



## Supporting Online Material for

### **Macrovertebrate Paleontology and the Pliocene Habitat of *Ardipithecus ramidus***

Tim D. White,\* Stanley H. Ambrose, Gen Suwa, Denise F. Su, David DeGusta,  
Raymond L. Bernor, Jean-Renaud Boisserie, Michel Brunet, Eric Delson, Stephen Frost,  
Nuria Garcia, Ioannis X. Giaourtsakis, Yohannes Haile-Selassie, F. Clark Howell,  
Thomas Lehmann, Andossa Likius, Cesur Pehlevan, Haruo Saegusa,  
Gina Semprebon, Mark Teaford, Elisabeth Vrba

\*To whom correspondence should be addressed. E-mail: [timwhite@berkeley.edu](mailto:timwhite@berkeley.edu)

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### **Text S1. Aramis Bovid Postcranial Ecomorphology.**

The functional morphology of postcranial remains can be used to infer locomotor mode and, by extension, habitat preference (1). This approach--commonly considered an "ecomorphology" method--does not rely on species-level taxonomic identifications or assume stasis in habitat preference across evolutionary time, two major limitations of faunal-list based approaches (2). The postcranial ecomorphology approach has been most commonly applied to bovids, as they occupy a diverse range of habitat, yet are often habitat-specific (2-6). Furthermore, bovids are often under selection by predation, and employ locomotion as part of their escape strategy. They are therefore likely to have specific morphological adaptations for efficient movement across their typical substrate. The ecomorphology approach seeks to identify these adaptations to reconstruct locomotor mode and, by extension, habitat.

Postcranial ecomorphological methods are developed by measuring a particular skeletal element (such as the femur) in a large, taxonomically diverse sample of extant species in a given family (e.g., Bovidae). Each of the extant species is classified into a particular "habitat group" (e.g., Forest, Heavy Cover, Open, etc.) based on modern behavioral data. A discriminant function is constructed to predict habitat preference from the measurements. It is this function that is then applied to fossils. There are a number of potential methodological pitfalls in implementing this approach, as reviewed in (2).

Methods for inferring habitat preference from bovid postcrania were originally developed for femora (5) and metapodials (6). Neither of these methods are applicable to the Aramis sample, as no sufficiently complete femora and only one sufficiently complete metapodial were recovered (despite the 100% collection strategy employed). This led us to develop methods based on astragali (2) and phalanges (3, 4), because those elements are relatively abundant in the Aramis sample.

The astragalus and phalanx methods were based on measurements of between 122 and 218 modern bovid specimens, representing from 35 to 40 extant species (2, 3). Four habitat categories were used: "Forest" taxa are forest-dwellers; "Heavy Cover" taxa are those which frequent bush, woodland, swamp, and near-water habitats; "Light Cover" taxa are those which frequent light bush, tall grass, and hilly areas; "Open" taxa are those which frequent edge or ecotone, open country, and arid country (2). The raw accuracy of the astragalus method in classifying taxa to their assigned habitat group is 67% (2.7 times better than chance,  $p < 0.0001$ ; 2), whereas that of the phalanges is from 70.6% to 71.3% depending on whether the proximal, intermediate, or distal phalanx is used (2.8 times better than chance,  $p < 0.0001$ ; 3). However, analysis of the probabilities associated with individual habitat predictions allows confidence thresholds to be established that identify specific predictions, which have  $< 5\%$  chance of being in error, raising the effective accuracy of the methods to 95% (2, 3). We refer to these as 'significant' predictions, as they correspond to  $p < 0.05$ .

The result of applying these methods to the Aramis bovid sample is given in Fig. S1

and Table S2. Of 11 elements with statistically significant habitat predictions, 10 are “Forest” and 1 is “Heavy Cover.” This is an especially clear signal, as these methods typically produce more varied habitat predictions when applied to fossil samples (7, 8).

This ecomorphological approach is not immune from taphonomic effects. Since the methods require relatively intact specimens, a bias could be introduced if the remains of different bovid taxa were at differential risk of fragmentation (perhaps based on size). In that case, the measurable sample might reflect neither the entire fossil sample nor the actual bovid paleocommunity. We took two steps to control for this possible bias: “morphogroup” sorting and evaluation of non-metric traits.

For each element, we divided the entire Aramis bovid sample into morphological groups. Each morphogroup comprised specimens (intact and fragmentary) of a similar size and shape. Every morphogroup ended up including at least one specimen sufficiently complete to be measured. We were thus able to produce a habitat prediction for each morphogroup, assuming that the habitat prediction(s) for the more complete specimens in a morphogroup also apply to the more fragmentary specimens in that morphogroup. A comparison of the total number of specimens in each morphogroup provides a control for the possibility that fragmentation was non-random across the bovid remains sampled. This approach, when applied to the Aramis bovid astragali and phalanges, clearly indicates that virtually all of the 30 fragmentary specimens belong to morphogroups whose complete specimens are predominantly classified as “Forest” (Table S3).

We also examined a range of non-metric traits that have been proposed as being indicative of habitat (4), because such traits can often be evaluated in fragmentary specimens. Testing these features on modern bovid taxa indicates that few are of any value in predicting habitat, save for several traits of the phalanges (4). When these features are evaluated in the Aramis sample, they confirmed the “Forest” nature indicated by the metric predictions, despite being effectively independent.

## **Text S2. Aramis Cercopithecoid Postcranial Functional Morphology.**

### **Overview.**

The habitat preferences of the two Lower Aramis Member monkey taxa are critical for environmental reconstruction. Phylogenetically, it is likely that the numerically dominant colobine *K. aramisi* was arboreal based on the strongly arboreal habitus of extant colobines (9). This, in turn, indicates a more closed, wooded environment at Aramis (cf. 10). However, the inference of paleoenvironments based on taxonomic identifications of fauna has been faulted in general (e.g., 5), and questions have been raised about the Aramis colobine in particular (11-13), because some early colobines may have been predominantly terrestrial (14, 15). The postcranial remains of the Aramis cercopithecoids allow for the testing of these competing hypotheses.

The inference of locomotor mode based on postcranial morphology has been the subject of intense study in hominids, but has been comparatively neglected in cercopithecoids. Various morphological traits in cercopithecoids are often asserted as indicative of either arboreal or terrestrial locomotion based on limited evidence (16). The few empirical studies often use small sample sizes of a restricted range of taxa, and/or require sufficiently complete elements that often exclude the majority of the fossil sample under consideration (e.g., 17, 18). As such, we consider most of the features said to be indicative of locomotion in the cercopithecoid postcranium to be of unknown reliability, pending more systematic and comprehensive studies.

Even so, the elbow is clearly a key joint for distinguishing between arboreal and terrestrial locomotion. We scored the Aramis samples of cercopithecoid distal humerus, proximal radius, and proximal ulnae for 24 traits previously suggested to be indicative of locomotor mode. The results indicate that, based on current criteria, the overwhelming majority of these specimens show adaptations to arboreal locomotion. More limited metric analysis, constrained by the smaller available fossil sample preserving metric features (and a sparse dataset of corresponding metrics on extant taxa), support these non-metric results. Based on current criteria there is clear evidence of arboreal adaptations in the overwhelming majority of the examined Aramis cercopithecoid postcranial sample, and a paucity of terrestrial indicators.

### **Results.**

The morphological features said to be indicative of locomotor mode in the cercopithecoid postcranial skeleton have generally been described in multiple sources (16-36). The descriptions of these features, and their implications for locomotor inferences, often differ (at least slightly) among sources. As such, the following summary of the Aramis material typically references only a single source for each feature, often the same source (16, 18), with the aim of improved clarity and consistency regarding the specific descriptions used. More systematic and comprehensive studies are required to test the correlations between these traits and locomotor modes. Therefore, we use these traits with caution, and assign only very limited significance to the indications from any single trait.

*Humerus, Distal.*

Of the 10 distal humeri from Aramis that preserve scorable features, 9 are clearly “arboreal” based on current standards, while 1 (ARA-VP-6/787) is clearly “terrestrial” by those same standards. Eight traits (5 of which are preserved in at least 3 specimens) are consistent with the sample having 2 distinct “types” (a terrestrial ARA-VP-6/787 versus all other specimens), whereas 2 traits provide less of a dichotomy.

The distal projection of the medial border of the trochlea relative to the width of the main articular surface is said to be short in arboreal taxa, whereas ‘mixed’ and terrestrial taxa are said to have long projections (26). Of the 8 Aramis distal humeri scorable for this character, 7 clearly have “short” projections (best seen in ARA-VP-1/387), whereas in 1 (the “terrestrial” ARA-VP-6/787) the projection is longer.

The medial projection of the medial epicondyle, relative to the overall width of the distal end, is said to be “strong” in arboreal taxa but “weak” in terrestrial taxa (with the exception of *Theropithecus*, presumably due to manual foraging specializations) (16). Of the 3 Aramis distal humeri scorable for this character, all have “strong” medial projections of the medial epicondyle (best seen in ARA-VP-1/1864).

The retroflexion (posterior displacement) of the medial epicondyle is said to be less in arboreal taxa and greater in terrestrial taxa (16). Of the 4 Aramis distal humeri scorable for this character, all 4 have very limited retroflexion (best seen in ARA-VP-1/2975).

The posterior articular surface area is said to be large relative to the anterior-posterior thickness of the distal end in arboreal taxa, with terrestrial taxa having a relatively small surface and “mixed” taxa being intermediate (18). Of the 4 Aramis distal humeri scorable for this character, all have “large” surface areas (e.g., as seen in ARA-VP-1/398).

The depth of the olecranon fossa is said to be smaller than the width of the fossa in arboreal taxa, but greater (deeper) in terrestrial taxa (16). Of the 5 Aramis distal humeri scorable for this character, all have “shallow” fossae (e.g., ARA-VP-1/798).

Three other features of the distal humerus said to be indicative of locomotor mode are each preserved in fewer than 3 Aramis specimens, rendering them of questionable utility. Even so, they are uniformly of the “arboreal” condition in all specimens except the “terrestrial” ARA-VP-6/787.

Two features are less dichotomous in the Aramis distal humerus sample. The development of the lateral trochlear margin is said to be “weak” in arboreal taxa but “strong” in terrestrial or mixed taxa (16). In the Aramis sample, 2 specimens seem to have “weak” margins (including the otherwise “terrestrial” ARA-VP-6/787), whereas 5 others are “intermediate” in comparison with a limited sample of modern taxa. The orientation of the proximal border of the trochlea in posterior view is said to be “not angled” in arboreal taxa, but “angled” in terrestrial taxa (16). In the Aramis distal humeri, 2 borders are “not angled” (including the otherwise “terrestrial” ARA-VP-6/787) whereas 1 otherwise “arboreal” specimen has an apparently angled border.

*Humerus, Proximal.*

The single well-preserved proximal humerus in the Aramis assemblage (ARA-VP-1/902) preserves a range of traits said to be indicative of locomotor mode (e.g., 16, 18, 26, 30, 31). In all cases, the character states of these traits correspond with arboreal locomotion. The proximal articular surface of the head clearly projects proximally beyond the greater tubercle. The bicipital groove is anteroposteriorly shallow relative to its mediolateral width. The bicipital groove is narrow, relative to the overall width of the proximal end (but this has also noted as being present in the terrestrial *Theropithecus* (16). The greater tubercle appears to be long in its anterior-posterior extent, relative to the overall anterior-posterior dimension of the head in proximal view. The lesser tubercle is very large relative to overall humeral head size, and as compared to terrestrial forms. The insertion for the infraspinatus muscle, on the lateral surface of the greater tubercle, is deep and pronounced. There is no clear insertion scar for the coracobrachialis muscle just inferior to the lesser tubercle.

*Ulna, Proximal.*

Of the 10 proximal ulnae from Aramis that preserve scorable features, 9 are “arboreal” in the majority of traits and 1 is an even mix between “arboreal” and “terrestrial” traits (2 of each). Specifically, 5 specimens are “arboreal” in every trait (1 to 3 traits scored), 1 is “arboreal” in all traits save one (8 traits scored), and 3 are “arboreal” in a majority of scored traits (3 out of 5 traits in 2 specimens and 6 out of 8 traits in 1 specimen). The “terrestrial” character states are found in only 4 of the 8 traits evaluated, as described below.

The retroflexion (angulation) of the olecranon in medial view relative to the main shaft axis is said to differ between arboreal and terrestrial taxa, with the former lacking retroflexion and the latter having it (16). Of the 5 ulnae preserving this trait, all lack retroflexion (“arboreal”).

The medial concavity of the olecranon is said to be deep in arboreal taxa and not deep in terrestrial taxa (16), presumably relative to the overall size of the element. Of the 4 ulnae that preserve this feature, 3 are apparently deep (“arboreal”) and 1 shallow (“terrestrial”). The lone “terrestrial” specimen has many other traits held to be indicative of arboreality.

The anterior extent of the coronoid process (relative to the medial-lateral width of the proximal end) is said to be “low” in arboreal taxa but “relatively high” in terrestrial and “mixed” taxa (18). Of the 5 ulnae preserving this trait, all are relatively low (“arboreal”).

The anterior tip of the coronoid is said to be anterior-pointing in medial view in arboreal taxa, while terrestrial taxa have superiorly curved tips (16). Of the 8 ulnae that preserve this trait, all appear to have anteriorly pointing (“arboreal”) rather than superiorly curved coronoid tips.

The relative dimensions of the radial notch are said to differ between arboreal and terrestrial taxa, with the notch of arboreal forms being expanded in the proximal-distal dimension relative to the medial-lateral dimension, whereas terrestrial forms exhibit the reverse, and “mixed” taxa are “intermediate” (18). Of the 4 ulnae preserving this trait, 2 have the “arboreal” condition, while 1 has the “terrestrial” condition and 1 is “intermediate.” The 2 “non-arboreal” specimens both have other traits said to be indicative of arboreality (6 of 8 traits in one case).

