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Stable Isotope Studies of Paleoenvironment and Paleoclimate from Afar, Ethiopia

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Stable Isotope Studies of Paleoenvironment and Paleoclimate from Afar, Ethiopia

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of
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DEDICATION

To my wife Hanna, my daughter Bezawit and my mother Aynalem.

In memory of my father, Kubsa, who would have loved to see this.

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ABSTRACT

The sedimentary deposits of the Hadar Formation at Dikika and the Mount Galili Formation at Galili preserve a wealth of paleoenvironmental and paleoclimatic records spanning the last 5.29 Ma. Stable carbon and oxygen isotopic compositions of herbivore tooth enamel were analyzed for more than 600 specimens of 15 different taxa from 10 stratigraphic intervals. The application of carbon and oxygen isotopes here aims principally at reconstructing shifts in the relative abundance of C₄ grasses, and its implications for climate indicators including temperature, aridity, and seasonality. The full range of $\delta^{13}\text{C}_{\text{enamel}}$ values throughout the Plio-Pleistocene signifies a wide range of foraging strategies by the fauna, which in turn reflects the mosaic of vegetation at Dikika and Galili. Estimates of ecosystem carbon isotope composition ($\delta^{13}\text{C}_{\text{ecosystem}}$, which is given by average $\delta^{13}\text{C}_{\text{enamel}}$ of each large vertebrate taxon weighted by the respective faunal abundance and the estimated daily biomass consumption) is used to assess shifts in the ecosystem-scale proportion of C₃ and C₄ vegetation. In the Plio-Pleistocene, the general paleoenvironmental conditions varied from wooded grassland to grasslands with the total amount of C₄ grass cover on the landscape varying between 35% and 91%. Likewise, the paleohabitat reconstructions indicate the presence of grassland, wooded grassland, woodland habitats throughout the Pliocene and in Middle Pleistocene but the relative proportion of the habitats has changed substantially with time. Although this

result agrees with the general trend towards more open grassland since the Late Miocene, a rebound of closed habitats and C₃ resources from closed canopy woodlands or forests is evident in the middle Pliocene between 3.42 Ma and 3.24 Ma. These changes in the proportion of habitats could have affected the distribution and availability of preferred food resources and has an implication on the interaction of the animals on the paleolandscape and competition for resources.

$\delta^{18}\text{O}_{\text{enamel}}$ values also show a wide range of variation within each stratigraphic member and through time. Temporal variation of $\delta^{18}\text{O}_{\text{enamel}}$ values within a given taxon, as well as differences among sympatric taxa, document different aspects of the environment and climate, including changes in drinking water source, seasonality, and periods of strong evaporation. Estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ based on the most ^{18}O -depleted hippo tooth enamel, displays values of -1.94‰ (VSMOW) and -5.24‰ (VSMOW) in the Middle Pleistocene of Asbole and middle Pliocene of Galili, respectively. A major shift in the isotopic composition of water at ~ 3.0 Ma was accompanied by a 6.0‰ increase from middle Pliocene to the present. While a +3.8‰ shift from early to middle Pliocene was documented. The isotopic composition of meteoric water between 4.6 Ma and 4.38 Ma was most ^{18}O -enriched compared to the rest of the Pliocene estimates. Likewise, an increase in the estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ values was documented in the Awash Valley and elsewhere in East Africa, which indicate a regional climate change since the early Pliocene. An increase in the aridity, which is expressed as mean annual water deficit (*i.e.*, the difference between potential evapotranspiration and mean annual precipitation) is also evident since the early Pliocene. These changes during the Pliocene in the region may in

part be attributed to a regional decrease in the amount of precipitation and changes in the moisture source superimposed on global climate changes.

CHAPTER ONE

INTRODUCTION

The Plio-Pleistocene sedimentary deposits at Dikika and Galili, in the Afar region of Ethiopia preserve a wealth of geological and paleontological record, which could provide paleoenvironmental and paleoclimatic information relevant to hominin evolution, particularly for *Australopithecus* sp. and *Ardipithecus ramidus*. The middle Pliocene sediments of the Hadar Formation at Dikika and the early to middle Pliocene sediments of the Mount Galili Formation at Galili provide an opportunity to explore the paleoenvironmental and paleoclimatic changes in the region from both spatial and temporal perspectives. Although there is general consensus in the overall regional environmental and climate change throughout the Neogene, site-specific environmental and climate reconstructions at hominin sites show considerable variability. Thus, there is a need to augment data from different archives at individual sites and make a regional comparison, and further compare local records to the documented major global climatic events and assess if there is any link or lack thereof.

The use of carbon and oxygen stable isotopic composition of mammalian tooth enamel has been proven as a successful tool in the study of paleoenvironmental and paleoclimatic reconstruction of both hominin and non-hominin species in eastern and South Africa

(Lee-Thorp, 1989; Bocherens et al., 1996; Kohn et al., 1996; Kingston, 1999a; Sponheimer et al., 1999; Cerling et al., 2003a; Levin et al., 2008; White et al., 2009; Bedaso et al., 2010). However, compared to the other Miocene and Pliocene fossil localities elsewhere in Africa, previous stable isotope studies of mammalian tooth enamel from the Awash Valley have been sparse (Figure 1.1).

This Ph.D. dissertation focuses on the reconstruction of paleoenvironmental and paleoclimatic conditions using carbon and oxygen isotopic composition of herbivore tooth enamel. Tooth enamel samples were collected from Chorora (11–10.5 Ma), Galili (>5.29–>3.6 Ma), Dikika (>3.8–3.24 Ma) and Asbole (0.8–0.64 Ma). The tooth enamel isotope data presented here provides an opportunity to widen the temporal and spatial scale beyond a single sedimentary basin, and assess large-scale lateral variation of vegetation and habitat structure on the landscapes where early hominins lived.

1.1. Scope of the study

Dikika and Galili are multi-disciplinary paleanthropological projects generally aimed at understanding various aspects of paleobiology of early hominins as well as their cultural evolution. While this dissertation is especially concerned with reconstruction of the paleoenvironments of human evolution, and addresses the following hypotheses and objectives.

1.1.1 Hypothesis

1. The Plio-Pleistocene environmental and climatic condition in the Awash Valley were variable both with time and space, superimposed on the general trend towards more open vegetation and drier climatic conditions.
2. In the study area, Plio-Pleistocene climate change was driven by both global and local factors such as: rearrangement of continental land masses, opening and closing of seaways, and local topographic change associated with Rift Valley formation.

