



Dietary trends in herbivores from the Shungura Formation, southwestern Ethiopia

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Diet provides critical information about the ecology and environment of herbivores. Hence, understanding the dietary strategies of fossil herbivores and the associated temporal changes is one aspect of inferring paleoenvironmental conditions. Here, we present carbon isotope data from more than 1,050 fossil teeth that record the dietary patterns of nine herbivore families in the late Pliocene and early Pleistocene (3.6 to 1.05 Ma) from the Shungura Formation, a hominin-bearing site in southwestern Ethiopia. An increasing trend toward C₄ herbivory has been observed with attendant reductions in the proportions of browsers and mixed feeders through time. A high proportion of mixed feeders has been observed prior to 2.9 Ma followed by a decrease in the proportion of mixed feeders and an increase in grazers between 2.7 and 1.9 Ma, and a further increase in the proportion of grazers after 1.9 Ma. The collective herbivore fauna shows two major change points in carbon isotope values at ~2.7 and ~2.0 Ma. While hominin fossils from the sequence older than 2.7 Ma are attributed to *Australopithecus*, the shift at ~2.7 Ma indicating the expansion of C₄ grasses on the landscape was concurrent with the first appearance of *Paranthropus*. The link between the increased C₄ herbivory and more open landscapes suggests that *Australopithecus* lived in more wooded landscapes compared to later hominins such as *Paranthropus* and *Homo*, and has implications for key morphological and behavioral adaptations in our lineage.

stable isotopes | herbivores | fauna | tooth enamel | Shungura Formation

Environmental change in the Pliocene and Pleistocene is among the key drivers thought to have shaped the course of human evolution (1–3). Well-dated hominin-bearing sites that span this critical time period offer a unique opportunity to investigate the tempo and patterns of paleoenvironmental shifts. This, in turn, allows us to test hypotheses about the links between environmental change and morphological and behavioral adaptations in the hominin clade (4–6). The Shungura Formation in the lower Omo Valley of southwestern Ethiopia is a key site spanning the time from ~3.6 to ~1 Ma, which possesses an exceptionally rich record of fossil vertebrates including hominins. The formation consists of a stratigraphic sequence with a composite thickness of >760 m divided into 12 members (i.e., Basal, A, B, C, D, E, F, G, H, J, K and L). Each member is underlain by a volcanic tuff layer that allows accurate radiometric age attribution for the corresponding member (7, 8). Over 50,000 fossil specimens belonging to more than 14 mammalian families were recovered in the 1960s and 1970s by the International Omo Research Expedition, and field work has recently been resumed by the Omo Group Research Expedition (9, 10).

The hominin taxa from the Shungura Formation include *Australopithecus* sp., *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Homo* sp. (11, 12). The hominin fossil record is thus unique as it spans the time period between 3.0 and 2.0 Ma that coincides with the earliest records of *Homo* and *Paranthropus* (13, 14). As such, this sedimentary sequence provides the unique opportunity to test the role of the environment in the origin and

evolution of our genus. The sedimentological record indicates that the lower Omo Valley from Member A (3.6 Ma) through the middle of Member G (2.1 Ma) was dominated by a large meandering river (15). This was followed by a shift to lacustrine conditions in middle and upper Member G (2.1 to 1.9 Ma), and a return to fluvial conditions in Members H through L (1.9 to 1.0 Ma) (16). Paleosols in the lower part of the Shungura sequence (Members A and B) indicate relatively high precipitation and a warm climate, with a shift to more sporadic precipitation and a generally drier climate in Member C and above (17). Stable isotopes from pedogenic carbonates suggest that Members B through G were dominated by extensive woodlands, with a shift to wooded grasslands above Member G, i.e., after 2 Ma (18). The evidence of paleobotanical remains (fossil wood, fruits, and pollen) (19–21) and micromammals (22, 23) corroborates that Members A and B had more extensive woodlands and forests than later members, and that environmental conditions became more open above Member G, after 2 Ma. Previous analyses of large mammals reinforce these interpretations, with shifts in taxonomic abundances at about 2.9 Ma, and higher proportions of grazing species first around 2.5 to 2.4 Ma (24, 25), then at the base of Member G at 2.3 Ma (25, 26), and more markedly after 2 Ma (27). Even though these environmental changes are well documented in the Shungura Formation from 3.6 to 2 Ma, it has been suggested that the Omo remained more wooded than other parts of the Omo-Turkana Basin (West Turkana, East Turkana)

Significance

Studying the diet of fossil herbivores is a critical aspect of understanding past ecology. Here, we present carbon isotope data from the collective herbivore fauna in the Shungura Formation, Ethiopia, a key sequence for the study of mammalian evolution in eastern Africa. We document temporal patterns in the diet of nine mammalian herbivore families in the late Pliocene and early Pleistocene. The diet of herbivores has significantly changed in the last 3.5 Ma, and major dietary transitions are observed in several taxa around ~2.7 Ma and then at ~2.0 Ma. These patterns reflect response of the fauna to major ecological and environmental changes and provide a comparative framework for the study of hominin diet during this time.

