Isotopic evidence for the timing of the dietary shift toward C_4 foods in eastern African *Paranthropus*

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New approaches to the study of early hominin diets have refreshed interest in how and when our diets diverged from those of other African apes. A trend toward significant consumption of C_4 foods in hominins after this divergence has emerged as a landmark event in human evolution, with direct evidence provided by stable carbon isotope studies. In this study, we report on detailed carbon isotopic evidence from the hominin fossil record of the Shungura and Usno Formations, Lower Omo Valley, Ethiopia, which elucidates the patterns of C_4 dietary utilization in the robust hominin *Paranthropus*. The results show that the most important shift toward C_4 foods occurred at ∼2.37 Ma, within the temporal range of the earliest known member of the genus, *Paranthropus aethiopicus*, and that this shift was not unique to *Paranthropus* but occurred in all hominins from this fossil sequence. This uptake of C_4 foods by hominins occurred during a period marked by an overall trend toward increased C_4 grazing by cooccurring mammalian taxa from the same sequence. However, the timing and geographic patterns of hominin diets in this region differ from those observed elsewhere in the same basin, where environmental controls on the underlying availability of various food sources were likely quite different. These results highlight the complexities of dietary responses by hominins to changes in the availability of food resources.

hominin diet | carbon isotope | paleodiet | bioapatite

Our understanding of the dietary significance of the peculiar dentognathic and cranial morphological features of the robust hominin genus *Paranthropus* has been revamped in the past decade, with much remaining to be learned. Since initial discoveries more than 50 y ago, distinct morphological similarities of southern African *Paranthropus robustus* and eastern African *Paranthropus boisei* have sustained the notion that the generic dietary inclination of *Paranthropus* was toward diets of hard objects (1, 2). However, new evidence requires a cleft interpretation of the distinctive characters that conjoin these two species, with dental microwear and stable carbon isotope studies now providing direct evidence for significant differences in their diets (3–5). While both microwear and isotope data are consistent with the interpretation of hard-object consumption for *P. robustus* (6, 7), dental microwear revealed no evidence of hard-object consumption for *P. boisei* (5), and stable isotope analysis further suggested a diet of C_4-dominated foods for this eastern African species (3, 4, 8). The combined evidence for *P. boisei* is now most consistent with consumption of large quantities of low-quality forage that may require processing by repetitive loading of the masticatory apparatus. Thus, with both dental microwear and stable isotope data for both *P. robustus* and *P. boisei*, it now appears that either their highly derived masticatory apparatus may not reflect a common adaptation for the consumption of hard foods or that the derived morphology of this genus may have been coopted for the consumption of items that presented novel mechanical challenges such as grasses or sedges. Answering such questions, however, requires that we understand how the diet of *Paranthropus* changed over time, and in particular during the early evolution of the genus. Was the diet of either *P. boisei* or *P. robustus* similar to that of the earliest members of the genus, or did the diets of both diverge from an earlier type of diet?

Key to addressing the pattern and timing of dietary shift(s) in *Paranthropus* is an appreciation of the morphology and dietary habits of the earliest member of the genus, *Paranthropus aethiopicus*, and how those differ from what is observed in later representatives of the genus. Fossils attributed to *P. aethiopicus* are radiometrically constrained between *ca*. 2.7 to 2.3 Ma, with the oldest specimens recovered from the Upper Ndolanya Beds at Laetoli (9, 10). The youngest are held to derive from Shungura Formation Member F according to perceived changes in mandibular premolar morphology, mandibular corpus depth and breadth, and elongation of the molar row from earlier "robust" forms to those characteristic of *P. boisei sensu stricto* (11–14). Radiometric ($^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$) dates constrain the age of *P. boisei* between *ca*. 2.3 and 1.34 Ma, with the oldest definitive specimens deriving from Member G of the Shungura Formation and the youngest known from Bed II of Olduvai Gorge (15, 16). Meanwhile, the estimated age of *P. robustus* from southern Africa is *ca*. 2 to 1 Ma based on biochronological data combined with uranium–lead radiometric ages for speleothems and cosmogenic nuclide dates for clastic sediments in paleokarst caves (17–22).

Phylogenetic analyses of large suites of craniodental characters consistently favor the hypothesis of *Paranthropus* monophyly (e.g., refs. 23–25). The most extensive fossil dataset analyzed

Significance

Reconstructing the dietary adaptations of our earliest ancestors is critical to understanding the evolution of our relationship with our environment. Here, we present carbon isotope data from hominins of the Shungura and Usno Formations, both part of the Pliocene to Pleistocene Omo Group, Ethiopia, a key sequence for the study of hominin evolution in eastern Africa. Our data show that about 2.37 Ma the diet of both robust and gracile hominins shifted profoundly toward consumption of C_4-derived foods (largely grasses and sedges), within the temporal range of an early member of the genus *Paranthropus aethiopicus*. This dietary shift in both groups of hominins occurred during a period marked by similar patterns for coeval herbivore taxa.

