Herbivore enamel carbon isotopic composition and the environmental context of Ardipithecus at Gona, Ethiopia

Naomi E. Levin*†
Department of Geology and Geophysics, University of Utah, Salt Lake City, Utah 84112, USA

Scott W. Simpson*
*Department of Anatomy, Case Western Reserve University School of Medicine, Cleveland, Ohio 44106, USA, and
Laboratory of Physical Anthropology, Cleveland Museum of Natural History, Cleveland, Ohio 44106, USA*

Jay Quade*
Department of Geosciences, University of Arizona, Tucson, Arizona 85721, USA

Thure E. Cerling*
Department of Geology and Geophysics, University of Utah, Salt Lake City, Utah 84112, USA

Stephen R. Frost*
Department of Anthropology, University of Oregon, Eugene, Oregon 97403, USA

ABSTRACT

Ardipithecus **fossils found in late Miocene and early Pliocene deposits in the Afar region of Ethiopia, along with** *Sahelanthropus tchadensis* **from Chad and** *Orrorin tugenensis* **from Kenya, are among the earliest known human ancestors and are considered to be the predecessors to the subsequent australopithecines (***Australopithecus anamensis* **and** *Australopithecus afarensis***). Current paleoenvironmental reconstructions suggest a wooded habitat for both** *Ardipithecus kadabba* **and** *Ardipithecus ramidus* **but more open and varied environments for other hominids living in Africa during the late Miocene and early Pliocene. To further evaluate the environmental context of** *Ardipithecus***, we present stable carbon isotope data of 182 fossil herbivore teeth from** *Ardipithecus***-bearing fossil deposits in the Gona Paleoanthropological Research Project area, in the Afar region of Ethiopia. The sampled teeth include representatives of all major fossil herbivore taxa and the majority of the mammalian biomass that lived in the same time and place as the hominids. When compared to extant herbivores from East Africa, the spectra of isotopic results from herbivores found in late Miocene** *Ar. kadabba* **and early Pliocene** *Ar. ramidus* **sites at Gona are most similar to isotopic values from extant herbivores living in bushland and grassland regions and**

*E-mails: Levin: naomi@gps.caltech.edu; Simpson: sws3@cwru.edu; Quade: jquade@geo.arizona.edu; Cerling: thure.cerling@utah.edu; Frost: sfrost@uoregon.edu.
†Current address: Division of Geological and Planetary Sciences, California Institute of Technology, MC100-23, 1200 E. California Blvd., Pasadena, California 91125, USA.

dissimilar to those from herbivores living in closed-canopy forests, montane forests, and high-elevation grasslands. The tooth enamel isotopic data from fossil herbivores make it clear that *Ardipithecus* at Gona lived among a guild of animals whose diet was dominated by C_4 grass, and where there is no record of closed-canopy vegetation.

INTRODUCTION

Ecological change is considered to be a key component to understanding the tempo and mode of human evolution (Laporte and Zihlman, 1983; Potts, 1998; White et al., 2006). The few late Miocene and early Pliocene deposits that do contain hominid fossils (Toros-Menalla in Chad, the Middle Awash, Gona, and Galili in Ethiopia, and the Tugen Hills, Kanapoi, and Lothagam in Kenya) suggest that these early hominids were associated with a range of environments, including shrublands, heterogeneous woodlands, closed woodland/forests, and rain forests (Wolde-Gabriel et al., 1994, 2001; Wynn, 2000; Haile-Selassie, 2001; Vignaud et al., 2002; Cerling et al., 2003a; Haile-Selassie et al., 2004; Pickford et al., 2004; Semaw et al., 2005; Urbanek et al., 2005; White et al., 2006). Late Miocene and early Pliocene hominid fossils, *Ardipithecus kadabba* and *Ardipithecus ramidus*, occur in the Middle Awash and Gona study areas, in the Afar region of Ethiopia (White et al., 1994; Haile-Selassie, 2001; Semaw et al., 2005; Simpson et al., 2007) (Fig. 1). The presence of *Ardipithecus* fossils from coeval deposits less than 100 km apart provides an opportunity to evaluate the environmental context of *Ardipithecus* beyond the scale of a single paleoanthropological research project area. In the Middle Awash study area, *Ar. kadabba* and *Ar. ramidus* specimens are associated with other fossils that suggest that they were restricted to wooded environments, avoided open environments, and likely lived in highland settings (WoldeGabriel et al., 1994, 2001). There is considerable overlap in the faunal composition of fossils found associated with late Miocene *Ar. kadabba* and early Pliocene *Ar. ramidus* in the Middle Awash and Gona study areas. However, fossil assemblages from Gona display distinct differences in faunal proportions, including a lower relative percentage of tragelaphine bovids and colobine primates (Semaw et al., 2005), suggesting that *Ar. ramidus* may have accessed a broader range of environments than documented in the Middle Awash study area.

Stable isotopes provide an additional perspective on the environmental context of *Ardipithecus* (WoldeGabriel et al., 2001; Semaw et al., 2005; White et al., 2006). The carbon isotopic composition of herbivore tooth enamel is a reliable dietary indicator that can be used to identify the relative contribution of grasses, trees and shrubs, and closed-canopy resources in an animal's diet. The carbon isotopic composition of teeth can be ecosystem specific (Cerling et al., 2003b, 2004) and, within a fossil context, provide information on the dietary preferences of the animals among which hominids lived. The carbon isotopic composition of tooth enamel, which reflects diet in an animal's early adult years, strongly complements morphological data, which reflect long-term evolutionary trends.

In this paper, we compare fossil tooth enamel isotopic results from *Ardipithecus*-bearing deposits at Gona to similar data from extant mammals in Ethiopia and across eastern Africa. This comparison makes it clear that early hominids at Gona, in both the late Miocene and early Pliocene, lived in an ecologically diverse environment that included abundant grasses.

BACKGROUND

Geology and Fossil Fauna

Late Miocene and early Pliocene fluvial and lacustrine deposits from the Gona Paleoanthropological Research Project (GPRP) study area, in the Afar region of Ethiopia, contain abundant vertebrate fossil remains, including hominids (Semaw et al., 2005; Simpson et al., 2007; Kleinsasser et al., this volume; Quade et al., this volume). The deposits containing *Ar. kadabba*, assigned to the 6.5–5.2 Ma Adu-Asa Formation, occur in small packages of sediment between stacked basalt flows (Simpson et al., 2007; Kleinsasser et al., this volume). The *Ar. ramidus*–bearing deposits in the Gona study area come from the Sagantole Formation (5.2–3.9 Ma), which is composed of basalts and fluviolacustrine sediments that rest conformably on the Adu-Asa Formation and are bound on the east by the As Duma fault. East of the As Duma fault, Pliocene and Pleistocene sediments of the Hadar and Busidima Formations have filled the basin, which formed as the result of movement along the As Duma fault (Quade et al., this volume) (Fig. 2).

In the Adu-Asa Formation, *Ar. kadabba* and other mammalian fauna are found in three fossiliferous horizons, above the Bodele Tuff (6.48 ± 0.22 Ma), above the Sifi Tuff, and at the level of the Kobo'o Tuff (5.44 ± 0.06 Ma) (Kleinsasser et al., this volume). Herbivore fossil fauna associated with *Ar. kadabba* include specimens of Colobinae and Cercopithecinae, *Nyanzachoerus syrticus*, Hippopotamidae, multiple bovid taxa, Giraffidae, *Eurygnathohippus* cf. *feibeli*, Rhinocerotidae, and *Anancus*. This assemblage bears similarities to that found in coeval deposits of the Adu-Asa Formation in the Middle Awash area (WoldeGabriel et al., 2001; Haile-Selassie et al., 2004). The fossil-bearing sediments in the Adu-Asa Formation at Gona include laminated siltstones, sands, and conglomerates indicative of both lacustrine and fluvial environments (Kleinsasser et al., this volume; Quade et al., this volume). High sedimentation rates, the lack of well-developed paleosols, and extensive basalts in the
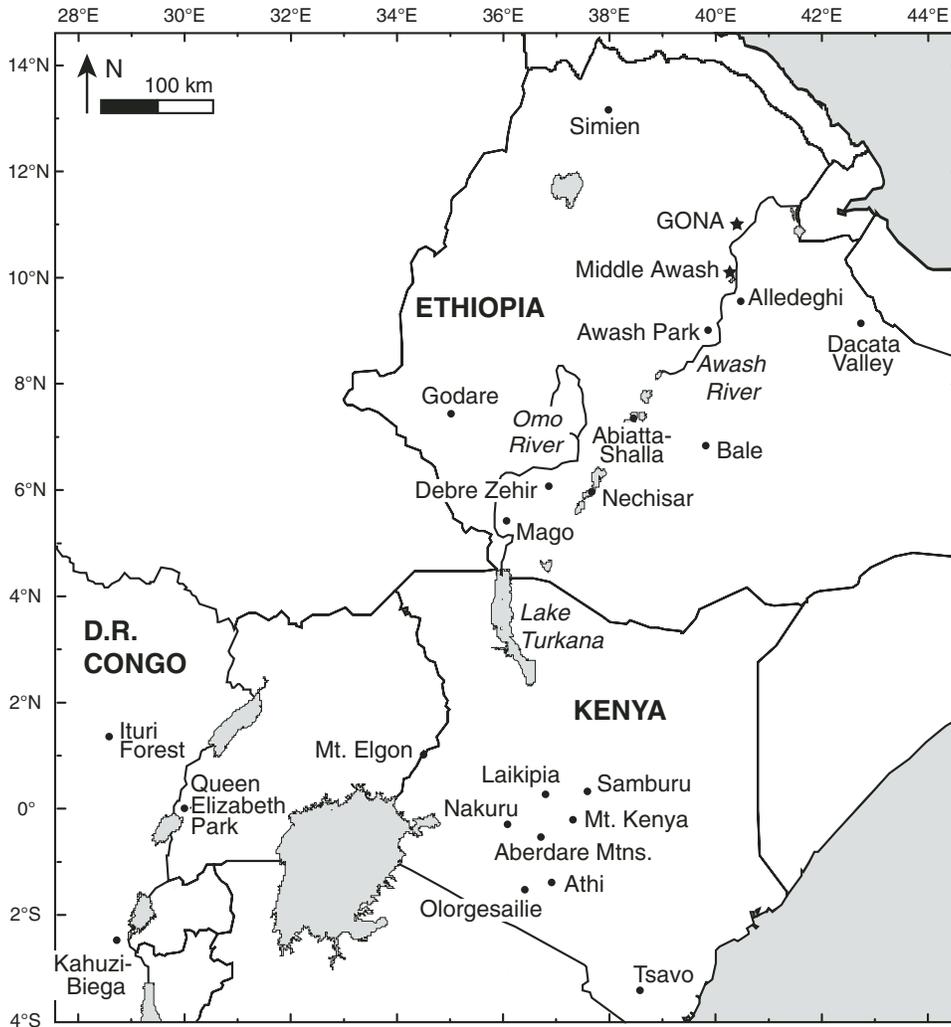
Figure 1. Map of sampling localities for modern teeth. Fossil localities discussed in text at length are marked with stars.

Adu-Asa Formation suggest active deposition in narrow floodplains confined by large expanses of basalt flows.

Ar. ramidus and other mammalian fossils are found predominantly in marginal lacustrine or marshy settings within the Sagantole Formation (Semaw et al., 2005; Quade et al., this volume). The herbivore fossil fauna associated with *Ar. ramidus* include Colobinae and Cercopithecinae, three suid species, Hippopotamidae, multiple bovid taxa, Giraffidae, Equidae, at least three proboscidean taxa, and Rhinocerotidae. To date, more than 130 fossil localities have been identified in the Sagantole Formation at Gona. Most of these localities can be confidently assigned to the Segala Noumou (4.6–4.2 Ma) or As Duma (<5.2–4.6 Ma) Members. The Segala Noumou and As Duma Members have been intensively studied at their type locations between the Sifi and Busidima Rivers (Quade et al., this volume). The fossil sites in the As Duma Member all occur at the same stratigraphic level and paleoenvironmental setting, the shallow margins of a lake where it lapped onto an active basaltic cinder cone. Mammalian fossils from the Segala Noumou Member are found in gastropod-rich tufas formed

in shallow lakes or marshes and in bedded siltstones that represent the overbank deposits of small rivers. The faunal compositions from sites in the As Duma and Segala Noumou Members are indistinguishable biostratigraphically. Sediments containing the Gona Western Margin South (GWMS) sites are exposed south of the Sifi River (Fig. 2). Unlike areas north of the Sifi, the geology of this area is not known in detail. Sediments in this area strongly resemble those of the Segala Noumou Member, with which we provisionally correlate them. The stratigraphic position of other sites, including GWM10 and 11 (part of the same sedimentary package), GWM45, and GWM18, is less clear, except that they lie stratigraphically above the top of the Adu-Asa Formation (<5.2 Ma) and below the top of the Sagantole Formation (>3.9 Ma).

Carbon Isotopes in Vegetation

Carbon isotope ratios ($^{13}C/^{12}C$) of C_3 and C_4 plants are distinct because they use different photosynthetic pathways to metabolize CO_2 (Farquhar et al., 1989). In East Africa, the

majority of shrubs and trees uses the C_3 pathway, whereas most grasses use the C_4 pathway, except for those growing at high elevations (above ~3000 m) (Tieszen et al., 1979; Young and Young, 1983). Stable carbon isotope ratios are commonly reported relative to the isotopic standard Vienna Peedee belemnite (VPDB) and presented as δ values in per mil (‰) units, wherein $\delta^{13}C = ([^{13}C/^{12}C]_{sample}/[^{13}C/^{12}C]_{standard} -1) \times 1000‰$. The $\delta^{13}C$ values of C_3 plants range from −36.5‰ to −22‰ and between −15‰ and −11‰ for C_4 vegetation in equatorial Africa (Cerling and Harris, 1999; Cerling et al., 2004). Plants that use the Crassulacean Acid Metabolism (CAM) photosynthetic pathway have $\delta^{13}C$ values intermediate to C_3 and C_4 plants, but

because CAM plants (e.g., cacti and succulents) do not make a large contribution to the diets of most extant mammals, they are not usually considered in the interpretation of $\delta^{13}C$ values of herbivore tooth enamel. Cerling et al. (2003c) reported that $\delta^{13}C$ values of C_3 plants from savannas and bushlands in Kenya average −27.0 ± 0.2‰, whereas plants from the subcanopy in the Ituri Forest average −34.0 ± 1.5‰. The $\delta^{13}C$ values of C_3 plants growing in an open-canopy forest average −27.8 ± 0.3‰, and they more closely resemble isotopic values of C_3 plants in savannas and bushlands than those in closed-canopy ecosystems. The ^{13}C-depleted values of C_3 plants in the Ituri Forest are due to the "canopy effect" (van der Merwe, 1991), wherein

