



Isotopic evidence for an early shift to C₄ resources by Pliocene hominins in Chad

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Foods derived from C₄ plants were important in the dietary ecology of early Pleistocene hominins in southern and eastern Africa, but the origins and geographic variability of this relationship remain unknown. Carbon isotope data show that *Australopithecus bahrelghazali* individuals from Koro Toro in Chad are significantly enriched in ¹³C, indicating a dependence on C₄ resources. As these sites are over 3 million years in age, the results extend the pattern of C₄ dependence seen in *Paranthropus boisei* in East Africa by more than 1.5 million years. The Koro Toro hominin fossils were found in argillaceous sandstone levels along with abundant grazing and aquatic faunal elements that, in combination, indicate the presence of open to wooded grasslands and stream channels associated with a greatly enlarged Lake Chad. In such an environment, the most abundant C₄ plant resources available to *A. bahrelghazali* were grasses and sedges, neither of which is usually considered as standard great ape fare. The results suggest an early and fundamental shift in hominin dietary ecology that facilitated the exploitation of new habitats.

Recent stable carbon isotope and microwear studies of early hominin diets have challenged widely held perceptions that the development of their robust craniomandibular morphology, large molars and premolars, and thick enamel, are adaptations for processing hard foods associated with increasingly xeric environments in the Pliocene and Pleistocene (1, 2). In particular, carbon isotope (¹³C/¹²C) ratios of fossil tooth enamel have demonstrated previously unsuspected contributions to australopithecine diets. Most ^δ¹³C data obtained for *Australopithecus africanus* and *Paranthropus robustus* in South Africa suggest significant dietary contributions from ¹³C-enriched biomass (3–7), which can be seasonally variable (8, 9). [By convention, ¹³C/¹²C ratios are expressed as parts per 1,000 in the δ notation relative to the VPDB standard, as $\delta^{13}\text{C} \text{‰} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$.] In eastern Africa, data for *Paranthropus boisei* suggest a very strong C₄ emphasis by ~1.8 Ma (10, 11). *Ardipithecus ramidus* from Aramis is a notable exception, showing little engagement with C₄ resources despite their abundance in the local environment (12). On present evidence, the earliest known evidence for C₄ consumption is observed in three of four *A. africanus* Makapansgat individuals from the Late Pliocene at ~2.8 Ma (4).

Australopithecus bahrelghazali is the only Pliocene hominin, and indeed the only primate, to have been found at the Koro Toro (KT) sites (KT12 and KT13) in the Chad Basin, well beyond the abundant fossil occurrences in the Rift Valley to the East, and the southern African sites to the South (Fig. 1) (13–15). Biochronological estimates for both sites indicate ages of 3–3.5 Ma (13, 15), whereas cosmogenic ¹⁰Be/⁹Be nuclide dating of the KT 12 sediments containing the *A. bahrelghazali* holotype specimen, KT12/H1, provides an age of 3.58 ± 0.27 Ma (16). These dates suggest contemporaneity with *Australopithecus afarensis* in eastern Africa.

The fragmentary remains of several *A. bahrelghazali* individuals occur in a poorly consolidated, perilacustrine, clayey sandstone together with terrestrial (Suidae, *Loxodonta*, *Stegodon*, *Giraffa*,

Parmularius, *Antidorcas*, *Sivatherium*, *Cerathotherium*, *Hipparion*, *Bovini*, *Kobus*) and freshwater (Perciformes, Siluriformes, *Trionyx*, cf. *Tomistoma*, Anatidae, *Hexaprotodon*, and Lutrinæ indet.) taxa (13–15, 17). Relative abundances of bovids at KT13 show a predominance of open-country grazers (17), including Reduncini indicative of edaphic grasslands (18). The lack of *Aepyceros*, Tragelaphini, and primates (other than *A. bahrelghazali*) suggests a paucity of woodland or thicket (13–15, 17), but the occurrence (~10% of terrestrial fauna) of *Giraffa* (19) indicates the continued presence of some tree cover in the Pliocene sites. Existing faunal enamel $\delta^{13}\text{C}$ data are consistent with these observations, showing overall C₄ plant dominance (20). Together, the paleoenvironmental data indicate a northern Chad Basin landscape with extensive grasslands and sparser trees, bordering an expanded lake and associated stream channels.

