicate that C_4 foods were a significant component to hominin diets as early as 3.76 Ma.

Cercopithecids. The $\delta^{13}C$ values of the cercopithecids sampled from Woranso-Mille represent diets that ranged in proportions of C_3 and C_4 resource use (Figs. 1 and 2). The $\delta^{13}C$ values of colobines average $-11.9 \pm 1.3‰$ ($n = 9$) and represent diets of either pure C_3 vegetation or with minor amounts of C_4 plants and/or water-stressed C_3 vegetation. The $\delta^{13}C$ values of *T. oswaldi* cf. *darti* sampled from Woranso Mille average $-3.4 \pm 1.8‰$ ($n = 39$) and represent diets that are compatible with the inclusion of a large proportion of C_4 foods. The $\delta^{13}C$ values from the other papionin samples, referred to as non-*Theropithecus* papionins henceforth, average $-8.8 \pm 3.9‰$ and range from $-12.0‰$ to $-2.6‰$ ($n = 9$), reflective of diets that included little to no C_4 vegetation for some animals and a majority of C_4 vegetation for others.

Collectively, the *T. oswaldi* cf. *darti* teeth yield the highest $\delta^{13}C$ values among all primates sampled from Woranso-Mille. They are distinct from $\delta^{13}C$ values of the non-*Theropithecus* papionins, colobines, and hominins and from $\delta^{13}C$ values of all other nonprimate taxa ($P < 0.001$), except for hippopotamids. The $\delta^{13}C$ values of *T. oswaldi* cf. *darti* from Woranso-Mille are indistinguishable from the oldest *Theropithecus* sampled from the Turkana Basin, *Theropithecus brumpti* (21), but significantly lower than $\delta^{13}C$ values from *T. oswaldi* that are younger than 2.0 Ma in Turkana, from Olorgesailie in Kenya, and from Swartkrans, Makapansgat, and Sterkfontein in South Africa (18, 21–24) (Fig. 2). All fossil *Theropithecus* $\delta^{13}C$ values are significantly higher than the carbon isotope data available for extant primates in Africa (Dataset S3). Our data are consistent with studies from several sites in South Africa that show that *Theropithecus* consumed more C_4 vegetation than other cercopithecids and contemporaneous hominins (Fig. 2 and Fig. S2) (18, 22–24).