1.1.2 Objectives

1. To reconstruct the dietary adaptation of the mammalian fauna and assess changes with time through the Pliocene and Pleistocene
2. To reconstruct the relative proportion of C_3 and C_4 vegetation on the paleolandscape as reconstructed from ecosystem carbon isotopic estimate of larger mammals
3. To reconstruct the habitat structure on the paleolandscape in each stratigraphic members in the middle Pliocene between 5.3 and 3.24 Ma and Middle Pleistocene between 0.8 Ma and 0.64 Ma pertaining early hominin species
4. To estimate the oxygen isotopic composition of meteoric water in the study area
5. To reconstruct the variation in the aridity by calculating the water deficit based on calibration of the modern fauna and meteorological data.
6. To develop a new method to estimate the paleotemperature using data from co-occurring hippopotami and crocodiles

1.2. Structure of Dissertation

The dissertation is composed of six chapters. The first chapter outlines the general goal of the study. The second chapter “Paleoenvironmental reconstruction of the Asbole fauna (Busidima Formation, Afar, Ethiopia) using stable isotopes” was published in *Geobios* (Bedaso et al., 2010), where carbon and isotopic data of tooth enamel from the Middle Pleistocene, between 0.8 Ma and 0.64 Ma were presented. The third chapter, “Dietary and paleoenvironmental reconstruction using stable isotopes of herbivore tooth enamel from middle Pliocene Dikika, Ethiopia: Implication for *Australopithecus afarensis* habitat and food resources” has been submitted to the *Journal of Human Evolution* (Bedaso et al., in review), where carbon and isotopic data of tooth enamel from the middle Pliocene, >3.8 Ma–3.24 Ma is presented. The fourth chapter, “Carbon and oxygen isotopic signature of tooth enamel as a proxy for the Pliocene paleoenvironment and paleoclimate from Mount Galili Formation, Ethiopia” is ready to be submitted to *Palaeogeography, Palaeoclimatology, Palaeoecology*, where the data presented encompass the interval between 5.3 Ma and >3.6 Ma. Chapter five presents a synthesis of the regional paleoclimatic changes through time and discusses the possible factors (global and regional) that control the climatic condition of the region in the Plio-Pleistocene. While chapter six synthesizes the regional environmental changes from both temporal and spatial perspectives, and discusses the types of habitat present and changes in their relative proportion through time. Chapter five and six are planned to be submitted to the journals *Global and Planetary Change* and *American Journal of Physical Anthropology*, respectively, later this year.

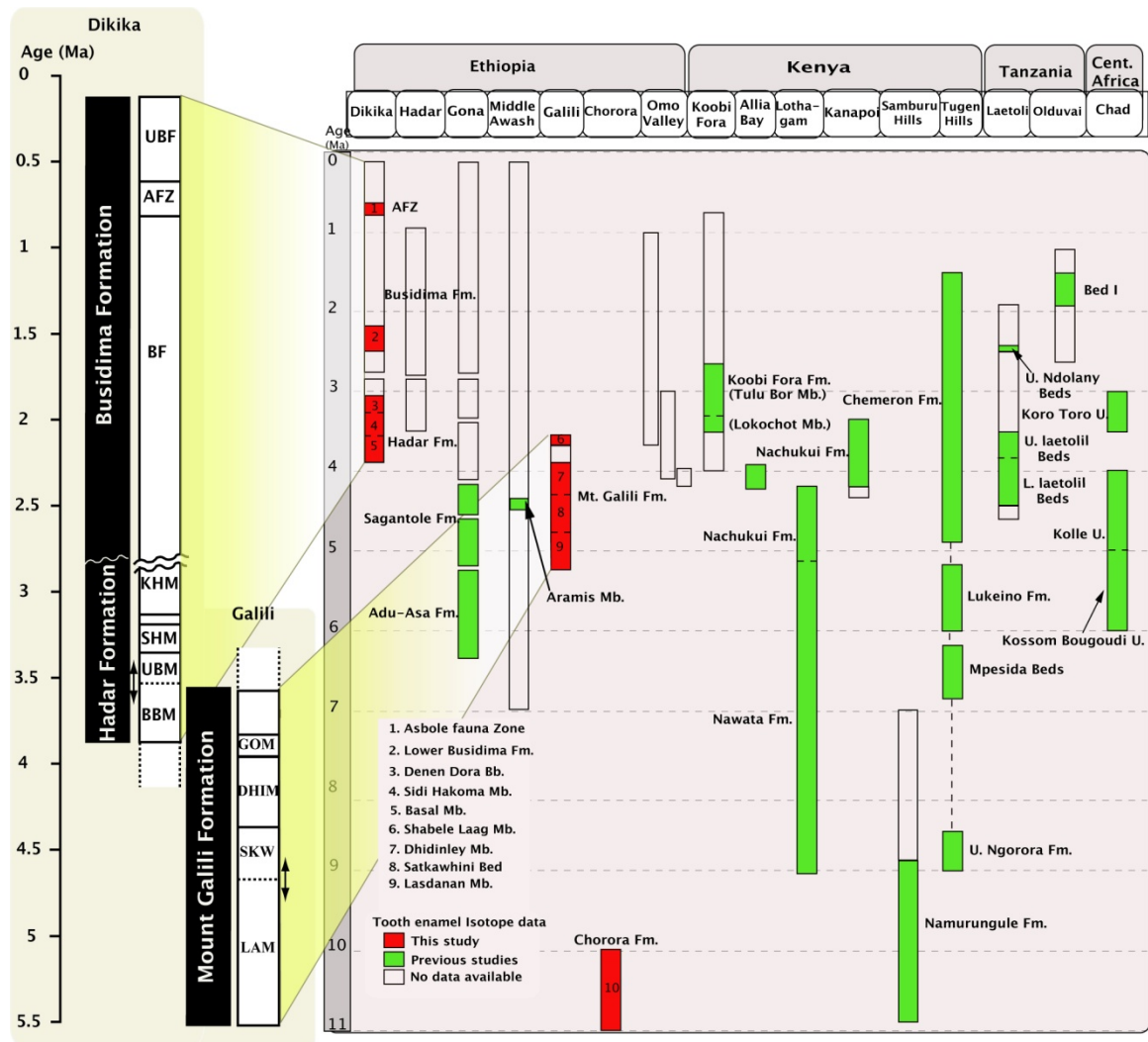


Figure 1.1 Stratigraphic sections exposed in eastern and Central Africa hominid localities. Green-filled sections have stable isotopic data from herbivore tooth enamel. Unfilled sections lack enamel data. The red-filled sections in Ethiopia are contributed by this study. These stable isotopic analyses of tooth enamel cover ten intervals (*i.e.*, Chorora Formation, 11–10.5 Ma, Lasdanan Member, 5.29–4.38 Ma, Satkawhini beds ~4.6–>4.38 Ma, Dhidinley Member, 4.38–3.92 Ma, Shabele Laag Member, 3.92–>3.6 Ma, base of Basal Member, >3.8–~3.6 Ma, upper Basal Member, ~3.6–3.42 Ma, Sidi Hakoma Member, 3.43–3.24 Ma, lower Busidima Formation, 2.6–1.3 Ma, and Asbole fauna zone, 0.8–0.64 Ma).