Figure 2. Map and schematic cross section of fossil localities in the western portion of the Gona Paleoanthropological Research Project study area where fossil teeth were sampled. Sites from the As Duma and Segala Noumou Members in the Sagantole Formation are labeled with site number. All other sites are labeled with site prefix and number. The prefixes for site names Gona Western Margin (GWM) and Gona Western Margin South (GWMS) are abbreviated accordingly. For detailed geological maps and cross sections of the Adu-Asa and Sagantole Formations at Gona, see Kleinsasser et al. (this volume) and Quade et al. (this volume).
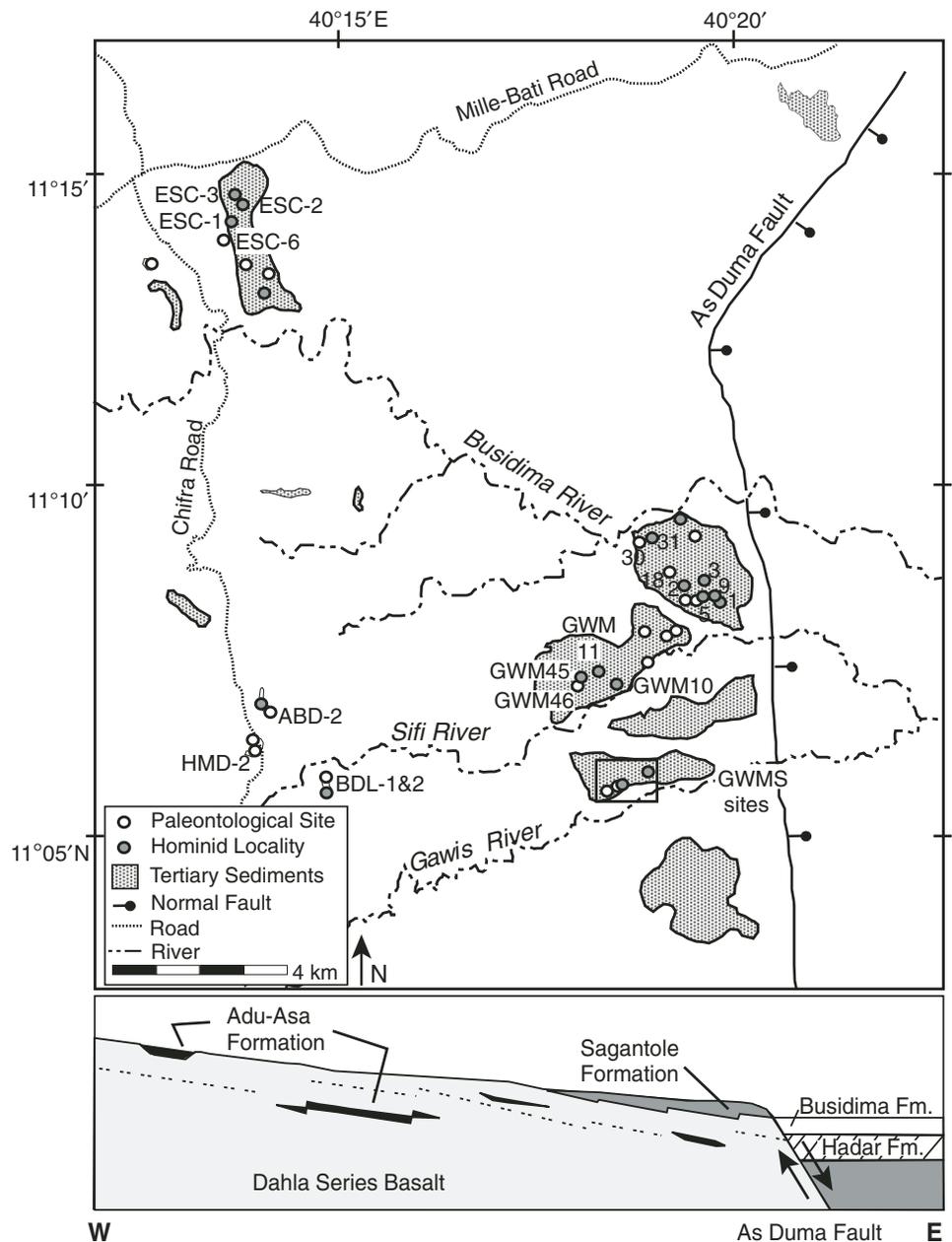
δ^{13}C values of plants are reduced by recycling of CO_2 within the forest canopy. This distinction within C_3 plants is important because the dietary composition of herbivores living in a closed-canopy ecosystem can be detected in the fossil record (MacFadden and Higgins, 2004). The δ^{13}C values of C_3 plants can increase by several per mil when water-stressed (Farquhar et al., 1989). The δ^{13}C values of C_4 grasses in East Africa also vary with water stress. The three main subpathways of C_4 photosynthesis include nicotinamide adenine dinucleotide phosphate (NADP), nicotinamide adenine dinucleotide (NAD), and phosphoenolpyruvate carboxykinase (PCK). The δ^{13}C values of mesic (NADP subpathway) grasses average -11.8 ± 0.2‰, whereas xeric (NAD, PCK subpathways) grasses have a lower average δ^{13}C value, -13.1 ± 0.3‰ (Cerling et al., 2003c).

Interpretation of Fossil δ^{13}C Values

The reconstruction of herbivore paleodiet and paleovegetation from δ^{13}C values of fossil teeth and paleosol carbonate involves several steps. One must estimate three values: δ^{13}C of atmospheric CO_2, the carbon isotope enrichment factor between atmospheric CO_2 and plants, and the carbon isotope enrichment factor between diet and tooth enamel or between vegetation and paleosol carbonate. The enrichment factor is the isotopic difference between two phases, and it is represented by $\varepsilon^*_{A\text{-}B}$, where $\varepsilon^*_{A\text{-}B} = ([\delta^{13}C_{PhaseB} + 1000]/[\delta^{13}C_{PhaseA} + 1000] - 1) \times 1000$. ε^* is used instead of the fractionation factor ($\alpha_{A\text{-}B} = [\delta^{13}C_{PhaseB} + 1000]/[\delta^{13}C_{PhaseA} + 1000]$), in order to present isotopic differences in per mil (‰). ε^* refers to isotopic differences between two phases that may not be in isotopic equilibrium (Cerling and Harris, 1999).

The δ^{13}C values of vegetation, teeth, and soil carbonates must be considered with respect to the δ^{13}C value of the atmosphere in which they formed. The δ^{13}C values of Atlantic Ocean benthic foraminifera can be used as recorders of δ^{13}C values of atmospheric CO_2 ($\delta^{13}C_{atmCO_2}$), assuming that the δ^{13}C values of foraminifera reflect surface dissolved inorganic carbon, which is in equilibrium with atmospheric CO_2. The ε^* value between atmospheric CO_2 and benthic foraminifera ($\varepsilon^*_{CO_2\text{-}foram}$) can be estimated for the past 30 k.y. from benthic foraminifera δ^{13}C values (Zachos et al., 2001) and the $\delta^{13}C_{atmCO_2}$ value of air trapped in ice cores (Indermühle et al., 1999; Smith et al., 1999). With the Cenozoic record of benthic foraminifera δ^{13}C values from Zachos et al. (2001), the calculated $\varepsilon^*_{CO_2\text{-}foram}$ can be used to determine $\delta^{13}C_{atmCO_2}$ values for the late Miocene and early Pliocene fossils deposits at Gona (Table 1). These estimated values are more ^{13}C-enriched than today's $\delta^{13}C_{atmCO_2}$ value (-8‰), which has decreased over the past 150 yr due to the combustion of ^{13}C-depleted fossil fuels (Keeling et al., 1979, 1995; Francey et al., 1999). Assuming that modern plants fix carbon from the present atmosphere with consistent $\varepsilon^*_{atmosphere\text{-}plant}$ values as in the past, $\varepsilon^*_{atmosphere\text{-}plant}$ can be estimated and used to estimate plant δ^{13}C values for time periods when $\delta^{13}C_{atmCO_2}$ values were different from today's values (Table 1).

The carbon isotope enrichment factor between herbivore diet and animal tissue ($\varepsilon^*_{diet\text{-}tissue}$) has been determined experimentally for domestic and laboratory animals and estimated for wild animals (Cerling and Harris, 1999; Passey et al., 2005). For

TABLE 1. ESTIMATED δ^{13}C VALUES FOR ATMOSPHERIC CO_2, VEGETATION, TOOTH ENAMEL, AND SOIL CARBONATE

	Present	0–30 ka	Sagantole Formation	Adu-Asa Formation
Time Interval (Ma)	0.0	0–0.03	5.2–3.9	6.5–5.2
δ^{13}C benthic foraminifera* (‰, VPDB)	—	0.6	0.4	1.0
δ^{13}C atmospheric CO_2[†] (‰, VPDB)	−8.0	−6.5	−6.7	−6.1
δ^{13}C vegetation[§] (‰, VPDB)				
Closed-canopy C_3	−31.4	−30.0	−30.1	−29.6
C_3	−27.0	−25.5	−25.7	−25.1
C_4	−12.0	−10.5	−10.6	−10.0
δ^{13}C tooth enamel[#] (‰, VPDB)				
Closed-canopy C_3	−17.6	−16.1	−16.3	−15.7
C_3	−13.1	−11.6	−11.7	−11.1
C_4	2.2	3.7	3.5	4.1
δ^{13}C soil carbonate** (‰, VPDB)				
Closed-canopy C_3	−17.7	−16.2	−16.4	−15.8
C_3	−13.2	−11.7	−11.8	−11.2
C_4	2.1	3.6	3.4	4.0

Note: VPDB is an abbreviation for the isotopic standard Vienna Peedee belemnite.

*Average δ^{13}C values of Atlantic benthic foraminifera were calculated from Zachos et al. (2001).

[†]Present δ^{13}C value of atmospheric CO_2 is from Francey et al. (1999), and the 0–30 ka value is from air trapped in ice cores from Smith et al. (1999) and Indermuhle et al. (1999). δ^{13}C values of atmospheric CO_2 for the fossil time intervals at Gona were calculated from benthic foraminifera δ^{13}C values, assuming that the enrichment factor between atmospheric CO_2 and benthic foraminifera was the same for these time intervals as it was for the 0–30 ka interval.

[§]Average values for modern plants from Cerling et al. (2003c). Values for plants from other time intervals were calculated using the observed enrichment factor between δ^{13}C values of atmospheric CO_2 and of each vegetation type for the present time interval.

[#]Expected enamel δ^{13}C values for animals consuming only the respective vegetation type, assuming a diet-enamel enrichment of +14.1‰, as discussed in the text.

**Expected δ^{13}C values of soil carbonates formed under different vegetation types, assuming plant to soil carbonate enrichment factor of +14‰.

large ruminant mammals, Cerling and Harris (1999) estimated a $\varepsilon^*_{\text{diet-tissue}}$ of 14.1 ± 0.5‰ for tooth enamel. This enrichment factor is consistent with the experimental results from Passey et al. (2005) for domestic cows, which show a $\varepsilon^*_{\text{diet-enamel}}$ value of 14.6 ± 0.3‰, but it is distinct from the $\varepsilon^*_{\text{diet-enamel}}$ value of 13.3 ± 0.3‰ found for the modern domestic pig, *Sus scrofa*. In this paper, we use the $\varepsilon^*_{\text{diet-enamel}}$ value of 14.1 ± 0.5‰ (Cerling and Harris, 1999) to interpret tooth enamel $\delta^{13}C$ values for all herbivore taxa because we do not know enough about the digestive physiologies of the fossil species to adjust the enrichment factors accordingly.

Carbonate-rich soils form in seasonally dry environments. The $\delta^{13}C$ values of soil carbonates that form at depths greater than 30 cm record the carbon isotope composition of vegetation growing in the soil during carbonate formation (Cerling, 1999). The carbon isotope enrichment factor between vegetation and soil carbonate depends on a combination of equilibrium and kinetic fractionation processes and can range between 13‰ and 16‰, depending on plant productivity, atmospheric CO_2 concentration, and soil properties (Cerling, 1999).

A summary of our estimates for $\delta^{13}C$ values of atmospheric CO_2, plants in different ecosystems, herbivore enamel, and soil carbonate is listed in Table 1. This approach to adjusting expected $\delta^{13}C$ values of enamel and paleosol carbonates according to changing $\delta^{13}C_{\text{atmCO}_2}$ values through time is similar to the approach used by Passey et al. (2002).

METHODS

Sample Collection

Tooth enamel was sampled from existing collections of herbivore skulls and isolated mandibles in several national parks and reserves in Ethiopia (Abiatta-Shalla, Alledeghi, Awash, Mago, Nechisar, Bale, and Simien) (Fig. 1), the Natural History Museum at the University of Addis Ababa, and the headquarters of the Ethiopian Wildlife Conservation Organization in Addis Ababa. These collections were supplemented by cranio-dental remains found on survey in the national parks and the Gona Paleoanthropological Research Project study area, which increased the sample size to 142 teeth from 122 individuals. The $\delta^{13}C$ values of tooth enamel from herbivores found in modern Ethiopian environments were compared to carbon isotopic data of teeth from similar taxa living in the mountain regions and rift valleys in Kenya and Uganda, and forests in the Democratic Republic of the Congo (D.R.C.) (Fig. 1). Modern collection localities are characterized using the ecoregion classification system defined by Olson et al. (2001) (Table 2). Ecoregions are large areas of land (~150,000 km²) that contain geographically distinct assemblages of natural communities that share a large majority of species, ecosystem dynamics, and environmental conditions (Olson et al., 2001).

For isotopic analysis, 182 fossil teeth from paleontological localities in the Adu-Asa and Sagantole Formations at Gona were sampled for isotopic analysis. This sample includes all mammalian taxa available except for hominids, micromammals, and carnivores (e.g., cercopithecids, suids, hippopotamids, bovids, giraffids, equids, rhinocerotids, and proboscideans). Bulk samples (GONBULK) of fragmented large herbivore teeth (e.g., suid, bovid, proboscidean, etc.) and complete teeth accessioned by the National Museums of Ethiopia were sampled. When possible, we sampled third molars, teeth that have formed after the adult diet has been adopted. Teeth formed prior to weaning may have ^{13}C-depleted $\delta^{13}C_{\text{enamel}}$ values compared to teeth formed with only an adult diet because milk contains a high proportion of lipids, which are depleted in ^{13}C relative to carbohydrates and proteins (DeNiro and Epstein, 1978).

Enamel from fragmentary GONBULK samples was separated from dentine and ground using a mortal and pestle, yielding up to 20 mg of powder. Accessioned specimens were sampled in the National Museum of Ethiopia in Addis Ababa, using a diamond bit and a hand-held drill. These teeth were sampled in a shallow vertical groove or pit removing 1–3 mg of enamel powder. All teeth were cleaned or wiped with ethanol before sampling, and great care was taken to avoid dentine, cementum, and matrix in the sample powder. Only one sample was taken from each fossil tooth. Modern teeth were sampled using a similar approach, but, in some cases, several teeth were sampled from a single individual, and single teeth were sampled in multiple places.

When present in stratigraphic section with fossil-bearing sediments at Gona, paleosol carbonates were collected from carbonate (Bk) horizons in paleo-Vertisols at least 30 cm below the upper boundary of the paleosol. Paleosol carbonates were collected at these depths to avoid the influence of ^{13}C-enriched atmospheric CO_2 on carbonate $\delta^{13}C$ values. Paleosol carbonates sampled for isotopic analysis in this study represent different substrates than the fossil teeth that were sampled, which come from nonpedogenic horizons.

Sample Treatment

All GONBULK sample powders were treated with 3% H_2O_2 for 30 min and 1 *M* acetic acid for 15–30 min, rinsed after each treatment with deionized water, and then dried at 60 °C before analysis. For the majority of modern teeth and accessioned fossil teeth, untreated powders were analyzed first. If enough powder remained after the initial isotopic analysis of the untreated portion, the sample was treated in the same manner as the GONBULK samples, except they were treated with 0.1 *M* acetic acid instead of 1 *M* acetic acid.

Isotopic Analysis and Notation

All GONBULK sample powders were reacted in 100% H_3PO_4 in a constant temperature bath at 50 °C. The resultant CO_2 was extracted offline and then analyzed on a Finnigan Delta S mass spectrometer at the University of Arizona.