The medial-lateral dimension of the radial notch (presumably relative to the width of the shaft to avoid redundancy with the “radial notch proportions” trait) is said to be narrow in arboreal taxa and wide in terrestrial and “mixed” taxa (18). Of the 4 ulnae preserving this trait, 2 are narrow (“arboreal”) while 2 are wide (“terrestrial”). However, the 2 ulnae with wide radial notches both have other traits said to be indicative of arboreality.

The shape of the trochlear notch is said to be relatively narrow at the distal end in arboreal taxa and relatively wide in terrestrial taxa (18). Of the 2 ulnae that preserve this trait, one is clearly “arboreal,” while the other is intermediate between “narrow” and “wide.” The “intermediate” specimen has many other traits said to be indicative of arboreality.

The trochlear notch is said to be shallow in medial view in arboreal taxa but deep in terrestrial taxa (16) presumably relative to the proximal-distal dimension of the notch. Of the 5 ulnae that preserve this trait, 4 appear to have relatively deep notches (“terrestrial”) while 1 appears to have a shallow notch (“arboreal”). The specimens with deep (“terrestrial”) notches have other traits said to be indicative of arboreality, and often many of those traits. For example, *ARA-VP-1/541* preserves all 8 scored traits, and is “arboreal” for all traits besides trochlear notch depth. In general, this one trait accounts for about half of the “terrestrial” character states seen in the entire sample.

#### *Radius, Proximal.*

Five traits of the proximal radius were examined in the Aramis sample, which contains 18 proximal radii that preserve at least one of the traits. The proximal radius traits were more difficult to score than those for the other elements. In addition, as noted by Krentz (16, p. 409): “Among the forelimb bones, the radius has been the most difficult to analyze in terms of correlating morphological traits and locomotor behaviours. Studies of the radii of Old World Monkeys ... have produced mixed and inconsistent results.” As such, less weight is assigned to the proximal radius results than those of the other element portions considered here. No strong evidence for terrestrial adaptation is apparent.

The shape of the radial head is sometimes said to be circular in arboreal taxa and oblong in terrestrial taxa, but see Krentz’s (16) review of contradictory claims in the literature on this count, and the degree of variation in extant primates. Of the 9 Aramis radii that preserve this feature, 7 are more oblong, whereas 2 are more circular.

The slope of the radial head, presumably relative to the main axis of the shaft in medial view, is said to be less angled in arboreal taxa and strongly angled in terrestrial taxa (16). Of the 9 Aramis specimens that preserve this feature, 1 is clearly not angled (“arboreal”), but in the remainder it is unclear whether the degree of angulation observed should be considered “strongly angled” or “less angled.”

The projection of the radial tuberosity above the shaft is sometimes said to be greater in arboreal taxa compared to terrestrial taxa (16), although other work (20) found no clear correlation between this feature and locomotion. Of the 13 Aramis radii preserving this feature, 2 had non-projecting tuberosities, whereas the appropriate scoring of the projection of the remainder was unclear.

The lateral border of the radial tuberosity is said to be “sharp” in terrestrial taxa (16). Of the 12 Aramis radii that preserve this feature, 6 are clearly not sharp, while 4 are sharp and 2 are of “intermediate” morphology.

The robustness of the radial shaft is said to be less in arboreal taxa (with slender shafts) than terrestrial taxa (with stout shafts) (16). By comparison with extant taxa (17), all 12 Aramis radial shafts appear to be slender (“arboreal”).

### **Text S3. Stable carbon and oxygen isotope analysis of mammalian tooth enamel from Lower Aramis Member Vertebrate Paleontology Localities.**

#### **Introduction and overview**

Stable carbon and oxygen isotope ratios of tooth enamel carbonate (bioapatite) of tropical mammals are now widely used to reconstruct their diets and habitat preferences (37-44). Isotopic analysis of fossil enamel of mammals from the Lower Aramis Member of the Sagantole Formation in the Middle Awash study area can provide insights into the habitats occupied by *Ardipithecus ramidus*.

The results of isotopic analysis of enamel of 177 individual mammals representing approximately 28 taxa from five *Ardipithecus*-bearing vertebrate paleontology collection localities in the Lower Aramis Member indicate the presence of small areas of closed canopy forest within a regional mosaic of local woodland to more distant wooded grassland. Compared to penecontemporary localities at Gona (c. 70 km to the north) (43), the Lower Aramis Member setting was substantially drier. The environments associated with *Ardipithecus ramidus* were more densely wooded compared to penecontemporary sites in the Apak Member of the Nachukui Formation at Lothagam in the Turkana Basin, Kenya (38). Enamel oxygen isotope ratios suggest that Lothagam was more arid and Gona had more permanent water than the Lower Aramis Member.

The carbon isotopic composition of *Ardipithecus ramidus* is closely similar to that of fossil baboons (*Pliopapio alemui*) in the Lower Aramis Member. It reflects diets that included small amounts of <sup>13</sup>C-enriched plants and/or animals that fed on such plants. *Ardipithecus* consumed slightly more of these resources than modern savanna woodland chimpanzees (45-46), but substantially less than Plio-Pleistocene hominids (47-48).

Environmental variation in tropical African ecosystem stable isotope ratios is summarized below in order to guide inferences about the diet and habitat preferences of the Lower Aramis Member local ecological community. Descriptions of samples, sample preparation and analysis methods, and results, interpretations and comparisons with modern and fossil ecosystems follow.

#### **Stable Carbon and Oxygen Isotope Variation in Tropical Ecosystems**

Stable carbon and oxygen isotope ratios are conventionally expressed using the  $\delta$  (delta) notation as parts per thousand (permil, ‰) difference from the ratios of international standards, calculated as  $\delta\text{‰} = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$ , where R is <sup>13</sup>C/<sup>12</sup>C or <sup>18</sup>O/<sup>16</sup>O. The standard for carbon is the Pee Dee Formation *Belemnitella* (PDB) fossiliferous carbonate. Oxygen isotope ratios are measured relative to PDB or to Standard Mean Ocean Water (SMOW) (49). Table S5 presents  $\delta^{18}\text{O}$  values relative to both standards to facilitate comparisons with previous studies that have used one standard. PDB is converted to SMOW using the formula:  $\delta^{18}\text{O}_{\text{SMOW}} = (\delta^{18}\text{O}_{\text{PDB}} \times 1.0389) + 30.90994$ .

Pre-industrial era atmospheric CO<sub>2</sub> had a  $\delta^{13}\text{C}$  value of -6.5‰, but combustion of <sup>13</sup>C-depleted fossil fuels during the last century has lowered this to approximately -8.0‰ (50). Levin *et al.* (43) estimate a  $\delta^{13}\text{C}$  value of -6.7‰ for atmospheric CO<sub>2</sub> during deposition of the “Sagantole Formation” at Gona. To compare modern with fossil species, 1.5‰ will be added to modern or subtracted from fossil  $\delta^{13}\text{C}$  values. Corrections are unnecessary for  $\delta^{18}\text{O}$  values.

Plants fix atmospheric CO<sub>2</sub> via two major photosynthetic pathways that discriminate to different degrees against isotopically “heavy” air molecules (<sup>13</sup>CO<sub>2</sub>). Tropical savanna grasses that use the C<sub>4</sub> pathway are adapted to strong sunlight, high temperatures and low CO<sub>2</sub> concentrations (51). Heliophilous (sun-loving) C<sub>4</sub> grasses can grow in light shade beneath open canopy woodlands, but the grass layer is poorly developed in the deep shade of closed canopy woodlands, and is absent from forests (52). C<sub>4</sub> plants in the central Rift Valley of Kenya and other parts of eastern Africa have  $\delta^{13}\text{C}$  values averaging -12.5‰ (39, 53, 54). Their discrimination against <sup>13</sup>CO<sub>2</sub> is small (~5‰), and is relatively insensitive to environmental variation (50-51).

Plants that use the C<sub>3</sub> photosynthetic pathway include trees, shrubs and most (but not all) herbaceous dicots; and grasses adapted to the shaded forest understory, high elevation cold tropical alpine, and high latitude environments. They discriminate strongly against <sup>13</sup>CO<sub>2</sub> (~20‰), and they have average  $\delta^{13}\text{C}$  values of -26.5‰ (39, 53, 54). However, their discrimination against air <sup>13</sup>CO<sub>2</sub> varies substantially, mainly in response to stomatal conductance, which is strongly influenced by humidity and water stress (51). C<sub>3</sub> leaf  $\delta^{13}\text{C}$  values can vary by up to 3-6‰ within species in response to water stress, and are highest in hot, dry environments (51). Closed canopy forests trap <sup>13</sup>C-depleted biogenic CO<sub>2</sub> from C<sub>3</sub> plant decomposition and root respiration. High concentrations of <sup>13</sup>C-depleted biogenic CO<sub>2</sub> lowers plant  $\delta^{13}\text{C}$  values near the forest floor and creates vertical stratification in plant and animal  $\delta^{13}\text{C}$  values (53-58).

Many tropical succulent plant genera, including *Aloe*, *Sansevieria* and *Euphorbia*, use the CAM (Crassulacean Acid Metabolism) photosynthetic pathway, and have  $\delta^{13}\text{C}$  values that are nearly as high as those of C<sub>4</sub> plants (59, 60). CAM plants are typically insignificant components of herbivore diets, but may be included in some omnivore diets (61).

Bioapatite carbonate is derived from all dietary macronutrients via blood CO<sub>2</sub> and CO<sub>3</sub>. Breath CO<sub>2</sub> of non-ruminants is closely similar to the whole diet  $\delta^{13}\text{C}$  value (62), whereas that of ruminants is systematically enriched by up to 4‰ relative to diet (63). Ruminant herbivore bioapatite carbonate (bone, dentine and enamel CO<sub>3</sub>)  $\delta^{13}\text{C}$  is enriched by approximately 14‰ relative to the diet (63-65), while that of rodents and carnivores, and presumably other non-ruminants such as primates and suids, is enriched by 8.5‰-10‰ (62, 66, 67). The large diet-apatite difference for ruminants may be due to cogeneration of large amounts of <sup>13</sup>C-depleted methane and <sup>13</sup>C-enriched CO<sub>2</sub> by methanogenic digestive tract symbionts (68, 69). Equids and suids generate less methane than ruminants (70, 71) so their diet-breath and diet-apatite spacing should be less than that of ruminants, as has been observed for cows *versus* pigs (63).

Methanogenesis in pigs increases significantly with a high fiber diet (71), so the diet-bioapatite  $^{13}\text{C}$  difference may vary within some herbivorous and omnivorous non-ruminant species depending on diet composition.

Collagen-apatite differences of cercopithecine monkeys in the Kibale Forest are on average 1.9‰ less than those of ruminants (4.55‰ and 6.46‰, respectively) (57). Assuming a diet-collagen enrichment of 5‰ for all species regardless of diet or digestive physiology (66), then the diet-apatite enrichment for Cercopithecinae is approximately 10‰. Ruminant  $\text{C}_4$  hypergrazers such as Hippotragini, Bovini and Alcelaphini, and  $\text{C}_3$  browsers such as Tragelaphini and Giraffidae have average bioapatite end-member  $\delta^{13}\text{C}$  values of approximately +2‰ and -12‰, respectively, as expected given the 14‰ difference between the means for  $\text{C}_3$  and  $\text{C}_4$  plants, and a diet-apatite enrichment of 14‰. Mixed feeders such as eland, kudu, impala and gazelle have intermediate values. The canopy effect permits discrimination of forest floor from forest canopy and open habitat species (56). Forest floor species have bioapatite  $\delta^{13}\text{C}$  values more negative than -12.5‰ (57, 58).

The oxygen isotope ratio of meteoric water controls that of food webs (72). Surface water  $\delta^{18}\text{O}$  values are closest to those of rainfall. Preferential evaporation of isotopically “light” water ( $\text{H}_2^{16}\text{O}$ ) leads to isotopic enrichment of remaining liquid water in near-surface soils (72). Evapotranspiration from plant leaves causes substantial enrichment of leaf water and organic matter  $\delta^{18}\text{O}$  values (73). Enrichment is highest at low relative humidity (74), and thus should be highest in  $\text{C}_3$  plants that retain their leaves through the dry season. A canopy effect analogous to that in  $\text{CO}_2$  lowers leaf  $\delta^{18}\text{O}$  values near the humid forest floor, mainly in response to humidity effects on stomatal conductance (75). Grasses cease growth and desiccate during the dry season, unless they grow in microhabitats with high soil moisture availability such as riparian environments (76). Therefore green grass leaf water and tissues synthesized during the humid growing season should have lower  $\delta^{18}\text{O}$  values compared to those of  $\text{C}_3$  leaves during dry seasons. Grasses with shallow roots growing in drier soils in open habitats should have somewhat higher  $\delta^{18}\text{O}$  values than grasses growing in moist soils. Moreover, because  $\text{C}_4$  grasses have substantial diurnal intra-leaf variation in water  $^{18}\text{O}$  enrichment (74), daytime grazers may also ingest plant waters with higher  $\delta^{18}\text{O}$  values higher than nocturnal species such as hippopotamus. The latter should most closely reflect the  $\delta^{18}\text{O}$  value of surface, soil and meteoric water.

Plant water  $\delta^{18}\text{O}$  increases with evaporative water deficit ( $\text{WD} = \text{mean annual evaporation minus mean annual precipitation}$ ) (77), so species that obtain a substantial amount of water from leaves should have a close correlation between WD and tissue  $\delta^{18}\text{O}$  values. Such species are classified as evaporation-sensitive (ES). Their difference in  $\delta^{18}\text{O}$  values from those of evaporation-insensitive (EI) species such as hippo can serve as an index of aridity (77).

