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Isotopic Evidence for Dietary Variability in the Early Hominin *Paranthropus robustus*

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Traditional methods of dietary reconstruction do not allow the investigation of dietary variability within the lifetimes of individual hominins. However, laser ablation stable isotope analysis reveals that the $\delta^{13}C$ values of *Paranthropus robustus* individuals often changed seasonally and interannually. These data suggest that *Paranthropus* was not a dietary specialist and that by about 1.8 million years ago, savanna-based foods such as grasses or sedges or animals eating these foods made up an important but highly variable part of its diet.

Both dental microwear texture analysis (*1*) and stable carbon isotope analysis (*2*–*5*) have demonstrated that the diets of South African australopiths were variable on the whole, but it has not been clear how the diets of individual hominins varied during their lifetimes. Here we provide evidence for short-term (seasonal and interannual) dietary change within the lifetimes of individual hominins, using a laser ablation method for stable isotope analysis (*6*). This method allows analysis along the growth axis of hominin teeth at submillimeter increments, making it possible to trace an individual's dietary history.

In tropical environments, virtually all trees, bushes, shrubs, and forbs use the C_3 photosynthetic pathway, whereas grasses and some sedges use the C_4 photosynthetic pathway (*7*, *8*). C_3 plants are depleted in ^{13}C [~ –27 per mil (‰)] as compared to C_4 plants (~ –12‰). The carbon isotopes in plants are incorporated into the tissues of consumers, with some additional fractionation (*9*, *10*), and consequently carbon isotope ratios of tooth enamel can reveal the degree to which an animal consumed C_3 or C_4 resources. This allows determination of whether a hominin ate C_3 foods, such as the forest fruits and leaves consumed by extant apes, or if they supplemented their diets with savanna-based C_4 foods, such as grasses or animals eating those plants (*2*).

We analyzed the enamel of four permanent teeth of *Paranthropus robustus* from Swartkrans, South Africa [found in member 1 at the site, dated ~1.8 million years ago (Ma)] using laser ablation stable isotope analysis (*11*). We also analyzed enamel of three contemporaneous browsing herbivores (*Raphicerus* sp.) from Swartkrans to control for postmortem alteration of carbon isotope ratios. We also counted the tooth growth increments (perikymata) that outcropped to the enamel surface between and adjacent to each ablation track on the hominin specimens to temporally constrain the isotope data where possible (Fig. 1). The number of days represented by perikymata is 9 days in humans and extant apes, with ranges from 6 to 12 days in humans and extant apes (*12*). Because the actual periodicities of perikymata in fossil teeth cannot be known without sectioning them, we assumed that the periodicity for *Paranthropus* was 7 days for this study (*12*).

The mean of all carbon isotopic analyses for *Raphicerus* demonstrates that diagenesis has not obliterated the biogenic carbon isotopic compositions, because it indicates a C_3 diet like that of *Raphicerus'* modern congeners (*13*) and of other known browsing herbivores from the site (Table 1 and table S1; $\delta^{18}O$ values are discussed in fig. S1) (*2*). Moreover, the expected small range in variation within individual *Raphicerus* teeth (a maximum of 0.9‰) shows that fossilization has not induced significant carbon isotopic variation at the spatial resolution of our analyses (Fig. 2). In contrast, there is strong variability within individual hominin teeth. The mean range of variation within individual teeth is 3.4‰ for *Paranthropus*, whereas the mean range for *Raphicerus* is only 0.7‰ ($P < 0.05$, Mann-Whitney *U* test, Table 1), showing that these hominins had more variable diets. In two out of four hominin teeth, the amplitude exceeds 4‰, which, at face value, suggests that their consumption of C_4 resources (tropical grasses or sedges or animals eating these foods) varied by ~40%. However, this isotopic signal is attenuated because of protracted mineral uptake during amelogenesis and our sampling protocol, which required some mixing of enamel layers (*14*).