The $\delta^{13}C$ data from colobines come from at least two species at Woranso-Mille: *Cercopithecoides* cf. *meaveae* and one or more larger colobines. We do not have enough $\delta^{13}C$ data from each taxon to detect differences among them, but they are all consistent with diets dominated by C_3 vegetation, with $\delta^{13}C$ values that are indistinct from the non-*Theropithecus* papionins and *Giraffa* sp. at Woranso-Mille ($P > 0.1$) but significantly lower than $\delta^{13}C$ values of *Theropithecus*, hominins, and the nonprimate mammals at Woranso-Mille (Fig. 1). The $\delta^{13}C$ values from colobines at Woranso-Mille are indistinct from $\delta^{13}C$ values published from fossil colobines at other localities in Ethiopia and South Africa (Fig. 2) (14, 22, 25, 26); however, they are significantly higher than carbon
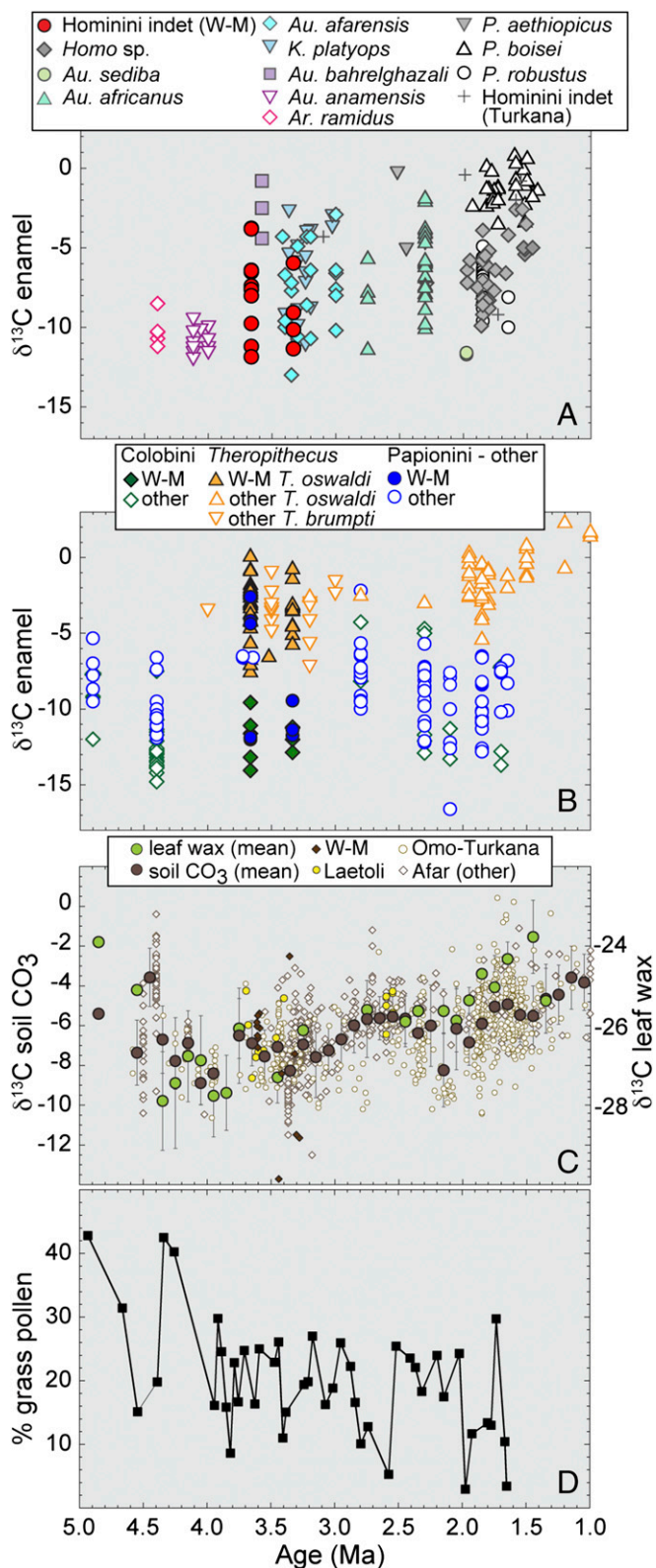
Fig. 2. The $\delta^{13}C$ values of African fossil hominin (*A*) and cercopithecid (*B*) tooth enamel and (*C*) soil carbonate and leaf wax C_{30}-acid and (*D*) the percentage of grass pollen from eastern Africa. Published fossil hominin and cercopithecid $\delta^{13}C$ data are from refs. 1, 2, 4, 14, 16–29, and 31–34. Soil carbonate $\delta^{13}C$ values are plotted as means for 100-ky age bins to view long-term trends but are also plotted for individual soils from the Omo-Turkana, Afar, and Laetoli regions (9, 37, 41, 42, 56–65); ages are assigned as in original publication or using the assignment provided in ref. 66. Mean leaf

isotope data from extant colobines (Dataset S3), which might indicate either a small component of C_4 in their diet, a difference in digestive physiology, or that the C_3 resources they consumed had higher $\delta^{13}C$ values than the plants consumed by extant primates in tropical evergreen and rainforests.

The $\delta^{13}C$ values of non-*Theropithecus* papionins at Woranso-Mille overlap with $\delta^{13}C$ values of hominins, colobines, giraffids, and *Tragelaphus* but are significantly lower than those of *T. oswaldi* cf. *darti*, the non-*Tragelaphus* bovids, hippopotamids, *N. euilus*, and Proboscidea. Among the nine teeth sampled, six yield $\delta^{13}C$ values $< -9‰$ ($-11.4 \pm 1.0‰$, $n = 6$) and overlap with the colobine $\delta^{13}C$ data; however, three of the teeth (all from the 3.76–3.57 Ma interval) yield distinctively higher $\delta^{13}C$ values ($-3.7 \pm 1.0‰$), indicating diets with significant amounts of C_4 vegetation. There is nothing about the size, morphology, or anatomical position of these teeth that set them apart; as such, we interpret these data to indicate that either (*i*) some non-*Theropithecus* papionins overlapped in their dietary behavior with *Theropithecus* and consumed large amounts of C_4 vegetation or (*ii*) they are early *Theropithecus* that used C_4 resources but with tooth morphology that is not distinct enough to characterize them as *Theropithecus*. The $\delta^{13}C$ values of the Woranso-Mille non-*Theropithecus* papionins are not significantly different from $\delta^{13}C$ of other fossil non-*Theropithecus* papionins from Ethiopia, Tanzania, and South Africa (14, 18, 22–29) (Fig. 2).