Bioapatite  $\delta^{18}\text{O}$  reflects that of ingested water, which includes drinking water, leaf water, and metabolic water formed from dietary carbohydrates, and proteins (44, 78). Dry grass cannot contribute significantly to animal water budgets, so grazers are

generally more water-dependent than browsers (79, 80), and they should drink more  $^{18}\text{O}$ -depleted surface water during the dry season. Grazing herbivores that drink more permanent surface water, for example hippopotamus, have lower bioapatite  $\delta^{18}\text{O}$  values than water-independent  $\text{C}_3$  browsing species such as giraffe (77, 81). Mixed feeders such as impala consume more grass during the rains and more browse during dry seasons (82), and such species should have high intra-tooth variation in carbon and oxygen isotope ratios. Water-dependent carnivores and other faunivores should have among the lowest values in an ecosystem (78, 83). Plant stems have substantially lower  $\delta^{18}\text{O}$  values than leaves because they have low evaporative surface areas (73, 74). Fruits, pith, roots and underground storage organs should also have lower  $\delta^{18}\text{O}$  values than leaves. Frugivores and omnivores such as primates, root-eating suids and termite-feeding insectivores (aardvark and aardwolf) should have relatively low bioapatite  $\delta^{18}\text{O}$  values (83).

### **Materials and Methods of Enamel Purification and Isotopic Analysis**

Tooth enamel bioapatite is dense, highly crystalline, non-porous and highly resistant to diagenesis, and can preserve its in-vivo isotopic composition with high fidelity for millions of years (37, 84). Fossil bone and tooth dentine (including ivory) bioapatite are poorly crystalline, porous and susceptible to diagenetic alteration and isotopic exchange, and are unsuitable for isotopic analysis (85).

Small fragments of tooth enamel representing 177 individuals of species identified to family, genus, tribe (for bovids), or species were selected and sampled (by T.W.). Represented were most of the available larger mammal taxa from 5 vertebrate paleontology fossil collection localities of the Lower Aramis Member of the Sagantole Formation. Most (61%) are from ARA-VP-1, 23% came from ARA-VP-6, 11% from SAG-VP-7, 3% from KUS-VP-2, and 1% from ARA-VP-17. Samples were analyzed at the Environmental Isotope Paleobiogeochemistry Laboratory, Department of Anthropology, University of Illinois. Samples were submitted to S.A. "blind", i.e., without taxonomic identifications. Most samples were well preserved, with mainly translucent white, gray to dark caramel-colored enamel. Surfaces of many specimens had surface patches of soft, whitened decayed, pitted enamel, indicating localized hydration and decalcification, and many had adhering dentine. All dentine and decayed, hydrated enamel was removed with a diamond grit 1 mm diameter dental burr in a rotary tool (Kupa Inc. KP-3000) set to approximately 20% of maximum speed to avoid thermal decomposition of carbonate. Drilling was performed while viewing under a low-power stereomicroscope to insure complete removal of dentine and altered enamel. Samples weighing  $\leq 15$  mg after cleaning were powdered either with the diamond burr, or by grinding manually with an agate mortar and pestle. Tools were cleaned with 1 M HCl and distilled water between samples to prevent cross-contamination.

Fossil enamel was pretreated to remove diagenetic carbonates using the protocol developed by Balasse *et al.* (86). Samples weighing 5-15 mg were placed in 1.5 ml plastic microcentrifuge tubes with 1.5 ml NaOCl (50% Clorox : water) for 20 hours, and rinsed 4X with distilled water. Samples were then treated with 0.1 M acetic acid (0.1 ml per mg) for 4 hours, rinsed 4X with distilled water, and freeze-dried. Purified

enamel bioapatite samples weighing 600-700  $\mu\text{g}$  were reacted with three drops of 100% phosphoric acid at 70°C in individual vessels in a Kiel III automated carbonate reaction, two-stage cryogenic distillation device, interfaced with a Finnegan MAT252 isotope ratio mass spectrometer (Thermo-Finnegan Corp.) for isotopic analysis of purified  $\text{CO}_2$ . National Bureau of Standards NBS18 and NBS19 carbonate standards were analyzed along with fossil enamel samples. Means and standard deviations of 35 replicates of NBS19 for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  are  $2.00 \pm 0.07\text{‰}$  and  $28.72 \pm 0.21\text{‰}$ , respectively, and for 26 replicates of NBS18, they are  $-4.96 \pm 0.09\text{‰}$  and  $7.04 \pm 0.16\text{‰}$ , respectively.

Comparisons with results of other studies are complicated in some cases by differences in pretreatments. Treatment of bone with 1.0 M acetic acid causes recrystallization of bone apatite (87), and may have a small effect on enamel as well (88). Recrystallization would tend to fix the diagenetic carbonate phase, leading to incomplete removal. Experiments by Koch *et al.* (89) show that 0.1 M acetic acid caused minimal alteration. Pretreatment methods used for Aramis fossil enamel in this study, described in detail in Balasse *et al.* (86), are based on Koch *et al.* (89). Levin *et al.* (43) report that treatment with 2% NaOCl and 1M acetic acid increased the  $\delta^{13}\text{C}$  of modern enamel by 0.2‰, and fossil enamel of Mio-Pliocene fossils from Gona by an average of  $0.4 \pm 0.7\text{‰}$ . However, the shift in fossils was not constant across the full range from  $\text{C}_3$  to  $\text{C}_4$ : treatment tended to increase  $\delta^{13}\text{C}$  by approximately 1.15‰ in samples that were around 0‰, and decrease it by  $\sim 0.5\text{‰}$  in samples around -10‰. The regression line (slope = 1.15) of treated *versus* untreated fossil enamel from Gona crosses that for modern treated *versus* untreated enamel (slope = 1.01) at around -5.3‰ (43). This crossover point is likely to be the average  $\delta^{13}\text{C}$  value of the diagenetic phase. The y-intercept of 0.957 shows that untreated fossil enamel of  $\text{C}_4$  feeders is about 1.0‰ higher than treated enamel. When comparing treated enamel from the Lower Aramis Member to untreated enamel from Gona, approximately 1.0‰ should be *added* to Gona  $\delta^{13}\text{C}$  values at the  $\text{C}_4$  end of the range, and 0.5‰ *subtracted* in the  $\text{C}_3$  end of the range. Values for mixed feeders in the vicinity of -5‰ need no correction.

The magnitude of the effect of treatment on enamel  $\delta^{18}\text{O}$  values is not reported for Gona by Levin *et al.* (43), but is known to vary between fossil sites (90, 91). Diagenetic alteration of oxygen isotopes is faster than carbon isotopes (84), so data on treatment effects on Gona enamel is needed for accurate inter-site comparison of fossil enamel  $\delta^{18}\text{O}$  values. Untreated enamel from Gona has been excluded from calculations of averages presented below, except as noted for Gona primates, all of which were untreated.

### Results of Enamel Carbonate Isotope Analysis

Table S5 provides individual  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values, and means and standard deviations for 26 large mammal taxa. Text Figure 4 of the current manuscript contains bivariate graphs of these data plotted as individual analyses and as means and standard deviations. Oxygen isotope values are referenced to SMOW. Figure S2 compares the means and standard deviations of the Lower Aramis Member mammals to those of

roughly contemporaneous fauna from Gona (43). The overall context of these results is presented in (92).

Systematic differences in isotopic composition within individual taxa between Lower Aramis Member sites are not apparent. The wide range of carbon isotope ratios (-14.8‰ to +3.3‰), and oxygen isotope ratios (21.6‰ to 38.6‰) demonstrates that the Lower Aramis Member sample set preserves its *in-vivo* isotopic composition. If diagenesis had systematically affected the isotopic composition of these teeth, or if pretreatment did not completely remove diagenetic carbonate, then the stable isotope ratios would converge on those of the diagenetic contaminant, and the range for both isotopes would be reduced.

Fossil species whose modern congeners can serve as probable analogs for diet and habitat preferences (38, 43, 53, 56, 57, 77, 81) have the isotopic compositions expected for a mosaic of mesic to semi-arid tropical African forest, woodland and savanna mosaic biomes. For example,  $\delta^{13}\text{C}$  values range from -14.8‰ for *Kuseracolobus aramisi*, whose closest living relatives are arboreal C<sub>3</sub> folivorous monkeys, to +3.3‰ for an alcelaphine, whose modern representatives such as wildebeest and hartebeest are C<sub>4</sub> hypergrazers. Giraffids and colobines have among the lowest  $\delta^{13}\text{C}$ , as expected for complete C<sub>3</sub> browsers, and the highest  $\delta^{18}\text{O}$  values, reflecting consumption of water-stressed upper canopy leaves. Hippopotamids have high  $\delta^{13}\text{C}$ , reflecting C<sub>4</sub> grass consumption, and among the lowest  $\delta^{18}\text{O}$  values, indicating regular access to riparian surface water and predominantly nocturnal feeding on grasses growing on moist soils (77, 78, 81). Oxygen isotope ratios range from 21.6‰ for a hippo, and 22.8‰ for *Enhydriodon* (an otter), as expected for an aquatic water-dependent carnivore, to 38.2‰, for *Sivatherium* (Giraffidae) and 38.6‰ for *Tragelaphus*, as expected for canopy- and above-ground-feeding C<sub>3</sub> folivores. These data completely span--but do not exceed--the full range of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values expected for mesic to semi-arid tropical African forest, woodland and savanna mosaic ecosystems (39, 43, 38-58, 60, 78, 83). Description of results on different taxa and comparison with similar modern and fossil species are presented below.

### Primates

Among the primates, *Kuseracolobus aramisi* has lower average  $\delta^{13}\text{C}$  values than *Pliopapio alemui* (-12.6‰ versus -10.9‰). The mean for *Kuseracolobus* includes one individual with an unusually high  $\delta^{13}\text{C}$  value of -7.5‰. Removing this outlier decreases the mean to -12.9‰. The mean difference between these species is consistent with that observed between modern forest-dwelling arboreal folivorous colobus monkeys and more terrestrial omnivorous baboons (56, 58). Arboreal and terrestrial monkeys in the Kibale (Uganda) and Ituri (Democratic Republic of Congo) forests have average bioapatite  $\delta^{13}\text{C}$  values of -14.6‰ and -15.0‰, respectively, *after* adjusting by +1.5‰ for pre-industrial air CO<sub>2</sub> isotopic dilution (57, 58). Extremely low  $\delta^{13}\text{C}$  values at Kibale and Ituri are due to a strong canopy effect. Kibale Forest *Colobus* has a slightly lower mean  $\delta^{13}\text{C}$  value than *Papio* (57). Using modern baboons as a referential model for diet (93, 94), higher  $\delta^{13}\text{C}$  for *Pliopapio* would indicate feeding in more open habitats and consuming small amounts of C<sub>4</sub> and CAM plants and/or small animals

(insects, vertebrates) that feed on such plants. These  $^{13}\text{C}$ -enriched plant species are virtually absent from Kibale forest and from other colobine diets (95, 96), but *Euphorbia candelabrum* is frequently consumed by baboons in Queen Elizabeth National Park, Uganda (61).

Two Lower Aramis Member *Kuseracolobus* individuals have  $\delta^{13}\text{C}$  values (-14.2‰, -14.8‰) low enough to indicate a completely closed canopy forest like that at Kibale. Modern *Colobus guereza* home range core areas (defined as the area accounting for 50% sightings in a home range) for 8 groups in the Kibale Forest range from 0.5 to 1.6 hectares (95). The rarity of very low  $\delta^{13}\text{C}$  values indicates that closed forest patches of this size were present, though uncommon, in the Lower Aramis Member.

Aramis colobines have higher  $\delta^{18}\text{O}$  values than associated papionines (33.0‰ and 32.0‰, respectively). This mean difference of 1‰ also occurs among their modern relatives in the Ituri and Kibale forests (57, 58), and is consistent with greater folivory, and thus ingestion of  $^{18}\text{O}$ -enriched leaf water and carbohydrates by colobines.

Untreated *K. aramisi* and *P. alemui* enamel samples from the Sagantole Formation at Gona have average  $\delta^{13}\text{C}$  values of -9.4‰ and -7.3‰, respectively. After subtracting 0.5‰ from these averages to correct for treatment effects, their corrected  $\delta^{13}\text{C}$  values (-9.9‰ and -7.8‰) remain significantly less negative than those of their congeners at Aramis, and indicate both species consumed small amounts of  $\text{C}_4/\text{CAM}$ -based foods. This conclusion is unremarkable for Gona *Pliopapio*, because modern and fossil baboons all eat small amounts of  $\text{C}_4/\text{CAM}$  plants (97). However, because  $^{13}\text{C}$ -enriched plants are absent from all modern colobine species diets (96), high *Kuseracolobus*  $\delta^{13}\text{C}$  values at Gona seem anomalous. Assuming that corrected Gona values are accurate, then lower  $\delta^{13}\text{C}$  values for primates in the Lower Aramis Member indicate the presence of more densely wooded environments than at Gona.

Gona *Kuseracolobus* and *Pliopapio* have similar average  $\delta^{18}\text{O}$  values. However, compared to their Aramis conspecifics, primates at Gona have substantially lower  $\delta^{18}\text{O}$  values (25.6‰ and 24.1‰, respectively), reflecting either much higher humidity and/or more regular access to surface water, or lower average meteoric water  $\delta^{18}\text{O}$  values.

*Ardipithecus ramidus* is represented by five individuals. Three teeth (M1, M2, M3) were sampled from the ARA-VP-6/500 skeletal individual. The average of these three specimens is used for calculating the species mean and standard deviation in Table S1. The variation in isotope ratios between these teeth is less than that observed within robust australopithecine teeth (98). The mean  $\delta^{13}\text{C}$  of  $-10.63 \pm 1.03\text{‰}$  is slightly higher than (but not significantly different from) the mean of  $-10.91 \pm 0.69\text{‰}$  for *Pliopapio* (student's T-test, two-tailed,  $p=0.50$ ). One individual (ARA-VP-1/700) has a  $\delta^{13}\text{C}$  value of -8.5‰, which is significantly higher than the mean in this small sample. High  $\delta^{13}\text{C}$  and relatively high  $\delta^{18}\text{O}$  suggests that this individual consumed more  $\text{C}_4/\text{CAM}$ -based resources than other *A. ramidus* individuals. Using estimates of food web carbon isotopic compositions and diet-bioapatite enrichment discussed above, the diets of the

four individuals with the lowest  $\delta^{13}\text{C}$  values ranged from approximately  $9-15 \pm 6\%$   $\text{C}_4/\text{CAM}$ , and  $28 \pm 6\%$   $\text{C}_4/\text{CAM}$  for ARA-VP-1/700.