TABLE 2. LOCATION AND DESCRIPTION OF MODERN ENVIRONMENTS SAMPLED

Location	Ecoregion	Latitude (°N)	Longitude (°E)	Elevation (m)	Country	Locations included
Abiatta-Shalla	Somali acacia-commiphora bushlands and thickets	7.5	38.6	1580–1700	Ethiopia	Abiatta-Shalla NP* and Bulbula town
Alledeghi	Somali acacia-commiphora bushlands and thickets	9.2	40.4	840	Ethiopia	
Athi Plains	Northern acacia-commiphora bushlands and thickets	−1.4	36.9	1640	Kenya	Athi Game Ranch, Nairobi NP*, Kitengela, Ngong, Lukenya Hills, Athi River, Sukari Ranch, Kikuyu, Embu Kjabe, Limuru
Dacata Valley	Ethiopian montane forests	9.1	42.4	1350	Ethiopia	Near Babille town
Bale	Ethiopian montane moorland & montane grasslands/woodlands	6.8	39.8	3000–4000	Ethiopia	
Debre Zehir	Somali acacia-commiphora bushlands and thickets	6.1	36.9	1550	Ethiopia	
Godare	Ethiopian montane forests	7.4	35.0	900	Ethiopia	
Gona	Somali acacia-commiphora bushlands and thickets	11.1	40.3	500–900	Ethiopia	
Ituri Forest	Northeastern Congolian lowland forests	1.4	28.6	770	D.R.C.	
Kahuzi-Biega	Albertine Rift montane forests	−2.5	28.8	1800–2500	D.R.C.	Mountain and lowland sectors
Kenya Mountains	East African montane forests	−0.4	36.6	2000–4000	Kenya	Mt. Kenya NP, Mt. Elgon NP, and Aberdare NP*
Laikipia	Northern acacia-commiphora bushlands and thickets	0.3	36.8	1700	Kenya	
Mago	Somali acacia-commiphora bushlands and thickets	5.5	36.0	400	Ethiopia	
Nakuru	Northern acacia-commiphora bushlands and thickets	−0.3	36.1	1870	Kenya	
Nechisar	Somali acacia-commiphora bushlands and thickets	6.0	37.6	1250	Ethiopia	
Olorgesailie	Northern acacia-commiphora bushlands and thickets	−1.5	36.4	619	Kenya	
Queen Elizabeth Park	Victoria Basin forest-savanna mosaic	0.0	30.0	950	Uganda	
Samburu	Northern acacia-commiphora bushlands and thickets	0.4	37.6	1100	Kenya	
Simien	Ethiopian montane moorland & montane grasslands/woodlands	13.2	38.0	3100–3800	Ethiopia	
Tsavo	Northern acacia-commiphora bushlands and thickets	−3.4	38.6	560	Kenya	
Turkana	Masai xeric grasslands and shrublands	4.0	36.0	360–450	Kenya	

Note: Ecoregion descriptions are from Olson et al. (2001). D.R.C.—Democratic Republic of Congo.
*NP—National Park.

Corrections were based on internal Carrara Marble standards calibrated to the NBS-19 calcite standard. Some of the GONBULK samples and all other tooth enamel and carbonates were analyzed using an online carbonate device, the Finnigan Carboflo, reacted in 100% H_3PO_4 with silver capsules at 90 °C and analyzed on a Finnigan MAT 252 at the University of Utah. Internal Carrara Marble and tooth enamel standards (MRS and MHS), calibrated to NBS-19, were used for the University of Utah analyses.

Statistics were performed using SYSTAT10. Significance (alpha) for statistics was set at $p < 0.05$. The post-hoc Scheffe analysis of variance (ANOVA) was used for all of the multipair comparisons. When comparisons were made between modern and fossil $\delta^{13}C_{enamel}$ values and between fossil time periods, the fossil data were adjusted to be compatible with modern $\delta^{13}C_{atm\text{-}CO_2}$ values using enrichment factors of −1.4‰ and −1.9‰ for the Sagantole and Adu-Asa data respectively (Table 1).

RESULTS

Analytical Precision

Repeat analyses of tooth enamel yielded consistent $\delta^{13}C$ values within and between the laboratories at which they were analyzed. Among fossil samples that were analyzed in different runs at the Utah laboratory, absolute differences between repeat analyses averaged 0.2 ± 0.2‰ for $\delta^{13}C$ ($n = 33$). The $\delta^{13}C$ values of enamel standards had a standard deviation of 0.15‰ over the course of the analyses performed for this study. For the Arizona laboratory, $\delta^{13}C$ values of the Carrara marble analyzed with the enamel samples had a standard deviation of 0.07‰, and their average was not distinct from the long-term averages of the analyses of these standards in that laboratory.

Some of the GONBULK samples originally analyzed at Arizona and published in Semaw et al. (2005) were reanalyzed

at the Utah laboratory to test interlaboratory precision and data compatibility. The average absolute difference in $\delta^{13}C$ values for samples analyzed in both laboratories was $0.2 \pm 0.2‰$ ($n = 40$).

Effects of Treatment on Isotopic Results

In general, there is a strong 1:1 relationship between $\delta^{13}C$ values of treated and untreated powders in both fossil and modern tooth enamel (Fig. 3). The average residual between the treated and untreated $\delta^{13}C$ values is $0.1 \pm 0.6‰$ for modern teeth and $0.4 \pm 0.7‰$ for fossil teeth. Among different fossil assemblages sampled (Adu-Asa Formation, As Duma Member, Segala Noumou Member, and the GWMS sites), there are no differences in treated versus untreated regressions for $\delta^{13}C_{enamel}$ values.

There is a substantial body of literature on the effects of treating tooth enamel powder prior to isotopic analysis (e.g., Lee-Thorp and van der Merwe, 1991; Koch et al., 1997; Passey et al., 2002). Although treatment of tooth enamel is intended to eliminate organic material and nonstructural carbonate, it can also produce new compounds or cause isotopic fractionation in existing ones (Lee-Thorp, 2000). From the treatment data presented in this study, it is clear that there are systematic differences in the ways that the fossil and modern enamel isotopic values respond to the same treatment (Fig. 3); however, it is unclear which value, treated or untreated, best represents animal diet.

A substantial amount of sample powder can be lost during sample treatment, leaving insufficient amounts of powder for analysis when the initial sample powder is small ($\leq$1mg). Sample loss during treatment makes some of the smaller specimens inaccessible for isotopic analysis. Given the uncertainty in the value of treatment, we decided to collect small enamel powder samples from some specimens and leave them untreated for analysis.

Out of 182 fossil teeth sampled for this study, 32 remained untreated. All $\delta^{13}C$ values from the untreated samples fall within the range of the treated values for each taxon at each site, and they do not affect the interpretation of any of the values. None of the primate tooth enamel powders was treated. The untreated primate values (in addition to the other untreated values) could be "converted" to be equivalent to treated values using the regression equations established from the Gona fossil samples (Fig. 3). However, for this study, none of the untreated values has been adjusted to be compatible with treated values, or vice versa.

Diagenesis in Tooth Enamel

In general, tooth enamel $\delta^{13}C$ ($\delta^{13}C_{enamel}$) values have been shown to be resistant to diagenetic overprinting (Wang and Cerling, 1994). Among fossil teeth from the Adu-Asa and Sagantole Formations at Gona, $\delta^{13}C_{enamel}$ values span and are restricted to the spectrum of expected $\delta^{13}C_{enamel}$ values. Analyses of teeth from fossil animals known to be obligate browsers and grazers, like the deinothere and gomphotheres (Cerling et al., 1999; Zazzo et al., 2000; Cerling et al., 2003a; Kingston and Harrison, 2007), yield $\delta^{13}C_{enamel}$ values indicative of strict
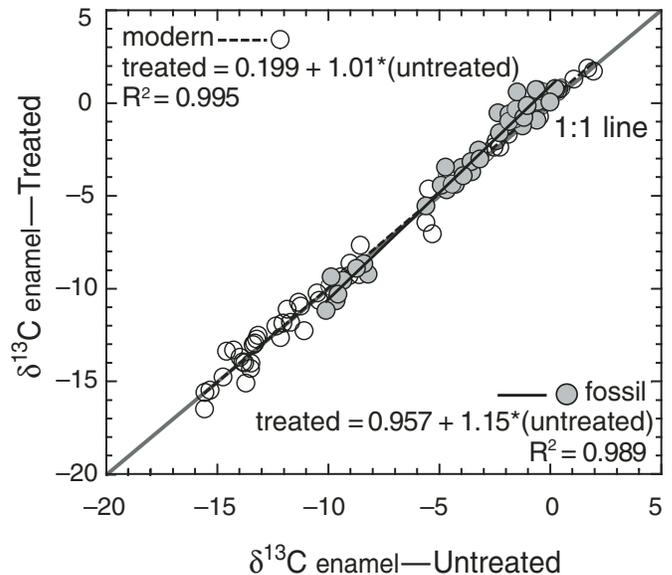

Figure 3. Scatter plot of $\delta^{13}C$ values (VPBD) of untreated and treated enamel for the same sample, in ‰ units, for modern and fossil tooth enamel. Linear regression equations for modern and fossil enamel are reported on plot.

C_3 and C_4 diets, as shown in a later section of this paper. These data provide confidence that the dietary signature from $\delta^{13}C_{enamel}$ values is preserved in the fossil record.

General Patterns: Modern Teeth

The $\delta^{13}C_{enamel}$ values from modern East African environments (Fig. 4) provide a framework for interpreting $\delta^{13}C_{enamel}$ values of fossil taxa at Gona. We first present $\delta^{13}C_{enamel}$ values from modern and fossil assemblages, grouped by location, to demonstrate how $\delta^{13}C_{enamel}$ values vary with environment, and, in later sections, we present the isotopic data grouped by taxon. The $\delta^{13}C_{enamel}$ values of tooth enamel (modern and fossil) sampled from Ethiopia are available in the GSA Data Repository.[1]

The $\delta^{13}C_{enamel}$ values of modern teeth were obtained from locations that encompass the spectrum of environments found in East Africa today, including bushlands, grasslands, lowland forests, montane forests, and montane moorlands (Table 2; Fig. 4). The $\delta^{13}C_{enamel}$ values from animals sampled from the Ituri Forest, in the northeastern Congolian lowland forest ecoregion, range from $-26.0‰$ to $-14.1‰$ ($n = 35$) and have a median value of $-16.2‰$, which is close to the expected average $\delta^{13}C_{enamel}$ value for animals consuming vegetation in a C_3 closed-canopy forest (Fig. 4A; Table 1). The $\delta^{13}C_{enamel}$ values from animals living in the Albertine Rift montane forests at Kahuzi-Biega have a median value of $-14.6‰$ and range from $-17.8‰$ to

---

−11.3‰ (*n* = 73) (Fig. 4B). The $\delta^{13}C_{enamel}$ values from mammals in the Ethiopian highlands (Bale and Simien National Parks) range between −15.5‰ and −6.5‰ (*n* = 21), and, although they are higher than $\delta^{13}C_{enamel}$ values from the lowland and montane forests at Ituri and Kahuzi-Biega, they still are centered near the expected value for animals on a strict C_3 diet (median $\delta^{13}C_{enamel}$ = −12.0‰) (Fig. 4C). Herbivores sampled from all other bushlands, shrublands, grasslands, and the Kenyan mountains (Aberdare Mountains, Mount Kenya, and Mount Elgon) have more positive $\delta^{13}C_{enamel}$ values that span the full spectrum of values expected for animals consuming C_3 and C_4 plants, with median values ranging from −12.0‰ in the Kenyan mountains (*n* = 37) to +0.2‰ in the grasslands of the Athi Plains (*n* = 65) (Figs. 4D–4H).

Carbon isotope data from extant herbivore teeth show distinct distributions of $\delta^{13}C_{enamel}$ values among East African ecoregions. Mean $\delta^{13}C_{enamel}$ values from the Ituri Forest are consistent with a C_3 diet (−16‰) (Fig. 4A), but a tail of ${}^{13}C$-depleted values indicates the reliance by some animals on subcanopy vegetation, as documented in Cerling et al. (2004). There is no carbon isotope evidence for C_4 grasses in the diets of the animals living in the closed-canopy Ituri Forest. Mean $\delta^{13}C_{enamel}$ values of herbivores from Kahuzi-Biega indicate a C_3 diet, with some of the ${}^{13}C$-depleted values nearing the expected value for closed-canopy diets (Fig. 4B). The shape and range of the Kahuzi-Biega histogram appear to be similar to the histogram from animals that lived in the montane moorlands, woodlands, and grasslands within Bale and Simien National Parks. Grazing animals at Bale and Simien are expected to yield $\delta^{13}C_{enamel}$ values indicative of C_3 diets because high-elevation grasses use the C_3 pathway. However, some $\delta^{13}C_{enamel}$ values from the Ethiopian highlands reach up to −6.5‰ and indicate that these animals may migrate to lower elevations where they have access to C_4 grass. No animals sampled from Ituri, Kahuzi-Biega, or the Ethiopian highlands rely solely on C_4 vegetation. Bovids are the only herbivores from the Kenyan mountains with $\delta^{13}C_{enamel}$ values that indicate a significant dietary intake of C_4 grass.

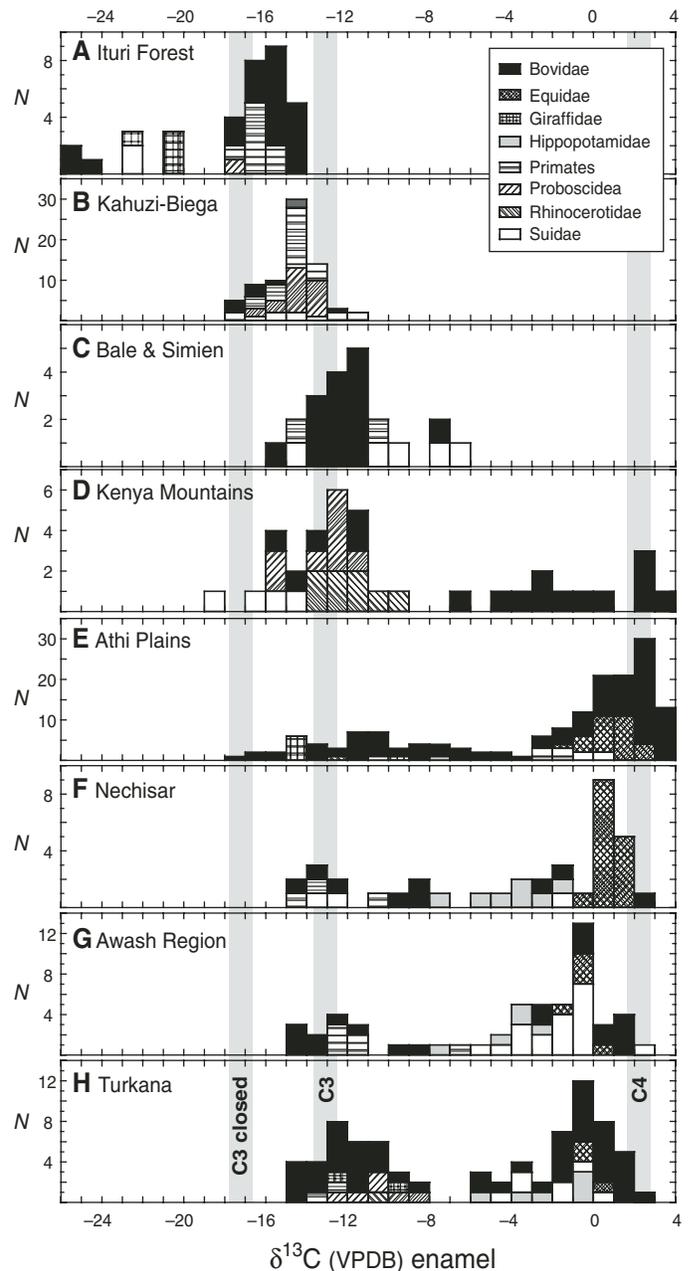Figure 4. Histograms of $\delta^{13}C$ values in ‰ of tooth enamel from extant herbivores in East Africa plotted by location: (A) Ituri Forest, Democratic Republic of Congo (D.R.C.) (Cerling et al., 2004); (B) Kahuzi-Biega Forest, D.R.C.; (C) Bale and Simien National Parks in the Ethiopian highlands; (D) Kenya Mountains, including data from the Aberdare Mountains, Mt. Kenya, and Mt. Elgon (Cerling et al., 1999; Harris and Cerling, 2002; Cerling et al., 2003b, 2003c); (E) Athi Plains, which includes samples from the grasslands near the Athi River and in the Nairobi vicinity, Kenya (Cerling et al., 1999, 2003b, 2003c; Harris and Cerling, 2002); (F) Nechisar Park, Ethiopia; (G) Awash region of Ethiopia, including samples from Awash National Park, the Alledeghi Wildlife Reserve, and the Gona Paleoanthropological Research Project study area; and (H) Turkana, including samples collected from Mago National Park in Ethiopia (this study) and from regions around Lake Turkana in Kenya (Cerling et al., 2003b, 2003c). Gray vertical bars represent averages of expected $\delta^{13}C_{enamel}$ values for herbivores eating strict diets of C_3 plants from a closed-canopy forest, C_3 plants from a forest or bushland, and C_4 grasses, based on calculations described in Table 1.