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thus far yields a strongly supported majority-rule consensus tree that *P. aethiopicus* is the sister of a clade comprising *P. boisei* + *P. robustus*, while a Bayesian inference analysis of these same character data provides a maximum-credibility majority-rule tree positing a unique sister relationship between *P. aethiopicus* and *P. boisei* (26). The differences between these two sets of analyses have nontrivial implications for the evolutionary history of the genus, but most workers appear to accept an anagenetic (i.e., ancestor–descendant) relationship between *P. aethiopicus* and *P. boisei* in East Africa (1, 11, 14, 27–30). As noted above, studies of teeth and mandibles have suggested a change at *ca*. 2.2 to 2.3 Ma (i.e., within lowermost Member G of the Shungura Formation) from morphologies associated with *P. aethiopicus* to those found in *P. boisei* (11–14).

P. aethiopicus is generally distinct and more primitive than both *P. boisei* and *P. robustus* in possessing an unflexed cranial base, a large postglenoid process, a shallow glenoid fossa, a posteriorly protruding and laterally flaring cerebellum, an extremely prognathic face, a relatively larger canine, and an extensive compound temporal-nuchal crest in males. At the same time, it also displays a number of craniodental features shared with *P. boisei* and *P. robustus* that are likely related to enhanced masticatory capabilities. These features include a sagittal crest suggesting prominent temporalis muscles, the incisor alveoli being constrained by the bicanine line, the anterior projection of the zygomatics relative to the pyriform aperture resulting in midfacial dishing, a greatly thickened palate, extensive overlap of the squamosal suture, high facial hafting, a wide supraglenoid gutter, a large cross-sectional area of the mandibular corpus in the molar region, large premolars and molars, molarized lower premolar roots, and cheek teeth with hyperthick enamel (table S1 in ref. 26). *P. boisei* displays further enlargement of the premolars and molars at the expense of the incisors and especially the canines, a more orthognathic face, a deep glenoid fossa with a barrel-shaped articular eminence, a deeper mandibular symphysis, and more expanded talonids on the premolar (especially P_4) crowns.

The emergence of extensive isotopic datasets of eastern African hominin taxa, largely from the southern Omo-Turkana Basin of Kenya, has revealed a general trend toward increasing utilization of C_4 foods by early hominins, culminating in *P. boisei*'s becoming a C_4 specialist (~80% of C_4 resources; refs. 4, 8, 31). However, despite what is now a large number of samples analyzed, the period between 3 and 2 Ma from the Omo-Turkana Basin remains poorly understood owing to a sedimentary hiatus in much of the southern portion of the basin (32). As a result, temporal patterns of C_4 utilization are poorly characterized for *P. aethiopicus*, early *Homo*, and other taxa that emerged during this crucial interval in human evolution. Fortunately, this interval is well represented in the sediments of the Ethiopian portion of the Omo-Turkana Basin, in fossils deriving from the Shungura and Usno Formations of the Lower Omo Valley (ref. 12; location shown in Fig. 1) and the strata contain a continuous and detailed record of the evolution of early *P. aethiopicus* to later *P. boisei*. Given the sequentially derived masticatory morphologies of both *P. aethiopicus* and *P. boisei*, one might expect to see evidence of dietary change accompanying the appearance of both species, especially around 2.3 to 2.2 Ma where there is a perceived transition from the former to the latter taxon. Similarly, if *P. robustus* evolved from a *P. aethiopicus*-like ancestor, one might hypothesize a dietary shift between them of a magnitude similar to that between *P. aethiopicus* and *P. boisei*. Here, we report data that fill a major gap in the stable isotopic record of these taxa to test the aforementioned hypotheses regarding dietary shift(s) in *Paranthropus* and their potential morphological consequences. We use fresh and extensive fossil hominin stable isotope data from the Shungura and Usno Formations to further our understanding of C_4 food utilization between 3 and 2 Ma which at this point is virtually unknown. As we show below, the time series of hominin stable isotopes from the Shungura and Usno Formations of the Lower Omo Valley records a dramatic change within the temporal range of the genera *Paranthropus* and *Homo*.