The mean  $\delta^{18}\text{O}$  of *Ardipithecus* is 1.4‰ lower than that of *Pliopapio*, and this difference is statistically significant ( $p = 0.04$ ). Similarity in  $\delta^{13}\text{C}$  and lower  $\delta^{18}\text{O}$  suggest that compared to *Pliopapio*, *Ardipithecus* relied more on drinking water and/or consumed more fruits and animals that consumed small amounts of  $\text{C}_4/\text{CAM}$  plants. It is obvious that the number of individuals sampled and analyzed needs to be increased should additional individuals with naturally spalling enamel become available.

Few chimpanzee data are available for comparison with *A. ramidus*. Biopapatite  $\delta^{13}\text{C}$  values of chimpanzees from the Kibale forest are similar to those of sympatric colobus monkeys and baboons, and their low values reflect the canopy effect. Hair  $\delta^{13}\text{C}$  values of chimpanzees in grassy woodlands in Tanzania and wooded grasslands in Senegal (45, 46) do not show the canopy effect, but are low enough to be consistent with nearly pure  $\text{C}_3$  diets. These data suggest that *A. ramidus* was not restricted to the most closed habitats at Aramis, and unlike chimpanzees sampled to date, most individuals ate small quantities of  $\text{C}_4/\text{CAM}$ -based foods.

### **Carnivora**

Among Aramis carnivores, Hyaenidae have lower average  $\delta^{13}\text{C}$  values than modern East African spotted hyenas (56), suggesting greater predation on browsing prey. They also have low  $\delta^{18}\text{O}$  values compared to most of the herbivores, reflecting greater reliance on drinking water. Sample numbers for *Crocota* and *Hyaenictis* are inadequate to evaluate interspecific differences in diet and habitat selection. *Agriotherium*, a large member of the Ursidae (bears), has the highest  $\delta^{18}\text{O}$  value among the carnivores, a result consistent with morphological and dental microwear evidence for an omnivorous/herbivorous diet (99). As noted above, the low  $\delta^{18}\text{O}$  value for *Enhydriodon* is expected for an aquatic water-dependent carnivore. Only one individual bear and otter at Aramis were available for isotopic analysis. Although their inferred diets and habitat preferences are congruent with their  $\delta^{18}\text{O}$ , reliable averages cannot be calculated for these extremely rare taxa until samples of at least five individuals can be analyzed (100). Isotopic analyses of early Pliocene carnivores have not been reported for other sites in eastern Africa, but Plio-Pleistocene carnivores from South Africa also have low  $\delta^{18}\text{O}$  values compared to herbivores (78, 101).

### **Proboscidea**

The proboscideans from Aramis fall into two groups: *Deinotherium* is identified as a pure  $\text{C}_3$  browser by its low  $\delta^{13}\text{C}$  values (average  $-12.5\text{‰}$ ), while *Anancus* and Elephantidae are  $\text{C}_4$  grazers, with  $\delta^{13}\text{C}$  values of  $-0.4\text{‰}$  and  $-1.6\text{‰}$ , respectively. These carbon isotope results are consistent with results from Gona and Lothagam (38, 43). Very low  $\delta^{18}\text{O}$  values ( $< 25\text{‰}$ ) for two *Deinotherium* and two *Anancus* suggest habitual drinking and feeding in humid habitats close to permanent water. Water obtained from feeding on plant stems and bark would also contribute to low  $\delta^{18}\text{O}$ . Gona *Anancus* average  $\delta^{18}\text{O}$  values are lower than those from Aramis ( $25.8\text{‰}$  versus  $28.1\text{‰}$ ), again

suggesting higher humidity and/or more regular access to surface water, or lower average meteoric water  $\delta^{18}\text{O}$  values at Gona.

### **Hippopotamidae**

Moderately high  $\delta^{13}\text{C}$  and very low  $\delta^{18}\text{O}$  values for Aramis hippopotamids demonstrate that they fed mainly on fresh grass in or near permanent water. Their average  $\delta^{18}\text{O}$  value (26.9‰) is significantly lower than that of early Pliocene Lothagam (Apak Member) and modern eastern African hippopotamids (81, 102). Gona hippo  $\delta^{18}\text{O}$  values (43) are, on average, significantly lower (23.7‰), indicating lower surface water/meteoric water  $\delta^{18}\text{O}$  compared to Aramis.

### **Suidae**

Suids from Aramis fall into two diet and habitat groups. *Kolpochoerus deheinzlini* is a browser/mixed feeder, with a very wide range of  $\delta^{13}\text{C}$  values (-3.2‰ to -9.9‰), similar to the range of modern bushpig (*Potamochoerus*) collected along transects from savanna to dry montane forest habitats in the Kenya Rift Valley (56). The *Kolpochoerus*  $\delta^{13}\text{C}$  values are substantially less negative than those from the Kibale and Ituri forests (57, 58), indicating the absence of extensive closed canopy forest at Aramis. *Nyanzachoerus kanamensis* and *N. jaegeri* at Aramis were both  $\text{C}_4$  grazers, with mean  $\delta^{13}\text{C}$  values of -1.7‰ and -0.7‰, respectively. Very low average  $\delta^{18}\text{O}$  values for *N. jaegeri* (26.2‰) compared to *N. kanamensis* (30.0‰) indicate the former was more dependant on habitats with fresh grass and/or more permanent surface water. *Kolpochoerus* and *Nyanzachoerus*  $\delta^{13}\text{C}$  values for Aramis are closely similar to those for Gona. However, average  $\delta^{18}\text{O}$  values are substantially lower at Gona (43), again suggesting more permanent water there.

### **Rhinocerotidae**

Rhinocerotidae selected for analysis at Aramis were not identifiable to genus. The wide range of  $\delta^{13}\text{C}$  values (-8.5‰ to +1.6‰) includes two distinct modes: high values (-1.0‰ to +1.6‰) indicate a grazing species, consistent with the morphology and mesowear of *Ceratotherium efficax* (main text), and its modern congener, the white rhino. Intermediate values for the second mode (-2.6‰ to -5.7‰) suggest a mixed feeding species. The most negative value is consistent with the browsing feeding habits of modern *Diceros* (black rhinoceros). A similar range of  $\delta^{13}\text{C}$  values occurs among Gona Rhinocerotidae. The rarity of low  $\delta^{18}\text{O}$  values suggest generally less dependence on permanent water and plants in moist habitats compared to proboscideans. Gona average  $\delta^{18}\text{O}$  values are 5.1‰ lower (43), again suggesting more permanent water compared to the Lower Aramis Member.

### **Equidae**

*Eurygnathohippus* has high  $\delta^{13}\text{C}$  and relatively low  $\delta^{18}\text{O}$  values, indicating water-dependent grazing. Although modern equids such as zebra are pure grazers (103), their  $\delta^{13}\text{C}$  values are not as high as those of other hypergrazing bovids (Bovini, Hippotragini and Alcelaphini). Cerling *et al.* (53) suggest that equids have lower  $\delta^{13}\text{C}$  values because they eat some  $\text{C}_3$  plants, or consume  $^{13}\text{C}$ -depleted subtypes of  $\text{C}_4$  plants. However, this is inconsistent with direct observations of their hypergrazing diets, so they may have

lower values because they do not co-generate as much  $^{13}\text{C}$ -depleted methane and  $^{13}\text{C}$ -enriched  $\text{CO}_2$ . Gona equid  $\delta^{13}\text{C}$  values are 2‰ lower than at Aramis (43), apparently reflecting consumption of small amounts of  $\text{C}_3$  plants. Gona  $\delta^{18}\text{O}$  values are 3.4‰ lower than those from Aramis, again suggesting more permanent water at Gona. Lothagam Apak Member *Eurygnathohippus* has slightly lower average  $\delta^{13}\text{C}$  and similar  $\delta^{18}\text{O}$  values (39).

### **Giraffidae**

Giraffids (*Giraffa* and *Sivatherium*) at Aramis have very low  $\delta^{13}\text{C}$  and very high  $\delta^{18}\text{O}$  values, as expected for canopy-feeding  $\text{C}_3$  folivores. Their  $\delta^{13}\text{C}$  values are significantly lower than from those from Gona (43), suggesting more substantial tree cover at Aramis. High giraffid  $\delta^{13}\text{C}$  values at Gona indicate consumption of some  $\text{C}_4/\text{CAM}$  plants, which is unexpected because they are absent from modern giraffe diets (104). *Giraffa* and *Sivatherium* average  $\delta^{18}\text{O}$  values at Aramis are 36.1‰ and 36.8‰, respectively. One giraffid has among the highest  $\delta^{18}\text{O}$  in the Gona Sagantole Formation (33.8‰), but the average for all Gona Giraffidae is 25‰. These data suggest a substantial ecological difference between the wetter Gona Sagantole Formation sites and the drier Lower Aramis Member.

### **Bovidae**

Bovidae from the Lower Aramis Member include members of six tribes, including Tragelaphini, Bovini, Aepycerotini, Hippotragini, Alcelaphini, and Neotragini. They span the full range of grazing to browsing adaptations. Their carbon isotopic compositions are generally consistent with the dietary adaptations of their modern representatives (105).

Tragelaphines are generally considered browsers, but some species consume small amounts of grass (106). They occupy a wide range of habitats, from mesic forest to arid wooded grassland. Moderately low  $\delta^{13}\text{C}$  values indicate that the Aramis tragelaphines also had diets with very small amounts of  $\text{C}_4$  grass, like those of modern kudu (106-108). Unlike modern bushbuck (*Tragelaphus scriptus*) in the central rift of Kenya and the Kibale Forest of Uganda (56, 57), the canopy effect is not evident in the Lower Aramis Member values, indicating that they did not feed extensively in closed canopy forest habitats. Their low mean and small standard deviation in  $\delta^{13}\text{C}$  ( $-9.8 \pm 0.9\text{‰}$ ) contrasts greatly with the higher mean and SD ( $-7.6 \pm 2.8\text{‰}$ ) for Gona contemporaries (43), which indicates consumption of more  $\text{C}_4$  plants than their modern congeners. However, Gona tragelaphine  $\delta^{13}\text{C}$  values are bimodal, with modal averages of  $-9.3 \pm 1.0\text{‰}$  ( $n = 8$ ), and  $-4.1 \pm 0.8\text{‰}$  ( $n = 4$ ), respectively. The more negative mode is slightly higher than that for Aramis; the higher mode is anomalous for all tragelaphines, including mixed feeders such as nyala and sitatunga (108).

Tragelaphines have the lowest  $\delta^{18}\text{O}$  values among the Lower Aramis Member bovids, and those with values less than  $\sim 30\text{‰}$  were likely to have fed in wetter woodland microhabitats. Gona  $\delta^{18}\text{O}$  values average 25.4‰, which are substantially lower than those at Aramis (31.7‰). Tragelaphines in the Lower Aramis Member apparently occupied more closed but drier habitats than at Gona.

Two genera of Bovini from Aramis may have different dietary adaptations. *Ugandax* sp. indet. from ARA-VP-1 has intermediate  $\delta^{13}\text{C}$  values (-4.4‰), indicating feeding on both  $\text{C}_3$  and  $\text{C}_4$  plants, whereas *Ugandax* cf. *gautieri* from ARA-VP-6 and ARA-VP-17 has a high average  $\delta^{13}\text{C}$  (0.32‰). *Simatherium* has the highest average (2.1‰) in the Aramis sample set, indicating that it was a pure grazer. Both genera have moderately high  $\delta^{18}\text{O}$  values, suggesting feeding in more open habitats away from permanent surface water. Bovini from Gona have substantially lower  $\delta^{13}\text{C}$  values than those of Aramis *Simatherium*, but are closer to *Ugandax* (43). The Gona Bovini mean  $\delta^{18}\text{O}$  value is 5.5‰ lower, indicating greater access to surface water and fresh grass at Gona.

Modern neotragines are small antelopes, and are predominantly browsers and mixed feeders whose very small territories may lack drinking water (109). Neotragines from Aramis have the low/intermediate  $\delta^{13}\text{C}$  values of browse-dominated mixed feeders (56). Their very high mean  $\delta^{18}\text{O}$  value indicates they obtained most of their water from leaves, as do modern savanna neotragines such as dik-dik (*Madoqua*) (43, 56).

Alcelaphini include one individual identified to tribe, and four to the genus *Damalops*. The former has the highest  $\delta^{13}\text{C}$  of the entire Aramis sample set, as expected from the hypergrazing diet of its modern congeners such as the hartebeest and wildebeest (39, 43, 103, 110). With the second-highest  $\delta^{18}\text{O}$  value in the Lower Aramis Member sample set, it probably obtained a significant proportion of its water from water-stressed grasses in the driest open environment in this area. Three *Damalops* individuals also have very high  $\delta^{13}\text{C}$  values, as expected for Alcelaphini. However one has an anomalously low value, indicating a pure  $\text{C}_3$  browsing diet. This tooth should be re-identified and re-sampled to confirm this anomalous result.

*Aepyceros* from Aramis has the high  $\delta^{13}\text{C}$  variance expected of a flexible mixed feeder in grassy woodland habitats, like its modern congener, the impala (53, 56, 80, 83, 84, 108). Its wide range of  $\delta^{18}\text{O}$  values indicates that some individuals were relatively water-independent, and did not feed in humid woodland understory habitats. *Aepyceros* at Gona has similar  $\delta^{13}\text{C}$  values (43). Some variation may represent intra-tooth seasonal variation, which could be large, because some impala populations graze in the wet season and browse in the dry season (82). The average  $\delta^{18}\text{O}$  value of *Aepyceros* at Gona is 9.3‰ lower than at Aramis, which again suggests more permanent water for plants and animals at Gona.

Hippotragines from Aramis have high  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values, as expected from the grazing habits and open habitat preferences of their modern congeners, the oryx, and roan and sable antelope (53).