Hence, *A. bahrelghazali* survived in an environment more open than that inhabited by most other Pliocene taxa including its contemporary *A. afarensis* in eastern Africa (18, 21–23). Their survival in such a habitat was possibly facilitated by dietary niche expansion to include novel C₄ resources, the exploitation of which is uncommon among extant great apes including savanna-dwelling chimpanzees (24, 25), although more common among many savanna baboons (26, 27). The appearance of C₄ resources among early hominins would represent a significant ecological shift, but the timing and geographical variability across Africa remains unclear. Here, we explore *A. bahrelghazali*'s diet by comparing the carbon isotope composition of their tooth enamel against that of the coexisting fauna, and against the published data for early hominins elsewhere.

Results

A. bahrelghazali $\delta^{13}\text{C}$ values range from –0.8 to –4.4‰. They are similar to, but reach slightly lower values than, those of the Alcelaphini, Reduncini, Equidae, Suidae, and Proboscidea from the KT sites (Fig. 2, Table S1). The detailed laser scan data for two of the hominids are given in Table S2. The results indicate a predominance of C₄ dietary resources (~55–80% by linear interpolation). Carbon isotope data alone cannot distinguish whether carbon of C₄ origin was from plant or animal sources, but in this case, the high proportions suggest that the primary C₄ dietary resources were plant staples. Consumption of animals (e.g., termites, rodents, grazing herbivores) reliant on the abundant

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Fig. 1. Map of Africa showing the Chad Basin and the location of the KT12 and KT13 sites, and the hominin sites in South Africa and eastern Africa from which the $\delta^{13}\text{C}$ data shown in Fig. 3 were obtained.

C_4 vegetation cannot be excluded and they may have formed components of the diet, as inferred for the South African australopithecines (5, 7, 28). Very high proportions of animal food, however, are not plausible for hominins given that even recent humans such as the Kalahari San rely most heavily on plant foods (~80%) and less on game (29). Moreover, hominins lack the appropriate dental morphology. Therefore, we focus on C_4 plants in the discussion below.

It is readily apparent that the *A. bahrelghazali* $\delta^{13}\text{C}$ values differ from those of most hominins analyzed so far (Fig. 3). They differ from $\delta^{13}\text{C}$ values for *Ar. ramidus*, which largely reflect C_3 resource consumption (Kruskal–Wallis test and Conover–Inman pairwise comparisons; $P < 0.001$). *A. bahrelghazali* is more enriched in ^{13}C than the South African australopithecines *A. africanus* and *P. robustus* ($P < 0.01$). In contrast, its $\delta^{13}\text{C}$ values are not significantly different from those of *P. boisei* from the Olduvai and Lake Turkana regions in East Africa, where mean $\delta^{13}\text{C}$ ($x = -1.3 \pm 0.9\text{‰}$) suggests as much as 85% of carbon from C_4 sources (10, 11).

Discussion

Although necessarily few because of the low numbers of *A. bahrelghazali* tooth specimens, the $\delta^{13}\text{C}$ data demonstrate that a reliance on C_4 resources is not an aberration confined to *P. boisei*, but that it had a much earlier genesis. The Chadian australopithecines occupied a largely open landscape dominated by C_4 plants, in which traditional hominoid woodland or forest-derived resources were sparse, so a significant C_4 dietary component might be considered unsurprising. However, both tropical grasses and sedges, which form the major and minor C_4 components of the flora in the open, low to midlatitude regions of Africa, respectively (30–32), are unusual foods for hominoids.