A Single Change Point in the Trend toward C_4 Food Consumption in *Paranthropus*

We measured $\delta^{13}C$ values from 86 hominin specimens deriving from Members B to G of the Shungura Formation and equivalent strata of the Usno Formation of the Lower Omo Valley, Ethiopia (stratigraphic units and ages are summarized in Fig. 2 and in ref. 33), filling the critical gap in the record of $\delta^{13}C$ values of hominins from the southern part of the Omo-Turkana Basin (ref. 31 and Fig. 2). For the purpose of characterizing isotopic patterns within and between various taxa, we categorize the hominin dental specimens into two simplified groups that can generally be distinguished by morphological features of isolated and often fractured dental specimens: 1) the robust hominins, exclusively composed of the genus *Paranthropus* and 2) hominins that are not attributable to *Paranthropus* and would thus be attributed to other known taxa such as *Australopithecus, Kenyanthropus*, or *Homo*. The *Paranthropus* lineage in our data includes two species: *P. aethiopicus* (Members C through F; specimens dating to 2.60 to 2.28 Ma) and *P. boisei* (Member G; specimens dating to 2.27 to 2.12 Ma). The other specimens in our dataset include those with features sufficient to enable ascription to *Australopithecus afarensis* (Member B; specimens dating to 3.20 to 3.02 Ma) and *Homo* (Members F through G; specimens dating to 2.31 to 2.02 Ma), as well as indeterminate specimens (Members C through G; specimens dating to 2.83 to 2.22 Ma) that are here recognized as "Hominini indet."

With the detailed time series from *ca*. 3 to 2 Ma provided by the Shungura and Usno Formations, we used change point detection (34) to automatically identify abrupt transitions in the distribution

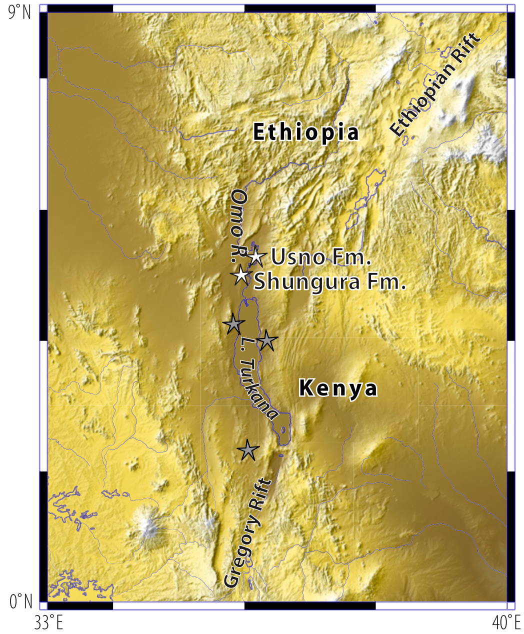

Fig. 1. Map showing location of the fossiliferous Shungura and Usno Formations of the Lower Omo Valley, Ethiopia (white stars), within the Omo-Turkana Basin. The Omo-Turkana Basin is a closed hydrographic and sedimentary basin with water and sediment input predominantly derived from the Omo River. The basin marks the intersection of the Ethiopian Rift with the Gregory Rift within the East African Rift System. Gray stars show other fossiliferous localities of the southern portion of the basin in Kenya discussed in the text. More detailed maps showing the distribution of samples within the outcrop region of the Shungura and Usno Formations are found in *SI Appendix*, Fig. S3.