### Discussion and Conclusions

Relatively low *Kuseracolobus*, giraffid, tragelaphine and *Deinotherium*  $\delta^{13}\text{C}$  values, and low  $\delta^{18}\text{O}$  values for some suids and proboscideans, indicate that small patches of closed canopy forests may have been present at Aramis, although woodlands to grassy woodlands probably dominated the mosaic of floral habitats. A small number of

individuals, mainly alcelaphines, rhinocerotidae, hippotragines and some impala and bovines fed in drier open environments on water-stressed C<sub>4</sub> plants. Open habitat grazers comprise a small proportion of the Aramis mammal assemblage (92). Low  $\delta^{13}\text{C}$  values for Hyaenidae suggests that browsing prey contributed more to their diet compared to their modern congeners in grazer-dominated open savanna environments (56). This is consistent with the dominance of the Aramis fauna by browsing tragelaphines and arboreal colobines (see main text for details).

The comparatively low  $\delta^{13}\text{C}$  values of larger mammals from Aramis suggest more closed habitats than in the penecontemporary *Ar. ramidus*-bearing deposits at Gona and the Apak Member of the Nachukui Formation at Lothagam. Lothagam, where hominids are extremely rare compared to Gona and Aramis (111), was overall the driest of these early Pliocene (4-5 Ma) fossil localities. Penecontemporary sites in the Tugen Hills, Kenya, have small numbers of isotopically analyzed specimens that are identified only to the family level (112), precluding meaningful comparisons to other sites. The larger numbers of specimens from early Pliocene sites in Chad (113), which are identified to the genus level, have generally higher  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values compared to those from the Lower Aramis Member, indicating drier conditions at those sites.

Substantially lower average oxygen isotope ratios for the entire penecontemporary Gona mammal community (43) indicate either more humid and cooler environments, more permanent surface water, and/or lower meteoric water  $\delta^{18}\text{O}$  values. More permanent surface water is consistent with the depositional setting there because most fossils at Gona were recovered from paludal (swampy), fluvial, and marginal lacustrine sediments (114).

The Gona mammal community oxygen isotopic composition most closely resembles that of a savanna woodland mammal community on the Morea Estate, South Africa, which is located in one of the highest rainfall regions of the tropical zone in South Africa (83). Assuming no diagenesis, the similarity of Gona to Morea may reflect the abundance of permanent surface water rather than higher rainfall. The predominantly riparian setting of Gona contrasts with the Lower Aramis Member of the Sagantole Formation in the Middle Awash, where fluvio-lacustrine sediments are virtually absent, and fossils were recovered primarily from terrestrial distal floodplain sediments and paleosols (115, 116). The higher, less compressed range of herbivore enamel oxygen isotope ratios at Aramis, particularly the large difference between water-dependent hippopotamids and canopy-feeding giraffids, is consistent with a drier setting far from riparian environment (77). As noted in the main text, the high range of  $\delta^{18}\text{O}$ --particularly the large difference between water-independent (evaporation-sensitive) Giraffidae (*Giraffa* and *Sivatherium*) and water-dependent, (evaporation-insensitive) Hippopotamidae (9.6‰)--indicates a mean annual evaporative water deficit of approximately 1,500 mm (77). This interpretation is consistent with other evidence for dry woodlands in the western three-quarters of the Lower Aramis Member paleotransect (92, 116).

The absence of carbon isotopic evidence for extensive closed canopy environments at Gona suggests that the environments sampled were relatively unstable, frequently resetting the floral habitat succession to open habitats, perhaps due to frequent fluctuations in lake levels or to rapid migration of fluvial channel systems, and/or frequent tectonic activity. Although the wider range and generally higher oxygen isotope ratios of Aramis fauna suggest a drier overall environment compared to Gona, lower  $\delta^{13}\text{C}$  values demonstrate the presence of more closed wooded habitats, including patches of closed canopy forest that were dense enough to generate the lowest *Kuseracolobus*  $\delta^{13}\text{C}$  values. This may signal a more stable, rift-axial landscape at Aramis, with a more developed floral succession.

Comparisons of the isotopic composition of Aramis and Gona mammals are predicated on the assumption that the Gona samples preserve their *in-vivo* isotopic composition. Levin *et al.* (43) state “[t]he tooth enamel data from fossil herbivores at Gona make it clear that *Ardipithecus* lived among a guild of species whose diet was dominated by  $\text{C}_4$  grass, and where there is no closed canopy vegetation.” However, the compressed range of  $\delta^{13}\text{C}$  values for Gona species is not consistent with an open habitat with high water availability for plant growth. As noted above in the section on stable carbon and oxygen isotope variation in tropical ecosystems, water stress increases  $\text{C}_3$  plant leaf  $\delta^{13}\text{C}$  (51). Therefore the humid Gona waterside setting should have lower  $\delta^{13}\text{C}$  values for giraffids, *Kuseracolobus*, *Pliopapio* and tragelaphines. However, they all have higher  $\delta^{13}\text{C}$  values than expected for their modern congeners in a wide range of humid to semi-arid habitats, and are substantially higher than their congeners at Aramis.

Compression of Gona  $\delta^{13}\text{C}$  values is also evinced on the  $\text{C}_4$  side of the food web. As noted above, water stress does not significantly affect  $\text{C}_4$  plant  $\delta^{13}\text{C}$  (50, 51). Several grazing species at Gona, including *Eurygnathohippus*, Bovini, Hippotragini and *Anancus*, have mean  $\delta^{13}\text{C}$  values that are 1-2‰ more negative than their congeners at Aramis. If Gona were more open, then it should have, on average, slightly higher grazer  $\delta^{13}\text{C}$  compared to Aramis. Because oxygen isotopes are more susceptible to diagenesis than carbon isotopes (84), a small compression of the carbon isotope range could be accompanied by a larger shift and compression of the Gona enamel carbonate  $\delta^{18}\text{O}$  values toward the isotopic composition of the diagenetic phase. The substantial difference in oxygen isotope ratios between Aramis and Gona may thus be more apparent than real. If so, then another foundation for the inference that *Ardipithecus* occupied more open grassy habitats at Gona should be reconsidered.

The Lower Aramis Member can be placed in a broader eastern and central African late Neogene comparative environmental context. Enamel carbon and oxygen isotopes from Late Miocene (6.5-5 Ma) fossil assemblages at Gona (Adu-Asa Formation) and Lothagam (Nawata Formation) tend to be lower than those of all Plio-Pleistocene sites (3-40, 43, 102) including Aramis. Late Miocene paleosol carbonates from the Adu-Asa Formation at Gona (43) and *Ar. kadabba*-bearing localities in the Middle Awash (117) are also consistent with the results of enamel stable isotopes. At Lothagam, paleosol carbonate data are insufficient to identify significant differences between the early Pliocene Apak Member and the late Miocene Upper and Lower Nawata members (38).

Late Miocene sites in Chad also have lower herbivore enamel  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  relative to later sites in Chad (113), but are overall higher relative to those in the Lower Aramis Member. Later Pliocene and early Pleistocene eastern and central African fossil sites at Gona in Ethiopia, Chad, Laetoli in Tanzania, and Tugen Hills, Lothagam and Kanapoi in Kenya (4.0-2.5 Ma) tend to have higher enamel  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values (38, 42, 43, 111-113). These data might indicate the presence of more closed habitats from 7 to 5 million years ago (Ma), and the spread of more open habitats after 4 Ma, but this is a hypothesis requiring further testing on controlled biological and geological samples.

Within the Lower Aramis Member *Ar. ramidus* is most common in the more wooded portion of the available paleotranssect (116). The presence of herbivores with high enamel  $\delta^{13}\text{C}$  values demonstrates the presence of grassy settings in the region. However, this does not directly translate to the abundance of grassy versus wooded biotopes because most herbivore species can be classified as either grazing ( $\text{C}_4$ ) or browsing ( $\text{C}_3$ ) dietary specialists whose diet selection is not strongly influenced by the overall abundance of these plant types (118, 119). Moreover, grazing herbivores tend to be more abundant than browsers because the latter are more selective feeders on generally more unpalatable, chemically defended plants (76, 120, 121). Therefore the frequency of species with high enamel  $\delta^{13}\text{C}$  values does not translate directly into an environmental signal indicating grassland. Paleosol carbonate carbon isotopes provide an unbiased estimation of the proportions of woody and grassy plant biomass (122), and these data demonstrate that the Sagantole Formation at Gona and the Lower Aramis Member supported predominantly woodland to grassy woodland environments (43, 116).

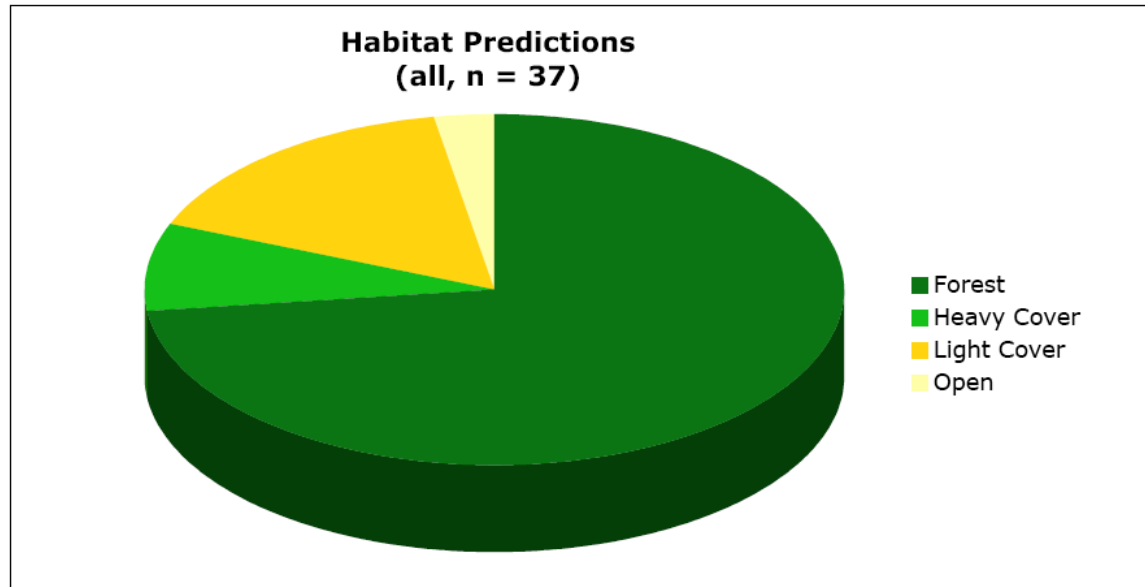
As noted above, *Ardipithecus ramidus* ranged across the more wooded portions of the Lower Aramis Member landscape. The isotopic composition of *Ardipithecus* tooth enamel in the Lower Aramis Member is consistent with woodland habitat preferences, and is supported by evidence of the habitat preferences of associated species as well as paleosol stable isotope ratios. The rarity of hominids in more open habitats at other late Miocene and early Pliocene sites is consistent with the new isotopic data, and suggests that although a mosaic of wooded grassland to predominantly woodland habitats was available prior to ~4 Ma, the earliest hominids preferred more closed local environments.

Isotopic analyses of late Miocene and early Pliocene hominids from other sites have not been reported, but comparisons can be made with later hominids from South Africa and Tanzania. The oxygen isotopic composition of *Ardipithecus* is approximately 2.5‰ higher than that of *Au. africanus* and indistinguishable from that of *Au. robustus* (101, 123). However, oxygen isotope ratios have not been systematically reported for southern African mammals, precluding further comparisons and interpretations.

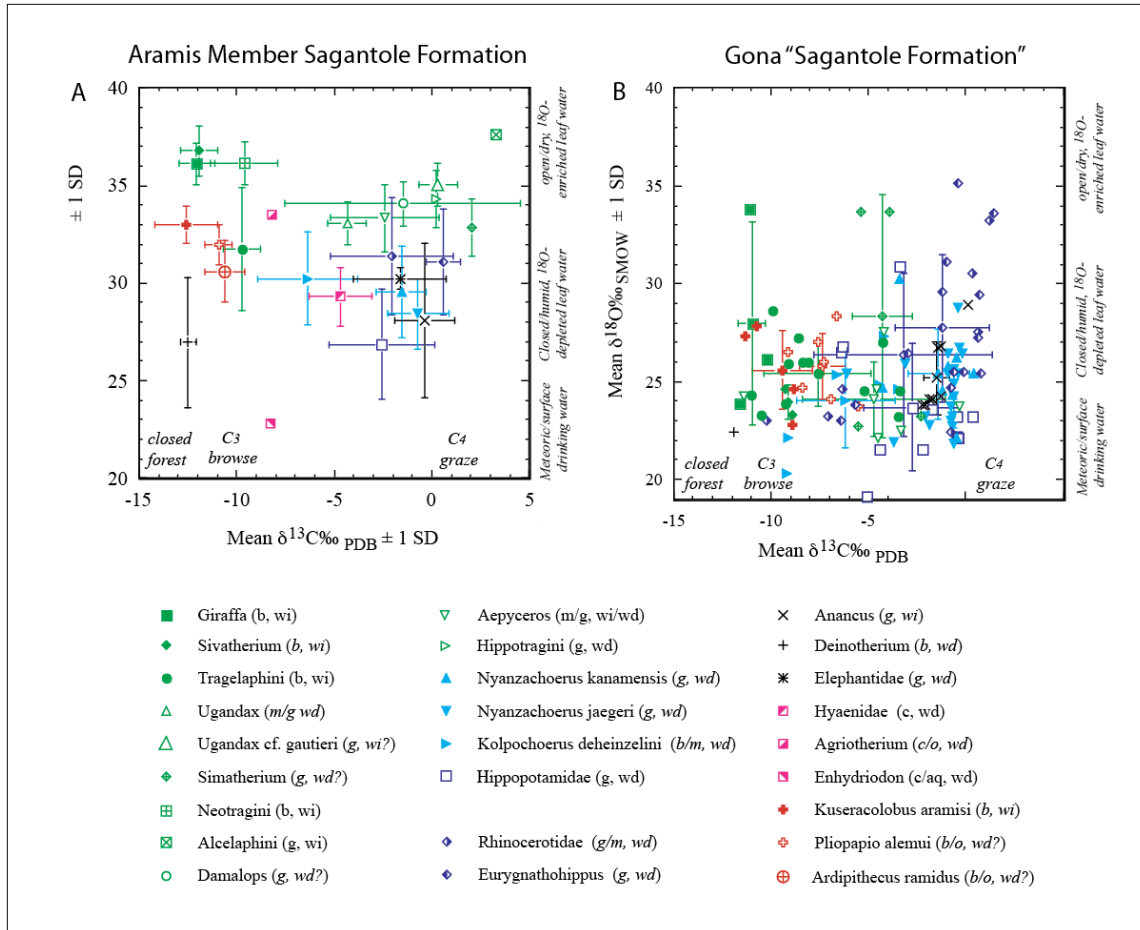
Carbon isotopic analyses of 45 individuals representing several Plio-Pleistocene hominid species ranging in age from ~3.0 to 1.5 Ma permit informed comparisons with *Ardipithecus ramidus*. *Au. africanus*, *Au. robustus*, and early *Homo* from South Africa (47), and *H. habilis* from Olduvai Gorge (48), have mean mean  $\delta^{13}\text{C}$  values ranging

from  $-6.8$  to  $-8.2\text{‰}$ , and all have very high intraspecific variation. These data demonstrate that they were flexible mixed feeders on widely varying proportions of  $C_3$  and  $C_4$ /CAM-based resources. No trend toward increasing  $C_4$ /CAM consumption is apparent through time (48, 98, 101). However, *Au. boisei* from Olduvai Gorge and Peninj, Tanzania, have  $\delta^{13}\text{C}$  values averaging  $-1.0\text{‰}$ , suggesting diets with 77-81%  $C_4$  (48).