C_4 , or Kranz, grasses are challenging for herbivores generally, and because hominins lack dental and digestive adaptations of grazing taxa to cope with the bundle sheath cell walls and abundant silica phytoliths (30), one must consider whether plant parts other than leaves/blades may have been the major

focus. Jolly (33) famously suggested a gelada baboon analogy for early hominin diet focused on exploitation of grass seeds and rhizomes. However, the seeds are seasonally restricted, small food packages that are costly to harvest, and most grass rhizomes are not fleshy storage organs (see figure 1j in ref. 34), so the potential value of these resources for hominins has been neglected (see 28). Nevertheless, East African savanna baboons regularly exploit all of the above-ground, fresh parts of taxa such as *Cynodon* and *Sporobolus* on a seasonal basis (26, 35–38). The more nutritious and lower fiber grass meristems may be exploited year-round (36, 37). Furthermore, some tropical grasses including *Sporobolus rangei* have fleshy tubers or corms that form an important component of Amboseli baboons' diets (26, 35, 37).

Several studies have suggested that exploitation of energy-rich geophytes or underground storage organs (USOs) (bulbs, corms, tubers, and rhizomes) represented an important adaptive shift in hominin evolution, especially as related to the transition to early *Homo* (e.g., 39–41). In general, most USOs are C_3 . The main exceptions are the C_4 members of the Cyperaceae (sedges), many of which produce tubers and more occasionally, corms, in addition to rhizomes and stolons. Species in the C_4 genus *Cyperus* form prominent and highly productive components of the vegetation fringing African tropical and subtropical wetlands including the Chad basin (42). The nutritive value of the rhizomes of the most abundant C_4 taxa fringing Lake Chad today, *Cyperus papyrus*, *Cyperus laevigatus*, and *Cyperus articulatus* (42) remains unclear given the prevalence of indigestible structural carbohydrates and/or secondary compounds (43). *Cyperus* species also occur in both swamp, and drier sandy or loamy settings where there is seasonal moisture (43); many of these taxa of “grassier” habit bear fleshy tubers or corms (e.g., *Cyperus rotundus*, *Cyperus esculentus*, *Cyperus blismoides*, *Cyperus obtusiflorus*) or swollen bases (e.g., *Cyperus bulbosus*, *Cyperus amauropus*, *Cyperus merkeri*) that are eaten by both baboons and humans

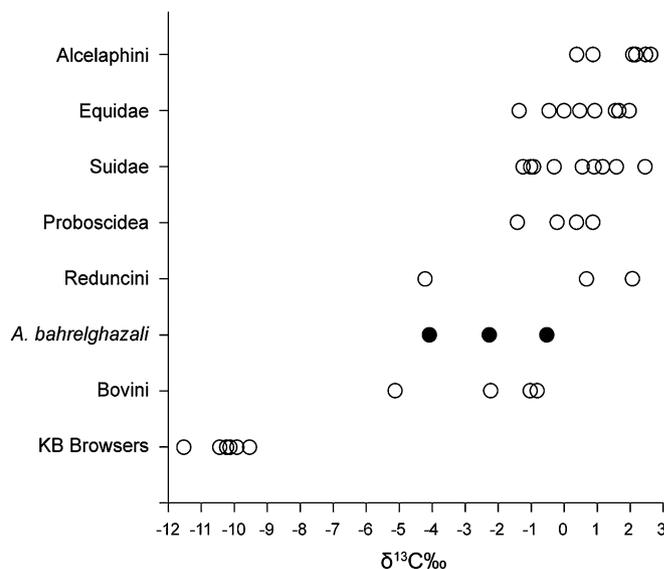


Fig. 2. Plot of $\delta^{13}\text{C}$ values for *A. bahrelghazali* and Alcelaphini, Equidae, Suidae, Proboscidea, Reduncini, and Bovini from the KT sites, and data for *Paracamelus* sp., *Giraffa* sp., and *Diceros bicornis* from the nearby, but older, site of Kossom Bougoudi (labeled KB browsers). Data for KT12 and KT13 from this study are combined with published data (20) for KT sites, and for KB (data provided in Table S1). The KB browsers are shown here to indicate values for C_3 feeders in the region, because although *Giraffa* fossils are present in the KT sites (20), no suitable tooth enamel was available for $\delta^{13}\text{C}$ analysis.