The $\delta^{13}C_{enamel}$ values from Nechisar Park, the Athi Plains, the Awash region, and Turkana indicate significant consumption of C_4 plants, consistent with the ecoregion classification of these areas as grasslands, shrublands, and bushlands (Figs. 4E–4H). A near bimodal distribution of $\delta^{13}C_{enamel}$ values of herbivores at Turkana indicates that most of the herbivores are either obligate browsers (C_3 consumers) or grazers (C_4 consumers), with the exception of the hippopotamids and some bovids, which yield intermediate $\delta^{13}C_{enamel}$ values. The distribution of $\delta^{13}C_{enamel}$ values from herbivores living in grassland, shrubland, and bushland ecoregions indicates the predominant consumption of C_4 plants,

and it is distinct from the distribution of $\delta^{13}C_{enamel}$ values of herbivores living in high-elevation or forested ecoregions, where diets are dominated by C_3 plants.

General Patterns: Fossil Teeth

Fossil teeth were sampled from four stratigraphic groupings at Gona, the late Miocene Adu-Asa Formation, the early Pliocene Segala Noumou and As Duma Members of the Sagantole Formation, and the early Pliocene Gona Western Margin South (GWMS) sites in the Sagantole Formation (Fig. 2). Eleven teeth were analyzed from other sites in the Sagantole Formation (GWM10, 11, 45, and 18), but we cannot place them confidently in any of these groupings. The data from these teeth will only be presented in the section that reviews $\delta^{13}C_{enamel}$ values by taxon. Fossils sampled from the Adu-Asa Formation are from sites in three stratigraphic horizons: one in lacustrine sediments above the Bodele Tuff (6.48 ± 0.22 Ma), another in fluvial sediments above the Sifi Tuff, and the highest level is associated with the Kobo'o Tuff (5.44 ± 0.06 Ma) (Kleinsasser et al., this volume). Most fossils sampled for isotopic analysis are associated with the Kobo'o Tuff and are considered together with the fossils sampled from the lower stratigraphic horizons.

The $\delta^{13}C_{enamel}$ values from the Adu-Asa fossils range between −15.7‰ to +0.8‰ and have a median value of −5.1‰ ($n = 35$) (Fig. 5D). Median $\delta^{13}C_{enamel}$ values for fossil teeth from the As Duma ($n = 76$), Segala Noumou ($n = 32$), and GWMS ($n = 28$) assemblages are −2.4‰, −2.8‰, and −1.6‰, respectively (Figs. 5A–5C). Fossil teeth from the As Duma Member include the most teeth sampled from one fossil assemblage at Gona, and they have the largest range in $\delta^{13}C_{enamel}$ values (−11.9‰ to +1.5‰) among fossil assemblages from the Sagantole Formation.

The $\delta^{13}C_{enamel}$ values of teeth from the Adu-Asa Formation suggest that the diets of some herbivores (suids, bovids, and giraffids) were dominated by C_3 plants, whereas other herbivores (hippopotamids, equids, and proboscidea) relied heavily on C_4 grasses. The presence of herbivores with C_4-dominated diets distinguishes fossil taxa of the Adu-Asa Formation from herbivores living in modern forests, where they do not eat C_4 grass (Figs. 4A–4B).

The distributions of $\delta^{13}C_{enamel}$ values from the Sagantole Formation fossil assemblages most resemble $\delta^{13}C_{enamel}$ values of extant herbivores living in bushlands, thickets, and grassland ecoregions, where there is a mix of C_3 and C_4 vegetation (Figs. 4E–4H). The fossil taxa from the Sagantole Formation with ^{13}C-depleted $\delta^{13}C_{enamel}$ values indicative of C_3 diets (colobines, bovids, giraffids, and rhinocerotids) are the same taxa that display ^{13}C-depleted $\delta^{13}C_{enamel}$ values in bushland and grassland ecoregions today. The suids are an exception because *Kolpochoerus deheinzelini* from the Sagantole Formation yields $\delta^{13}C_{enamel}$ values as low as −10.5‰, indicative of a C_3-dominated diet, whereas most extant suids living in bushlands and thickets today have diets dominated by C_4 grass. The details of $\delta^{13}C_{enamel}$ values from the fossil suids at Gona are discussed in a later section of this paper.

Carbon Isotope Results by Taxa

Cercopithecidae

Modern primate teeth sampled from Ethiopia include the papionins, *Papio hamadryas hamadryas* (sacred baboon), *P. h. anubis* (olive baboon), and *Theropithecus gelada* (gelada baboon), and the cercopithecins, *Chlorocebus aethiops* (vervet) and *Cercopithecus neglectus* (de Brazza's monkey). We compared the $\delta^{13}C_{enamel}$ values of these extant Ethiopian cercopithecids to those of similar taxa from Kenya and the D.R.C. They were also compared to the papionin *Cercocebus agilis* (agile mangabey), the cercopithecin *Cercopithecus mitis* (the diadem or blue monkey), the colobines *Procolobus badius* (red colobus) and *Colobus angolensis* (Angolan black-and-white colobus), as well as hominoids *Gorilla gorilla* (gorilla) and *Pan troglodytes* (chimpanzee). Teeth tentatively allocated to the fossil papionin *Pliopapio alemui* and the colobine monkey *Kuseracolobus aramisi* were sampled from the As Duma and Segala Noumou Members of the Sagantole Formation. Fossils of *P. alemui* are
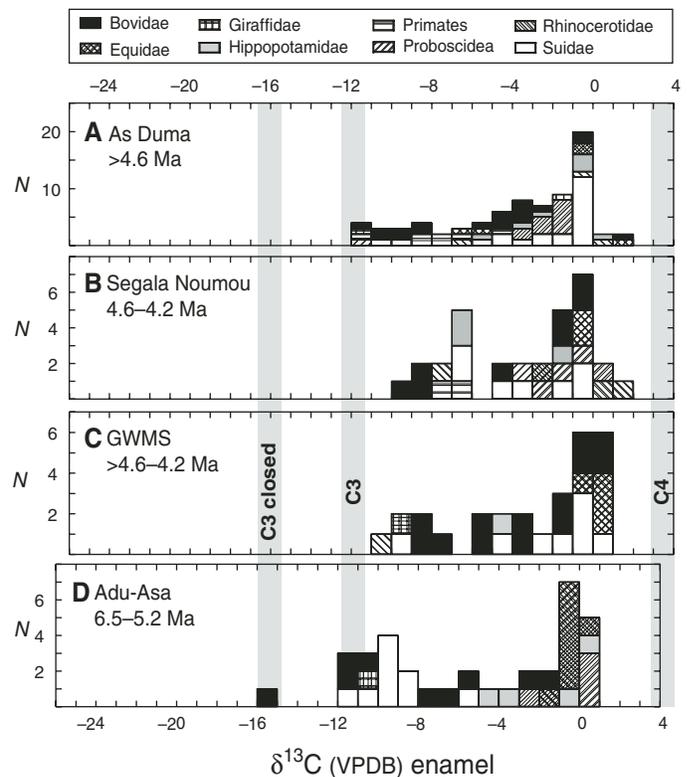

Figure 5. Histograms of $\delta^{13}C$ values in ‰ of tooth enamel for fossil herbivores from (A) the As Duma Member, (B) the Segala Noumou Member, and (C) Gona Western Margin South (GWMS) sites in the Sagantole Formation, and (D) the Adu-Asa Formation. The axis for the Adu-Asa plot (D) is shifted −0.6‰ to account for changes in $\delta^{13}C$ values of atmospheric CO_2 (see Table 1). Gray vertical bars represent averages of expected $\delta^{13}C_{enamel}$ values for herbivores eating strict diets of C_3 plants from a closed-canopy forest, C_3 plants from a forest or bushland, and C_4 grasses.

twice as common as *K. aramisi* fossils in the Sagantole Formation at Gona (Semaw et al., 2005).

The $\delta^{13}C_{enamel}$ values of modern primate teeth span a large range (>13‰) of values expected for herbivore tooth enamel (Fig. 6). The $\delta^{13}C_{enamel}$ values of primates from the Ituri Forest are less than −15‰ and are lower than $\delta^{13}C_{enamel}$ values from the majority of extant primates living elsewhere in eastern Africa. Baboons (*Papio anubis*, *P. hamadryas*, and *T. gelada*), which live in many different environments today, exhibit a large range in $\delta^{13}C_{enamel}$ values, between −16.7 ± 0.5‰ (n = 2) in the Ituri Forest and −5.2 ± 1.4‰ (n = 3) at Laikipia. A single tooth from *T. gelada*, a grass-eating baboon, sampled from Simien yields a $\delta^{13}C_{enamel}$ value of −10.2‰. The $\delta^{13}C_{enamel}$ values of extant colobine monkeys sampled from the forests at Ituri and Kahuzi-Biega in the D.R.C. average −15.5 ± 1.3‰ (n = 5) (Fig. 6).

The $\delta^{13}C_{enamel}$ values of fossil primates *P. alemui* and *K. aramisi* are enriched in ^{13}C relative to $\delta^{13}C_{enamel}$ values of extant East African primates. The $\delta^{13}C_{enamel}$ values for *P. alemui* average −7.3 ± 1.2‰ (n = 7), and those from *K. aramisi* average −9.4 ± 1.5‰ (n = 5). There are no significant distinctions in $\delta^{13}C_{enamel}$ values between specimens found in the As Duma or Segala Noumou Members for either *P. alemui* or *K. aramisi*. When compared to each other, $\delta^{13}C_{enamel}$ values of *P. alemui* are significantly higher than those of *K. aramisi*. The $\delta^{13}C_{enamel}$ values of *P. alemui* are most similar to $\delta^{13}C_{enamel}$ values of extant papionins than to any of the other primates, but they are significantly higher than $\delta^{13}C_{enamel}$ values of the baboons from

Ituri and all non-papionin primates in the comparison. The $\delta^{13}C_{enamel}$ values of *K. aramisi* do not vary from $\delta^{13}C_{enamel}$ values of any of the extant primates, except they have higher $\delta^{13}C_{enamel}$ values than those measured for the cercopithecines from Ituri and Kahuzi-Biega, gorillas at Kahuzi-Biega, and the colobine *P. badius* at Ituri.

There are two useful observations from the extant primate $\delta^{13}C_{enamel}$ data that help us interpret $\delta^{13}C_{enamel}$ values from fossil primates at Gona: (1) primates living in closed-canopy systems are isotopically distinctive, and (2) papionin diet can be variable. The ^{13}C-depleted $\delta^{13}C_{enamel}$ values (<−15‰) of primates from the Ituri Forest are indicative of animals living in a closed-canopy forest and are consistent with other primate isotopic data from closed-canopy ecosystems (Schoeninger et al., 1998; Carter, 2001). All of the $\delta^{13}C_{enamel}$ values from the fossil primates at Gona are more enriched in ^{13}C than those from primates living in closed-canopy forests, precluding the possibility that the fossil primates lived in a closed-canopy environment. The large range in $\delta^{13}C_{enamel}$ values from extant papionins indicates that their diet is variable and can include some C_4 vegetation, as also observed by Codron et al. (2006). The overlap in $\delta^{13}C_{enamel}$ values between the extant and fossil papionins suggests that *P. alemui*, the more prevalent non-hominoid primate at Gona, may have had dietary behaviors similar to extant baboons and consumed varying amounts of C_4 plants, including grass leaves, seeds, or rhizomes. Lower $\delta^{13}C_{enamel}$ values for *K. aramisi* show that these fossil colobines ate proportionately more C_3 vegetation than *P. alemui*.

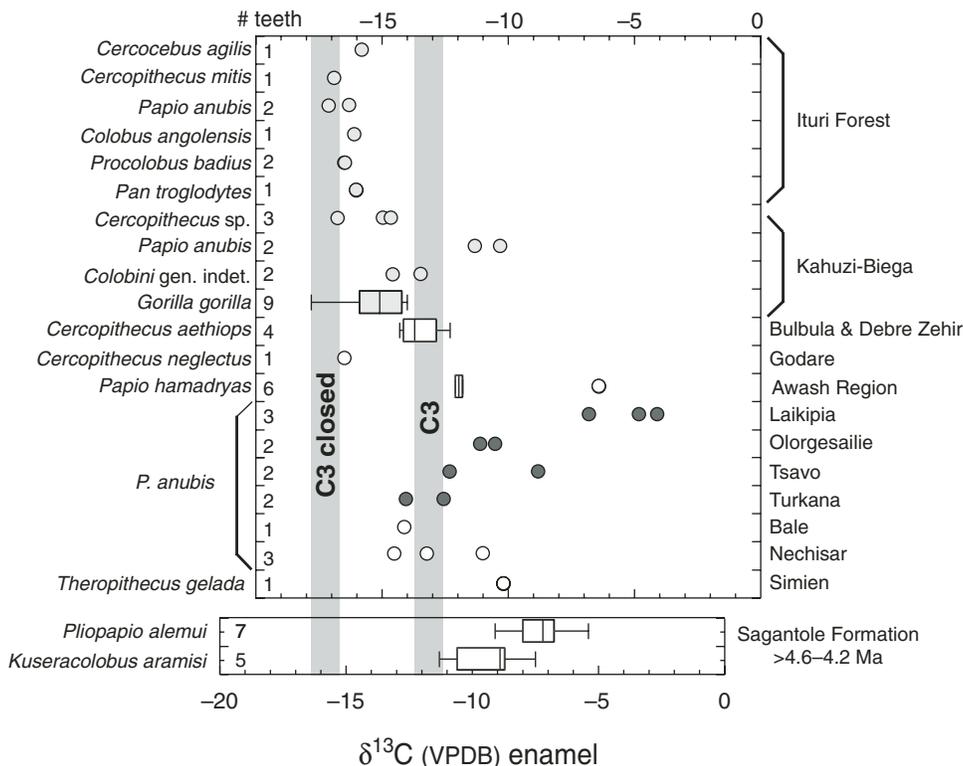Figure 6. Box plot of $\delta^{13}C$ values in ‰ of extant and fossil primate teeth. In the box plot, median values are marked by a vertical line within the box, the edges of the boxes represent quartile values, the horizontal lines indicate the range, and outliers are plotted as circles. The $\delta^{13}C_{enamel}$ values for taxa with three or fewer samples are plotted as circles. Axes for the plots of fossil $\delta^{13}C_{enamel}$ values are offset from modern $\delta^{13}C_{enamel}$ values based on calculations for changes in $\delta^{13}C_{atm-CO_2}$ values described in Table 1. The $\delta^{13}C_{enamel}$ values from the Democratic Republic of Congo (D.R.C.) (Cerling et al., 2004), Kenya (T.E. Cerling et al., 2007, personal commun.), and Ethiopia are plotted in light gray, dark gray, and white, respectively. Gray vertical bars represent averages of expected $\delta^{13}C_{enamel}$ values for herbivores eating strict diets of C_3 plants from a closed-canopy forest and C_3 plants from a forest or bushland. The estimate for $\delta^{13}C_{enamel}$ values formed from a diet of C_4 plants is excluded because it lies off the plot.