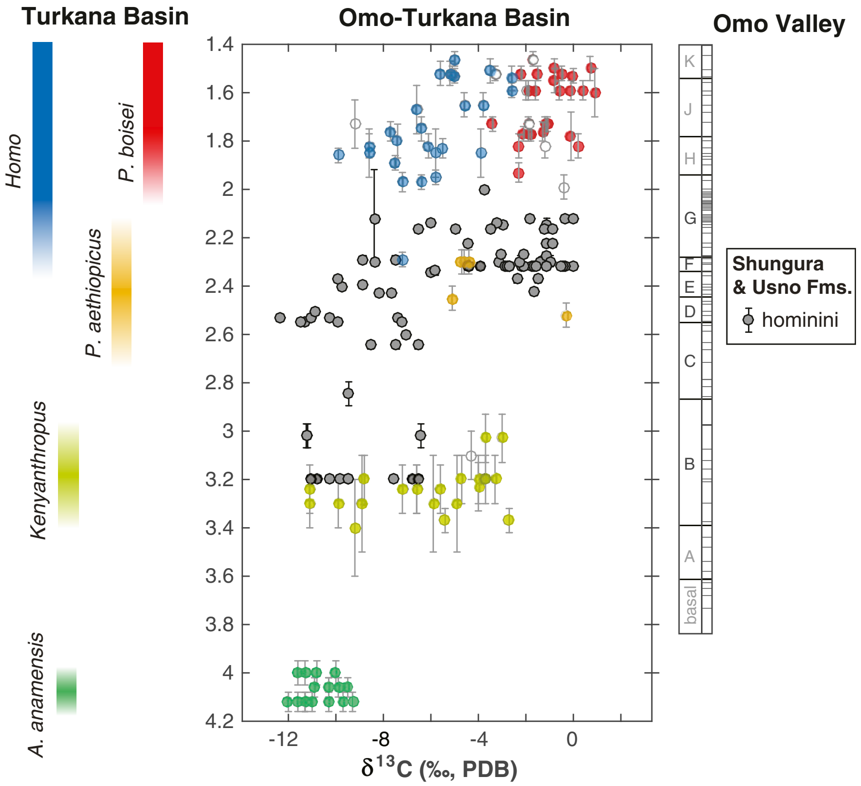

Fig. 2. Temporal trend of hominin $\delta^{13}C$ values from previous data of the southern portion (Turkana Basin) of the Omo-Turkana Basin (ref. 31; symbols coded to species shown at left) with a significant gap filled by $\delta^{13}C$ values of hominins from the *ca.* 3 to 2 Ma interval of the Shungura and Usno Formation in the Omo Valley in the northern portion of the Omo-Turkana Basin (gray points).

of all hominin $\delta^{13}C$ values. This change point detection algorithm separated the time series into two segments divided by a single change point that occurs within submember E3 (*ca.* 2.39 to 2.35 Ma; Figs. 3 and 4). Prior to this change point, the median $\delta^{13}C$ value of all Hominini samples is −9.4‰ (samples from Member B to submember E3), indicating diets predominantly derived from C_3-derived food sources. After 2.37 Ma, the time series shifts abruptly toward values indicating predominantly C_4-derived food sources (median $\delta^{13}C = -2.1$‰; samples from submember E3 to Member G). Thus, this change point demonstrates a rapid and dramatic shift toward increased C_4 food consumption by hominins of the Lower Omo Valley at *ca.* 2.37 Ma.

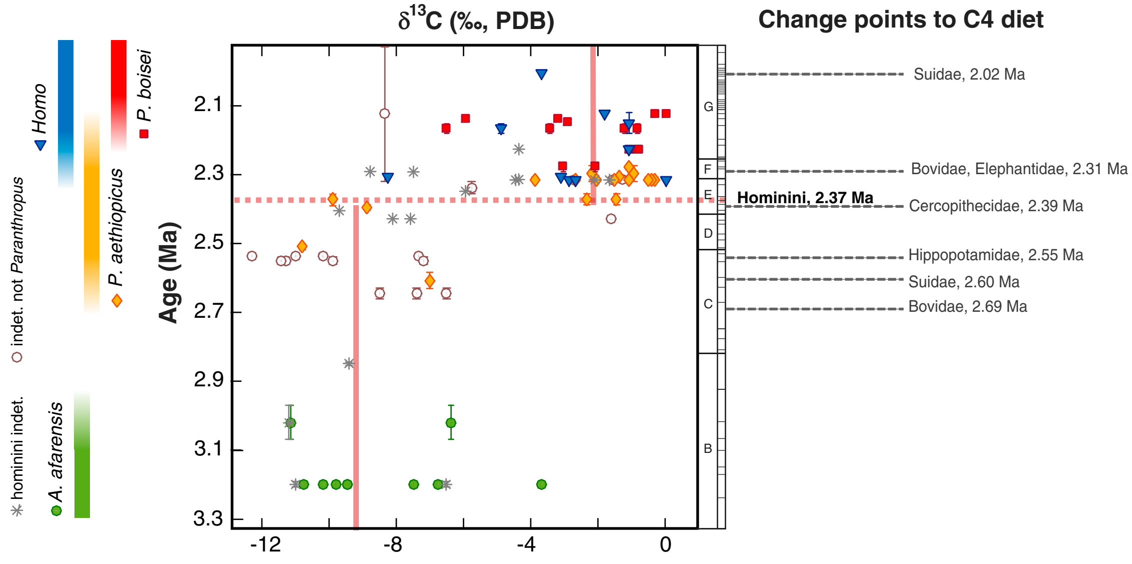

Fig. 3. Detailed view, from Fig. 2, of $\delta^{13}C$ values of hominin samples of the Shungura and Usno Formations of the Omo Valley shown with taxonomic attributions. Red dashed line indicates a change point in all $\delta^{13}C$ values with median values above and below the change point indicated by red solid lines. Similarly determined change points toward increased C_4 food consumption (higher $\delta^{13}C$ values) for other mammalian families (33) are shown along the right axis.