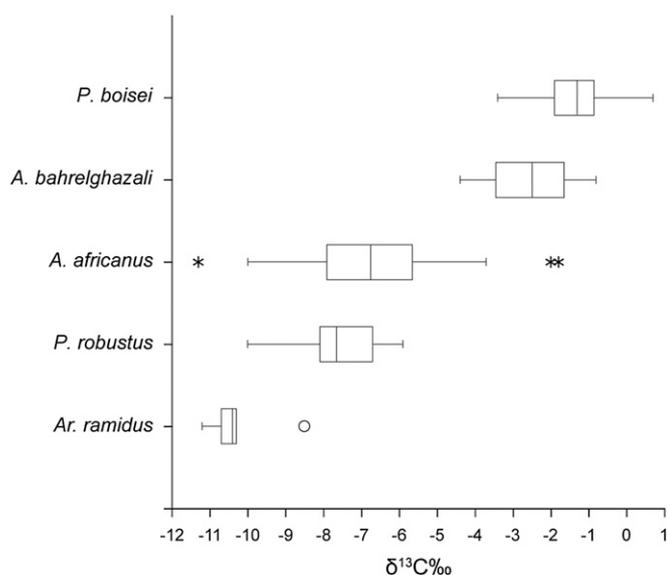


Fig. 3. Box-and-whiskers plot of the $\delta^{13}\text{C}$ data for all probable hominins (excluding *Homo*) published to date. The high C_3 and C_4 contributions to the diets of *Ar. ramidus* and *P. boisei*, respectively, mark out distinctive diets toward both ends of the C_3 to C_4 spectrum. *A. africanus* data stand out for their high variability, which is atypical among fossil and extant mammals. Data sources are ref. 13 for *Ar. ramidus*, the South African australopith data as summarized in ref. 8, and the *P. boisei* data in refs. 11 and 12.

today (36–38, 43). Ethnohistoric sources suggest that *Cyperus usitatus*, *Cyperus fulgens*, and *C. esculentus* were important plant resources for Late Stone Age foragers in the semiarid South African Karoo (44). The above-ground parts of many sedges are also eaten. For instance, humans use the culms of *C. papyrus* as casual or famine foods (43) and baboons the flowers and bulbs of *Cyperus grandibulbosus* (38).

Given the nature of the Chad basin environment, it would seem that abundant edible C_4 plant resources were available to *A. bahrelghazali*, including the below- and above-ground parts of several grass and sedge taxa. Moreover, many of the invertebrate and vertebrate fauna are likely to be enriched in ^{13}C in a C_4 -rich biome. The remaining (C_3) portion of *A. bahrelghazali*'s diet may have included C_3 macrophytes, as suggested in ref. 41, or the more “traditional” hominoid foods such as fruits, pods, flowers, and insects. The semiarid terrestrial flora that today stretches away from the current Lake Chad and colonizes the dunes includes *Hyphaene thebaica* (doum palm), *Acacia nilotica*, and *Ficus ingens* (42), all of which produce widely consumed fruits and pods (e.g., refs. 35–38). The presence of *Giraffa* in the KT sites suggests that similar species might have been present in the Pliocene environment.

Whether the *A. bahrelghazali* individuals relied on C_4 grasses or sedges, or both, these resources are seldom consumed (if at all) by most primates. Savanna baboons are a notable exception as they spend significant amounts of time foraging for C_4 plants (26, 35–38), although the sparse existing $\delta^{13}\text{C}$ data for these baboons in East Africa show a lower reliance on such resources than one might expect based on foraging time. Bone collagen and enamel values for modern *Papio anubis* individuals ($n = 3$, respectively) suggest C_4 contributions of $<20\%$ in East Turkana and Naivasha (45) and $\sim 50\%$ in Laikipia (46). Many of the main C_4 plant resources (i.e., grasses and sedges) are high in fiber and/or complex starches, although some parts, such as grass meristems, offer higher nutrient rewards. For instance, the tubers of cultivated *C. esculentus* varieties are high in structural carbohydrates and lignin (47). In comparison with baboons, values

for the hominins *A. bahrelghazali* and *P. boisei* suggest higher C_4 contributions. A focus on the C_4 plant parts as suggested above may be consistent with observations that occlusal microwear in *A. anamensis*, *A. afarensis*, and *P. boisei* (1, 48) lack indications for the processing of hard items.