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The authors declare no competing interest.

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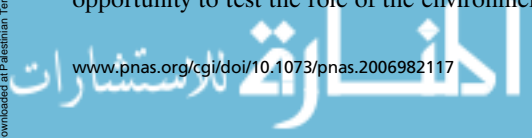
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and provided a partial refugium for woodland species (e.g., Tragelaphini) (18, 28, 29).

Here we use stable isotope data from herbivore tooth enamel to characterize the diet of large mammals from the Shungura Formation. The use of stable isotopes is predicated upon our understanding of carbon isotope fractionation during photosynthesis in C₃ plants (i.e., trees, shrubs, herbs, and temperate and high-altitude grasses) and C₄ plants (mainly tropical grasses and sedges) (30–32). As plants are the primary source of carbon for herbivores, the distinct isotopic signature of foods consumed is recorded in body tissues (e.g., bones and teeth) with a relatively consistent fractionation factor. Thus, the carbon isotopic values of tooth enamel reflect the diet of herbivores and can be used to infer the vegetation available on the landscape (33–35). Although isotopic data have been reported for a few taxonomic groups from the Shungura Formation (25, 36, 37), a detailed isotopic record of the broader large herbivore fauna is currently lacking. Here, we present dietary trends in nine mammalian families using >1,050 fossil specimens from the Shungura Formation and provide a fresh perspective on the ecological context of hominins in the late Pliocene and early Pleistocene.

Results

In this section we report on analyses of carbon isotope values from each mammalian family binned at the stratigraphic level of members (Fig. 1 and Dataset S1). Mammalian families are presented in the order of their abundance (i.e., from the most to the least abundant in terms of number of identified specimens) with median $\delta^{13}\text{C}$ values and ranges provided for each taxon. It should be noted that, overall, the relative abundance of browsers decreases through time as noted in previous work (24–26).

Bovidae. The bovids analyzed comprise 414 specimens belonging to five tribes: Reduncini, Tragelaphini, Aepycerotini, Alcelaphini, and Bovini. Collectively, the bovids show a trend toward increasing C₄ resource consumption through time, with statistically significant differences in $\delta^{13}\text{C}$ values between some members. While the transition from Member A to B shows a shift from C₃ and mixed C₃–C₄ diets to a broader dietary spectrum of C₃, mixed C₃–C₄, and C₄ diets (Wilcoxon rank-sum test, $P = 0.02$), a shift toward higher $\delta^{13}\text{C}$ values and more C₄-dominated diets was observed between Members B and C (t test, $P < 0.01$).

Reduncini. Samples from Reduncini have a median $\delta^{13}\text{C}$ value of -0.7‰ , with values ranging from -13.4 to $+2.6\text{‰}$ (although the minimum values are driven by two outliers) ($n = 90$). The data indicate that reduncins had a predominantly mixed C₃–C₄ diet during the earlier members of the formation (i.e., Member B) and shifted to a C₄-dominated diet during later periods.

Aepycerotini. Samples of Aepycerotini have a median $\delta^{13}\text{C}$ value of -2.2‰ , with values ranging from -9.2 to $+2.5\text{‰}$ ($n = 96$). The overall dietary pattern for *Aepyceros* indicates a mixed C₃–C₄ diet in the earlier members (Members A and B) followed by a shift to a C₄-dominated diet in Members C through F, and a slight change back to a diet dominated by mixed C₃–C₄ resources in the upper Members G through L.

Tragelaphini. The median $\delta^{13}\text{C}$ value for tragelaphin bovids ($n = 104$) is -5.2‰ with $\delta^{13}\text{C}$ values ranging from -11.6 to $+3.0\text{‰}$. This indicates a diet dominated by mixed C₃–C₄ resources.