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CHAPTER TWO

PALEOENVIRONMENTAL RECONSTRUCTION OF THE ASBOLE FAUNA USING STABLE ISOTOPES, BUSIDIMA FORMATION, AFAR, ETHIOPIA

2.1. Introduction

Measurements of natural variations in stable isotope ratios have become vital tools in fields as diverse as geochemistry, hydrology, ecology, and anthropology. The application of stable isotopes to paleoceanography and marine paleoclimatology has been spectacularly successful, revealing both long-term trends in marine climate and the response of the oceans to short-term orbital forcing and sudden events (Imbrie et al., 1984, Zachos et al., 1993). Isotopic reconstruction of conditions on land is more difficult, however, because terrestrial ecosystems and climates exhibit greater spatial and temporal heterogeneity and the isotope systems applied in these settings are more complex. Even so, over the past decade, there has been a surge in studies of continental paleoclimates and paleoenvironments, spurred by the increased need to understand the response of the more variable land ecosystems to past climate change (*e.g.*, Swart et al., 1993).

Analyses of stable isotopes of carbon and oxygen extracted from fossils have contributed substantially to our understanding and ability to reconstruct paleoenvironmental and paleoclimatic parameters in the Neogene of tropical Africa, which is characterized by

mixed C₃ and C₄ vegetation (Lee-Thorp, 1989; Morgan et al., 1994; Bocherens et al., 1996; Kohn et al., 1996; Cerling et al., 1997a,b; Kingston, 1999a,b; Sponheimer et al., 1999; Sponheimer and Lee-Thorp, 1999a,c; Zazzo et al., 2000). These approaches have been critical in documenting ecological shifts, elucidating hominin dietary adaptations, constraining vegetation types in past ecosystems, characterizing habitat heterogeneity in space and time, revealing dietary niche partitioning in fossil terrestrial communities, and correlating climatic perturbations and oscillations in terrestrial ecosystems (Kingston & Harrison, 2007). The present study uses stable isotopes of mammalian tooth enamel to assess the paleoclimate conditions and understand the distribution of different types of vegetation between 0.8-0.64 Ma at Asbole in the Awash Valley of Ethiopia—a site which has a direct relevance to the understanding of the paleoenvironmental contexts of Pleistocene hominins in the Horn of Africa (Geraads et al., 2004; Wynn et al., 2008).

2.2 Controls on the isotopic composition of tooth enamel

Stable carbon and oxygen isotopic analysis of tooth enamel has been established as a valuable tool for reconstructing terrestrial paleoenvironments (Koch, 1998; Kohn and Cerling, 2002, Kingston & Harrison et. al., 2007, Bocherens et al., 1996, Franz-Odenaal et al., 2002; Cerling et al., 2003b; Schoeninger et al., 2003, Boisserie et. al., 2005). Tooth enamel is an ideal substrate for preserving stable isotopic signatures because it is almost entirely inorganic and has very low porosity (>96% inorganic component by weight and < 1% organic material; Wang and Cerling, 1994). The inorganic mineral phase of tooth enamel is hydroxyapatite (Ca₁₀(PO₄)₆(OH)₂), a relatively stable mineral in surface weathering environments. As such, tooth enamel is less susceptible to diagenesis than

bone or dentine because of its lower organic content, higher density, and larger crystalline size (Ayliffe et al., 1994; Bryant et al., 1994). Enamel forms by accretion without remodeling and mineralization is complete prior to tooth eruption. Like enamel, dentin grows by accretion with little remodeling (Lowenstam & Weiner, 1989). However, because of its resistance to diagenetic alteration, enamel is the most suitable fossilized material of vertebrates for paleoenvironmental study using stable isotopes (Wang and Cerling, 1994).

2.2.1 Carbon Isotope

The interpretation of carbon isotopic composition of tooth enamel is based on differences in carbon isotope fractionation between plants that use the two major photosynthetic pathways (C_3 and C_4), and the consumption of C_3 and C_4 vegetation by mammalian fauna (Smith & Epstein, 1971). The C_3 pathway is most common, occurring in the vast majority of trees and shrubs, as well as those herbs and grasses with cool and relatively moist (*i.e.*, non-evaporative) growing seasons. C_3 plants have $\delta^{13}C$ values (mean $\approx -27\text{‰}$, range -22 to -35‰) that are much lower than those of atmospheric CO_2 ($\approx -7.7\text{‰}$; O'Leary, 1988). C_4 photosynthesis is less common and occurs in grasses and some sedges and herbs, but only those that grow under sufficiently dry and/or warm (*i.e.* evaporative) growing season climates in which this energy-intensive pathway is able to gain a competitive advantage over the C_3 pathway. C_4 plants have $\delta^{13}C$ values (mean $\approx -13\text{‰}$, range -19 to -9‰) that are more similar to those of the atmosphere (O'Leary, 1988). The crassulacean acid metabolism (CAM) pathway is least common, occurring in succulent plants adapted to arid climates. CAM plants fix CO_2 by both pathways, separating their use of each

pathway during high and low light conditions, and thus exhibit a range of $\delta^{13}\text{C}$ values intermediate between those of C_3 and C_4 plants (Ehleringer & Monson, 1993).

Dietary differences are recorded in developing tissues of animal such as teeth with a relatively constant fractionation factor (Cerling and Harris, 1999). Because most C_4 plants are tropical grasses, (Koch 1998) suggest stable carbon isotope values can readily distinguish grazing from browsing mammals.

2.2.2. Oxygen Isotope

The oxygen isotopic composition of mammalian tooth enamel is a function of the isotopic composition of oxygen that enters and exits the body (Kohn, 1996). Biogenic phosphate (hydroxyapatite) is precipitated in equilibrium with body water, which is mostly comprised of ingested water (Longinelli, 1984; Luz et al., 1984). Because mammals larger than 1 kg have a constant body temperature near 37°C , hydroxyapatite is precipitated in these species at a constant temperature, which allows for the oxygen isotopic signature of the ingested material to be recorded without the effects of temperature dependent fractionation. The body's main oxygen sources are atmospheric O_2 , liquid water and oxygen bound in food, of which only the latter two are likely to cause differences in oxygen isotope values among sympatric taxa. Unlike atmospheric O_2 , the oxygen isotope composition of food and liquid water are highly variable, and thus likely to explain any differences found in the oxygen isotope compositions of animals within a local ecosystem. Liquid water enters the body through drinking and as free water in food. In most cases, liquid water in plant roots and stems is isotopically similar to

available drinking water, but leaf water can be relatively enriched in H_2^{18}O due to preferential evapotranspiration of the lighter H_2^{16}O molecule (Sternberg, 1989). Thus, animals that derive most of their water from plant leaves (such as *Giraffa* or *Litocranius*) ingest water enriched in ^{18}O compared to animals that drink regularly (such as *Equus* and *Phacocoherus*).