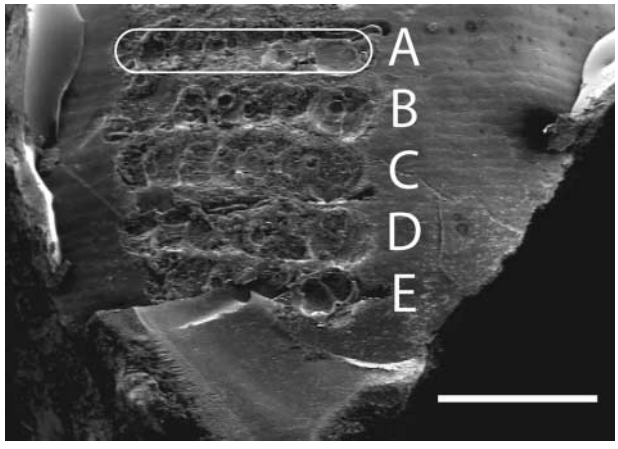

Fig. 1. A portion of the imbricational enamel of SKX 5939, on which the total number of perikymata between the first and last ablation samples shown (**A** to **E**) is 22, meaning that the interval represented by these samples is approximately 154 days (22 × 7). The day counts are only intended to be rough approximations sufficient to differentiate seasonal from interannual variability. The first visible ablation track is outlined in white. Perikymata are visible as faint horizontal lines across the tooth's surface. Scale bar, 1 mm.

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Thus, a change of 5.2‰, as seen in specimen SKX 5939, probably signifies a change from a diet dominated by C_4 resources to one of predominantly C_3 foods. Our data do not allow us to determine which C_4 resources *Paranthropus* consumed, although it is likely that grasses (seeds and roots), sedges (tubers and pith), and animal foods were all consumed to varying degrees.

Although all of the *Paranthropus* specimens show evidence of seasonal variability, there is also evidence of interannual variation that might reflect yearly differences in rainfall-related food availability (Fig. 2). Another possible explanation is that these individuals were migrating between more wooded habitats (favoring C_3 food consumption) and more open savannas (favoring C_4 resource consumption). Regardless, these results are very unlike what has been observed in our close relative the chimpanzee (*Pan troglodytes*). Some chimpanzees inhabit savanna woodland environments that are believed to be similar to those inhabited by early hominins [such as Mt. Assirik in Senegal (*15*)]. However, they do not consume C_4 resources to any measurable extent (*16*, *17*), and the carbon isotope compositions of their hair are not known to vary significantly from season to season (fig. S2) (*17*). Baboons (*Papio* spp.), in contrast, consume significant quantities of C_4 resources such as grass seeds and roots in some regions and some have variable $\delta^{13}C$ values (*18*). Thus, eurytopic *Papio* might be a more appropriate ecological analog for *P. robustus* (*19*).

A dental microwear study of the earlier (3.0 to 3.7 Ma) hominin *Australopithecus afarensis* found no evidence that its diet changed over time or in different habitats (*20*). In contrast, stable carbon isotope (*3*, *4*) and dental microwear texture analyses (*1*) of the slightly younger (~3.0 to ~2.4 Ma) hominin *A. africanus* demonstrated that its diet was far more variable. This suggests the possibility that a major increase in hominin dietary breadth was broadly coincident with the onset of increasing African continental aridity and seasonality after 3 Ma (*21*, *22*) and only shortly antedated the first probable members of the genera *Homo* and *Paranthropus* (*23*–*25*) and the earliest stone tools (*26*). The undoubted toolmaker *Homo* is thought to have been a dietary generalist that consumed novel foods such as large ungulate meat and tubers that are abundant in savanna environments (*27*–*30*). *Paranthropus*, in contrast, with its extremely large and flat cheek teeth, thick enamel, robust mandible, and heavily buttressed facial architecture, is often portrayed as a dietary specialist (*27*–*29*). Further, it has been argued that this specialization contributed to its extinction when confronted with increasingly dry and seasonal environments later in the Pleistocene, whereas *Homo*'s generalist adaptation was crucial for its success (*28*, *29*). Our results suggest that *Paranthropus* had an extremely flexible diet, which may indicate that its derived masticatory morphology signals an increase, rather than a decrease, in its potential foods. Thus, other biological, social, or cultural differences may be needed to explain the different fates of *Homo* and *Paranthropus* (*31*).