Alcelaphini. Samples from alcelaphin bovids ($n = 67$) have a median $\delta^{13}\text{C}$ value of $+1.0\text{‰}$ with values ranging from -6.9 to $+3.9\text{‰}$, indicating a relatively consistent C₄ diet. A shift toward higher $\delta^{13}\text{C}$ values within the C₄ diet category was observed between Members B and C (Wilcoxon rank sum test, $P < 0.01$).

Bovini. The median $\delta^{13}\text{C}$ value of bovin specimens ($n = 57$) is $+0.6\text{‰}$ with values ranging from -10.6 to $+4.4\text{‰}$. Except for Member A, in which values indicative of a mixed C₃–C₄ diet are displayed, the dietary pattern throughout the remainder of the sequence is a relatively consistent C₄-dominated diet.

Hippopotamidae. A mixed C₃–C₄ diet and a higher percentage of C₄ resources at times was observed in hippopotamids ($n = 81$), with an overall median value of -3.3‰ with minimum and maximum values of -8.7 and $+1.1\text{‰}$, respectively.

Cercopithecidae. This sample comprises 73 specimens identified as the genus *Theropithecus*. The overall median $\delta^{13}\text{C}$ value for *Theropithecus* is -2.9‰ with a -9.2 to $+0.4\text{‰}$ range. These data indicate a diet dominated by mixed C₃–C₄ and C₄ resources. A statistically significant difference (Wilcoxon rank-sum test, $P = 0.01$) in $\delta^{13}\text{C}$ values was observed between Members B and C with the latter having higher $\delta^{13}\text{C}$ values.

Suidae. This family ($n = 258$) comprises four genera: *Nyanzachoerus*, *Kolpochoerus*, *Notochoerus*, and *Metridiochoerus*. An overall increase in C₄ resource consumption with time was observed with significant shifts between some members. Among suids in general, the transition from Member B to C was accompanied by a notable change from a mixed C₃–C₄ and a C₄-dominated diet to a predominantly C₄ diet (Wilcoxon rank-sum test, $P < 0.01$), and the change from Member G to Member H also shows a shift toward higher $\delta^{13}\text{C}$ values within the C₄ diet category (Wilcoxon rank-sum test, $P < 0.01$).

Nyanzachoerus. Known from a small sample size ($n = 12$) in the lower members only, *Nyanzachoerus* has an overall median $\delta^{13}\text{C}$ value of -3.6‰ , indicating a diet of mixed C₃–C₄ resources.

Notochoerus. Specimens of *Notochoerus* ($n = 87$) have an overall median $\delta^{13}\text{C}$ value of -1.2‰ with a range between -7 and $+0.3\text{‰}$. Apart from some samples in Members A and B that show a mixed C₃–C₄ diet, the $\delta^{13}\text{C}$ results indicate that *Notochoerus* had a diet dominated by C₄ resources. A shift toward higher $\delta^{13}\text{C}$ values within the C₄ diet category was observed between Members G and H (Wilcoxon rank-sum test, $P = 0.01$).

Metridiochoerus. The median $\delta^{13}\text{C}$ value for *Metridiochoerus* ($n = 78$) is -0.9‰ with a range between -8.1 and $+1.6\text{‰}$. Throughout the formation, *Metridiochoerus* maintained a relatively consistent C₄-dominated diet, with the transition from Member G to H marked by a significant shift (Wilcoxon rank-sum test, $P = 0.01$) toward higher $\delta^{13}\text{C}$ values.

Kolpochoerus. The median $\delta^{13}\text{C}$ value for samples from *Kolpochoerus* throughout the Shungura Formation ($n = 81$) is -0.8‰ , with values ranging from -8.9 to $+0.9\text{‰}$. It appears that initially (i.e., Members A and B) *Kolpochoerus* was a mixed feeder but there was a later shift (with a statistically significant difference between Members B and C, Wilcoxon rank-sum test, $P < 0.01$) to a C₄-dominated diet in the upper members. Similarly, the transition from Member G to H was marked by a significant shift (Wilcoxon rank-sum test, $P = 0.01$) toward higher $\delta^{13}\text{C}$ values.

Elephantidae. The overall median $\delta^{13}\text{C}$ value of samples of elephants ($n = 86$) is -1.8‰ with values ranging from -12.4 to $+0.8\text{‰}$. A mixed C₃–C₄-dominated diet was observed in the lower members of the formation (i.e., Members A to E) that changed to predominantly C₄ resource consumption in the upper members (Members F through L). Across the members, a statistically significant shift to a higher incorporation of C₄ resources was observed between Members B and C (Wilcoxon rank-sum test, $P = 0.02$).