2.3 Geological context of the Asbole Fauna

Late Pliocene and early Pleistocene deposits at Asbole belong to the Busidima Formation which is dominated by fluvial sedimentation in an asymmetrical half graben (the Busidima half-graben; Wynn et al., 2008). The sediments of the Busidima Formation thicken towards the border fault at the western margin (Figure 1), as is typical of half-graben rift basins throughout the East African and other continental rift systems (Ebinger, 2002). As described in Alemseged & Geraads (2000) and Geraads et al. (2004), the “Asbole fauna” is bracketed between two widespread and mappable stratigraphic markers (i.e., the “top conglomerate” bed (~0.8 Ma) and the Bironita Tuff (0.64 Ma). The Bironita Tuff is correlated to a tuff from Bodo, Dawitoli, and Hargufia areas of the Middle Awash which has previously been dated at 0.64 ± 0.03 Ma (Clark et al., 1994). The age boundary of the “top conglomerate” is defined by the uppermost of a series of mappable conglomerates estimated at 0.8 Ma (Geraads et al., 2004). In this study we only analyzed Middle Pleistocene mammalian fossil specimens from the interval between these two markers. The majority of the fossils from Asbole derive from close proximity to a prominent paleochannel that can be mapped throughout the region (Figure 2.1).

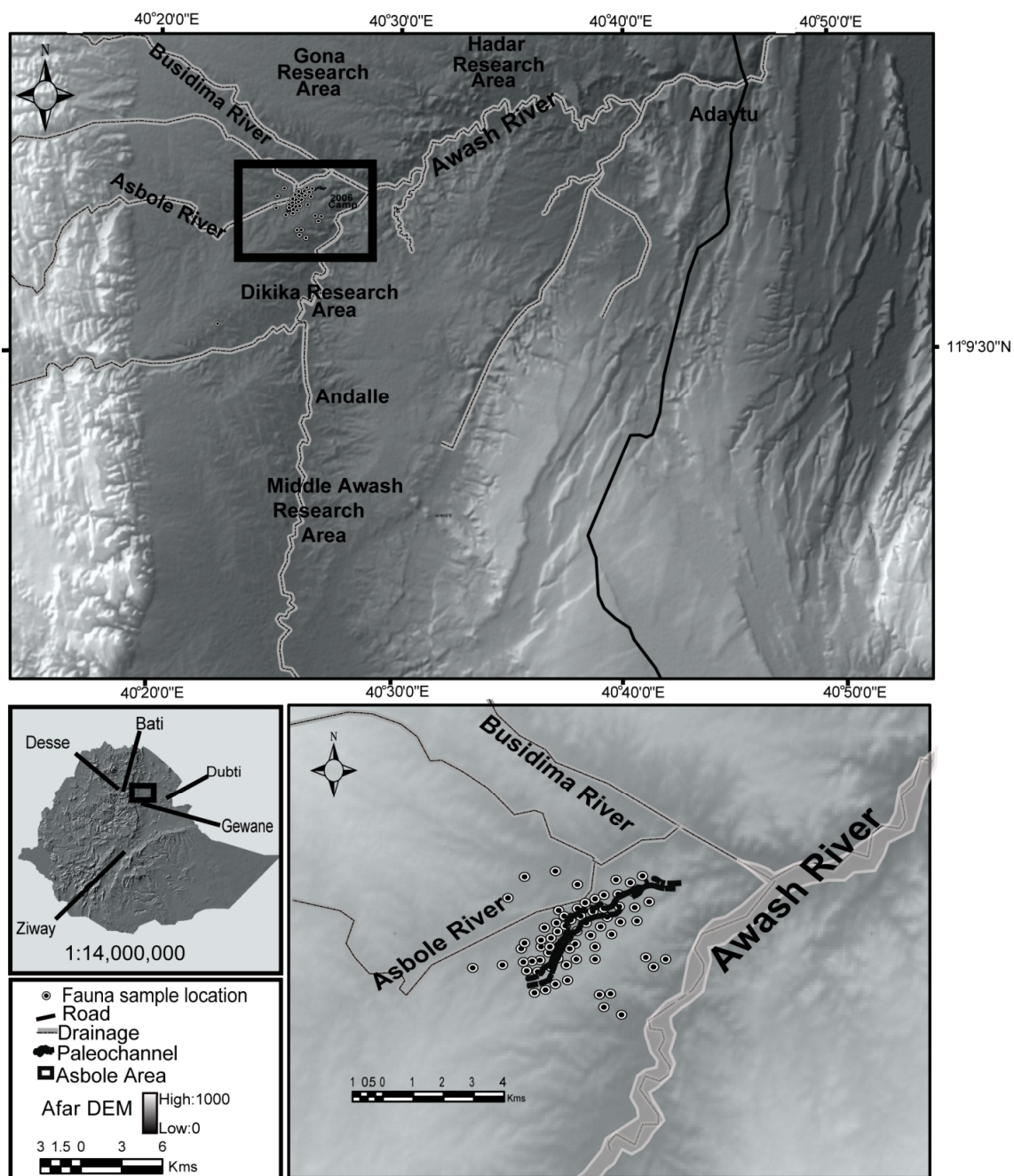


Figure 2.1 Location map of the Dikika Research Project (DRP) area showing the main modern drainages, and Asbole Paleochannel, a prominent ephemeral paleochannel mappable through the deposits, and illustrating the fossil tooth enamel sampling locations in relation to the paleochannel outcrop.

2.4 Methods

We analyzed the isotopic composition of a total of 80 samples (Figure 1) from 15 different mammalian taxa collected in December 2006 and previous field seasons (*i.e.* museum collections housed in the National Museum of Ethiopia). Bulk enamel samples were taken by drilling down the tooth along the growth axis with a 0.5 mm drill bit, cleaning the drill bit between sampling and care was taken to avoid dentine, cementum and matrix in the sample powder. About 20 mg of powder enamel was extracted from each tooth.

The powder produced was pretreated with 3% hydrogen peroxide followed by a 1 M acetic acid-calcium acetate buffer to remove organic matter and secondary carbonates, and thoroughly rinsed with distilled water (following standard procedures for the treatment of tooth enamel of Lee-Thorp and Van der Merwe 1987; Quade et al. 1992; Koch 1998). Approximately 5-7 mg of the treated powder was reacted with 103% H₃PO₄ in He flushed exetainer vials at 25°C for 24 hrs to produce the CO₂ analyte gas for analyses of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Isotope ratios were measured on a Thermo Fisher Scientific (Finnigan) Delta V 3 keV Isotope Ratio Mass Spectrometer and results are reported using the standard per mil notation where:

$$\delta^{13}\text{C} \text{ or } \delta^{18}\text{O} = \left(\frac{R_{\text{sample}}}{R_{\text{Standard}}} - 1 \right) * 1000$$

R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios in the sample and standard, respectively, for $\delta^{13}\text{C}$ and the $^{18}\text{O}/^{16}\text{O}$ ratios in the sample and standard, respectively, for $\delta^{18}\text{O}$. The reference standard is the international reference scale VPDB, which was normalized using replicate samples of IAEA reference materials NBS-18 and NBS-19.