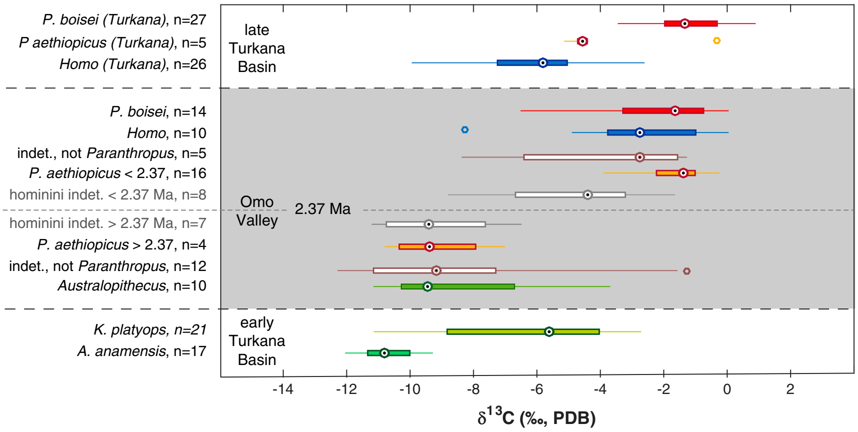

Fig. 4. Box plots of δ^{13}C values of hominin taxa from Fig. 2 separated into specimens above and below the change point of δ^{13}C values of hominins from the Shungura and Usno Formations (2.37 Ma). Also shown are taxa from the southern portion of the Omo-Turkana Basin (Turkana Basin) that straddle the record from the Shungura and Usno Formations (31). Boxes outline the interquartile range, with median value shown by enclosed circle. Whiskers show range exclusive of outliers shown as individual circles; outliers are defined as values greater than 1.5× interquartile range outside the box.

The magnitude of the δ^{13}C shift that accompanies this change point in hominin diets (7.3‰) is approximately equivalent to the largest total difference between any taxonomic category (i.e., the difference between median δ^{13}C values of *A. afarensis* and *P. boisei* = 7.8‰). Moreover, within both the pre-2.37-Ma and the post-2.37-Ma populations there is no taxonomic difference in median δ^{13}C values (Kruskal–Wallis, $P = 0.82$ for pre-2.37-Ma and $P = 0.22$ for post-2.37-Ma taxa exclusive of "Hominini indet."). For example, for samples prior to 2.37 Ma, there is no significant difference between median δ^{13}C values of specimens attributed to *Au. afarensis* (>2.9 Ma; median = −9.5‰, $n = 10$) and those belonging to *P. aethiopicus* (2.9 to 2.37 Ma, median = −9.4‰, $n = 4$; Mann–Whitney U, $P = 0.73$). Likewise, prior to the 2.37 Ma change point, *Au. afarensis* (> 2.9 Ma; median = −9.5‰, $n = 10$) shows indistinguishable δ^{13}C values from the "indet. not *Paranthropus*" group—that is, those specimens that are not attributable to *Paranthropus* but have features consistent with attribution to either *Australopithecus* or early *Homo* (median = −9.1‰, $n = 12$; Mann–Whitney U, $P = 0.60$). Meanwhile, after the 2.37 Ma change point, there is no significant difference between median δ^{13}C values of *Homo* and *Paranthropus* (Mann–Whitney U, $P = 0.22$). This result contrasts with the clear isotopic distinction between *Homo* and *Paranthropus* after 2 Ma that is observed in the data from the southern Omo-Turkana Basin (31). Our findings, therefore, suggest that this dietary shift toward C_4 food occurs simultaneously within both robust and gracile groups in the Lower Omo Valley. The distinction observed between the two groups in the later record of the southern Omo-Turkana Basin could suggest further niche partitioning in which *P. boisei* continues its use of C_4 resources whereas *Homo* becomes more generalist via consumption of C_3-derived carbon from plant or animal resources.

The 2.37-Ma dietary change point in carbon isotopic composition (δ^{13}C values) is marked by a comparatively small change in δ^{18}O values (*SI Appendix*, Fig. S1). In addition, while there are no significant differences in δ^{18}O values between hominin taxa identified to at least the genus level (*SI Appendix*, Table S2; Kruskal–Wallis, $P = 0.32$), there is a significant difference in pre- and post-2.37-Ma δ^{18}O values of the Hominini as a whole (Mann–Whitney U, $P < 0.0001$), suggesting that the dietary change in carbon sources is accompanied by other changes that affect δ^{18}O values of tooth enamel, which include diet, physiology, drinking water source, and climate, among others (35, 36).