Suidae

Extant suid teeth sampled include *Phacochoerus* sp. (warthog) and *Potomachoerus porcus* (bush pig) from Ethiopia and *Phacochoerus* sp., *Pot. porcus*, and *Hylochoerus meinertzhageni* (forest hog) from Kenya, Uganda, and the D.R.C. (Harris and Cerling, 2002). Warthogs are grouped on the genus level because morphologic distinctions between the common warthog (*Phacochoerus africanus*) and the desert warthog (*Phacochoerus aethiopicus*) (d'Huart and Grubb, 2001; Randi et al., 2002) were not made for this study. Fossil suidae sampled from Gona include *Nyanzachoerus syrticus* from the late Miocene and three sympatric taxa from the early Pliocene deposits, *Nyanzachoerus jaegeri*, *Nyanzachoerus kanamensis*, and *Kolpochoerus deheinzelini*. Of the early Pliocene suids found in the Sagantole Formation at Gona, *Ny. jaegeri* is the most common, followed by *K. deheinzelini* and then by *Ny. kanamensis*. Subtle morphological distinctions between *Ny. kanamensis* and *Ny. jaegeri* limit some of the identifications of isolated teeth to the genus level.

Extant suids from East Africa display the full spectrum of $\delta^{13}C_{enamel}$ values expected for herbivores (Fig. 7). Average $\delta^{13}C_{enamel}$ values for warthogs range from $-8.4 \pm 2.0‰$ ($n = 4$) at Bale to $-0.1 \pm 0.6‰$ ($n = 12$) at Nakuru. Within the Awash region alone, $\delta^{13}C_{enamel}$ values of warthogs range between $-5.6‰$ and $+2.2‰$ (average $-1.7 \pm 1.8‰$, $n = 18$). The $\delta^{13}C_{enamel}$ values of extant bush pigs range between $-16.1‰$ ($n = 1$) in the Ituri Forest and $-3.0 \pm 3.7‰$ ($n = 6$) in the Athi Plains. Forest hogs have the lowest $\delta^{13}C_{enamel}$ values among extant suids, averaging $-22.6 \pm 0.4‰$ ($n = 2$) at Ituri, $-16.3 \pm 1.8‰$ ($n = 4$) in the Kenyan mountains, and $-14.5‰$ ($n = 1$) in Queen Elizabeth Park.

The $\delta^{13}C_{enamel}$ values of fossil suids point to different dietary behaviors between the late Miocene and early Pliocene taxa (Fig. 7). The $\delta^{13}C_{enamel}$ values of *Ny. syrticus*, the late Miocene suid at Gona, average $-9.2 \pm 1.5‰$ ($n = 9$) and are responsible for a large portion of the C_3 signal in the histogram of $\delta^{13}C_{enamel}$ values of teeth from the Adu-Asa Formation (Fig. 5D). The $\delta^{13}C_{enamel}$ values of the small suid from the Sagantole Formation, *K. deheinzelini*, average $-6.2 \pm 2.3‰$ ($n = 7$), whereas $\delta^{13}C_{enamel}$ values of the nyanzachoeres from the Sagantole Formation average $-1.5 \pm 1.5‰$ ($n = 22$), $-1.4 \pm 1.6‰$ ($n = 8$), and $-2.1 \pm 1.3‰$ ($n = 5$) for *Ny. jaegeri*, *Ny. kanamensis*, and *Ny.* sp. indet., respectively. The $\delta^{13}C_{enamel}$ values of *Ny. syrticus* from the Adu-Asa Formation are significantly lower than $\delta^{13}C_{enamel}$ values of all suid species from the Sagantole Formation. Among suids from the Sagantole Formation, $\delta^{13}C_{enamel}$ values of *K. deheinzelini* are lower than $\delta^{13}C_{enamel}$ values of the nyanzachoeres.

The $\delta^{13}C_{enamel}$ values of the extant suids show that warthogs eat primarily C_4 plants, that bush pigs can have variable diets and will opportunistically feed on C_3 or C_4 vegetation, and that forest hogs are hyperbrowsers (Harris and Cerling, 2002). The $\delta^{13}C_{enamel}$ values of warthogs from Ethiopia extend the known isotopic range for extant warthogs. Low $\delta^{13}C_{enamel}$ values ($-10.8‰$ to $-6.5‰$) of warthogs at Bale National Park indicate diets with a significant C_3 plant component, which may be explained by consumption of C_3 grasses prevalent at high elevations in the Bale Mountains (>3000 m). Low $\delta^{13}C_{enamel}$ values ($-13‰$) of two adult molar teeth from a single warthog at Nechisar (Fig. 7) are unexpected, given the 1250 m elevation grassland setting at Nechisar. The large range of $\delta^{13}C_{enamel}$ values among warthogs from the Awash region suggests that

Figure 7. Box plot of $\delta^{13}C$ values in ‰ of extant and fossil suid teeth, plotted in same manner as Figure 6. Axes for the plots of fossil $\delta^{13}C_{enamel}$ values are offset from each other and from modern $\delta^{13}C_{enamel}$ values based on calculations for changes in $\delta^{13}C_{atm-CO_2}$ values described in Table 1. The $\delta^{13}C_{enamel}$ values from Uganda, the Democratic Republic of Congo (D.R.C.), Kenya (Harris and Cerling, 2002), and Ethiopia are plotted in black, light gray, dark gray, and white, respectively. Gray vertical bars represent averages of expected $\delta^{13}C_{enamel}$ values for herbivores eating strict diets of C_3 plants from a closed-canopy forest, C_3 plants from a forest or bushland, and C_4 grasses.
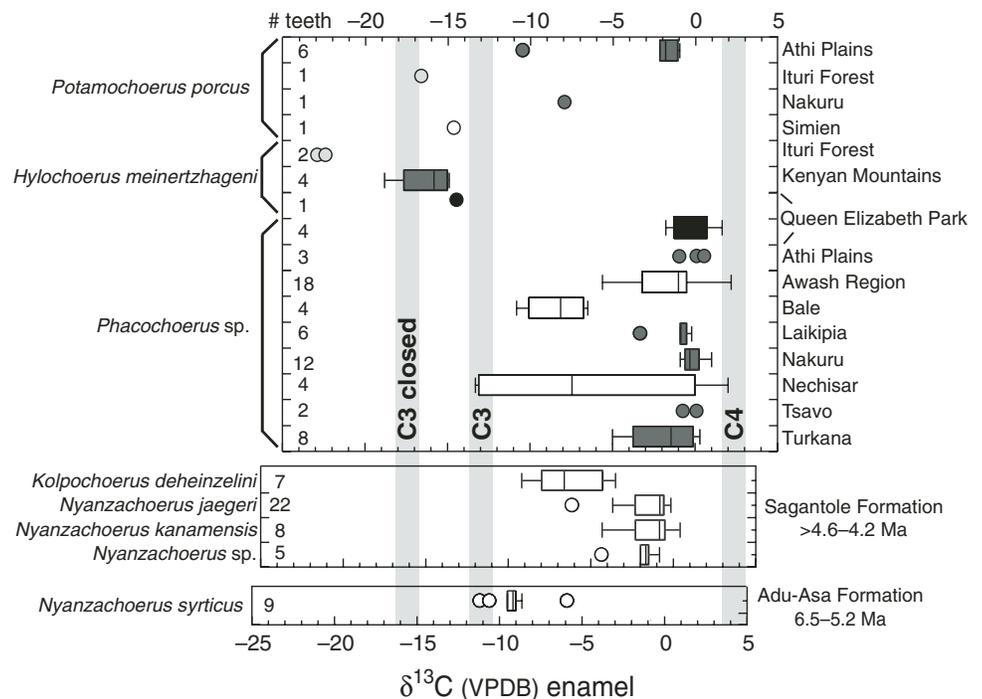
warthogs can have variable diets, even in environments where C_4 plants are the only available grass resources.

The $\delta^{13}C_{enamel}$ values of fossil suids at Gona indicate a dietary shift between the late Miocene, when suid diet was dominated by C_3 plants, and the early Pliocene, when suids had mixed C_3-C_4 and C_4-dominated diets. The isotope data suggest that *Ny. syrticus* was a browser living in a forest, woodland, or bushland, but not in a closed-canopy ecosystem. In contrast, the early Pliocene nyanzachoeres were grazers with $\delta^{13}C_{enamel}$ values indicative of diets similar to those of extant East African warthogs living at lower elevations (<2000 m). These results are consistent with isotopic data from *Ny. syrticus* and *Ny. jaegeri* from late Miocene and early Pliocene deposits at Kenya and Chad (Zazzo et al., 2000; Harris and Cerling, 2002).

While there is no significant difference in $\delta^{13}C_{enamel}$ values between *Ny. jaegeri* and *Ny. kanamensis*, there is a distinction between the nyanzachoeres and *K. deheinzelini* in the Sagantole Formation. The $\delta^{13}C_{enamel}$ values for *K. deheinzelini* are most similar to those of extant bush pigs, and the large range in values suggests a cosmopolitan diet. There are no published isotopic data from *K. deheinzelini* for comparison, but $\delta^{13}C_{enamel}$ values from younger taxa in the kolpochoere lineage (Zazzo et al., 2000; Harris and Cerling, 2002; Kingston and Harrison, 2007) indicate a shift toward an increased dependence on C_4 vegetation through the Pliocene.

Hippopotamidae

Hippopotamid teeth sampled from Ethiopia include the extant hippopotamus, *Hippopotamus amphibius*, from Nechisar and Awash Parks and fossil Hippopotamidae from the Adu-Asa and Sagantole Formations (Fig. 8A). The $\delta^{13}C_{enamel}$ values of *H. amphibius* average $-4.2 \pm 1.7‰$ ($n = 5$) at Awash Park and $-4.1 \pm 2.0‰$ ($n = 7$) at Nechisar Park. Among the fossils, $\delta^{13}C_{enamel}$ values average $-2.0 \pm 2.5‰$ ($n = 4$) and $-2.8 \pm 2.5‰$ ($n = 11$) for the late Miocene and early Pliocene hippopotamidae, respectively. The $\delta^{13}C_{enamel}$ values from fossil hippopotamids are indistinguishable from values of modern Ethiopian *H. amphibius*.

The carbon isotope data suggest that the diets of extant and fossil hippopotamids are dominated by C_4 plants but include a C_3 component. Mixed C_3-C_4 diets in extant and fossil hippopotamidae have also been observed elsewhere in Africa (Boisserie et al., 2005; Cerling et al., 2008; Harris et al., 2008).

Bovidae

Extant bovids sampled from Ethiopia include Alcelaphini, Bovini, Caprini, Cephalophini, Hippotragini, Neotragini, Reduncini, and Tragelaphini. The $\delta^{13}C_{enamel}$ values of extant bovids from Ethiopia were compared to $\delta^{13}C_{enamel}$ values of bovids from Kenya, Uganda, and the D.R.C (Cerling et al., 2003c, 2004) and used as references for interpreting $\delta^{13}C_{enamel}$ values of fossil bovids from Gona, which include Aepycerotini, Bovini, Reduncini, and Tragelaphini (Fig. 9). In the fossil deposits of the Sagantole Formation, Tragelaphini and Aepycerotini are equally common and together comprise ~80% of the bovid sample.

The $\delta^{13}C_{enamel}$ values of extant Ethiopian bovids plot within the ranges of corresponding tribes from elsewhere in East Africa (Fig. 9). An outlying $\delta^{13}C_{enamel}$ value among the Reduncini serves as one exception. Although $\delta^{13}C_{enamel}$ values of most Reduncini are indicative of diets of C_4 graze, the one *Redunca redunca* (Bohor reedbuck) sampled from the Bale Mountains yielded a $\delta^{13}C_{enamel}$ value of $-7.1‰$, suggesting the presence of C_3 plants in its diet. Like the other grazing animals sampled from Bale and Simien, in the Ethiopian highlands, the intermediate $\delta^{13}C_{enamel}$ value from this reedbuck indicates that it ate both C_3 and C_4 grass. The ^{13}C-depleted $\delta^{13}C_{enamel}$ values among Neotragini are from the Ituri Forest (Fig. 9) and indicate that these Neotragini (*Neotragus batesi*) eat ^{13}C-depleted plants from a closed-canopy setting. Cerling et al. (2004) classified these animals as subcanopy folivores.

In general, the $\delta^{13}C_{enamel}$ values of the late Miocene bovids from the Adu-Asa Formation lie outside the ranges of their modern analogs. The $\delta^{13}C_{enamel}$ value from cf. Hippotragini ($-10.2‰$) is considerably lower than values of modern grazing Hippotragini, and the $\delta^{13}C_{enamel}$ value of the cf. Reduncini specimen ($-5.4‰$) is similar only to the low outlier value from the extant Reduncini. The $\delta^{13}C_{enamel}$ value of the Antilopini ($-6.6‰$) from the Adu-Asa Formation does fall within the range of extant Antilopini. The $\delta^{13}C_{enamel}$ values of cf. *Tragelaphus* average $-13.6 \pm 2.9‰$ ($n = 2$) and are similar to those of extant Tragelaphini, whereas $\delta^{13}C_{enamel}$ values of *Tragelaphus* sp. are significantly more positive (average $-2.2 \pm 0.9‰$, $n = 2$) (Fig. 9).

The $\delta^{13}C_{enamel}$ values of bovids from the Sagantole Formation generally correspond to those of their extant counterparts. The $\delta^{13}C_{enamel}$ values of Aepycerotini range from $-11.4‰$ to $-0.3‰$ (average $-4.8 \pm 4.1‰$, $n = 6$) and are indistinct from $\delta^{13}C_{enamel}$ values of extant Aepycerotini. The $\delta^{13}C_{enamel}$ values of Bovini average $-3.9 \pm 1.3‰$ ($n = 4$) and lie within the extant range, except for those from the Ituri Forest and the Kenyan mountain region, which include data from the forest buffalo. Reduncini $\delta^{13}C_{enamel}$ values average $-0.7 \pm 1.1‰$ ($n = 2$) and are not distinct from those of extant Reduncini. Among $\delta^{13}C_{enamel}$ values of *Tragelaphus* sp., there are no distinctions between the different fossil assemblages within the Sagantole Formation, and when pooled together, they average $-6.8 \pm 3.4‰$ ($n = 20$) and range from $-11.0‰$ to $-0.1‰$. Although some $\delta^{13}C_{enamel}$ values of Tragelaphini from the Sagantole Formation overlap with the range of $\delta^{13}C_{enamel}$ values of extant Tragelaphini, they extend to values much higher ($-0.1‰$) than the high values measured in extant Tragelaphini ($-7‰$). The Tragelaphini are the only group of fossil bovids from the Sagantole Formation that do not have a range similar to their modern analogs.