Giraffidae. A consistently C₃ (browse)-dominated diet was observed in the giraffes throughout the sequence. The sample has a median $\delta^{13}\text{C}$ value of -12.4‰ and a narrow range between -14.9 and -10.4‰ ($n = 23$).

Equidae. Except for the mixed C₃–C₄ diet observed in some individual samples in Member B (which is significantly different

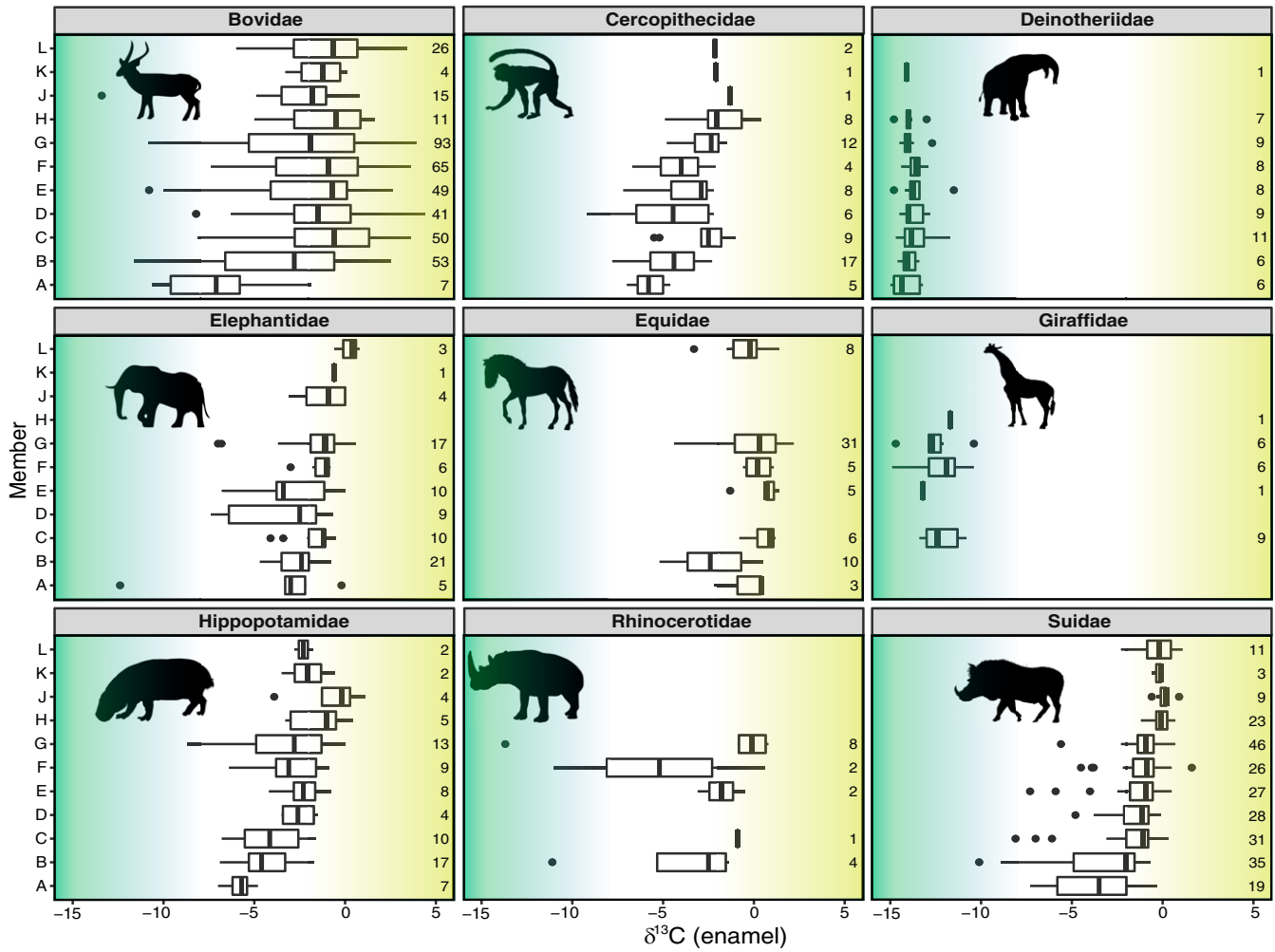


Fig. 1. Box and whisker plots of $\delta^{13}\text{C}$ values for the fossil tooth enamel data from Shungura Formation across nine mammalian families. Median values are marked by a vertical line within the box, the edges of the boxes represent the lower and upper quartile values, the whiskers extend from the edge of the box to the largest and smallest value no farther than $1.5 \times$ interquartile range, and outliers are plotted as black dots. Green, white, and yellow shades indicate C_3 browsers, $\text{C}_3\text{-C}_4$ mixed feeders, and C_4 grazers, respectively.