Our data show that by ~ 3.5 Ma *A. bahrelghazali* was fully engaged in exploiting C_4 biomass. The results imply that australopithecines had become broad generalists foraging opportunistically for locally abundant resources that included significant quantities of savanna resources, unlike chimps. Alternatively, they might imply an emerging specialism on grasses and/or sedges. In the former case, we should expect strong variability related to the environment differences, whereas in the latter we might expect most early australopithecine diets to reflect a strong C_4 focus in all habitats where both grasses and sedges are predominantly C_4 . This could be tested by isotopic analyses of temporally and morphologically similar *A. afarensis*, which generally inhabited more wooded environments in eastern Africa (18, 21, 22) and might be expected to consume more C_3 resources there if they were dietary generalists. Whatever the case, we suggest that a capacity to exploit C_4 resources provided the means to survive in environments completely unlike the earlier ancestral forests or denser woodlands.

Methods

Because there are very few *A. bahrelghazali* specimens and it was imperative to minimize the impact of sampling, we followed a dual approach using laser ablation (LA) mass spectrometry (following methods outlined in ref. 49) for $\delta^{13}\text{C}$ determination of two of the hominin specimens, and standard acid hydrolysis preparation for the third hominin and all of the fauna. LA analysis permitted isotopic determination from a minute enamel sliver previously dislodged from KT12/H1a during morphometric measurements. Although this method is minimally invasive, there are drawbacks, including lower precision (49), and lack of comparability for $^{18}\text{O}/^{16}\text{O}$ ratios because the laser releases all oxygen species in enamel. Therefore, we first compared $\delta^{13}\text{C}$ results for the two methods, using two fossil teeth in our collection (LT4 and LT6), and thereafter, three KT faunal specimens. The results showed reasonable agreement (see Table S3 for the KT data). LT4 and LT6 were subsequently used as internal standards to monitor the response of the laser and to calibrate the data. We considered that the lower isotopic homogeneity in enamel was outweighed by the requirement for a standard of similar mineralogy to the samples, given the sensitivity of LA to this factor (SI Methods).

All teeth were cleaned as outlined in SI Methods. Enamel powders destined for standard 100% H_3PO_4 hydrolysis mass spectrometry were pretreated first (SI Methods) before analysis in a GasBench II coupled to a Thermo Finnigan Delta V. Multiple measurements of NBS 19 and laboratory calcium carbonate standards, using H_3PO_4 hydrolysis, indicated precision better than 0.1‰ for $^{13}\text{C}/^{12}\text{C}$, and 0.2‰ for $^{18}\text{O}/^{16}\text{O}$, whereas multiple ($n = 10$) determinations of the fossil enamel fragments (LT4 and LT6) gave means for $\delta^{13}\text{C}$ of -7.73 ± 0.15 and $-1.20 \pm 0.06\%$, respectively.

For LA mass spectrometry, the sample tooth or fragment was placed alongside the two enamel standards in a laser chamber, and purged with helium, usually overnight. CO_2 was generated by firing a New Wave MIR 10 CO_2 laser in several bursts, whereafter the gas was cryogenically purified and introduced to the continuous-flow gas chromatography–isotope ratio mass spectrometry system (details are given in SI Text, including data and comparisons in Tables S2 and S3). All data were blank corrected. The two internal enamel standards (LT4 and LT6), gave long-term $\delta^{13}\text{C}$ means of -8.03 ± 0.8 ($n = 45$) and -0.49 ± 1.01 ($n = 53$), respectively. The data for unknowns were calibrated using a regression calculated from the two standards, for each run. All measurements were performed in the University of Bradford (Bradford, UK) Stable Light Isotope Laboratory.

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