Table 1. Carbon isotope means, ranges, perikymata counts (PKM), and estimated number of days (perikymata × 7) for the total sampling intervals of specimens in this study. Oxygen isotope compositions are produced in tandem with the carbon isotope data and are further discussed in fig. S1. SD, standard deviation; na, not applicable.

Specimen	$\delta^{13}C$ (‰)	$\delta^{13}C$ range (‰)	PKM (*n*)	Days (*n*)
Paranthropus				
SK 24605	−7.3	1.3	47	329
SK 24606	−6.1	4.4	70	490
SKX 5939	−5.4	5.2	92	644
SKW 6427	−8.6	2.5	63	441
Mean	−6.9	3.4	68	467
SD	1.4	1.8	19	131
Raphicerus				
SKX 14150	−9.9	0.6	na	na
SKX 8494	−9.8	0.5	na	na
SKX 8535a	−8.6	0.9	na	na
Mean	−9.4	0.7	na	na
SD	0.7	0.2	na	na

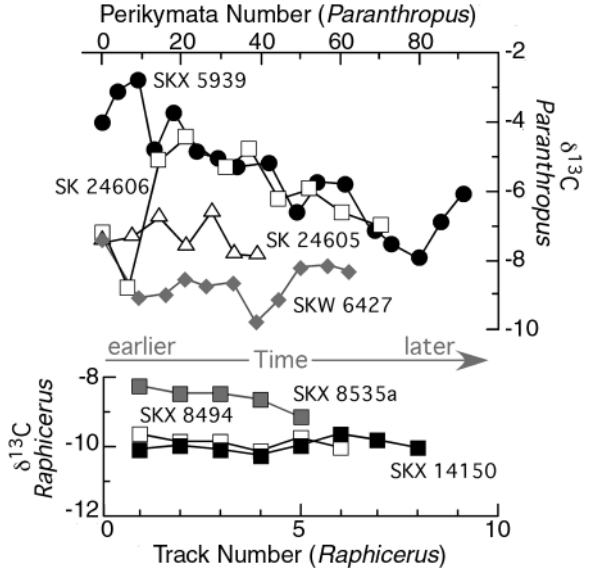

Fig. 2. $\delta^{13}C$ of multiple ablation samples along the growth axes of teeth of the early hominin *P. robustus* (top) and the browsing bovid *Raphicerus* sp. (bottom). Precision as gauged by reproducibility of internal enamel and CO_2 standards analyzed concurrently with each specimen was found to be 0.2, 1.1, 0.3, and 0.5‰ for SKX 5939 (black circles), SK 24606 (white squares), SK 24605 (white triangles), and SKW 6427 (gray diamonds), respectively. A perikymata count of 50 should be roughly equivalent to 1 year's crown formation. It is also important to note that each sample could incorporate carbon consumed over many months because of protracted mineral uptake during amelogenesis (*14*). This effectively attenuates the primary dietary signal, meaning that the intratooth variability observed here significantly underestimates actual dietary variability. Determination of the full amplitude of diet change awaits further study of enamel maturation parameters in hominoids [as in (*14*)]. The lack of variability within the *Raphicerus* teeth suggests that temporal differences in C_3 vegetation $\delta^{13}C$ values were very small and would not have contributed significantly to the variability in *Paranthropus*.

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Table S1
References

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Human Hair Growth Deficiency Is Linked to a Genetic Defect in the Phospholipase Gene *LIPH*

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The molecular mechanisms controlling human hair growth and scalp hair loss are poorly understood. By screening about 350,000 individuals in two populations from the Volga-Ural region of Russia, we identified a gene mutation in families who show an inherited form of hair loss and a hair growth defect. Affected individuals were homozygous for a deletion in the *LIPH* gene on chromosome 3q27, caused by short interspersed nuclear element–retrotransposon–mediated recombination. The *LIPH* gene is expressed in hair follicles and encodes a phospholipase called lipase H (alternatively known as membrane-associated phosphatidic acid–selective phospholipase A1α), an enzyme that regulates the production of bioactive lipids. These results suggest that lipase H participates in hair growth and development.