C_3–C_4 Dietary Change Is Independent of Functional Morphology

One of the most remarkable aspects of the rapid shift toward C_4 food consumption in the Omo Valley hominins is that the change occurs among samples of the same species, *P. aethiopicus*, where those prior to the 2.37-Ma change point show a median δ^{13}C value of −9.4‰, contrasting with later samples that have a median δ^{13}C value of −2.11.4‰. Given the derived masticatory morphology of both *P. boisei* and *P. aethiopicus*, it would have been reasonable to hypothesize a stepwise dietary change toward C_4 diets for both species originations. Indeed, isotopic data from *Paranthropus* of the southern Omo-Turkana Basin were consistent with such a hypothesis (31), showing a stepwise increase in δ^{13}C values. However, with the more detailed and larger sample from the Lower Omo Valley, earliest *P. aethiopicus* shows very little evidence of consumption of C_4 foods, with the major change point occurring well after the emergence of *P. aethiopicus* but prior to the accepted emergence of *P. boisei*. Thus, although features of an enhanced masticatory apparatus evinced by *P. aethiopicus* are already in place by *ca.* 2.7 Ma (i.e., within Member C of the Shungura Formation), these features considerably antedate the marked increase in the degree of C_4 food consumption at 2.37 Ma within the *Paranthropus* lineage. The shift toward C_4 foods seems to coincide only with the appearance of minor refinements in craniodental morphologies that potentially portend an enhancement, rather than fundamental change, in trophic capabilities. Thus, the shift toward a C_4-dominated diet within *P. aethiopicus* from the Shungura Formation shows a significant delay compared to the evolution of the defining morphological features of the species. Once a C_4-dominated diet is in place within late *P. aethiopicus* there is no evidence for significant change in C_4 food consumption through the later temporal range of *P. boisei* that would accompany the "refinements" in canine reduction, orthognathism, and the features noted above (ref. 26 and *SI Appendix*, Table S1).

The 2.37 Ma change point that defines the robust australopiths' shift toward C_4 consumption also occurs simultaneously within the *Australopithecus, Homo* and "indet. not *Paranthropus*" group, which prior to the 2.37 Ma change point show median δ^{13}C values of −9.4‰ ($n = 22$), while after 2.37 Ma gracile forms (*Homo* and the "indet. not *Paranthropus*" group) show median δ^{13}C values of −2.7‰ ($n = 15$). Dentognathic morphological changes observed within this group are not accompanied by any significant change in median δ^{13}C values. Thus, neither of the synchronous dietary transitions of robust or gracile hominins are marked by other significant changes in dental anatomy that might otherwise signal such a dietary change, although such an absence of evidence might be an artifact of the incomplete nature of the largely isolated and fragmentary dental specimens available. While we argue that the significant change point toward C_4 consumption does not coincide with the species transition from *P. aethiopicus* to *P. boisei* at *ca*. 2.30 Ma, we recognize that the attribution of the sampled dental specimens to either one of these taxa, and especially to *P. aethiopicus*, is, of course, critical to interpreting our results. The basis for the taxonomic attributions used in this study, and their potential effect on our conclusions is further explored in *SI Appendix*, including *SI Appendix*, Fig. S2 and Table S1.