We can only make general observations from the fossil bovid isotope data, given (1) the difficulty of making taxonomic identifications from isolated teeth, (2) the still-developing taxonomy of bovids from the late Miocene and early Pliocene in Ethiopia, and (3) the small number of isotopic analyses for some of the taxa from each fossil assemblage. All of the isotopic data from the fossil bovid teeth

A Hippopotamidae

B Giraffidae

C Rhinocerotidae

D Proboscidea

Figure 8. Box plot of $\delta^{13}C_{enamel}$ values in ‰ of large extant herbivores and their fossil forms from the Adu-Asa and Sagantole Formations, plotted in a similar manner as Figure 6. Axes for the plots of fossil $\delta^{13}C_{enamel}$ values are offset from each other and from modern $\delta^{13}C_{enamel}$ values based on calculations for changes in $\delta^{13}C_{atm-CO_2}$ values described in Table 1. Gray vertical bars represent averages of expected $\delta^{13}C_{enamel}$ values for herbivores eating strict diets of C_3 plants from a closed-canopy forest, C_3 plants from a forest or bushland, and C_4 grasses.
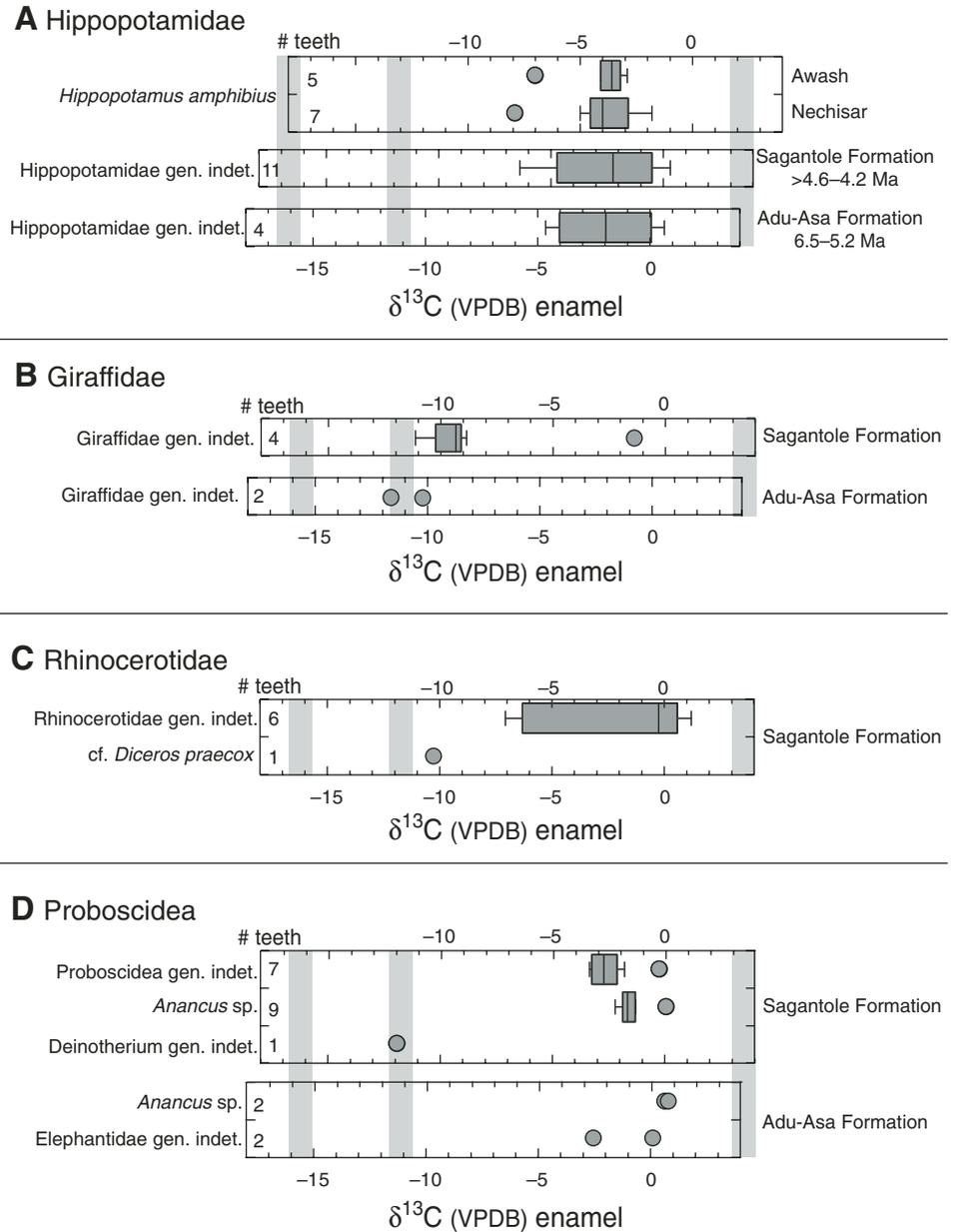
at Gona plot within the expected range of $\delta^{13}C_{enamel}$ values from animals eating C_3 and C_4 plants (Fig. 9), but most of the $\delta^{13}C$ values are intermediate and do not represent diets composed solely of C_3 or C_4 vegetation. The $\delta^{13}C_{enamel}$ values of bovids from the Adu-Asa Formation indicate that these animals relied more heavily on C_3 vegetation, whereas $\delta^{13}C_{enamel}$ values of bovids from the Sagantole Formation suggest an increased reliance on C_4 vegetation in the early Pliocene. The $\delta^{13}C_{enamel}$ values from the Sagantole bovids generally match those of their modern counterparts. However, $\delta^{13}C_{enamel}$ values of *Tragelaphus* sp. indicate a broad range of C_3 and C_4 diets, unlike extant tragelaphines, which exclusively eat C_3 plants. If these teeth represent one bovid species, then it had a very

diverse diet, like extant Antilopini and Aepycerotini. Alternatively, the large range in $\delta^{13}C_{enamel}$ values among Tragelaphini from the Sagantole Formation may indicate that more than one taxon is represented by *Tragelaphus* sp.

Giraffidae

The sample of giraffid teeth from the Adu-Asa and Sagantole Formations includes those identified to family. The $\delta^{13}C_{enamel}$ values of giraffids from the Adu-Asa Formation average -10.9 ± 1.0‰ ($n = 2$), and those from the Sagantole Formation average -9.8 ± 1.7‰ ($n = 3$), with one outlier value of -1.4‰ (Fig. 8B). The isotopic data from all giraffids, except for the outlier value, indicate diets dominated by C_3 plants, consis-
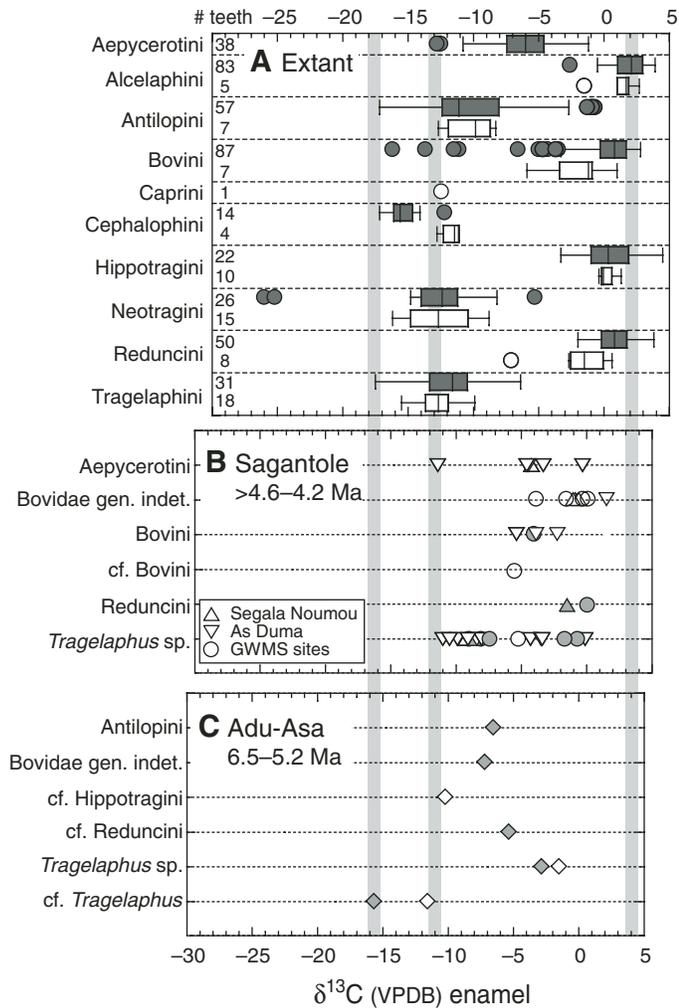
Figure 9. Bovid $\delta^{13}C_{enamel}$ values in ‰. (A) Box plot of $\delta^{13}C_{enamel}$ values from extant East African bovids grouped by tribe. The $\delta^{13}C_{enamel}$ values from bovids in Kenya, the Democratic Republic of Congo (D.R.C.), and Uganda (Cerling et al., 2003c, 2004) are plotted in dark gray, whereas white boxes represent the data from Ethiopia. (B–C) Point plots of $\delta^{13}C_{enamel}$ values from the Sagantole and Adu-Asa fossil assemblages. The $\delta^{13}C_{enamel}$ values from untreated fossil samples are plotted as filled symbols. Axes for the plots of fossil $\delta^{13}C_{enamel}$ values are offset from each other and from modern $\delta^{13}C_{enamel}$ values based on calculations for changes in $\delta^{13}C_{atm-CO_2}$ values described in Table 1. Gray vertical bars represent averages of expected $\delta^{13}C_{enamel}$ values for herbivores eating strict diets of C_3 plants from a closed-canopy forest, C_3 plants from a forest or bushland, and C_4 grasses.

tent with isotopic data from late Miocene giraffids from Chad (Zazzo et al., 2000) and early Pliocene giraffids from Tanzania (Kingston and Harrison, 2007).

Equidae

Extant equid teeth sampled from Ethiopia include *Equus grevyi* (Grevy's zebra), *E. burchelli* (Burchell's zebra), and *E. africanus somalicus* (Somali wild ass). All fossil equid teeth sampled

from the Adu-Asa Formation were assigned to *Eurygnathohippus* cf. *feibeli*, and those from the Sagantole Formation are classified as *Eurygnathohippus* sp.

The $\delta^{13}C_{enamel}$ values of most East African equids, ancient and modern, overlap and fall within a narrow range of −2‰ to +2‰ (Fig. 10). More subtle, but statistically significant, distinctions include *E. burchelli* from the Athi Plains and Nechisar, which have higher $\delta^{13}C_{enamel}$ values compared to those at Samburu and Nakuru. Among the fossil material from Gona, there are no significant differences among equid $\delta^{13}C_{enamel}$ values from the different fossil assemblages. The $\delta^{13}C_{enamel}$ values of *E*. cf. *feibeli* teeth from the late Miocene average −0.6 ± 0.5‰ (*n* = 8), and the $\delta^{13}C_{enamel}$ values of early Pliocene *Eurygnathohippus* sp. average −1.2 ± 2.4‰ (*n* = 13). The $\delta^{13}C_{enamel}$ values of two specimens from the As Duma Member (*Eurygnathohippus* sp.) average −6.1 ± 0.5‰ and are significantly lower than the $\delta^{13}C_{enamel}$ values of other equids from the As Duma Member and from other sites in the deposits of the Sagantole Formation (Fig. 10).

These isotopic results demonstrate that most fossil equidae from Gona, in both the late Miocene and early Pliocene deposits, were grazers and fed primarily on C_4 grass, like extant *Equus* in eastern Africa today. The low (−6‰) $\delta^{13}C_{enamel}$ values from two *Eurygnathohippus* sp. teeth in the As Duma Member suggest a diet with a large input of C_3 vegetation. However, given the fragmentary nature of these two teeth (both are unaccessioned GONBULK specimens), we must consider the possibility that these teeth might have formed early in life and represent a pre-adult diet. In bovids, the influence of mother's milk depletes $\delta^{13}C_{enamel}$ values by less than 1‰ (Balasse, 2002; Zazzo et al., 2002). The magnitude of this effect is likely similar for equids, which, like bovids, have milk with a low fat content (Oftedal, 1984). Consequently, the pre-weaning effect cannot account for the entire offset (~4‰) in $\delta^{13}C_{enamel}$ values of these equid teeth; a diet consisting of some C_3 plants likely explains the relatively ^{13}C-depleted $\delta^{13}C_{enamel}$ values.

Rhinocerotidae

The rhinoceros teeth sampled from the Sagantole Formation are fragmentary enamel pieces and are identified to family, except for one specimen identified as cf. *Diceros praecox*. No rhinoceros teeth were sampled from the Adu-Asa Formation. The $\delta^{13}C_{enamel}$ values of the rhinocerotids from the Sagantole Formation average −2.0 ± 3.7‰ (*n* = 6), but within this sample, two teeth have $\delta^{13}C_{enamel}$ values less than −6‰ (Fig. 8C). The specimen identified as cf. *Diceros praecox* has a $\delta^{13}C_{enamel}$ value of −10.3‰.

The isotopic data suggest that the diets of rhinocerotids contained varying amounts of C_3 and C_4 plants. The diets of the fossil rhinocerotids from Gona may have had similar diets to extant rhinocerotids, which include both a browsing and a grazing species, but it is unclear how the Pliocene fossil rhinocerotids are related to the extant forms (Geraads, 2005). Other isotopic studies have found a similar range in diets of rhinocerotids from the early Pliocene in Africa (Zazzo et al., 2000; Cerling et al., 2003a; Kingston and Harrison, 2007).