In order to calculate the $\delta^{13}\text{C}$ of the total large vertebrate diet in the ecosystem, we calculated a weighted average of the $\delta^{13}\text{C}_{\text{enamel}}$ value, weighted using the relative abundance of each taxon multiplied by an estimate of the daily food intake of respective species:

$$\bar{\delta}^{13}\text{C}_{\text{Ecosystem}} = \frac{\sum (X_{\text{taxa}} Q) \bar{\delta}^{13}\text{C}_{\text{enamel, taxa}}}{\sum (X_{\text{taxa}} Q)} + \Delta_{\text{enamel-diet}}$$

Where, X_{taxa} is relative faunal abundance expressed as a fraction, $\bar{\delta}^{13}\text{C}_{\text{enamel, taxa}}$ is the average value for each taxon in per mil (‰) and (Q) is the average daily food intake in kg/day of taxa, and $\Delta_{\text{enamel-diet}} = -14\text{‰}$ is an offset between diet and enamel $\delta^{13}\text{C}$ (Kohn and Cerling 2002). The daily food intakes of most of the taxa were estimated based on the calibration of food consumption of African mammals to mean body size (Delany and Happold 1979). Dietary intake and body mass data from *Gazella granti*, *Gazella thomsoni*, *Aepyceros melampus*, *Connochaetes taurinus*, *Syncerus caffer*, *Hippopotamus amphibius* and *Loxodonta africana* from Delany and Happold (1979) were used to calibrate a regression line to estimate dietary intake of all other taxa in this study based on average body mass.

We calculated the percentage of estimated C₄ biomass in the animal diet for each taxon based on a linear mixing model between pure C₃ and C₄ biomass with values of -13‰ and +1‰, respectively).

For oxygen isotopic composition, we calculated the enrichment factor (ϵ) between two groups of taxa (evaporation sensitive and insensitive) as:

$$\epsilon_{ES-EI} = \left(\frac{R_{ES}}{R_{EI}} - 1 \right) * 1000$$

We used this variable to estimate aridity, which is quantified as water deficit (WD), equal to the difference between Mean Annual Thornthwaite Potential Evapotranspiration (PET) and Mean Annual Precipitation (MAP). For modern comparable climates in Ethiopia, we estimated WD using data from the Ethiopian National Meteorological Agency.

2.5 Carbon isotope, results and interpretation

$\delta^{13}\text{C}_{\text{enamel}}$ values of the Asbole fossils range between -11.4 to +3.1‰ and thus span the entire range of pure C₃ and C₄ consumers (Table 1). $\delta^{13}\text{C}_{\text{enamel}}$ values of tooth enamel from the Asbole faunal zone indicate that some herbivores, such as *Chlorocebus* and giraffids, consumed dominantly C₃ plants, while most bovid tribes of Bovidae (Bovini, Reduncini, Alcelaphini, Hippotragini) consumed C₄ grasses, and other tribes, Tragelaphini and Antilopini showed mixed C₃/C₄ feeding strategies. Other herbivores (hippopotamids, rhinocerotids, equids, suids, Proboscidea and *Theropithecus*) relied heavily on C₄ grasses while a few large Rodentia sampled exhibit mixed C₃/C₄ feeding strategies (Figure 2.2 and 2.3; Table 2.1). The results from each major taxonomic category are discussed in detail below.

2.5.1 Rhinocerotidae

The only rhinoceros identified in the “Asbole faunal zone” is *Diceros* cf. *bicornis* (Geraads et al., 2004). *Ceratotherium* may also be present, but definite evidence is still lacking, because distinction of the two living African genera is difficult based on fragmentary remains (Geraads et al., 2004). $\delta^{13}\text{C}_{\text{enamel}}$ value of the single *Diceros* from the Asbole fauna zone is -5.5‰ (n= 1).

Table 2.1 Stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of fossil tooth enamel and modern samples collected from Asbole during 2006 and prior field seasons.

DRP No	Sample no	ID	Family	Tribe	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
ASB 340	Zk-EN 34	<i>Connochaetes</i>	Bovidae	Alcelaphini **	0.4	-0.5
ASB 283	Zk-EN 27	<i>Damaliscus</i>	Bovidae	Alcelaphini**	0.9	1.2
ASB 262	Zk-EN 19	<i>Megalotragus</i>	Bovidae	Alcelaphini**	2.5	-0.1
ASB 341	Zk-EN 36	<i>Gazella granti</i>	Bovidae	Antilopini**	-5.7	-0.8
ASB 264	Zk-EN 20	<i>Gazella</i> (other)	Bovidae	Antilopini**	-4.7	4.6
ASB 248	Zk-EN 16	<i>Gazella</i> (other)	Bovidae	Antilopini**	-7.7	4.2
ASB 139	Zk-EN 5	<i>Gazella</i> (other)	Bovidae	Antilopini**	-5.5	5.2
ASB 116	Zk-EN 51	<i>Gazella granti</i>	Bovidae	Antilopini**	-3.3	3.2
ASB 220	Zk-EN 52	<i>Gazella</i>	Bovidae	Antilopini**	-8.0	3.1
	Zk-EN 53	<i>Gazella</i>	Bovidae	Antilopini**	-6.4	-2.0
ASB 184	Zk-EN 54	<i>Gazella</i>	Bovidae	Antilopini**	-4.2	2.3
ASB 259	Zk-EN 18	Bovini	Bovidae	Bovini	0.7	0.3
ASB 236	Zk-EN 14	Bovini	Bovidae	Bovini	1.8	-2.2
ASB 226	Zk-EN 13	Bovini	Bovidae	Bovini	-2.3	0.1
ASB 206	Zk-EN 12	Bovini	Bovidae	Bovini	2.5	2.2
ASB 194	Zk-EN 10	Bovini	Bovidae	Bovini	-0.9	0.1
ASB 178	Zk-EN 7	Bovini	Bovidae	Bovini	0.9	1.7
ASB 134	Zk-EN 4	<i>Pelorovis</i>	Bovidae	Bovini	-0.1	5.8
ASB 370	Zk-EN 42	<i>Pelorovis</i>	Bovidae	Bovini	0.8	0.1
	Zk-EN 61	Bovini	Bovidae	Bovini	2.7	3.2
ASB 96	Zk-EN 62	Bovini	Bovidae	Bovini	1.2	1.3
ASB	Zk-EN 63	Bovini	Bovidae	Bovini	3.3	0.4
ASB 26	Zk-EN 64	Bovini	Bovidae	Bovini	0.0	0.3
ASB 305	Zk-EN 31	<i>Chlorocebus</i>	Cercopithecidae	Cercopithecini	-8.9	-0.6
ASB 192	Zk-EN 9	Hippotragini	Bovidae	Hippotragini	1.1	3.8
	Zk-EN 65	Hippotragini	Bovidae	Hippotragini	0.1	0.8
ASB 388	Zk-EN 44	<i>Kobus</i>	Bovidae	Reduncini*	2.3	1.7
ASB 381	Zk-EN 43	<i>Kobus</i>	Bovidae	Reduncini*	1.9	2.1