Compared to *Ardipithecus*, all analyzed later hominid species samples indicate consumption of substantially more  $C_4$ /CAM-based foods. These foods may have included grasses, fruits, and succulent leaves of CAM plants, the starchy parts of sedges, termites and other  $C_4$ -feeding insects, and the meat of  $C_4$ -feeding vertebrate animals (47, 48). The low  $\delta^{13}\text{C}$  values of most *Ar. ramidus* individuals at Aramis indicates a diet more similar to that of modern chimpanzees in savanna woodlands (45, 46) and baboons (97) than to the diets of later Plio-Pleistocene hominids. These findings are consistent with morphological evidence from the *Ardipithecus* masticatory system (124).



**Figure S1. Pie chart of habitat predictions for Aramis based on the “ecomorphology” of bovid astragali and phalanges sufficiently complete for measurement (n=37).** This includes both “significant” and “non-significant” predictions (see Text S1).



**Figure S2. Stable carbon and oxygen isotope ratios comparing Aramis and Gona.**

Plotted as bivariate means  $\pm$  one standard deviation  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of mammal tooth enamel from the Lower Aramis Member of the Sagantole Formation in the Middle Awash Valley (**A**), and taxa from the Sagantole Formation at Gona (**B**) that were also analyzed from the Lower Aramis Member. Individual values for Gona samples are also plotted in (B). See Text S3.

**Table S1. Distribution data for large mammal taxa from the Lower Aramis Member of the Sagantole Formation, in the Middle Awash, Ethiopia.** Localities arranged west to southeast along the Lower Aramis Member erosional exposure arc. Numbers of identified specimens (dental) correspond to large mammal taxa per Text Fig. 1C. Note the relative faunal poverty of the large Sagantole localities (yellow column) at the southeastern pole of the paleotranssect.

Large mammal taxa	WEST					SOUTHEAST
	KUS-VP-2	ARA-VP-17	ARA-VP-6	ARA-VP-1	SAG-VP-7	SAG-VP-1+3
<b>ARTIODACTYLA</b>						
Hippopotamidae indet.	1		1	15	15	1
<i>Cainochoerus</i> sp. nov.	1		2	4		
<i>Kolpochoerus deheinzlini</i>	3	1	5	11	1	
<i>Nyanzachoerus jaegeri</i>			1	6	3	
<i>Nyanzachoerus kanamensis</i>	1		2	35	2	
Neotragini			11	12		
cf. <i>Aepyceros</i>	1		4	51	15	
<i>Damalops</i> sp.			2	6	1	
? <i>Gazella</i>				1		
cf. <i>Simatherium</i>			1	4		
cf. <i>Ugandax</i> cf. <i>gautieri</i>		1	6	3	1	
<i>Ugandax</i> sp.				2		
<i>Tragelaphus kyloae</i>	21	5	64	588	42	
<i>Praedamalis</i>			1	1		
<i>Kobus preoricornis</i>			1	1	2	
<i>Giraffa</i> sp.			3	8		
<i>Sivattherium</i> sp.				9		
Alcelaphini All			2	8	2	
Tragelaphini All	21	6	67	591	42	
Neotragini All		1	11	13	0	
Aepycerotini All	1		4	53	15	
Antilopini All			1	1		
Bovini All		1	7	10	1	
Hippotragini All			1	1		
Reduncini All			3	13	4	
<b>CARNIVORA</b>						
Hyaenidae			28	42	2	1
Canidae indet.						
<i>Enhydriodon</i> sp.				1		
cf. <i>Lutra</i> sp.			1			
cf. <i>Torolutra</i> sp.			1			
<i>Agriotherium</i> sp.		1		2	2	
cf. <i>Dinofelis</i> sp.			2		1	
? <i>Dinofelis</i> sp.				1		

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<i>Felis</i> small			3	6		
<i>Felis</i> medium			2	2		
<i>Felis</i> indet.			1	2		2
<i>Machairodus</i> sp.			1			1
<i>Panthera</i> sp.			1			
<b>PERISSODACTYLA</b>						
<i>Ceratotherium</i> sp. nov.				5	1	
<i>Diceros</i> sp.				1		
<i>Eurygnathohippus</i> sp.	2		8	45	6	1
<b>PRIMATES</b>						
<i>Pliopapio alemui</i>	11	1	55	164	7	
<i>Kuseracolobus aramisi</i>	20	2	69	225	8	
<i>Ardipithecus ramidus</i>	6	1	45	54	3	
<b>PROBOSCIDEA</b>						
<i>Anancus</i> sp.				3		
<i>Deinotherium</i> sp.				2		
Elephantidae indet.				10	1	
<b>TUBULIDENTATA</b>						
<i>Orycteropus</i> sp.	1		6	24		
Outcrop area estimate (sq. m)	3808	4322	18116	90646	21096	205621
Total <i>Ardipithecus</i>	7	1	44	49	3	0
Total catalogued specimens	225	71	2173	3199	225	10

**Table S2. Habitat predictions for Aramis based on the “ecomorphology” of bovid astragali and phalanges.** AST = Astragalus, PPX = Proximal Phalanx, IPX = Intermediate Phalanx, DPX = Distal Phalanx. Significant predictions are those where the specific probability of the prediction (from the discriminant function) indicates that the classification is accurate in > 95% of cases (2).

<b>ELEMENT</b>	<b>HABITAT</b>	<b># OF SPECIMENS</b>	<b># SIGNIFICANT (&gt;95%)</b>
AST	Forest	11	6
	Heavy Cover	1	1
	Light Cover	0	0
	Open	0	0
PPX	Forest	3	0
	Heavy Cover	0	0
	Light Cover	2	0
	Open	0	0
IPX	Forest	6	4
	Heavy Cover	0	0
	Light Cover	3	0
	Open	1	0
DPX	Forest	7	0
	Heavy Cover	2	0
	Light Cover	1	0
	Open	0	0
<b>TOTAL</b>	<b>Forest</b>	<b>27</b>	<b>10</b>
	<b>Heavy Cover</b>	<b>3</b>	<b>1</b>
	<b>Light Cover</b>	<b>6</b>	<b>0</b>
	<b>Open</b>	<b>1</b>	<b>0</b>

**Table S3: Table showing bovid-based habitat predictions for Aramis by “morphogroup.”** All astragali and phalanges, including those too fragmentary to measure, were divided into morphological groups based on shared size and shape. The number of specimens in each morphogroup is given in parentheses. For each morphotype, the habitat predictions for those specimens sufficiently complete to measure are given. It is likely that the remainder of specimens in the morphotype share the same habitat prediction, despite being too fragmentary to measure directly. This was done in an effort to lessen the possible bias due to potential size-based differences in fragmentation rates (see text).

<b>MORPHOGROUP</b>	<b>HABITAT</b>	<b># MEASURED SPECIMENS</b>	<b># SIGNIFICANT (&gt;95%)</b>
I (n = 11)	Forest	3	2
	Heavy Cover	0	0
	Light Cover	3	0
	Open	0	0
II (n = 16)	Forest	5	2
	Heavy Cover	0	0
	Light Cover	3	0
	Open	1	0
III (n = 38)	Forest	18	6
	Heavy Cover	2	0
	Light Cover	0	0
	Open	0	0
IV (n = 2)	Forest	1	0
	Heavy Cover	1	1
	Light Cover	0	0
	Open	0	0

**Table S4. Mesowear data for large mammal taxa from the Lower Aramis Member of the Sagantole Formation, in the Middle Awash Valley, Ethiopia.**

Specimen ID	Element	Side	Shape	Relief	Score
<b><i>Aepyceros</i></b>					
ARA-VP-1/232	M2	rt.	round	high	3
ARA-VP-1/274	M3	rt.	sharp	high	2
ARA-VP-1/419	M3	lt.	round	high	3
ARA-VP-1/520	M2	lt.	round	high	3
ARA-VP-1/520	M3	lt.	round	high	3
ARA-VP-1/106	M3	lt.	round	high	3
ARA-VP-1/1336	M3	lt.	round	high	3
ARA-VP-1/1508	M2	lt	round	high	3
ARA-VP-1/2535	M1	lt.	round	high	3
ARA-VP-1/2563	M3	lt.	round	high	3
ARA-VP-6/6	M2	rt.	round	high	3
ARA-VP-6/2122	M3	lt.	round	high	2
SAG-VP-7/73	M2	lt.	round	high	3
SAG-VP-7/73	M3	lt	sharp	high	2
					2.8
<b><i>Alcelaphini</i></b>					
ARA-VP-1/522	M2	lt	round	high	5
ARA-VP-7/121	M2	lt.	round	high	3
					4
<b><i>Bovini</i></b>					
ARA-VP-1/1904	M2	rt.	round	high	4
ARA-VP-6/79	M2	lt.	round	high	3
ARA-VP-6/451	M2	rt.	blunt	low	6
					4.3
<b><i>Giraffa</i></b>					
ARA-VP-1/88	M2?	lt	round	high	3
ARA-VP-1/2455	M2?	lt.	sharp	v. high	2
ARA-VP-1/2839	M2?	rt.	sharp	v. high	2
ARA-VP-6/86	M2?	lt.	sharp	v. high	2
ARA-VP-6/438	M1	lt.	sharp	v. high	2
ARA-VP-6/438	M2	lt.	sharp	high	2

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					2.2
<b>Neotragines</b>					
ARA-VP-6/460	M2	lt.	sharp	high	2
ARA-VP-6/1257	M2	lt.	sharp	high	1
					1.5
<b>Tragelaphines</b>					
ARA-VP-1/524	M2	rt.	v. high	round	3
ARA-VP-1/1939	M2	rt.	v. high	sharp	2
ARA-VP-1/3005	M3	lt.	v. high	sharp	2
ARA-VP-1/3007	M2	rt.	high	round	3
ARA-VP-1/3117	M2	rt.	high	round	3
ARA-VP-1/38	M3	lt.	v. high	sharp	1
ARA-VP-1/58	M2	lt.	v. high	sharp	2
ARA-VP-1/60	M2	lt.	v. high	sharp	1
ARA-VP-1/61	M2	rt.	v. high	sharp	1
ARA-VP-1/262	M2	lt.	v. high	round	2
ARA-VP-1/349	M3	lt.	high	round	4
ARA-VP-1/373	M3	rt.	high	sharp	2
ARA-VP-1/415	M3	lt.	v. high	sharp	2
ARA-VP-1/431	M3	lt.	high	round	3
ARA-VP-1/526	M3	lt.	v. high	sharp	2
ARA-VP-1/667	M3	lt.	v. high	sharp	2
ARA-VP-1/827	M3	rt.	v. high	sharp	1
ARA-VP-1/3355	M3	lt.	v. high	sharp	1
ARA-VP-6/1254	M3	lt.	v. high	sharp	1
ARA-VP-17/18	M3	lt.	v. high	sharp	1
					2.0
<b><i>Eurygnathohippus</i></b>					
ARA-VP-1/995	M1	rt.	blunt	low	5
ARA-VP-1/2424	M1	rt.	blunt	low	7
ARA-VP-2/4	M1	rt.	round	low	4
ARA-VP-3/1D	M1	lt.	blunt	low	7
ARA-VP-9/2	M1	rt.	blunt	low	5
ARA-VP-3/1E	M2	lt.	blunt	low	5
ARA-VP-6/12	M2	lt.	blunt	low	6

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ARA-VP-6/18	M2	rt.	blunt	low	7
ARA-VP-9/2	M2	rt.	blunt	low	6
ARA-VP-12/5	M2	rt.	blunt	low	5
ARA-VP-1/995	M3	lt.	blunt	low	7
ARA-VP-1/498	M3	rt.	blunt	low	5
ARA-VP-1/2704	M3	lt.	blunt	low	6
ARA-VP-2/4	M3	rt.	round	low	4
ARA-VP-3/1F	M3	lt.	blunt	low	6
ARA-VP-4/7	M3	lt.	blunt	low	7
ARA-VP-9/2	M3	rt.	high	round	3 (early wear)
ARA-VP-3/33	M3	rt.	blunt	low	7
ARA-VP-1/995	P4	lt.	blunt	low	5
ARA-VP-1/2518	P4	rt.	blunt	low	7
ARA-VP-2/4	P4	lt.	blunt	low	5
ARA-VP-3/1C	P4	lt.	blunt	low	7
ARA-VP-6/18	P4	rt.	blunt	low	6
ARA-VP-12/5	P4	rt.	blunt	low	6
					5.75

**Table S5. Stable carbon and oxygen isotope ratios of mammalian tooth enamel from the Lower Aramis Member of the Sagantole Formation, in the Middle Awash Valley, Ethiopia.** Three teeth from the *ARA-VP-6/500* skeleton have been averaged before calculating the mean  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of *Ardipithecus ramidus*. See main text and Text S3 for details.