Figure 10. Box plot of $\delta^{13}C$ values in ‰ of extant and fossil equids. Plotted in the same manner as Figure 6, except note the different scale. Axes for the plots of fossil $\delta^{13}C_{enamel}$ values are off-set from each other and from modern $\delta^{13}C_{enamel}$ values based on calculations for changes in $\delta^{13}C_{atm-CO_2}$ values described in Table 1. The $\delta^{13}C_{enamel}$ values from Kenya (T.E. Cerling, 2007, personal commun.) and Ethiopia are plotted in dark gray and white, respectively. Gray vertical bars represent averages of expected $\delta^{13}C_{enamel}$ values for herbivores eating strict diets of C_4 plants. Estimates for $\delta^{13}C_{enamel}$ values formed from a strict diet of C_3 plants from a closed-canopy forest and C_3 plants from a forest or bushland are excluded because they lie off the plot.
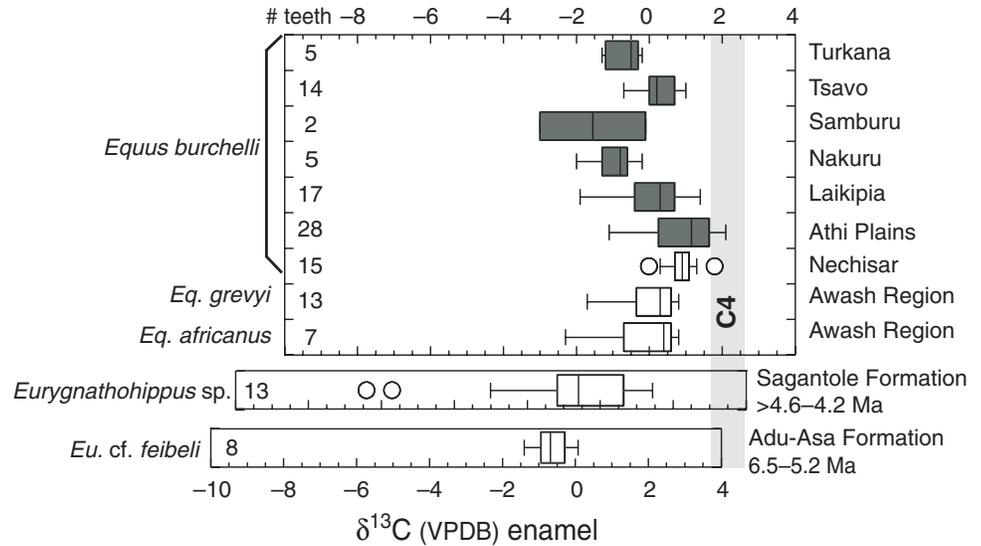
Proboscidea

The fossil proboscidea from Gona include gomphotheres (*Anancus* sp.) and elephantids from the Adu-Asa Formation, and gomphotheres (*Anancus* sp.), deinotheres (*Deinotherium* sp.), and unclassified proboscidea (Proboscidea gen. indet.) from the Sagantole Formation. Most of the proboscidean teeth sampled from the Sagantole Formation are enamel fragments and are difficult to identify in more detail. The $\delta^{13}C_{enamel}$ values of *Anancus* sp. and elephantids from the Adu-Asa Formation average +0.8 ± 0.1‰ (n = 2) and −1.2 ± 1.9‰ (n = 2), respectively (Fig. 8D). The $\delta^{13}C_{enamel}$ values of *Anancus* sp. and Proboscidea gen. indet. from the Sagantole Formation average −1.5 ± 0.7‰ (n = 9) and −2.4 ± 1.1‰ (n = 7). The $\delta^{13}C_{enamel}$ value of the sole deinothere analyzed from the Sagantole Formation is −11.9‰.

The $\delta^{13}C_{enamel}$ values of proboscidea from the Adu-Asa and Sagantole Formations at Gona indicate that the diets of these large-bodied herbivores were dominated by C_4 grass in both the late Miocene and the early Pliocene, except for the dentally specialized deinothere, which had a strict diet of C_3 plants. These results are consistent with isotopic data of proboscidea from fossil sites in Kenya, Tanzania, and Chad (Cerling et al., 1999, 2003a; Zazzo et al., 2000; Kingston and Harrison, 2007).

Summary

Examination of the herbivore tooth enamel isotopic data by each taxon confirms the perspective on late Miocene and early Pliocene environments at Gona provided by the $\delta^{13}C_{enamel}$ histograms in Figure 5. There is no isotopic evidence for a closed-canopy forest at Gona in the late Miocene or early Pliocene. The presence of suids, hippopotamids, bovids, equids, rhinocerotids, and proboscideans with C_4-dominated diets makes the fossil sites at Gona very different from the modern closed-canopy Ituri Forest, the forests at Kahuzi-Biega, and the Ethiopian highlands, where there is little to no C_4 component in herbivore diets.

Although some fossil taxa from the Adu-Asa and Sagantole Formations at Gona (e.g., primates, suids, and bovids) have $\delta^{13}C_{enamel}$ values that are similar to their extant forms in forest and highland environments, they are also similar to $\delta^{13}C_{enamel}$ values of analog taxa living in woodland and bushland ecoregions. The $\delta^{13}C_{enamel}$ values of fossil herbivores from the Adu-Asa and Sagantole Formations at Gona suggest that the vegetation at Gona during the late Miocene and early Pliocene was most similar to mixed C_3-C_4 woodlands or bushlands today.

Paleosol Carbonates

Paleosols in the Sagantole Formation at Gona are dark brown and clay rich with occasional manganese and iron-oxide staining, and they have either blocky ped structures or are massive in outcrop. Carbonate nodules collected from paleosols are 0.5–2 cm in diameter and are from distinct carbonate (Bk) horizons. In general, the early Pliocene paleosols at Gona are not as mature as the paleosols found in the younger Busidima Formation (Levin et al., 2004; Quade et al., 2004, this volume). There are no well-developed soils in the sedimentary sequences that contain fossil sites in the As Duma Member of the Sagantole Formation or in the Adu-Asa Formation at Gona.

Pedogenic carbonates were sampled from paleosols in the Sagantole Formation within <2 km radii of paleontological localities in the Segala Noumou Member, the GWMS fossil sites, and the fossil locality GWM45. Pedogenic carbonate nodules sampled from 10 paleosols in the Segala Noumou Member within a 2 km radius of GWM3, an *Ar. ramidus* locality, yield $\delta^{13}C$ values that average −7.5 ± 1.6‰ and range from −10.4‰ to −3.9‰ (Fig. 11). Pedogenic carbonate nodules from four paleosols associated with GWMS fossil sites (<1 m directly above or a below a fossil horizon) yield $\delta^{13}C$ values that average −5.5 ± 1.1‰. Three nodules from a paleosol directly underlying a fossiliferous gravel
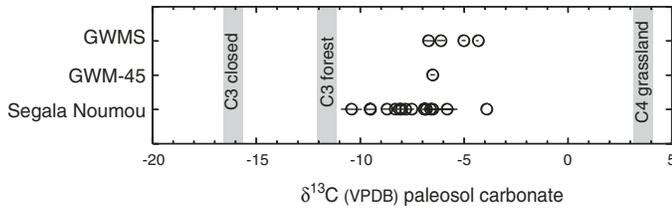
Figure 11. The $\delta^{13}C$ values in ‰ of paleosol carbonates associated with paleontological localities in the Sagantole Formation from the Gona Western Margin South (GWMS) sites, the GWM-45 site, and in the Segala Noumou Member. Plotted values are averages of multiple nodules from a single paleosol outcrop, and horizontal lines represent standard deviations. Gray vertical bars indicate approximate values that would be expected for soil carbonates forming beneath a canopy forest, C_3 plants in a forest or bushland, and a C_4 grassland during deposition of the Sagantole Formation when $\delta^{13}C_{atm-CO_2}$ was more enriched in ^{13}C.

and hominid locality, GWM45, have $\delta^{13}C$ values that average $-6.5 \pm 0.1‰$. A summary of the $\delta^{13}C$ values of soil carbonate from paleosols in the Sagantole Formation is presented in GSA Data Repository Table DR3 (see footnote 1). The $\delta^{13}C$ values of pedogenic nodules from the Sagantole Formation indicate the presence of both C_3 and C_4 vegetation but, generally, a greater proportion of C_3 plants (Fig. 11).

The C_3-dominated landscapes in the Sagantole Formation, as inferred from the soil carbonate record, contrast with the tooth enamel isotopic record, which suggests an abundance of C_4 vegetation. The $\delta^{13}C$ record from soil carbonates may represent just one end of the spectrum of environments in which animals lived. Differences between the records can be reconciled if C_3 plants grew in the well-watered areas where there was active deposition and soil formation, and if C_4 plants grew on slopes or topographic highs where depositional rates were lower. Active volcanic cones and basalt flows adjacent to the depositional environments in both the Adu-Asa and Sagantole Formations would have generated topographically and lithologically diverse landscapes that could support a variety of soil types and vegetation communities, including C_4 grasses.

Paleoelevation

In addition to identifying the degree of forestation and the presence of grasslands, $\delta^{13}C$ values from soil carbonates and teeth can also be indicators of paleoelevation. The altitudinal effect on $\delta^{13}C_{enamel}$ values is clear in modern data from the Ethiopian highlands, where only a few taxa have C_4 grass in their diet, despite the abundance of grasses (Fig. 4C). The presence of C_4 plants growing in soils and in the diets of most herbivores in the late Miocene and early Pliocene fossil assemblages at Gona precludes the possibility that these environments were above the altitudinal limit for growth of C_4 plants, which is between 2800 and 3200 m in East Africa today (Young and Young, 1983). However, this limit depends on climatic conditions (e.g., effective moisture and growing-season temperatures), and there

is evidence that it has moved upward in the past, during the Last Glacial Maximum, on Mt. Kenya, when C_4 grasses were abundant at 3080 m (Wooller et al., 2003). We do not know the location of this limit in East Africa in the late Miocene and early Pliocene, before the onset of Northern Hemisphere glaciation, but if C_4 grasses did exist at higher elevations during these periods, then they were accompanied by the environmental conditions, like warm growing-season temperatures, in which C_4 grasses thrive at lower elevations today.

The presence of fossil *Tachyoryctes*, a genus of mole rat, has been used as an indicator of high elevation for *Ardipithecus*-bearing deposits in the Middle Awash and Gona study areas (WoldeGabriel et al., 1994, 2001; Haile-Selassie et al., 2004; Semaw et al., 2005). *T. macrocephalus*, the giant mole rat, is currently found at Bale and Simien in the Ethiopian highlands and is restricted to 3200–4150 m (Yalden, 1985), above the elevation limit for C_4 grasses. However, another species, *T. splendens*, is found at lower elevations (1200–3200 m; Yalden et al., 1996), where C_4 vegetation thrives. Assuming that *Tachyoryctes* in the fossil record was restricted to similar elevations as the extant forms, and that C_4 plants in the late Miocene and early Pliocene were limited to environments below 3200 m, then *Ardipithecus* must have lived at elevations between 1200 and 3200 m. If the high-elevation limit of C_4 plants was above 3200 m in the late Miocene or early Pliocene, then the environments would have to be similar to those below that limit today, given the clear isotopic indicators of C_4 vegetation in the fossil record from the Adu-Asa and Sagantole Formations at Gona. Either of these interpretations would place late Miocene and early Pliocene *Ardipithecus* environments at elevations higher than the present elevation of *Ardipithecus*-bearing deposits in the Gona Paleoanthropological Research Project study area, which ranges between 800 and 950 m. Alternatively, the fossil *Tachyoryctes* may have had a lower elevation limit than its present forms, in which case there might have been little elevation change since the late Miocene or early Pliocene. This latter hypothesis is consistent with a kinematic model proposed by Redfield et al. (2003), which suggests little change in Afar topography since the late Miocene.

DISCUSSION

Regional Environments of *Ardipithecus*

The isotopic data from large herbivores and paleosol carbonates associated with *Ardipithecus* fossils at Gona indicate a different landscape from that described for either the *Ardipithecus*-bearing deposits in the Middle Awash, Ethiopia, or at Tabarin, Kenya. WoldeGabriel et al. (1994, 2001) and White et al. (2006) have suggested that *Ardipithecus* lived in wooded biomes and avoided open environments. Isotopic data from soil carbonates in these deposits suggest the presence of both C_3 and C_4 vegetation on the landscape, but the paleoenvironmental reconstructions are based primarily on the presence or absence of fossils with extant forms usually found in wooded or open

environments, respectively. For example, the characterization of *Ar. ramidus* habitat at Aramis as "varying from closed to grassy woodlands" is based on the presence of colobine monkeys and tragelaphine bovids (White et al., 2006; WoldeGabriel et al., 1994). Pickford and colleagues (2004) reconstructed the habitat at the Tabarin *Ar. ramidus* site as a rain forest from the presence of peafowl and tragulids. However, assignments of the habitat and diet of extant taxa to their fossil forms can be tenuous.

The carbon isotope data from Gona show that there were abundant C_4 grasses associated with paleohabitats where *Ardipithecus* lived and that the majority of the large mammalian herbivores with which *Ardipithecus* fossils are found sought C_4 plants for food. Considering the isotopic data from Gona, the assertion that there is a "scarcity of basal Pliocene hominid remains in non-woodland settings in the Middle Awash and beyond" (WoldeGabriel et al., 1994, p. 333) must be revised. However, this does not preclude the possibility that less than 100 km to the south, in the Middle Awash study area, *Ardipithecus* lived in closed, forested habitats. *Ardipithecus* fossils found in the Middle Awash study area may have been deposited in a more axial part of the basin than the Gona sediments, which were closer to the basin margin (Quade et al., this volume). The different paleoenvironmental reconstructions indicate that *Ardipithecus* may have inhabited a variety of landscapes and was not as ecologically restricted as previous studies have suggested (WoldeGabriel et al., 1994, 2001). Active tectonism, frequent volcanism, and the segmented nature of basalt-bounded grabens in this part of the Afar Rift during the late Miocene and early Pliocene could explain variation in *Ardipithecus* habitat within the 100 km that separates the Middle Awash and Gona project areas. Direct comparisons of the paleontological records and geological setting in the future will further clarify the paleobiology of *Ardipithecus*.

CONCLUSIONS

Carbon isotopic data show that extant East African herbivores living in closed-canopy forests, forests, and montane regions have $\delta^{13}C_{enamel}$ values that are distinct from those of herbivores living in bushlands and grasslands. When compared to data from modern environments, isotopic data of fossil herbivores from the *Ardipithecus*-bearing deposits at Gona most closely resemble the isotopic data from herbivores living in bushlands today. The $\delta^{13}C_{enamel}$ values of the fauna from the Miocene-Pliocene fossil deposits at Gona do not match $\delta^{13}C_{enamel}$ values of herbivores living in closed-canopy forests like the Ituri Forest, the forests in Kahuzi-Biega, or the mountainous regions in Kenya and Ethiopia. Examination of individual taxa confirms this and shows that the diets of the majority of taxa in the late Miocene at Gona were composed of a mixture of C_3 and C_4 plants, and, in the early Pliocene, they were dominated by C_4 grass. The carbon isotopic record from fossil teeth and soil carbonates shows that *Ardipithecus* at Gona was part of ecosystems in which C_4 grasses were a major component of the floral biomass.

REFERENCES CITED

Balasse, M., 2002, Reconstructing dietary and environmental history from enamel isotopic analysis: Time resolution of intra-tooth sequential sampling: International Journal of Osteoarchaeology, v. 12, p. 155–165, doi: 10.1002/oa.601.

Boisserie, J.-R., Zazzo, A., Merceron, G., Blondel, C., Vignaud, P., Likius, A., Mackaye, H.T., and Brunet, M., 2005, Diets of modern and late Miocene hippopotamids: Evidence from carbon isotope composition and microwear of tooth enamel: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 221, p. 153–174, doi: 10.1016/j.palaeo.2005.02.010.

Carter, M.L., 2001, Sensitivity of Stable Isotopes (^{13}C, ^{15}N and ^{18}O) in Bone to Dietary Specialization and Niche Separation among Sympatric Primates in Kibale National Park, Uganda [Ph.D. thesis]: Chicago, University of Chicago, 288 p.

Cerling, T.E., 1999, Stable carbon isotopes in palaeosol carbonates, *in* Thiry, M., and Simon-Coincon, R., eds., Palaeoweathering, Palaeosurfaces and Related Continental Deposits: International Association of Sedimentology Special Publication 27, p. 43–60.

Cerling, T.E., and Harris, J.M., 1999, Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies: Oecologia, v. 120, p. 347–363, doi: 10.1007/s004420050868.

Cerling, T.E., Harris, J.M., and Leakey, M.G., 1999, Browsing and grazing in elephants: The isotope record of modern and fossil proboscideans: Oecologia, v. 120, p. 364–374, doi: 10.1007/s004420050869.

Cerling, T.E., Harris, J.M., and Leakey, M.G., 2003a, Isotope paleoecology of the Nawata and Nachukui Formations at Lothagam, Turkana Basin, Kenya, *in* Leakey, M.G., and Harris, J.M., eds., Lothagam: The Dawn of Humanity: New York, Columbia University Press, p. 605–614.