DRP No	Sample no	ID	Family	Tribe	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
ASB 360	Zk-EN 41	<i>Kobus</i>	Bovidae	Reduncini*	-3.0	-2.0
ASB 357	Zk-EN 1	<i>Kobus</i>	Bovidae	Reduncini*	1.2	0.6
ASB 331	Zk-EN 33	<i>Kobus</i>	Bovidae	Reduncini*	0.3	0.6
ASB 299	Zk-EN 29	<i>Kobus</i>	Bovidae	Reduncini*	0.2	0.1
ASB 273	Zk-EN 23	<i>Kobus</i>	Bovidae	Reduncini*	1.1	1.8
ASB 186	Zk-EN 8	Reduncini	Bovidae	Reduncini*	0.3	0.3
ASB 124	Zk-EN 2	Reduncini	Bovidae	Reduncini*	-5.7	3.7
ASB 6	Zk-EN 66	<i>Kobus</i>	Bovidae	Reduncini*	1.8	1.2
ASB 132	Zk-EN 67	<i>Kobus</i>	Bovidae	Reduncini*	-2.6	2.5
ASB 182	Zk-EN 68	<i>Kobus</i>	Bovidae	Reduncini*	3.1	1.4
	Zk-EN 69	<i>Kobus</i>	Bovidae	Reduncini*	-0.2	2.0
ASB 390	Zk-EN 45	<i>Theropithecus oswaldi</i>	Cercopithicidae	Papionini	-0.1	-0.4
ASB 130	Zk-EN 3	<i>Taurotragus</i>	Bovidae	Tragelaphini**	-6.5	1.5
ASB 356	Zk-EN 38	<i>Taurotragus</i>	Bovidae	Tragelaphini**	-11.4	4.7
ASB 280	Zk-EN 26	<i>Taurotragus</i>	Bovidae	Tragelaphini**	-3.7	3.7
ASB 414	Zk-EN 47	<i>Elephas</i>	Elephantidae*		-1.4	-1.3
ASB 255	Zk-EN 17	<i>Hippopotamus</i>	Hippopotamidae*		-1.0	-0.5
ASB 155	Zk-EN 70	<i>Hippopotamus</i>	Hippopotamidae*		-1.5	-3.6
ASB 9	Zk-EN 71	<i>Hippopotamus</i>	Hippopotamidae*		-1.4	-6.3
ASB 279	Zk-EN 25	<i>Hystrix</i>	Rodentia		-1.6	-0.2
ASB 269	Zk-EN 22	<i>Hystrix</i>	Rodentia		-8.0	-0.9
ASB 392	Zk-EN 46	<i>Phacochoerus</i>	Suidae*		-0.4	1.2
ASB 322	Zk-EN 32	<i>Kolpochoerus majus</i>	Suidae*		-0.3	-0.5
ASB 268	Zk-EN 21	<i>Kolpochoerus majus</i>	Suidae*		0.2	0.9
ASB 242	Zk-EN 55	<i>Giraffa</i>	Giraffidae**		-8.5	1.3
ASB 224	Zk-EN 56	<i>Giraffa</i>	Giraffidae**		-8.9	8.4
ASB 176	Zk-EN 57	<i>Equus</i>	Equidae*		1.2	1.2
ASB 355	Zk-EN 39	<i>Equus</i>	Equidae*		0.4	2.9
ASB 342	Zk-EN 37	<i>Equus</i>	Equidae**		1.1	3.4
ASB 177	Zk-EN 58	<i>Equus</i>	Equidae*		1.0	0.6
ASB 178	Zk-EN 59	<i>Equus</i>	Equidae*		-0.6	-0.4
ASB 179	Zk-EN 60	<i>Equus</i>	Equidae*		1.0	1.3
ASB 165	Zk-EN 6	<i>Diceros</i>	Rhinocerotidae*		-5.5	-1.0
ASB 110	Zk-EN 72	<i>Elephas</i>	Elephantidae*		-0.4	-0.4

Notes: Samples used in the calculation of $e_{\text{ES-EI}}$ shown in Table 3 are indicated here:

* Evaporation Insensitive (EI) spices, ** Evaporation Sensitive (ES) species.

The isotopic data suggest that the dietary strategy of this *Diceros* was that of a mixed feeder with both C_3 and C_4 components, with approximately 53% C_4 grass consumed in its diet (Table 2.2). Previous studies on isotopic analysis of modern rhinocerotid teeth

clearly reflect dietary partitioning (Lee-Thorp, 1989; Bocherens et al., 1996; Cerling and Harris, 1999; Cerling et al., 2003b; Kingston and Harrison, 2007) with *Ceratotherium simum* yielding $\delta^{13}\text{C}_{\text{enamel}}$ values consistent with a variable to obligate C_4 grazing diet averaging about 0.0‰ and *Diceros bicornis* (black rhino) with a C_3 browsing diet with a mean of about -10.5‰ (Kingston and Harrison, 2007). Our analysis of the rhino tooth enamel from the Asbole faunal zone is consistent with *Diceros cf. bicornis*. The $\delta^{13}\text{C}_{\text{enamel}}$ values of *D. bicornis* from arid habitats such as Amboseli National Park are typically more ^{13}C -enriched than average (Bocherens et al., 1996), suggesting that Asbole was near the arid end of the habitat preference of *Diceros*, although this is based on a single specimen from Asbole.

2.5.2 Elephantidae

The fossil Elephantidae from Asbole consists only of *Elephas* (Geraads et al., 2004). $\delta^{13}\text{C}_{\text{enamel}}$ values of the only two Elephantidae analyzed averages -0.8‰ (n=2). $\delta^{13}\text{C}_{\text{enamel}}$ values of Elephantidae from the Asbole fauna zone indicate that the diets of these large-bodied herbivores were dominated by C_4 grass (*i.e.* 87% of the total diet were C_4 grasses, Table 2.2). These results and others suggesting variable grazing to intermediate foraging isotopic strategies of late Miocene and Pliocene fossil elephantids (Zazzo et al., 2000) contrast with the $\delta^{13}\text{C}_{\text{enamel}}$ of extant African *Loxodonta*, which indicate a diet generally dominated by C_3 biomass (Cerling et al., 1999). Hypotheses to explain this discrepancy include reduction of C_4 grasslands at the terminal Pliocene resulting in increased competition from other grazing taxa or incorrect phylogenetic assumptions linking fossil grazing lineages with modern browsing elephants (Cerling et al., 1999).

2.5.3 Equidae

The fossil Equidae from Asbole are represented by the genus *Equus* and because of limited fossil finds, further specific identification is not possible (Geraads et al., 2004). $\delta^{13}\text{C}_{\text{enamel}}$ values of the *Equus* from the Asbole Fauna averages $0.8 \pm 0.5\text{‰}$ (n=6). The isotopic data suggest that the dietary strategies of the Equids grazed primarily on C₄ grass (*i.e.*, 98% of the total diet, Table 2.2). These results are consistent with isotopic data of equid enamel, younger than about 7 Ma in tropical and sub-tropical Africa, including all modern samples, which yield $\delta^{13}\text{C}_{\text{enamel}}$ values in the range of -2‰ to $+3\text{‰}$, indicating C₄ dominated to exclusive C₄ grass diets (Morgan et al., 1994; Bocherens et al., 1996; Cerling et al., 1997b; Cerling et al., 2003a, b, Kingston and Harrison 2007).