from Member C, Wilcoxon rank-sum test, $P < 0.01$), the equids show a consistent C_4 diet with a median value of $+0.1\text{‰}$ and values ranging from -5.2 to $+2.2\text{‰}$ ($n = 68$).

Deinotheriidae. Throughout the formation, the deinotheres were consistent C_3 browsers, showing no change in their diet with a median $\delta^{13}\text{C}$ value of -14.0‰ and a range between -15.7

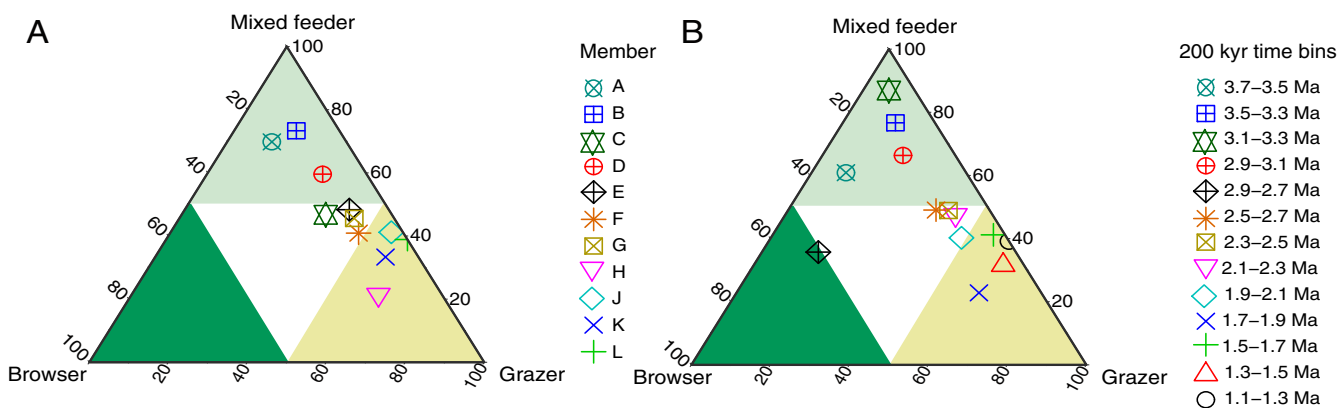


Fig. 2. Ternary diagram showing proportions of C_3 browsers, $\text{C}_3\text{-C}_4$ mixed feeders, and C_4 grazers at the member level (A) and for 200 kyr time bins (B). Each point in the figure represents the respective proportions in the specified time units. Triangle represents regions where $>50\%$ of the taxa are browsers, mixed feeders, or grazers in each category. Browser, mixed feeder, and grazer categories are adopted from ref. 39.



and -11.5‰ ($n = 65$). This is a narrow range compared to other taxa.

Rhinocerotidae. The 17 specimens assigned to the genus *Ceratotherium* show an overall median $\delta^{13}\text{C}$ value of -0.9‰ with values ranging from -13.7 to $+0.8\text{‰}$. Although there are specimens that indicate a mixed $\text{C}_3\text{-C}_4$ diet in some members (and a few outliers showing a C_3 -dominated diet), the genus overall has a clear C_4 diet. Moreover, it may also be that the few outliers belong to *Diceros* (a C_3 browser), misidentified as *Ceratotherium*, as the distinction between the two genera is considered problematic based solely on fragmentary dental remains (38).

Discussion

Herbivore Diet in the Pliocene and Pleistocene. In general, based on the grazer–mixed feeder–browser ternary classification (39–41) at the member level (Fig. 2A), three major periods are evident with differing ecological groupings: 1) herbivore fauna dominated by mixed feeders occurs in Members A, B, and D; 2) faunas with abundant mixed feeders and grazers in Members C, E, F, and G; and 3) grazer-dominated faunas in Members H, J, K, and L. The first and second groups also have statistically significant differences in $\delta^{13}\text{C}$ values between Members B and C, which is evident in multiple lineages (i.e., bovids, suids, cercopithecids, elephantids, and equids) that show an increase in C_4 food intake.