Tooth Enamel Oxygen Isotope Data. The $\delta^{18}O$ values of teeth samples from Woranso-Mille range from $-9.0‰$ to $+6.3‰$ (Fig. 1) and exhibit fewer taxonomic distinctions than observed for $\delta^{13}C$. The majority of taxa have overlapping $\delta^{18}O$ values, with the exception of the hippopotamid teeth, which are significantly lower than $\delta^{18}O$ values of all other taxa sampled from the 3.76–3.57 Ma time interval ($P < 0.02$), except for Proboscidea, *N. euilus*, and sivatheres. We did not make this comparison for the other time intervals, as we only sampled hippopotamids from the 3.76–3.57 Ma time interval. However, among the samples from the youngest time interval (3.47–3.2 Ma), there are no distinctions in $\delta^{18}O$ among taxa, except for $\delta^{18}O$ of sivatheres, which are significantly higher than those of *Theropithcus* and *N. euilus*. There are not enough samples from the middle time interval (3.57–3.47 Ma) to make meaningful comparisons. Among taxa that were sampled from multiple time intervals (all of the primates, giraffids, *Tragelaphus*, and *N. euilus*), there are no temporal distinctions in the distributions of $\delta^{18}O$ values, with the exception of *Theropithecus* and *N. euilus*, which exhibit an increase in mean $\delta^{18}O$ values of 3.0‰ and 3.9‰, respectively, between the 3.76–3.57 Ma and 3.47–3.2 Ma sampling intervals. The total range in $\delta^{18}O$ values among hominins (8.1‰) is similar to that for sympatric primates (6.5–7.8‰) and other mammals (5.0–11.0‰) at Woranso-Mille for which more than five teeth were sampled.

Absolute $\delta^{18}O$ values of fossil teeth are difficult to compare between fossil localities (30); however, the low $\delta^{18}O$ values of the hippopotamid teeth relative to most other taxa at Woranso-Mille are consistent with observations from other fossil sites in the Afar, including those with oxygen isotope data from hominins (1, 14). The offset between the giraffid and hippopotamid $\delta^{18}O$ values in the 3.76–3.57 Ma aged sediments at Woranso-Mille is $3.3 \pm 2.4‰$, which can be compared with the $\delta^{18}O$ giraffid−hippopotamid offset observed among fauna associated with *Ar. ramidus* at Aramis ($9.0 \pm 3.0‰$) (14) and with *Au. afarensis*

wax $\delta^{13}C$ values (C_{30} *n*-alkanoic acids) for 100-ky bins and percentage of grass pollen from the Deep Sea Drilling Project Site 231 are from refs. 38 and 40. Fossil ages are plotted as midpoints if the age constraint is a range of dates. In *A−C*, more positive $\delta^{13}C$ values indicate an increase in the contribution of C_4 vegetation. In *C*, error bars are 1σ on the mean.

at Hadar (5.4 ± 4.0‰) (1). The oxygen isotope data may indicate a slightly wetter environment in Woranso-Mille at 3.76–3.57 Ma that at Hadar (*ca.* 3.4 Ma) or Aramis (4.4 Ma), assuming the relationship between aridity and the offset in $\delta^{18}O$ values of giraffids and hippopotamids in eastern Africa today (30) applies to the Pliocene.

Soil Carbonates. Soil carbonates from hominin fossil-bearing sequences at Woranso-Mille yield mean $\delta^{13}C$ values of −6.1 ± 0.6‰ (*n* = 8) at Aralee Issie (3.76–3.57 Ma) and −9.2 ± 4.0‰ (*n* = 6) from Burtele and Nefuraytu (3.47–3.2 Ma) (Fig. S3 and Dataset S4). This distribution is similar to $\delta^{13}C$ values of soil carbonates from *Au. anamensis*-, *K. platyops*-, and *Au. afarensis*-bearing sequences (Fig. S3 and Dataset S5). The $\delta^{18}O$ values of soil carbonates at Woranso-Mille (−6.5 ± 0.9‰ at Aralee Issie and −3.7 ± 2.7‰ at Burtele and Nefuraytu) are within the range of $\delta^{18}O$ values for soil carbonates from other Pliocene hominin-bearing sequences in eastern Africa (Fig. S3).

Discussion

C₄ Resource Use Among Pliocene Hominins and Cercopithecids. The carbon isotope data from Woranso-Mille indicate that hominins included significant amounts of C_4 resources in their diets as early as 3.76 Ma (Fig. 2). In this regard, $\delta^{13}C$ values of the Woranso-Mille hominins indicate diets that are distinct from those of preceding taxa, *Au. anamensis* and *Ar. ramidus*, but similar to those of the majority of younger hominins, including *Au. afarensis*, *K. platyops*, and *Au. africanus*, although not to *Au. bahrelghazali* or *Au. sediba* (1, 2, 4, 14–20, 29, 31–34).