Species	Locality	Catalog #	LAB ID #	Analysis ID #	$\delta^{13}\text{C}\text{‰}_{\text{pdb}}$	$\delta^{18}\text{O}\text{‰}_{\text{pdb}}$	$\delta^{18}\text{O}\text{‰}_{\text{smow}}$
<i>Kuseracolobus aramisi</i>	ARA-VP-1	70	2	14140	-12.7	3.6	34.6
<i>Kuseracolobus aramisi</i>	ARA-VP-1	1380a	51	16230	-13.0	2.1	33.0
<i>Kuseracolobus aramisi</i>	ARA-VP-1	1483b	63	16243	-13.2	2.9	33.9
<i>Kuseracolobus aramisi</i>	ARA-VP-1	1483c	64	16244	-11.5	1.5	32.4
<i>Kuseracolobus aramisi</i>	ARA-VP-1	1713b	74	16255	-14.2	2.5	33.5
<i>Kuseracolobus aramisi</i>	ARA-VP-1	2180a	82	16972	-10.7	-0.1	30.8
<i>Kuseracolobus aramisi</i>	ARA-VP-1	2180b	108	17336	-10.7	1.0	32.0
<i>Kuseracolobus aramisi</i>	ARA-VP-1	2652	105	17467	-13.4	3.1	34.1
<i>Kuseracolobus aramisi</i>	ARA-VP-1	2853	111	17470	-7.5	1.2	32.1
<i>Kuseracolobus aramisi</i>	ARA-VP-1	2950	113	17342	-11.7	1.9	32.8
<i>Kuseracolobus aramisi</i>	ARA-VP-6	500b	94	17321	-12.9	1.3	32.2
<i>Kuseracolobus aramisi</i>	ARA-VP-6	500c	95	17322	-12.6	1.8	32.8
<i>Kuseracolobus aramisi</i>	ARA-VP-6	771a	141	17475	-13.8	3.0	34.0
<i>Kuseracolobus aramisi</i>	ARA-VP-6	771b	142	17422	-13.5	2.5	33.5
<i>Kuseracolobus aramisi</i>	ARA-VP-6	771c	143	17476	-13.7	1.3	32.2
<i>Kuseracolobus aramisi</i>	ARA-VP-6	771d	144	17424	-13.9	1.2	32.1
<i>Kuseracolobus aramisi</i>	ARA-VP-6	1686	150	17431	-13.0	1.8	32.8
<i>Kuseracolobus aramisi</i>	KUS-VP-2	118a	160	17444	-12.1	2.9	33.9
<i>Kuseracolobus aramisi</i>	KUS-VP-2	118b	161	17445	-12.8	3.0	34.0
<i>Kuseracolobus aramisi</i>	SAG-VP-7	1	162	17446	-14.8	1.7	32.6
<b>Mean</b>					<b>-12.59</b>	<b>1.99</b>	<b>32.96</b>
<b>1 St. dev.</b>					<b>1.62</b>	<b>0.92</b>	<b>0.95</b>
<b>N</b>	<b>20</b>				<b>20</b>	<b>20</b>	<b>20</b>
<i>Pliopapio alemui</i>	ARA-VP-1	133	7	14246	-11.0	1.5	32.5
<i>Pliopapio alemui</i>	ARA-VP-1	1316a	42	16220	-11.1	2.1	33.1
<i>Pliopapio alemui</i>	ARA-VP-1	1316b	43	16221	-11.1	2.3	33.3
<i>Pliopapio alemui</i>	ARA-VP-1	1483a(p)	62	16242	-11.1	-0.9	30.0
<i>Pliopapio alemui</i>	ARA-VP-1	1675a	70	16250	-11.8	2.2	33.2
<i>Pliopapio alemui</i>	ARA-VP-1	1713a	73	16254	-11.2	0.9	31.8
<i>Pliopapio alemui</i>	ARA-VP-1	2879	112	17341	-11.9	0.0	31.0
<i>Pliopapio alemui</i>	ARA-VP-1	2954	114	17343	-11.7	1.0	32.0
<i>Pliopapio alemui</i>	ARA-VP-6	771e	145	17425	-10.4	1.1	32.0
<i>Pliopapio alemui</i>	ARA-VP-6	771f	146	17426	-11.1	1.7	32.6
<i>Pliopapio alemui</i>	ARA-VP-6	771g	147	17427	-9.5	-0.2	30.7
<i>Pliopapio alemui</i>	SAG-VP-7	10a	166	17450	-10.0	0.0	30.9
<i>Pliopapio alemui</i>	SAG-VP-7	10b	167	17451	-10.4	1.4	32.3
<i>Pliopapio alemui</i>	SAG-VP-7	10c	168	17453	-10.6	1.3	32.2

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<b>Mean</b>					<b>-10.91</b>	<b>1.03</b>	<b>31.97</b>
<b>1 St. dev.</b>					<b>0.69</b>	<b>0.97</b>	<b>1.00</b>
<b>N</b>	<b>14</b>				<b>14</b>	<b>14</b>	<b>14</b>
<i>Ardipithecus ramidus</i>	ARA-VP-1	700	23	14230	-8.5	1.8	32.7
<i>Ardipithecus ramidus</i>	ARA-VP-1	1818	76	16257	-10.7	0.0	30.9
<i>Ardipithecus ramidus</i>	ARA-VP-1	3291	84	17310	-11.2	-1.8	29.0
<i>Ardipithecus ramidus</i>	ARA-VP-1	3290	86	17312	-10.3	-0.9	30.0
<i>Ardipithecus ramidus</i>	ARA-VP-1	<b>500-90</b>	121	17399	-10.2	1.1	32.1
<i>Ardipithecus ramidus</i>	ARA-VP-1	<b>500-113</b>	122	17400	-10.2	1.3	32.3
<i>Ardipithecus ramidus</i>	ARA-VP-1	<b>500-115</b>	123	17401	-10.8	2.1	33.0
<b>Mean</b>					<b>-10.25</b>	<b>0.50</b>	<b>31.43</b>
<b>1 St. dev.</b>					<b>0.87</b>	<b>1.45</b>	<b>1.50</b>
<b>N</b>		<b>7</b>			<b>7</b>	<b>7</b>	<b>7</b>
Hyaenidae	ARA-VP-1	326	14	14218	-1.8	0.1	31.0
Hyaenidae	ARA-VP-1	931	28	14236	-5.2	-0.6	30.3
Hyaenidae	ARA-VP-1	1195	38	16179	-4.9	-0.9	30.0
Hyaenidae	ARA-VP-1	1342	47	16225	-4.1	-0.5	30.4
Hyaenidae	ARA-VP-1	1342	48	16226	-4.5	-0.7	30.2
Hyaenidae	ARA-VP-1	1528	66	16246	-5.2	-1.3	29.5
Hyaenidae	ARA-VP-1	2423	100	17327	-2.0	-1.2	29.7
Hyaenidae	ARA-VP-6	534	131	17410	-6.6	-2.1	28.8
<b>Mean</b>					<b>-4.29</b>	<b>-0.90</b>	<b>29.98</b>
<b>1 St. dev.</b>					<b>1.66</b>	<b>0.64</b>	<b>0.66</b>
<b>N</b>	<b>8</b>				<b>8</b>	<b>8</b>	<b>8</b>
<i>cf. Crocuta aff. dietrichi</i>	ARA-VP-1	2809	109	17337	-4.67	-5.31	25.44
<i>cf. Crocuta aff. dietrichi</i>	ARA-VP-6	517	130	17409	-6.39	-2.16	28.68
<b>Mean</b>					<b>-5.53</b>	<b>-3.74</b>	<b>27.06</b>
<b>1 St. dev.</b>					<b>1.22</b>	<b>2.23</b>	<b>2.29</b>
<b>N</b>	<b>2</b>				<b>2</b>	<b>2</b>	<b>2</b>
<i>cf. Hyaenictis</i>	ARA-VP-6	1831	152	17433	-6.1	-2.4	28.4
<i>Agriotherium</i>	ARA-VP-1	1302	41	16219	-8.2	2.5	33.5
<i>Enhydriodon</i>	ARA-VP-1	2113	78	16259	-8.2	-7.9	22.8
<i>Anancus</i>	ARA-VP-1	450	18	14222	-0.4	1.3	32.2
<i>Anancus</i>	ARA-VP-1	1322	44	16968	1.4	-7.2	23.5
<i>Anancus</i>	ARA-VP-1	1357	49	16227	0.4	-0.3	30.6
<i>Anancus</i>	ARA-VP-1	1757	75	16256	-2.8	-6.4	24.3
<i>Anancus</i>	SAG-VP-7	8a	164	17448	-0.5	-1.1	29.7
<b>Mean</b>					<b>-0.36</b>	<b>-2.75</b>	<b>28.08</b>
<b>1 St. dev.</b>					<b>1.55</b>	<b>3.81</b>	<b>3.93</b>
<b>N</b>	<b>5</b>				<b>5</b>	<b>5</b>	<b>5</b>

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<i>Deinotherium</i>	ARA-VP-1	1401a	54	16233	-12.6	-5.8	24.9
<i>Deinotherium</i>	ARA-VP-1	1478	61	16241	-12.6	0.0	31.0
<i>Deinotherium</i>	ARA-VP-1	2742	106	17334	-11.9	-2.5	28.3
<i>Deinotherium</i>	KUS-VP-2	64b	157	17438	-12.9	-7.1	23.6
<b>Mean</b>					<b>-12.49</b>	<b>-3.84</b>	<b>26.95</b>
<b>1 St. dev.</b>					<b>0.41</b>	<b>3.21</b>	<b>3.31</b>
<b>N</b>	<b>4</b>				<b>4</b>	<b>4</b>	<b>4</b>
Elephantidae	ARA-VP-1	1582	67	16247	-0.2	0.2	31.1
Elephantidae	ARA-VP-6	494a	90	17316	-1.0	-1.0	29.9
Elephantidae	ARA-VP-6	494b	91	17317	-0.7	-0.5	30.4
Elephantidae	ARA-VP-6	494c	92	17319	-1.1	-1.3	29.5
Elephantidae	KUS-VP-2	64a	156	17437	-6.4	-1.0	29.9
Elephantidae	SAG-VP-7	8b	165	17449	-0.5	-0.4	30.5
<b>Mean</b>					<b>-1.64</b>	<b>-0.66</b>	<b>30.23</b>
<b>1 St. dev.</b>					<b>2.36</b>	<b>0.53</b>	<b>0.55</b>
<b>N</b>	<b>6</b>				<b>6</b>	<b>6</b>	<b>6</b>
Hippopotamidae	ARA-VP-1	2120	79	16977	-2.4	-7.0	23.7
Hippopotamidae	ARA-VP-1	2807	107	17355	-5.4	-5.3	25.4
Hippopotamidae	ARA-VP-6	764a	133	17412	-3.3	-2.2	28.7
Hippopotamidae	ARA-VP-6	764b	134	17471	0.4	-1.1	29.8
Hippopotamidae	ARA-VP-6	764b-2	135	17414	0.5	-0.8	30.1
Hippopotamidae	ARA-VP-6	764c	136	17472	-3.5	-2.4	28.4
Hippopotamidae	KUS-VP-2	66a	159	17443	-7.5	-9.0	21.6
Hippopotamidae	SAG-VP-7	59	177	17462	-1.6	-4.0	26.8
Hippopotamidae	SAG-VP-7	123	179	17465	-0.3	-3.4	27.4
<b>Mean</b>					<b>-2.57</b>	<b>-3.91</b>	<b>26.87</b>
<b>1 St. dev.</b>					<b>2.69</b>	<b>2.77</b>	<b>2.85</b>
<b>N</b>	<b>9</b>				<b>9</b>	<b>9</b>	<b>9</b>
<i>Nyanzachoerus kanamensis</i>	ARA-VP-1	184	8	14211	-2.0	0.7	31.7
<i>Nyanzachoerus kanamensis</i>	ARA-VP-1	302	11	14214	-2.0	0.7	31.6
<i>Nyanzachoerus kanamensis</i>	ARA-VP-1	304	12	14215	0.7	0.2	31.1
<i>Nyanzachoerus kanamensis</i>	ARA-VP-1	988	32	15465	-3.1	-2.6	28.3
<i>Nyanzachoerus kanamensis</i>	ARA-VP-1	996	34	16175	-2.5	0.5	31.5
<i>Nyanzachoerus kanamensis</i>	ARA-VP-1	1476a	57	16236	-2.3	-5.0	25.8
<i>Nyanzachoerus kanamensis</i> (advanced)	ARA-VP-1	2393	97	17324	0.1	-0.9	29.9
<i>Nyanzachoerus kanamensis</i> (advanced)	ARA-VP-1	2821	110	17338	-1.4	-4.1	26.7
<b>Mean</b>					<b>-1.56</b>	<b>-1.31</b>	<b>29.56</b>
<b>1 St. dev.</b>					<b>1.29</b>	<b>2.29</b>	<b>2.36</b>
<b>N</b>	<b>8</b>				<b>8</b>	<b>8</b>	<b>8</b>
<i>Nyanzachoerus jaegeri</i>	ARA-VP-1	1476b	58	16237	-1.5	-4.5	26.2
<i>Nyanzachoerus jaegeri</i>	ARA-VP-1	1476d	60	16239	-2.7	-4.7	26.1
<i>Nyanzachoerus jaegeri</i>	ARA-VP-1	2410	98	17325	0.9	-2.1	28.8