P. robustus Does Not Show the *P. boisei* Signature

Previous work has shown that *P. boisei* from the Turkana Basin in Kenya had much higher $\delta^{13}C$ values (median = −1.2‰) than did *P. robustus* (median = −7.4‰) from southern Africa. This pattern is replicated in specimens analyzed here, as *P. boisei* from the Shungura Formation has $\delta^{13}C$ values nearly 6‰ higher than those of its southern African congener. Moreover, *P. aethiopicus* also has much higher $\delta^{13}C$ values (median = −2.1‰) than *P. robustus*, although this difference is driven entirely by specimens postdating 2.37 Ma. Given the strongly similar and highly derived dentognathic morphologies of *P. robustus* and *P. boisei*, these differences are nonintuitive, but they gain support from the similarly surprising differences in the dental microwear of these taxa (5). What could be driving the greater consumption of ^{13}C-enriched foods (C_4 grasses and/or crassulacean acid metabolism plants) in eastern African *Paranthropus*? One possibility is that *P. robustus* was derived from an early population of *P. aethiopicus* (pre-2.37-Ma change point) and maintained the preference for C_3 resources of its ancestor. Another possibility is that these divergent diets are driven by environment. At first blush, this seems unlikely given that the environmental record of the Omo Valley is notable for the persistence of relatively abundant C_3 vegetation (37), while *P. robustus* is associated with abundant fauna from open environments (38, 39). Thus, one might expect the opposite pattern, more C_3 consumption by *Paranthropus* in the Omo Valley and more C_4 consumption in the ancient Sterkfontein Valley. A focus on tree cover, however, seems problematic given that the Omo hominins after 2.37 Ma, including *Homo*, appear to have focused on C_4 vegetation just as much as the southern Omo-Turkana Basin hominins despite the latter's occupying landscapes with more abundant C_4 plants (37). One possible key to this conundrum is that the dietary differences between *P. boisei* and *P. robustus* were driven primarily by the nutritional content of grasses, which is often much higher in eastern Africa due to nutrient-rich volcanic soils and a bimodal rainfall pattern (40). The grasses in the Sterkfontein Valley, in contrast, which grow in predominantly dolomitic soils and experience unimodal rainfall, are of much lower quality, especially during the dry season, and may have only been worth consuming during brief periods (40).

Niche Differentiation between Coeval Hominin Taxa

Despite the overall similarity in dietary patterns of cooccurring robust and gracile hominins within the Omo Valley, the combined dataset highlights significant geographic differences between coeval taxa from different regions of the Omo-Turkana Basin. For example, samples of coeval gracile australopiths, *Au. afarensis* and *Kenyanthropus platyops*, from the Omo and Turkana portions respectively, have significantly different median $\delta^{13}C$ values prior to 2.8 Ma (−9.4 and −5.6‰ respectively, Mann–Whitney U = 0.026), despite their similar ranges of $\delta^{13}C$ values (−11.1 to 3.7‰ and −11.1 to −2.7‰, respectively). Such differences between samples from different geographic regions within the same sedimentary basin may reflect underlying differences in the local habitats. The geographical patterns of depositional environments sets the stage for these ecological patterns, highlighting that the northern part of the basin is characterized by a perennial axial fluvial system, the paleo-Omo River, which would support persistently wooded conditions of gallery forests flanking the river (41). Meanwhile, the generally more open conditions of the southern part of the basin, lacking the forest refugium provided by the proto-Omo River, are characterized by more open adapted fauna and both earlier and more stepwise transitions to C_4-food consumption. A somewhat anomalous trend with respect to this paleogeographic pattern is observed within early *Homo*; diets of relatively older *Homo* from the Omo Valley (*ca*. 2.3 to 2.1 Ma) have already taken up the C_4-dominated diet, while the later *Homo* from the southern Turkana Basin (<*ca*. 2 Ma) show characteristically less C_4 food consumption. This new and detailed direct evidence of hominin diets lays the groundwork for further exploration of niche partitioning of hominins within the overall mammalian fauna. Paleobiogeographic patterns from the Shungura fauna show that *Homo* is associated with closed woodland species while *Paranthropus* often occurs with taxa representative of more open habitats (42). While our stable isotope data support the notion of more open environments for *Paranthropus*, the association of *Homo* with more closed woodland settings for *Homo* is not supported by the data. Although the faunal associations would have predicted results similar to what is observed in the southern Omo-Turkana Basin, the stable isotope data suggest that all hominins in the Omo Valley shifted toward C_4 foods at the same time. These patterns highlight the complexity of distinctive and specific behavioral patterns that may vary with habitat availability within a single sedimentary basin but are underpinned by larger-scale regional and temporal trends toward increasing abundance of C_4-supported ecosystems (31, 37, 43).

Comparison with Change Points toward C_4 Diets in Other Mammalian Taxa and Other Regions

While the hominin $\delta^{13}C$ record from the Shungura and Usno Formations shows a single abrupt shift toward C_4 foods at 2.37 Ma, the equivalent record from the southern Omo-Turkana Basin (31) shows two change points at ∼4 to 3.4 Ma and at some point prior to 1.8 Ma. However, these shifts are less-well-resolved because of temporal lacunae in the sedimentary and fossil record during which changes in the $\delta^{13}C$ record occurred. With the present combined record of the complete Omo-Turkana Basin, the change points from the southern Omo-Turkana Basin largely define the transitions between hominin species such as *Australopithecus anamensis*, *Kenyanthropus*, and *Paranthropus*, while the single change point from the Omo Valley occurs distinctly within the temporal range of *P. aethiopicus.* For example, the early change point of hominin $\delta^{13}C$ values in the southern Omo-Turkana Basin occurs across a gap in the fossil record that separates two taxa of gracile australopiths with distinct dental morphological features: *Au. anamensis* and *Kenyanthropus*. Similarly, the later change point of $\delta^{13}C$ values coincides roughly with the transition from early *Homo* to later *Homo erectus* and falls between the transition from *P. aethiopicus* to *P. boisei* in this part of the basin. The apparent correspondence of the timing of these two change points with morphological changes contrasts with our observations that the change point in $\delta^{13}C$ from the Omo Valley hominins occurs within the *P. aethiopicus* lineage. The 2.37-Ma change point observed in the Omo Valley hominin record also occurs after what may be a transition from late *Australopithecus* to early *Homo*, characterized by specimens that cannot at present be assigned to one genus or the other based on tooth morphology alone.