Because member-level stratigraphic units of the Shungura Formation do not represent equivalent temporal durations, this analysis of the grazer–mixed feeder–browser ternary diet classification was also calculated for 200 kyr time bins (Fig. 2B). Similarly, these finer timescale temporal bins show a high proportion of mixed feeders prior to ~ 2.9 Ma, a decrease in the proportion of mixed feeders and an increase in grazers from ~ 2.7 to 1.9 Ma followed by a high proportion of grazers after 1.9 Ma. The outlying high proportion of browsers from 2.9 to 2.7 Ma likely results from the small sample size in this time period with relatively abundant deinotheres and giraffes. This supports the argument that the faunal composition changed after 2.9 Ma and again after 1.9 Ma, based on the member-level analysis. Similar patterns have been reported from the Turkana Basin where $\text{C}_3\text{-C}_4$ mixed-feeder herbivores dominated the ecosystem prior to 2.5 Ma, to be replaced by dominantly grazing taxa after 2.5 Ma

(39). Despite these similarities, there are slight differences in the timing of shifts toward grazing-dominated fauna at the expense of mixed feeders, which occurs later (i.e., after 1.9 Ma) in the Shungura Formation compared to after 2.3 Ma in the southern portion of the Omo-Turkana Basin. This indicates the consistent presence of C_3 resources and further supports previous notions that the paleo Omo River provided broad gallery forests that served as a refugium for C_3 -browsing fauna under relatively stable hydrological conditions in an otherwise increasingly seasonal and arid basin (42, 43).

Temporal Patterns in the Diet of Herbivores. We used a nonparametric change-point analysis to detect distributional changes in the $\delta^{13}\text{C}$ values in the Shungura mammalian fauna. First, the analysis was conducted using the complete faunal isotopic dataset including the nine mammalian families (Fig. 3) and then replicated for each family that shows a significant change in distribution (Fig. 4). Considering the herbivore fauna as a whole, there are two major change points, first at ~ 2.7 Ma and then at ~ 2.0 Ma. The first change point occurs in lower Member C (C-4), where the $\delta^{13}\text{C}$ values change to a mixed $\text{C}_3\text{-C}_4$ - and C_4 -dominated distribution. The second change point occurs at upper Member G (G-28), where there is a change to a C_4 -dominated distribution. These change points are more or less congruent with the patterns portrayed by the ternary diagrams shown in Fig. 2. Assessing the mammalian families individually, five taxa show significant changes in the distribution of $\delta^{13}\text{C}$ values. The bovids show two major change points at ~ 2.7 and ~ 2.3 Ma. The first change point occurs at the same time as the ~ 2.7 -Ma change observed for the composite fauna (Member C unit 4). Even though significant differences are observed between the bovids in Members B (~ 3.4 to 2.8 Ma) and C (~ 2.8 to 2.5 Ma) (Fig. 1), this analysis indicates that a change in distribution occurred within Member C. Closer examination of the faunal composition between 2.8 and 2.7 Ma indicates a very small sample size for bovids during this time, which might have resulted in this later change point. The second change point occurs at ~ 2.3 Ma (at the base of Member F). These results are consistent with previous studies that reported changes in the abundance, species composition, morphology, and diet in the bovids at these two time periods (24–26, 36). The suids also show two major change points at ~ 2.6 and ~ 2.0 Ma. Similar to the bovids, despite the significant difference between Members