2.5.4 Suidae

In addition to their key role in biochronology, pigs are frequently utilized as paleoecological indicators. The fossil Suidae from Asbole are represented by *Metridiochoerus modestus* and *Kolpochoerus majus* (the most common species in Asbole; Geraads et al., 2004). $\delta^{13}\text{C}_{\text{enamel}}$ values of the Suidae average $-0.2 \pm 0.9\text{‰}$ (n=3). The suid specimens analyzed consist of two upper molars of *Kolpochoerus majus* and one lower third molar of *Metridiochoerus sp.* $\delta^{13}\text{C}_{\text{enamel}}$ values from both species indicate exclusively C₄ grazers (*i.e.*, 92% C₄ grasses, Table 2.2). By contrast, extant suids from eastern Africa display the full spectrum of herbivore $\delta^{13}\text{C}_{\text{enamel}}$ values. *M. modestus* had a diet based on grasses, as its close relative the warthog, but it is surprising to find similar dietary signals in *K. majus* that had much lower crowned teeth (although higher than in *Potamochoerus* or *Sus*) and M3s that are not more elongated than those of the early

members of *K. limnetes*, suggesting that increase in molar height and length are not required for grazing (Harris & Cerling, 2002).

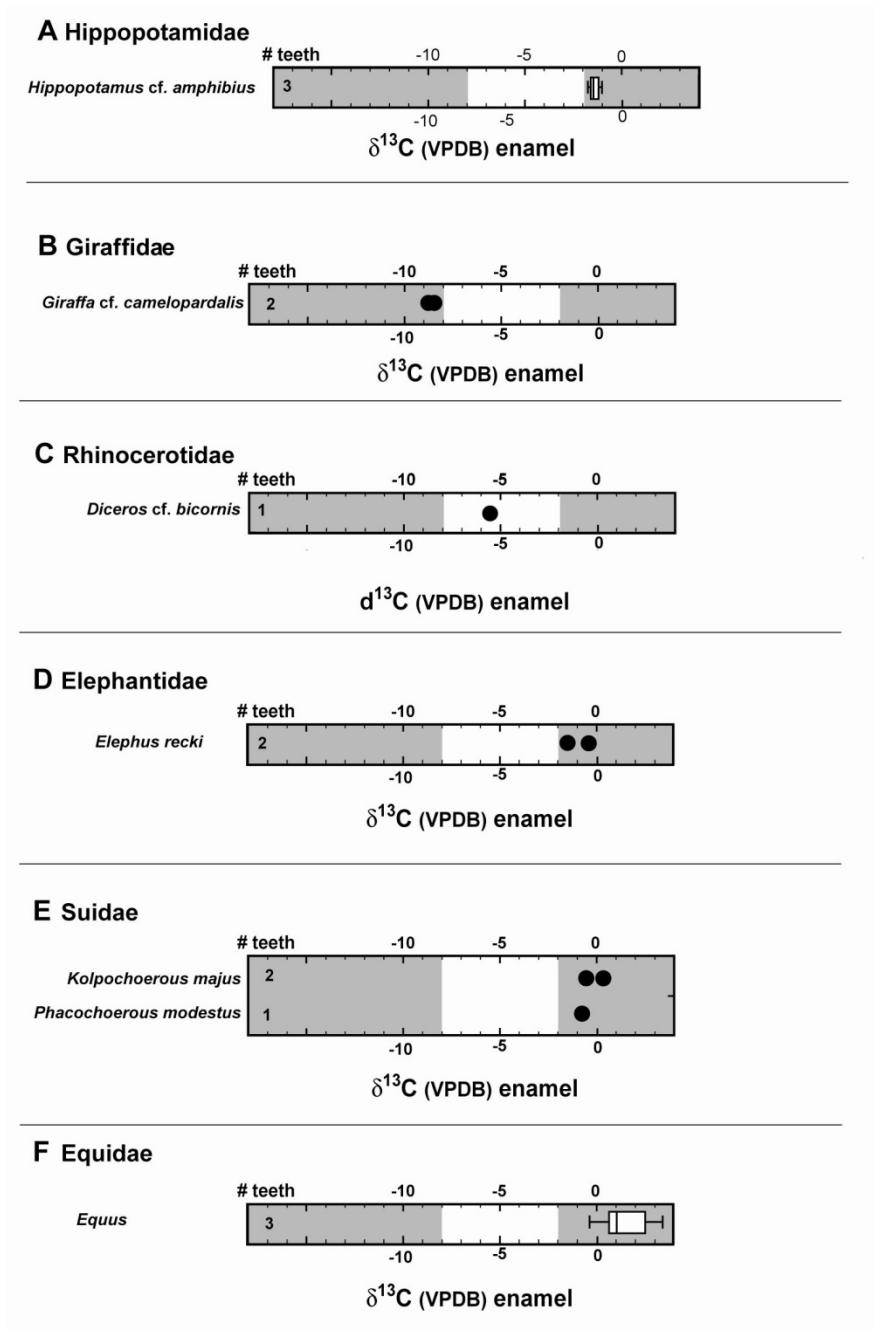


Figure 2.2 Box plots of $\delta^{13}\text{C}_{\text{enamel}}$ values (‰) large mammal teeth from the Asbole fauna. The edges of the box represent quartile values; the horizontal line indicates the range and the median values are represented by a vertical line within the box. $\delta^{13}\text{C}_{\text{enamel}}$ values for taxa represented by three or fewer samples are plotted as individual circles for each analysis.

2.5.5 Giraffidae

The fossil Giraffidae from Asbole are represented by *Giraffa* cf. *camelopardalis* (Geraads et al., 2004). $\delta^{13}\text{C}_{\text{enamel}}$ values of the Giraffidae averages $-8.7 \pm 0.3\text{‰}$ (n=2). The isotopic data from both *Giraffa* specimens indicate diets dominated by C_3 plants with 31% C_4 component, consistent with isotopic data from all modern and fossil *Giraffa* (Cerling & Harris, 1999; Kingston & Harrison, 2007; Cerling et al., 2008) showing that the specialized selective feeding strategy of the giraffe was already established in the Pliocene. Harris & Cerling (1998) report that late Miocene and early Pliocene sivatheres from East Africa have exclusive browsing isotopic signatures, but they become grazers in the late Pliocene. Similarly, a carbon isotopic signature of -1.2‰ was reported for an enamel fragment attributed to cf. *Sivatherium* recovered from the Pliocene GWM-5 block ($\sim 4.3\text{--}3.7$ Ma) at Gona (Semaw et al., 2005), indicating a foraging strategy dominated by C_4 grazing in the early to middle Pliocene.