The distinct $\delta^{13}C$ change point in the time series of the Omo Valley hominins (2.37 Ma) is also asynchronous with the timing of change points toward higher $\delta^{13}C$ values of teeth from families of other large mammals, with the exception of cercopithecids, which shifted toward C_4 diets at nearly the same time (2.39 Ma; ref. 33). Bovids, suids, and hippopotamids show various change points in $\delta^{13}C$ values toward C_4 diets that range from 2.69 to 2.55 Ma. Bovids and suids show additional change points toward C_4

diets at 2.31 to 2.02 Ma, respectively, while elephantids show a single change point at 2.31 Ma. Thus, multiple mammalian families increased C_4 food consumption at different time periods during the interval from 2.69 to 2.02 Ma. Previous work on the paleoecology of the Omo Valley mammalian faunas has suggested major events in the overall trend of ecological and environmental change occurred largely within Member C (*ca*. 2.8 Ma; refs. 44, 45) and again through Members D, E and F (*ca*. 2.5 to 2.3 Ma; ref. 44) and in Member G (*ca*. 2.3 Ma; ref. 46). Although the shift toward C_4 diets by Omo Valley hominins within Member E does not map directly on to any generalizable specific pattern of ecological change that characterizes the terrestrial vertebrate fauna during the period from 2.8 to 2.3 Ma, this singular shift in hominin diets does occur during a more extended period characterized by changing mammalian communities of predominantly C_4-grazing adapted taxa. One could conclude from what is now abundant isotopic data for early hominins and coeval mammalian faunas that specific dietary changes observed for individual taxa, such as the hominins, reflect behavioral changes that do not respond in a uniform or systematic way to any underlying ecological changes in the availability of resources.

Methods

Samples were selected from the Omo fossil database of the International Omo Research Expedition, housed in the National Museum of Ethiopia in Addis Ababa. Specimens sampled for stable isotopes were examined by F.E.G. and Z.A. and identified to the finest taxonomic category possible for isolated dental material. In some cases, a generic attribution could not be made; for these specimens identification is noted simply as "Hominini indet." However, many of these "indet." specimens from the interval from ~2.8 to 2.2 Ma had features clearly lacking attribution to *Paranthropus* and are thus identified as "indet. not *Paranthropus*" in order to differentiate cooccurring lineages of this interval. Age ranges of samples were determined using the assignment of each specimen to submember-level stratigraphy in the catalogs. The stratigraphic heights of these submembers (47) were fit to a height-age model using chronostratigraphic markers (48); see ref. 33 for detailed methodology.

Samples were extracted with caution from fractured surfaces to avoid damage to exterior surfaces, as in the methods described in ref. 49. Approximately 2 to 10 mg of powdered enamel was removed by abrasion with a diamond-tipped drilling bit in a Dremel rotary tool. The extracted powdered enamel sample was treated in 3% H_2O_2 (hydrogen peroxide) for 30 min and rinsed thoroughly with deionized water. This pretreated powder was reacted with 103% phosphoric acid (a solution of excess P_2O_5 in H_3PO_4, with a specific gravity of 1.93) at 25 °C for 24 h to produce CO_2 for isotopic analysis on a Thermo Fisher Scientific (Finnigan) Delta V isotope ratio mass spectrometer. Results are reported using per mil (‰) notation,

$$\delta(^{13}C^{18}O) = [R_{sample}/R_{standard} - 1]*10^3,$$

where R_{sample} is the ratio of heavy to light isotope ($^{13}C/^{12}C$ or $^{18}O/^{16}O$) of the sample and $R_{standard}$ is the same ratio for a reference standard; in this case values are both reported on the Vienna Pee Dee Belemnite standard (VPDB) scale. Statistical calculations and change point analysis were done with MATLAB using standard packages and the CPRBayes algorithm (50).

Data Availability. All study data are included in the paper and *SI Appendix*.

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