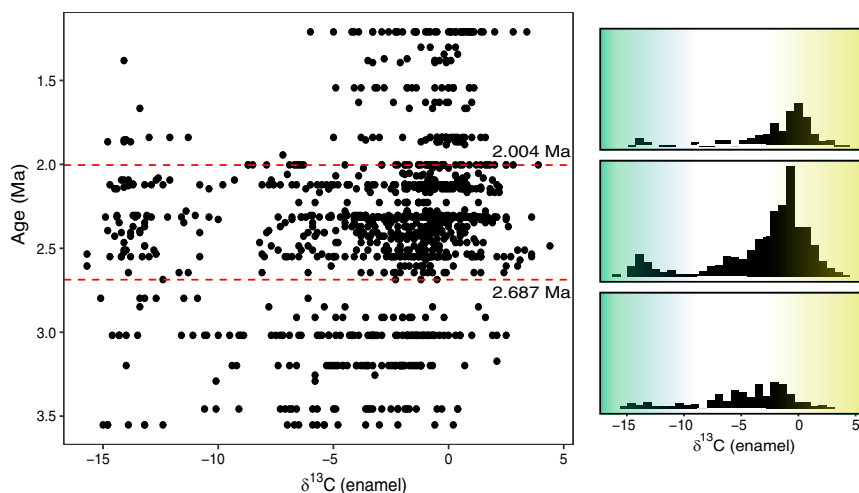


Fig. 3. Significant change points in the distribution of $\delta^{13}\text{C}$ values across herbivore mammalian lineages in the Shungura Formation (shown as red dashed line). The histograms (Right) show distribution of $\delta^{13}\text{C}$ values in each category before and after the major change points. Green, white, and yellow shades indicate C_3 browsers, $\text{C}_3\text{-C}_4$ mixed feeders, and C_4 grazers, respectively.

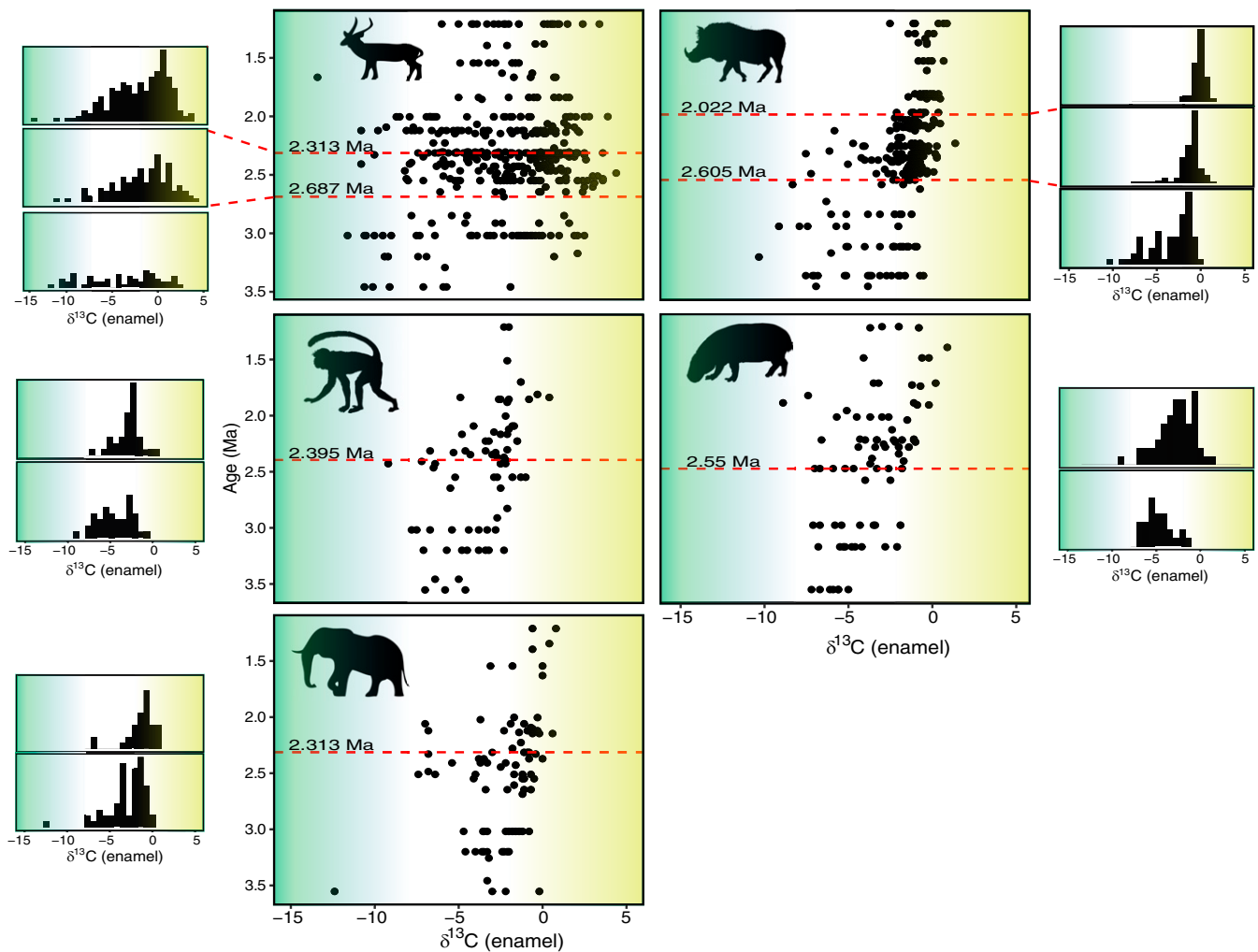


Fig. 4. Change points in mammalian families that show significant changes in the distribution of $\delta^{13}\text{C}$ values (shown as red dashed line). The histograms show distribution of $\delta^{13}\text{C}$ values for each taxa before and after the major change points. Green, white, and yellow shades indicate C_3 browsers, $\text{C}_3\text{-C}_4$ mixed feeders, and C_4 grazers, respectively.