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<i>Nyanzachoerus jaegeri</i>	ARA-VP-1	2650	104	17332	-0.1	-0.1	30.8
<i>Nyanzachoerus jaegeri</i>	SAG-VP-7	3	163	17447	0.3	-1.2	29.7
<i>Nyanzachoerus jaegeri</i>	SAG-VP-7	47	175	17460	0.8	-3.1	27.7
<i>Nyanzachoerus jaegeri</i>	SAG-VP-7	122	178	17479	-2.7	-1.2	29.6
<b>Mean</b>					<b>-0.70</b>	<b>-2.41</b>	<b>28.43</b>
<b>1 St. dev.</b>					<b>1.56</b>	<b>1.76</b>	<b>1.81</b>
<b>N</b>	<b>7</b>				<b>7</b>	<b>7</b>	<b>7</b>
<i>Kolpochoerus deheinzeli</i>	ARA-VP-1	645	20	14965	-3.2	1.6	32.5
<i>Kolpochoerus deheinzeli</i>	ARA-VP-1	806	26	14234	-9.1	-0.1	30.8
<i>Kolpochoerus deheinzeli</i>	ARA-VP-1	986	31	15464	-7.9	0.0	30.9
<i>Kolpochoerus deheinzeli</i>	ARA-VP-1	1250	39	16180	-5.2	-1.3	29.6
<i>Kolpochoerus deheinzeli</i>	ARA-VP-1	1476c	59	16238	-9.9	-4.9	25.9
<i>Kolpochoerus deheinzeli</i>	ARA-VP-1	1706	71	16252	-4.7	1.8	32.8
<i>Kolpochoerus deheinzeli</i>	ARA-VP-1	2611	103	17331	-4.8	-1.8	29.1
<b>Mean</b>					<b>-6.39</b>	<b>-0.66</b>	<b>30.23</b>
<b>1 St. dev.</b>					<b>2.56</b>	<b>2.29</b>	<b>2.36</b>
<b>N</b>	<b>7</b>				<b>7</b>	<b>7</b>	<b>7</b>
Rhinocerotidae	ARA-VP-1	711	24	14231	-3.7	3.5	34.5
Rhinocerotidae	ARA-VP-1	855	27	14235	-8.5	0.2	31.2
Rhinocerotidae	ARA-VP-1	1253	40	16181	-0.8	1.3	32.3
Rhinocerotidae	ARA-VP-1	1323	46	16224	1.1	5.2	36.3
Rhinocerotidae	ARA-VP-1	1360	50	16228	0.1	-1.5	29.3
Rhinocerotidae	ARA-VP-1	1382	52	16231	-4.4	0.8	31.7
Rhinocerotidae	ARA-VP-1	1399	53	16232	-2.6	-0.5	30.4
Rhinocerotidae	ARA-VP-1	1473	56	16235	-0.4	-0.7	30.1
Rhinocerotidae	ARA-VP-1	1588	68	16248	-1.0	0.4	31.3
Rhinocerotidae	ARA-VP-1	1671	69	16249	1.1	0.8	31.8
Rhinocerotidae	ARA-VP-1	1711	72	16253	1.4	2.7	33.7
Rhinocerotidae	ARA-VP-17	40	125	17403	-0.4	1.2	32.1
Rhinocerotidae	ARA-VP-6	768	140	17420	1.4	3.2	34.2
Rhinocerotidae	KUS-VP-2	65	158	17442	-5.7	-8.7	21.9
Rhinocerotidae	SAG-VP-7	16b	171	17456	-5.5	-1.0	29.9
Rhinocerotidae	SAG-VP-7	16c	172	17457	-5.3	-0.4	30.5
Rhinocerotidae	SAG-VP-7	16d	173	17458	-5.3	-0.4	30.5
Rhinocerotidae	SAG-VP-7	16e	174	17459	1.6	2.0	33.0
<b>Mean</b>					<b>-2.06</b>	<b>0.45</b>	<b>31.37</b>
<b>1 St. dev.</b>					<b>3.13</b>	<b>2.90</b>	<b>2.99</b>
<b>N</b>	<b>18</b>				<b>18</b>	<b>18</b>	<b>18</b>
<i>Eurygnathohippus</i>	ARA-VP-1	947	29	15462	0.7	-0.8	30.1
<i>Eurygnathohippus</i>	ARA-VP-1	995	33	15466	-0.4	-1.5	29.4
<i>Eurygnathohippus</i>	ARA-VP-1	1497	65	16245	0.8	-1.3	29.6
<i>Eurygnathohippus</i>	ARA-VP-1	2608	102	17330	-1.0	-6.2	24.6
<i>Eurygnathohippus</i>	ARA-VP-6	18	126	17404	0.1	1.8	32.8
<i>Eurygnathohippus</i>	ARA-VP-6	765a	137	17473	0.5	1.3	32.2
<i>Eurygnathohippus</i>	ARA-VP-6	765b	138	17417	0.9	2.1	33.1

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<i>Eurygnathohippus</i>	ARA-VP-6	765c	139	17418	2.3	2.0	33.0
<i>Eurygnathohippus</i>	SAG-VP-7	12a	169	17454	1.1	2.4	33.4
<i>Eurygnathohippus</i>	SAG-VP-7	16a	170	17455	0.2	-0.9	30.0
<i>Eurygnathohippus</i>	SAG-VP-7	46	176	17461	1.2	2.9	33.9
<b>Mean</b>					<b>0.59</b>	<b>0.17</b>	<b>31.09</b>
<b>1 St. dev.</b>					<b>0.88</b>	<b>2.65</b>	<b>2.73</b>
<b>N</b>	<b>11</b>				<b>11</b>	<b>11</b>	<b>11</b>
<i>Giraffa</i>	ARA-VP-1	52	1	14139	-11.8	5.0	36.0
<i>Giraffa</i>	ARA-VP-1	957	30	15463	-13.1	6.0	37.1
<i>Giraffa</i>	ARA-VP-6	67	127	17405	-12.4	3.6	34.7
<i>Giraffa aff. stillei</i>	ARA-VP-6	438	128	17406	-11.0	5.6	36.7
<b>Mean</b>					<b>-12.05</b>	<b>5.05</b>	<b>36.11</b>
<b>1 St. dev.</b>					<b>0.90</b>	<b>1.03</b>	<b>1.06</b>
<b>N</b>	<b>4</b>				<b>4</b>	<b>4</b>	<b>4</b>
<i>Sivatherium</i>	ARA-VP-1	1196	4	14143	-10.5	4.0	35.1
<i>Sivatherium</i>	ARA-VP-1	1052	36	16177	-12.3	5.5	36.6
<i>Sivatherium</i>	ARA-VP-1	1137	37	16178	-12.4	7.0	38.1
<i>Sivatherium</i>	ARA-VP-1	1329	45	16976	-12.4	6.1	37.2
<b>Mean</b>					<b>-11.91</b>	<b>5.68</b>	<b>36.77</b>
<b>1 St. dev.</b>					<b>0.94</b>	<b>1.26</b>	<b>1.30</b>
<b>N</b>	<b>4</b>				<b>4</b>	<b>4</b>	<b>4</b>
Tragelaphini	ARA-VP-1	72	3	14142	-10.2	-0.6	30.3
Tragelaphini	ARA-VP-1	114	6	14209	-8.7	2.3	33.3
Tragelaphus	ARA-VP-1	1019	35	16176	-8.1	4.4	35.5
Tragelaphus	ARA-VP-1	2145	80	16970	-9.2	-0.6	30.3
Tragelaphus	ARA-VP-1	2162	81	16998	-9.9	-2.5	28.4
Tragelaphus cf. moroitu	ARA-VP-1	279	9	14212	-8.8	-2.7	28.2
Tragelaphus cf. moroitu	ARA-VP-1	420	17	14221	-10.0	3.3	34.3
Tragelaphus cf. moroitu	ARA-VP-1	2413	99	17326	-8.9	-3.1	27.8
Tragelaphus cf. moroitu	ARA-VP-1	2590	101	17328	-9.6	-1.8	29.1
Tragelaphus cf. moroitu	ARA-VP-1	3096	118	17347	-9.9	-1.2	29.7
Tragelaphus cf. moroitu	ARA-VP-1	3100	119	17469	-10.8	2.0	33.0
Tragelaphus cf. moroitu	ARA-VP-1	3137	120	17313	-10.3	1.7	32.6
Tragelaphus cf. moroitu	ARA-VP-6	500a	93	17320	-11.3	2.2	33.2
Tragelaphus cf. moroitu	ARA-VP-6	1813	151	17432	-10.9	7.4	38.5
<b>Mean</b>					<b>-9.75</b>	<b>0.79</b>	<b>31.73</b>
<b>1 St. dev.</b>					<b>0.94</b>	<b>3.06</b>	<b>3.15</b>
<b>N</b>	<b>14</b>				<b>14</b>	<b>14</b>	<b>14</b>
<i>Ugandax</i>	ARA-VP-1	113	5	14208	-3.7	2.8	33.8
<i>Ugandax</i>	ARA-VP-1	281	10	14213	-5.0	1.3	32.3
<b>Mean</b>					<b>-4.35</b>	<b>2.08</b>	<b>33.06</b>
<b>1 St. dev.</b>					<b>0.98</b>	<b>1.05</b>	<b>1.08</b>
<b>N</b>	<b>2</b>				<b>2</b>	<b>2</b>	<b>2</b>

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<i>Ugandax cf. gautieri</i>	ARA-VP-17	17	124	17402	-0.3	3.9	34.9
<i>Ugandax cf. gautieri</i>	ARA-VP-6	451	129	17407	1.3	5.9	37.0
<i>Ugandax cf. gautieri</i>	ARA-VP-6	816	148	17428	0.0	2.2	33.2
<b>Mean</b>					<b>0.32</b>	<b>3.99</b>	<b>35.02</b>
<b>1 St. dev.</b>					<b>0.98</b>	<b>1.05</b>	<b>1.08</b>
<b>N</b>	<b>3</b>				<b>3</b>	<b>3</b>	<b>3</b>
<i>Simatherium</i>	ARA-VP-1	376	15	14219	1.79	0.85	31.79
<i>Simatherium</i>	ARA-VP-1	533	19	14223	2.32	2.87	33.87
<b>Mean</b>					<b>2.06</b>	<b>1.86</b>	<b>32.83</b>
<b>1 St. dev.</b>					<b>0.37</b>	<b>1.43</b>	<b>1.47</b>
<b>N</b>	<b>2</b>				<b>2</b>	<b>2</b>	<b>2</b>
Neotragini	ARA-VP-1	315	13	14217	-7.0	6.0	37.1
Neotragini	ARA-VP-6	745	132	17411	-10.6	5.0	36.0
Neotragini	ARA-VP-6	1839	154	17435	-10.3	3.6	34.6
Neotragini	ARA-VP-6	2133	155	17436	-10.4	5.6	36.7
<b>Mean</b>					<b>-9.59</b>	<b>5.05</b>	<b>36.12</b>
<b>1 St. dev.</b>					<b>1.72</b>	<b>1.08</b>	<b>1.11</b>
<b>N</b>	<b>4</b>				<b>4</b>	<b>4</b>	<b>4</b>
Alcelaphini	ARA-VP-1	418	16	14220	3.3	6.5	37.6
<i>cf. Damalops</i>	ARA-VP-1	2406	85	17311	-10.4	3.7	34.7
<i>Damalops</i>	ARA-VP-6	453	88	17314	2.4	3.7	34.7
<i>Damalops</i>	ARA-VP-6	459	89	17315	1.9	3.5	34.5
<i>cf. Damalops</i>	SAG-VP-7	121	96	17466	0.2	0.0	32.4
<b>Mean</b>					<b>-1.49</b>	<b>2.72</b>	<b>34.08</b>
<b>1 St. dev.</b>					<b>6.01</b>	<b>1.80</b>	<b>1.13</b>
<b>N</b>	<b>4</b>				<b>4</b>	<b>4</b>	<b>4</b>
<i>Aepyceros</i>	ARA-VP-1	665	21	14225	1.1	5.4	36.5
<i>Aepyceros</i>	ARA-VP-1	769	25	14232	-2.1	1.1	32.0
<i>Aepyceros</i>	ARA-VP-1	1410	55	16234	-4.0	2.9	33.9
<i>Aepyceros</i>	ARA-VP-1	1934	77	16258	-8.2	1.4	32.3
<i>Aepyceros</i>	ARA-VP-1	3045	115	17344	-1.1	1.4	32.4
<i>Aepyceros</i>	ARA-VP-1	3056	116	17345	-1.2	0.3	31.2
<i>cf. Aepyceros</i>	ARA-VP-1	3085	117	17468	-2.8	2.8	33.8
<i>Aepyceros</i>	ARA-VP-6	2122	153	17434	-1.1	3.6	34.6
<b>Mean</b>					<b>-2.44</b>	<b>2.36</b>	<b>33.35</b>
<b>1 St. dev.</b>					<b>2.78</b>	<b>1.66</b>	<b>1.72</b>
<b>N</b>	<b>8</b>				<b>8</b>	<b>8</b>	<b>8</b>
Hippotragini	ARA-VP-1	668	22	14228	0.0	4.3	35.3
?Hippotragini cf. <i>Predamalis</i>	ARA-VP-6	1560	149	17429	0.4	2.3	33.3
<b>Mean</b>					<b>0.21</b>	<b>3.28</b>	<b>34.29</b>

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1 St. dev.					0.26	1.41	1.45
N	2				4	4	4

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125. T.D.W. wrote and organized the paper. S.H.A. conducted all isotopic work after sampling by T.D.W. D.F.S. conducted numerical analysis. D.D. and G.S. integrated observations and provided text and SOM (D.D.), especially for primates and bovids. Other authors, listed alphabetically, contributed as follows on various taxa: M.T. and S.F. provided SEM analysis of the primate teeth and G.S. and R.L.B. provided mesowear data for the ungulates. Systematic work was apportioned as follows: overall fauna (T.D.W. and Y.H.S.), aardvarks (T.L. and M.B.), bovids (E.V.), carnivores (F.C.H. and N.G.), equids (R.L.B.), giraffids (A.L. and Y.H.S.), hippos (J.R.B.), cercopithecids (S.F. and E.D.), rhinos (I.X.G. and C.P.), proboscideans (H.S.).