Mammalian hair follicles are self-renewing organs that represent interesting models for the regulation of stem cells. Hair follicles cycle through periods of growth (anagen), involution (catagen), and rest (telogen) before regenerating at the onset of a new anagen growth phase (*1*–*3*). Hair follicle stem cells, permanent residents of the stem cell niche called the "bulge," communicate with the underlying dermal papilla cells and proliferate at anagen onset to generate the progenitor matrix cells required for new hair growth (*4*). The molecules that control morphogenesis and cycling of hair follicles and the mechanisms underlying hair loss are poorly understood. However, genetic studies of rare familial cases of alopecia (hair loss on the scalp) and hypotrichosis (deficiencies of hair growth) have yielded important information about some of the genes controlling hair growth, including human *hairless*, desmoglein 4 (*DSG4*), and corneodesmosin (*CDSN*) (*5*–*7*).

Previously, we described individuals within the aboriginal Finno-Ugric population of Russia with a genetic form of hair growth deficiency (*8*, *9*). To identify the genetic defect for this condition, we have now studied two ethnic groups of mixed Caucasian and Mongoloid origin living in the Volga-Ural region of Russia (Mari El and Chuvash). The Mari population belongs to the Finno-Ugric linguistic group and the Chuvash population to the Turks linguistic group. The ancestors of the Chuvash population were probably Volga Bulgars, extruded by Mongols from Volga Bulgaria, who settled in the territory occupied by the Mari ancestral populations. We analyzed 50 families with hypotrichosis (14 from Mari and 36 from Chuvash) identified in a genetic epidemiological study of 171,500 Mari individuals and 178,722 Chuvash individuals (see supporting online material).

Affected individuals were characterized by deficiencies of hair growth on the scalp and body starting at birth, but showed no other pathologies. The growth of scalp hairs was retarded or arrested, leading to short hair length. Hair loss on the scalp was occasionally seen in children and progressed with age (Fig. 1A and fig. S1). Histopathological analysis revealed abnormal morphology of hair follicles and dystrophy and fragility of the hairs in analyzed individuals (Fig. 1, B to D).

The parents of affected individuals were normal, and the segregation frequency suggested an autosomal-recessive form of inheritance. We conducted primary genotyping in Mari families with a set of STR (simple tandem repeat) markers

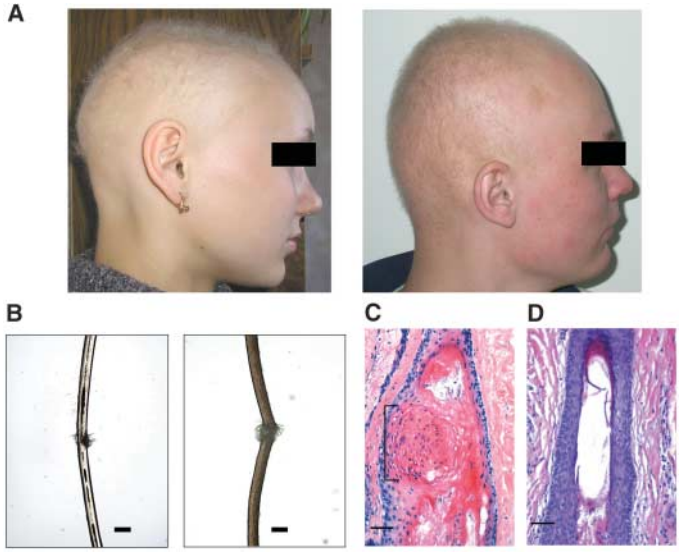

Fig. 1. Clinical presentation of hair growth defect and alopecia in Chuvash individuals. (**A**) Example of hypotrichosis and alopecia in a female adolescent (left) and a male adolescent (right). Note the sparse and short hairs on the scalp (shown with permission from the subjects). The phenotype is variable in males and females of different ages and can progresses to alopecia in adults. (**B**) Hair fibers from affected individuals showed common dystrophic structural alterations and signs of fracture and fragility. Scale bars, 100 μm. (**C** and **D**) Hair follicle histology in an affected individual (C) and in an unaffected control subject (D). Scale bars, 50 μm. In many follicles, the lower follicular infundibulum above the insertion of the sebaceous gland shows marked dilation with epithelial thinning and abnormal keratinization (brackets). There is a loss of the normal granular layer, with premature differentiation of the epithelium and a remarkable parakeratotic plug.

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