B and C at the member-level analysis, the later change point at 2.6 Ma results from a small sample size of suids between 2.8 and 2.6 Ma. The second change point at ~ 2.0 Ma is also consistent with the significant difference observed between Members G and H in this taxon. It also coincides with one of the two major change points observed for the herbivore fauna as a whole. These timings are also congruent with changes in dental morphology previously reported for this lineage (44). Likewise, the elephants show a change at 2.3 Ma consistent with previously reported dental morphology changes (45) and congruent with the change point observed in bovids. The hippopotamids, on the other hand, show a change at 2.55 Ma, slightly later than the change point in the bovids and suids. However, a close inspection of the isotope dataset shows a very small sample size of hippopotamids between 2.8 and 2.55 Ma, which might have resulted in this later change point. *Theropithecus* shows a change at ~ 2.4 Ma (Member E unit 2), which is similar to what has been observed in the hominins from the Shungura Formation (46). Apart from *Theropithecus* and the hominins, the other herbivores show changes in the distribution of $\delta^{13}\text{C}$ values that coincide with previously reported paleoecological changes in the Shungura Formation between Members B and C (24, 36), between Members F and G (26), and after Member G (27). While these previous studies analyzed selected taxa or different components of the fossil collections (e.g., collections from the French vs.

American expeditions), this comprehensive study includes the collective herbivore fauna from both the French and American collections and further confirms that real ecological changes indeed occurred in the Shungura Formation between 2.9 and 2.0 Ma.

Conclusion

Stable carbon isotope data from herbivores in the Shungura Formation indicate a trend toward increasing C_4 herbivory with attendant reductions in the proportions of browsers and mixed feeders. This is similar to other Pliocene and Pleistocene sites in eastern Africa (39). However, despite this increasing trend toward C_4 diets, the higher proportion of mixed feeders indicates relative environmental stability, compared to contemporaneous sites elsewhere in eastern Africa. Thus, more wooded habitats (i.e., C_3 resources) were available to hominins in the Shungura Formation compared to contemporaneous sites south of the basin on a landscape that was gradually becoming more open and dominated by C_4 resources. Among the major dietary shifts observed in herbivores, the shift at ~ 2.7 Ma, which indicates the expansion of C_4 grasses on the landscape, was concurrent with the first appearance of *Paranthropus* in the Shungura Formation (47). The hominin fossils from the sequence older than 2.7 Ma are attributed to *Australopithecus* or Hominini gen. et sp. indet, and these appear to have lived in more wooded landscapes

compared to later hominins such as *Paranthropus* and *Homo*. These results are also congruent with other studies that indicate *Australopithecus* lived in more wooded settings compared to later hominins such as early *Homo* (48, 49). Overall, the increasing expansion of C₄ grasses on the landscape at the expense of wooded habitats across depositional basins has further implications for key adaptations in our lineage such as morphological changes (e.g., loss of features that attest to arboreal adaptations) or behavioral changes (e.g., increased reliance on C₄ dietary resources by consuming either plant or animal resources) (27, 50, 51).

Materials and Methods

Fossil teeth were sampled at the National Museum of Ethiopia. Taxonomic assignments are based on a printed version of faunal databases in the National Museum of Ethiopia and updated electronic versions provided by R.B. and Z.A. The specimens were cleaned before sampling, and powdered enamel samples were extracted. The samples were pretreated with hydrogen

peroxide and acetic acid–calcium acetate buffer, and isotopic ratios were measured on a Thermo Fisher Scientific (Finnigan) Delta V Isotope Ratio Mass Spectrometer at the University of South Florida. Age estimates for fossil samples are based on a well-established chronology of stratigraphic units using radiometric dates and magnetostratigraphy (8, 16, 52). All statistical analyses including the nonparametric change point analysis (53) were performed using R statistical software.

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

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