Cerling, T.E., Harris, J.M., Leakey, M.G., and Mudida, N., 2003b, Stable isotope ecology of northern Kenya with emphasis on the Turkana Basin, *in* Leakey, M.G., and Harris, J.M., eds., Lothagam: The Dawn of Humanity: New York, Columbia University Press, p. 583–594.

Cerling, T.E., Harris, J.M., and Passey, B.H., 2003c, Diets of East African Bovidae based on stable isotope analysis: Journal of Mammalogy, v. 84, no. 2, p. 456–470, doi: 10.1644/1545-1542(2003)084<0456:DOEABB>2.0.CO;2.

Cerling, T.E., Hart, J.A., and Hart, T.B., 2004, Stable isotope ecology in the Ituri Forest: Oecologia, v. 138, p. 5–12, doi: 10.1007/s00442-003-1375-4.

Cerling, T.E., Harris, J.M., Hart, J.A., Kaleme, P., Klingel, H., Leakey, M.G., Levin, N.E., Lewison, R.L., and Passey, B.H., 2008, Stable isotope ecology of the common hippopotamus: Journal of Zoology, doi: 10.1111/j.1469-7998.2008.00450.x.

Codron, D., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D., and Codron, J., 2006, Inter- and intrahabitat dietary variability of Chacma baboons (*Papio ursinus*) in South African savannas based on fecal δ13C, δ15N, and %N: American Journal of Physical Anthropology, v. 129, p. 204–214, doi: 10.1002/ajpa.20253.

DeNiro, M.J., and Epstein, S., 1978, Influence of diet on the distribution of carbon isotopes in animals: Geochimica et Cosmochimica Acta, v. 42, p. 495–506, doi: 10.1016/0016-7037(78)90199-0.

d'Huart, J.-P., and Grubb, P., 2001, Distribution of the common warthog (*Phacochoerus africanus*) and the desert warthog (*Phacochoerus aethiopicus*) in the Horn of Africa: African Journal of Ecology, v. 39, p. 156–169, doi: 10.1046/j.0141-6707.2000.00298.x.

Farquhar, G.D., Ehleringer, J.R., and Hubick, K.T., 1989, Carbon isotope discrimination and photosynthesis: Annual Review of Plant Physiology and Plant Molecular Biology, v. 40, p. 503–537, doi: 10.1146/annurev.pp.40.060189.002443.

Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E., and Steele, L.P., 1999, A 1000-year high precision record of δ13C in atmospheric CO2: Tellus, v. 51B, p. 170–193.

Geraads, D., 2005, Pliocene Rhinocerotidae (Mammalia) from Hadar and Dikika (Lower Awash, Ethiopia), and a revision of the origin of modern African rhinos: Journal of Vertebrate Paleontology, v. 25, no. 2, p. 451–461, doi: 10.1671/0272-4634(2005)025[0451:PRMFHA]2.0.CO;2.

Haile-Selassie, Y., 2001, Late Miocene hominids from the Middle Awash, Ethiopia: Nature, v. 412, p. 178–181, doi: 10.1038/35084063.

Haile-Selassie, Y., WoldeGabriel, G., White, T.D., Bernor, R.L., Degusta, D., Renne, P.R., Hart, W.K., Ambrose, S., and Howell, F.C., 2004, Mio-Pliocene mammals from the Middle Awash, Ethiopia: Geobios, v. 37, p. 536–552, doi: 10.1016/j.geobios.2003.03.012.

Harris, J.M., and Cerling, T.E., 2002, Dietary adaptations of extant and Neogene African suids: Journal of Zoology, v. 256, p. 45–54.

Harris, J.M., Cerling, T.E., Leakey, M.G., and Passey, B.H., 2008, Stable isotope ecology of fossil hippopotamids from the Lake Turkana Basin of East Africa: Journal of Zoology, v. 275, p. 323–331, doi: 10.1111/j.1469-7998.2008.00444.x.

Indermühle, A., Stocker, T.F., Joos, F., Fischer, H., Smith, H.J., Wahlen, M., Deck, B., Mastroianni, D., Tschumi, J., Blunier, T., Meyer, R., and Stauffer, B., 1999, Holocene carbon-cycle dynamics based on CO2 trapped in ice at Taylor Dome, Antarctica: Nature, v. 398, p. 121–126, doi: 10.1038/18158.

Keeling, C.D., Mook, W.G., and Tans, P.P., 1979, Recent trends in the 13C/12C ratio of atmospheric carbon dioxide: Nature, v. 277, p. 121–123, doi: 10.1038/277121a0.

Keeling, C.D., Whorf, T.P., Wahlen, M., and van der Plicht, J., 1995, Inter-annual extremes in the rate of rise of atmospheric carbon dioxide since 1980: Nature, v. 375, p. 666–670, doi: 10.1038/375666a0.

Kingston, J.D., and Harrison, T., 2007, Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Implications for early hominin palaeoecology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 243, p. 272–306, doi: 10.1016/j.palaeo.2006.08.002.

Kleinsasser, L.L., Quade, J., McIntosh, W.C., Levin, N.E., Simpson, S.W., and Semaw, S., 2008, this volume, Stratigraphy and geochronology of the late Miocene Adu-Asa Formation at Gona, Ethiopia, *in* Quade, J., and Wynn, J.G., eds., The Geology of Early Humans in the Horn of Africa: Geological Society of America Special Paper 446, doi: 10.1130/2008.2446(02).

Koch, P.L., Tuross, N., and Fogel, M.L., 1997, The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite: Journal of Archaeological Science, v. 24, p. 417–429, doi: 10.1006/jasc.1996.0126.

Laporte, L.F., and Zihlman, A.L., 1983, Plates, climate and hominoid evolution: South African Journal of Science, v. 79, p. 96–110.

Lee-Thorp, J.A., 2000, Preservation of biogenic carbon isotope signals in Plio-Pleistocene bone and tooth mineral, *in* Ambrose, S.H., and Katzenberg, M.A., eds., Biogeochemical Approaches to Paleodietary Analysis: New York, Kluwer Academic/Plenum Press, p. 89–115.

Lee-Thorp, J.A., and van der Merwe, N.J., 1991, Aspects of the chemistry of modern and fossil biological apatites: Journal of Archaeological Science, v. 18, p. 343–354, doi: 10.1016/0305-4403(91)90070-6.

Levin, N.E., Quade, J., Simpson, S.W., Semaw, S., and Rogers, M.J., 2004, Isotopic evidence for Plio-Pleistocene environmental change at Gona, Ethiopia: Earth and Planetary Science Letters, v. 219, p. 93–110, doi: 10.1016/S0012-821X(03)00707-6.

MacFadden, B.J., and Higgins, P., 2004, Ancient ecology of 15-million-year-old browsing mammals within C3 plant communities from Panama: Oecologia, v. 140, p. 169–182, doi: 10.1007/s00442-004-1571-x.

Oftedal, O.T., 1984, Milk composition, milk yield and energy output at peak lactation: A comparative review: Symposia of the Zoological Society of London, v. 51, p. 33–85.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoureux, J.F., Wettengel, W.W., Hedao, P., and Kassem, K.R., 2001, Terrestrial ecoregions of the world: A new map of life on Earth: BioScience, v. 51, no. 11, p. 933–938.

Passey, B.H., Cerling, T.E., Perkins, M.E., Voorhies, M.R., Harris, J.M., and Tucker, S.T., 2002, Environmental change in the Great Plains: An isotopic record from fossil horses: The Journal of Geology, v. 110, p. 123–140, doi: 10.1086/338280.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., and Ehleringer, J.R., 2005, Carbon isotope fractionation between diet, breath CO2, and bioapatite in different mammals: Journal of Archaeological Science, v. 32, p. 1459–1470, doi: 10.1016/j.jas.2005.03.015.

Pickford, M., Senut, B., and Mourer-Chauviré, C., 2004, Early Pliocene Tragulidae and peafowls in the Rift Valley, Kenya: Evidence for rainforest in East Africa: Comptes Rendus Palevol, v. 3, p. 179–189, doi: 10.1016/j.crpv.2004.01.004.

Potts, R., 1998, Environmental hypotheses of hominin evolution: Yearbook of Physical Anthropology, v. 41, p. 93–136, doi: 10.1002/(SICI)1096-8644(1998)107:27+<93::AID-AJPA5>3.0.CO;2-X.

Quade, J., Levin, N., Semaw, S., Stout, D., Renne, P.R., Rogers, M., and Simpson, S., 2004, Paleoenvironments of the earliest stone toolmakers, Gona, Ethiopia: Geological Society of America Bulletin, v. 116, no. 11–12, p. 1529–1544, doi: 10.1130/B25358.1.

Quade, J., Levin, N.E., Simpson, S.W., Butler, R., McIntosh, W.C., Semaw, S., Kleinsasser, L., Dupont-Nivet, G., Renne, P., and Dunbar, N., 2008, this volume, The geology of Gona, Afar, Ethiopia, *in* Quade, J., and Wynn, J.G., eds., The Geology of Early Humans in the Horn of Africa: Geological Society of America Special Paper 446, doi: 10.1130/2008.2446(01).

Randi, E., d'Huart, J.-P., Lucchini, V., and Aman, R., 2002, Evidence of two genetically deeply divergent species of warthog, *Phacochoerus africanus* and *P. aethiopicus* (Artiodactyla: Suiformes) in East Africa: Mammalian Biology, v. 67, p. 91–96, doi: 10.1078/1616-5047-00013.

Redfield, T.F., Wheeler, W.H., and Often, M., 2003, A kinematic model for the development of the Afar Depression and its paleogeographic implications: Earth and Planetary Science Letters, v. 216, p. 383–398, doi: 10.1016/S0012-821X(03)00488-6.

Schoeninger, M.J., Iwaniec, U.T., and Nash, L.T., 1998, Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair: Oecologia, v. 113, p. 222–230, doi: 10.1007/s004420050372.

Semaw, S., Simpson, S.W., Quade, J., Renne, P.R., Butler, R.F., McIntosh, W.C., Levin, N., Dominguez-Rodrigo, M., and Rogers, M.J., 2005, Early Pliocene hominids from Gona, Ethiopia: Nature, v. 433, p. 301–305, doi: 10.1038/nature03177.

Simpson, S.W., Quade, J., Kleinsasser, L., Levin, N., McIntosh, W., Dunbar, N., and Semaw, S., 2007, Late Miocene hominid teeth from Gona project area, Ethiopia: American Journal of Physical Anthropology, v. 132, no. S44, p. 219.

Smith, H.J., Fischer, H., Wahlen, M., Mastroianni, D., and Deck, B., 1999, Dual modes of the carbon cycle since the Last Glacial Maximum: Nature, v. 400, p. 248–250, doi: 10.1038/22291.

Tieszen, L.L., Senyimba, M.M., Imbamba, S.K., and Troughton, J.H., 1979, The distribution of C_3 and C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya: Oecologia, v. 37, p. 337–350.

Urbanek, C., Faupl, P., Hujer, W., Ntaflos, T., Richter, W., Weber, G., Schaefer, K., Viola, B., Gunz, P., Neubauer, S., Stadlmayr, A., Kullmer, O., Sandrock, O., Nagel, D., Conroy, G., Falk, D., Woldearegay, K., Said, H., Assefa, G., and Seidler, H., 2005, Geology, paleontology and paleoanthropology of the Mount Galili Formation in the southern Afar Depression, Ethiopia—Preliminary results: Joannea Geologie und Paläontologie, v. 6, p. 29–43.

van der Merwe, N.J., 1991, The canopy effect: Carbon isotope ratios and food-webs in Amazonia: Journal of Archaeological Science, v. 18, p. 249–259, doi: 10.1016/0305-4403(91)90064-V.

Vignaud, P., Duringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boisserie, J.-R., de Bonis, L., Eisenmann, V., Etienne, M.-E., Geraads, D., Guy, F., Lehmann, T., Lihoreau, F., Lopez-Martinez, N., Mourer-Chauviré, C., Otero, O., Rage, J.-C., Schuster, M., Viriot, L., Zazzo, A., and Brunet, M., 2002, Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad: Nature, v. 418, p. 152–155, doi: 10.1038/nature00880.

Wang, Y., and Cerling, T.E., 1994, A model of fossil tooth and bone diagenesis: Implications for paleodiet reconstruction from stable isotopes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 107, p. 281–289, doi: 10.1016/0031-0182(94)90100-7.

White, T., Suwa, G., and Asfaw, B., 1994, *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia: Nature, v. 371, p. 306–312, doi: 10.1038/371306a0.

White, T.D., WoldeGabriel, G., Asfaw, B., Ambrose, S., Beyene, Y., Bernor, R.L., Boisserie, J.-R., Currie, B., Gilbert, H., Haile-Selassie, Y., Hart, W.K., Hlusko, L.J., Howell, F.C., Kono, R.T., Lehmann, T., Louchart, A., Lovejoy, C.O., Renne, P.R., Saegusa, H., Vrba, E.S., Wesselman, H., and Suwa, G., 2006, Asa Issie, Aramis, and the origin of *Australopithecus*: Nature, v. 440, p. 883–889, doi: 10.1038/nature04629.

WoldeGabriel, G., White, T.D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W.K., and Heiken, G., 1994, Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia: Nature, v. 371, p. 330–333, doi: 10.1038/371330a0.

WoldeGabriel, G., Haile-Selassie, Y., Renne, P.R., Hart, W.K., Ambrose, S.H., Asfaw, B., Heiken, G., and White, T., 2001, Geology and palaeontology of the late Miocene Middle Awash Valley, Afar Rift, Ethiopia: Nature, v. 412, p. 175–178, doi: 10.1038/35084058.

Wooller, M.J., Swain, D.L., Ficken, K.J., Agnew, A.D.Q., Street-Perrott, F.A., and Eglinton, G., 2003, Late Quaternary vegetation changes around Lake Rutundu, Mount Kenya, East Africa: Evidence from grass cuticles, pollen and stable carbon isotopes: Journal of Quaternary Science, v. 18, no. 1, p. 3–15, doi: 10.1002/jqs.725.

Wynn, J.G., 2000, Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, northern Kenya: Journal of Human Evolution, v. 39, p. 411–432, doi: 10.1006/jhev.2000.0431.

Yalden, D.W., 1985, *Tachyoryctes macrocephalus*: Mammalian Species, v. 237, p. 1–3, doi: 10.2307/3503827.

Yalden, D.W., Largen, M.J., Kock, D., and Hillman, J.C., 1996, Catalogue of the mammals of Ethiopia and Eritrea. 7. Revised checklist, zoogeography and conservation: Tropical Zoology, v. 9, p. 73–164.

Young, H.J., and Young, T.P., 1983, Local distribution of C_3 and C_4 grasses in sites of overlap on Mount Kenya: Oecologia, v. 58, p. 373–377, doi: 10.1007/BF00385238.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001, Trends, rhythms, and aberrations in global climate 65 Ma to present: Science, v. 292, p. 686–693, doi: 10.1126/science.1059412.

Zazzo, A., Bocherens, H., Brunet, M., Beauvilain, A., Billiou, D., Mackaye, H.T., Vignaud, P., and Mariotti, A., 2000, Herbivore paleodiet and paleoenvironmental changes in Chad during the Pliocene using stable isotope ratios of tooth enamel carbonate: Paleobiology, v. 26, no. 2, p. 294–309, doi: 10.1666/0094-8373(2000)026<0294:HPAPCI>2.0.CO;2.

Zazzo, A., Mariotti, A., Lécuyer, C., and Heintz, E., 2002, Intra-tooth isotope variations in late Miocene bovid enamel from Afghanistan: Paleobiological, taphonomic, and climatic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 186, p. 145–161, doi: 10.1016/S0031-0182(02)00449-2.