The expansion of hominin diets in the early Pliocene appears to be contemporaneous with the appearance of the first recognizable forms of *Theropithecus* (10, 35, 36). There are two well-known lineages of the genus, *T. brumpti*, largely restricted to the Turkana Basin, and the much more cosmopolitan *T. oswaldi*; both first appear *ca.* 3.8–3.6 Ma (10). The $\delta^{13}C$ values for the earliest *T. brumpti* show that it incorporated a large component of C_4 resources in its diet (21). The $\delta^{13}C$ values from Woranso-Mille extend this record of early C_4 consumption to the *T. oswaldi* lineage. The C_4-dominated diets of *Theropithecus* are unique among the cercopithecids; colobines maintain C_3-dominated diets through the Pliocene, and non-*Theropithecus* papionins always maintained a smaller component of C_4 in their diet than sympatric populations of *Theropithecus* (Fig. 2, Fig. S2, and Dataset S6). It is notable that $\delta^{13}C$ values of hominin teeth are consistently higher than $\delta^{13}C$ values of colobines throughout the Pliocene, indicating that (*i*) hominin and colobine diets were always distinct, (*ii*) hominins and colobines had different carbon isotope diet–tissue fractionation factors, reflecting differences in their physiologies, or (*iii*) hominins consumed some C_4 foods since 4.4 Ma.

Environmental Change. Environmental context is an important part to understanding the evolutionary implications of the dietary expansion among hominins and *Theropithecus* to include C_4 resources; however, it has been difficult to establish definitive links between diet and environment for fossil primates (4, 21). The incorporation of significant amounts of C_4 resources in primate diets in the early Pliocene occurred amid a gradual trend of increasing C_4 vegetation in Africa that began in the late Miocene (37–39) (Fig. 2). This increase in C_4 vegetation is generally viewed as a decrease in woody cover (37), but pollen records indicate that C_3 grasses were present throughout the Pliocene and into the Pleistocene (38, 40). Pollen abundances and $\delta^{13}C$ values of leaf waxes and soil carbonates indicate large proportions of grasses and C_4 plants in eastern Africa in the earliest Pliocene (5.0–4.0 Ma), with decreased amounts of C_4 vegetation and grasses by 4.0 Ma, followed by a small rise in C_4 vegetation between 3.9 and 3.7 Ma (37, 38, 40–42), which is coincident with the expansion of primate diets to include significant

amounts of C_4 resources. Although the coincidence makes it tempting to link the C_4 dietary expansion among hominins to environmental factors, there are reasons to be cautious: (*i*) the soil carbonate records are sparse from this time interval, and (*ii*) when $\delta^{13}C$ values of soil carbonates from hominin-bearing strata are compared directly (Fig. S3), there is no clear connection between environmental C_4 abundance and C_4-dominated diets among hominins. The oxygen isotope data from fossil giraffid and hippopotamid teeth may indicate wetter environments at Woranso-Mille than at both earlier and later hominin sites, but this could reflect local variation in water availability that is typical in eastern Africa today and does not necessitate any major climate change coincident with the inclusion of significant amounts of C_4 resources in hominin or *Theropithecus* diets. Given the collective data that are available, we do not see strong environmental trends that can be linked confidently to the C_4 dietary expansion among hominins and *Theropithecus*.

Dietary Breadth in Primate Communities. The combination of the expanded breadth in hominin diet and the appearance of the *T. oswaldi* lineage as early as 3.76 Ma marks a major change in African primate communities. The appearance of *Theropithecus* is important to hominin paleoecology because *Theropithecus* was a large fraction of the identifiable mammalian fossils at Woranso-Mille (10) and was predominant in nearly all eastern African mammalian communities from 3.5 Ma to 1.0 Ma (36). The increased range in $\delta^{13}C$ values of both hominins and cercopithecids after 3.76 Ma indicates that primate dietary breadth increased with the appearance of *Theropithecus*, which ultimately became a committed grazer (21). The use of both C_3 and C_4 foods by hominins likely reflects that they were generalists who could thrive in different environments, eating foods of varying quality and type (1, 4, 43). The inclusion of significant amounts of C_4 foods among hominins and papionins indicates niche broadening that appears unique among primates in the early Pliocene. We are not aware of significant dietary changes in other African mammalian orders at this time; Artiodactyla, Perissodactyla, and Probsocidea started to consume significant amounts of C_4 resources several million years earlier, in the late Miocene (39).

Relationship Between Diet and Morphology. The craniodental features characterizing australopiths are usually interpreted as a character complex associated with adaptations for hard-object, tougher, and more abrasive food resources (44, 45), although other interpretations such as those based on dental microstructure may not corroborate the former interpretation (46). The first appearance of these features is interpreted as an adaptation to eating a broader array of resources than hominins did previously (47, 48). However, the niche expansion indicated by dentognathic morphology at 4.2 Ma is not reflected in carbon isotope data (2, 4, 14). Intake of large amounts of C_4 foods as early as 3.76 Ma may represent a subsequent dietary change, wherein hominins further increased their dietary breadth (Fig. 2). Increasing enamel thickness, megadontia, and mandibular robusticity among Pliocene hominins is consistent with the consumption of more C_4 food resources, which might have included underground storage organs (i.e., rhizomes, corms) (1, 49, 50). The long-term relationships between dentognathic morphology and C_4 dietary intake is exhibited by correlations between $\delta^{13}C$ values and both postcanine and mandibular size for australopithecines (4); however, morphological changes are incremental and do not reflect the stepwise increase in C_4 resource consumption. We note that microwear data from *Au. anamensis* and *Au. afarensis* teeth are similar to one another and are not consistent with morphological changes that are often associated with

increased specialization for hard-object feeding; instead, they are consistent with diets of soft and tough foods (51).

Among papionins, adaptations to terrestrial behavior were already apparent by the late Miocene (52), and all evidence suggests that the earliest *Theropithecus* was fully terrestrial (10, 36, 53, 54). The main morphological changes that occurred in *Theropithecus* 3.8–1.0 Ma include increasing body size and the dentognathic specialization for grazing (36, 53, 55), but the evidence for C_4-dominated diets among the earliest *Theropithecus* fossils indicates that the grazing behavior precedes most of the dental specializations for eating grass, although we recognize that *Theropithecus*' initial use of C_4 grass may have focused on the nonblade part of grass.

Conclusions

Stable carbon isotope data from Woranso-Mille show that both hominins and *Theropithecus* included large proportions of C_4 foods in their diets as early as 3.76 Ma. This increased use of C_4 foods among both hominins and *Theropithecus* represents an expansion of dietary niche among primates to include both C_3 and C_4 resources that became typical in subsequent fossil primate communities for which there are isotopic data (Fig. S2). The C_4 dietary expansion was relatively late among primates, as other African mammalian orders had been consuming large amounts of C_4 foods since the late Miocene (39). For *Theropithecus*, the reliance on C_4 foods represents the initiation of its dietary specialization and its role as an abundant and widespread grazer within African mammalian communities (13). The evidence for C_4-dominated diets among the earliest identified specimens of *Theropithecus* precedes morphological specializations for grazing and provides a clear example of behavioral change preceding morphological adaptation. For hominins, the isotopic evidence for dietary expansion postdates the beginning of major

morphological dentognathic changes among australopiths (47, 48) and, as such, it represents a subsequent phase of increasing dietary breadth. The unequivocal incorporation of C_4 resources by hominins and cercopithecids as early as 3.76 Ma demonstrates that primates were expanding the types of food resources and potentially the environments that they were able to exploit.

Methods

Fossil teeth were sampled in the National Museum of Ethiopia in Addis Ababa. Teeth were cleaned with gentle abrasion before sampling. Hominin teeth were sampled along previously broken surfaces. Enamel powders were treated with 10% (vol/vol) H_2O_2 and 0.1 M buffered acetic acid solution for 15 min each, rinsed with deionized water three times after each treatment, and dried at 60 °C overnight before analysis. Soil carbonates were sampled from distinct pedogenic carbonate zones $\geq$ 50 cm below the contact with the overlying unit. After digestion in phosphoric acid, $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios of enamel and carbonate powders were measured on a Thermo MAT 253 isotope ratio mass spectrometer at Johns Hopkins University. External precision (1σ) of $\delta^{13}C$ and $\delta^{18}O$ values of the working fossil tooth enamel standards over the course of analysis was 0.3‰ and 0.2‰ for $\delta^{13}C$ and $\delta^{18}O$, respectively. Isotope data are reported relative to the Vienna Pee Dee Belemnite standard. Statistics were performed in Kaleidograph using an unpaired Wilcoxon–Mann–Whitney Rank Sum Test.

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