2.5.6 Hippopotamidae

Hippos are quite rare in Asbole, and are represented by *Hippopotamus* cf. *amphibius*, which is indistinguishable from the living *H. amphibius*, but no diagnostic feature allows a specific identification (Geraads et al., 2004). The average $\delta^{13}\text{C}_{\text{enamel}}$ value of the Asbole hippos is $-1.3 \pm 0.6\text{‰}$ (n= 3). The isotopic data indicate diets dominated by C_4 plants (*i.e.*, 83 % C_4 grasses). Reconstruction of fossil hippo diets has often been based on observations of cranio-dental morphology (Boisserie et. al., 2005). However, the degree of hypsodonty is a weak variable in hippos and cannot be used to distinguish dietary adaptations (Solounias et al., 1988; MacFadden et al., 1999). Stable carbon isotope

analyses of tooth enamel, on the other hand, provide more reliable information on fossil hippo diet. So far, data have been provided by (Morgan et al., 1994; Bocherens et al., 1996; Kingston, 1999; Zazzo et al., 2000; Franz-Odenaal et al., 2002; Cerling et al., 2003b; Schoeninger et al., 2003, Boisserie et. al., 2005), concluding that the $\delta^{13}\text{C}_{\text{enamel}}$ is rather variable in the modern form (-10.9 to +1‰) and that this range of value was almost the same since the Late Miocene (Boisserie et al., 2005). Our isotopic data suggest that the dietary strategies of the Hippopotamidae at Asbole were grazing and fed primarily on C_4 grass (i.e., here all the three data points indicate grazing on C_4 grasses), likely reflecting the aridity of Asbole and the resulting predominance of C_4 vegetation. On the other hand, both C_4 -dominated (Levin et al., 2008) and mixed C_3/C_4 diets have also been reported in different parts of Africa, (*e.g.*, Toros-Menalla, Chad, Boisserie et. al., 2005).

2.5.7 Bovidae

African bovids are a diverse group of mammals that live in habitats ranging from tropical rainforest to deserts (Cerling et al., 2003). Evolutionary pattern of this family has been linked specially to environmental change and faunal turnover during the Miocene and Plio-Pleistocene (Vrba, 1985, 1995; Bobe and Eck, 2001; Alemseged, 2003; Kingston and Harrison 2007).

As in most African paleontological sites, bovids are the most abundant mammalian taxa in the Asbole faunal assemblage, comprising 52 % of the analyzed sample. The samples from Asbole include representatives of the tribes Tragelaphini, Bovini, Hippotragini, Alcelaphini, Reduncini, and Antilopini (Figure 2.3).

Tragelaphini from Asbole are represented by the genus *Taurotragus* and *Tragelaphus scriptus* (Geraads et al., 2004) but all specimens analyzed here are probably from *Taurotragus*. Their $\delta^{13}\text{C}_{\text{enamel}}$ values average $-7.2 \pm 3.9\text{‰}$ (n=3). These isotopic data suggest that *Taurotragus* at Asbole was adapted to a wide range of diets with a suggested preference for browsing, but at least with significant C_4 component in the diet (41% C_4 grasses). Isotopic analyses of enamel and horn keratin of extant tragelaphines from South and East Africa indicate diets dominated by browsing (i.e. *Tragelaphus imberbis* and *Tragelaphus strepsiseros*), although there is evidence for mixed C_3/C_4 in *Taurotragus oryx* (Lee-Thorp, 1989; Cerling et al., 2003a; Sponheimer et al., 2003d), and this is in agreement with our results of the Asbole Tragelaphini.

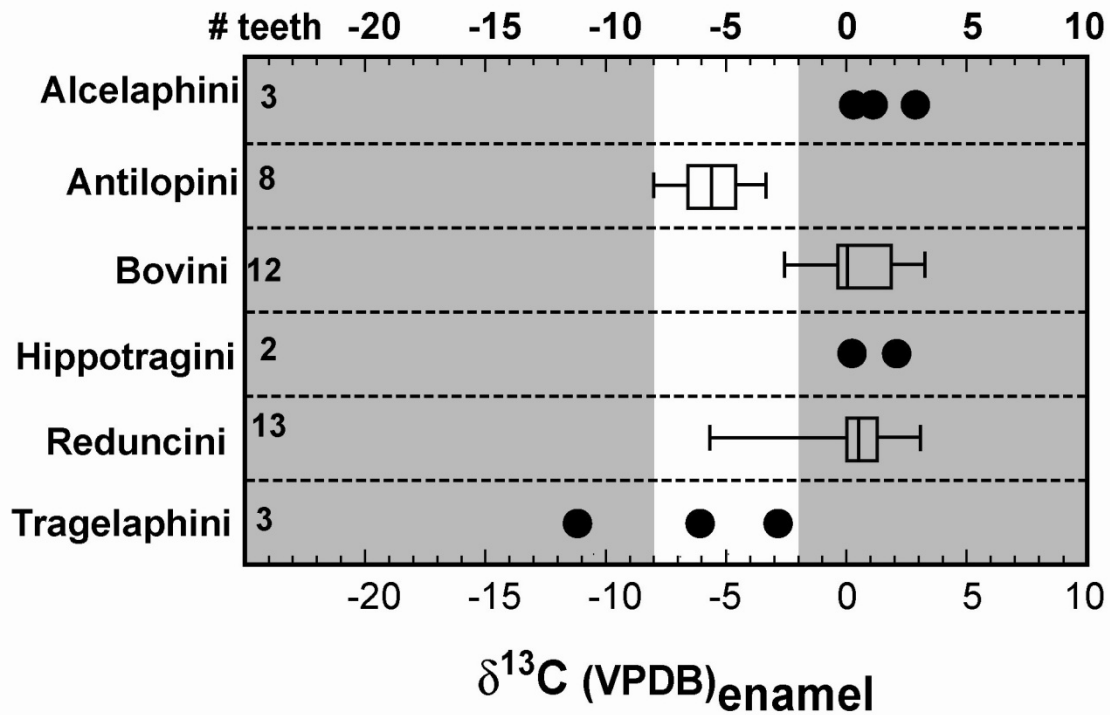


Figure 2.3 Box plot of $\delta^{13}\text{C}_{\text{enamel}}$ values (‰) of bovid teeth from Asbole fauna plotted in the same manner as Figure 2.2.

Bovini are represented at Asbole by an incomplete skull of the genus *Bos* (Geraads et al., 2004), but it is likely that some, if not most, of the teeth sampled here are from a buffalo, either *Syncerus caffer* or a long-horned form close to *Pelorovis*. $\delta^{13}\text{C}_{\text{enamel}}$ values of the samples analyzed have an average $\delta^{13}\text{C}_{\text{enamel}}$ value of $0.9 \pm 1.8\text{‰}$. (n=12). The isotopic data suggests that the dietary strategies of Bovini were generally grazing and fed primarily on C₄ grass (*i.e.*, 99% C₄ grass).

Alcelaphini from Asbole are represented by cf. *Connochaetes* sp. and *Damaliscus niro* (Geraads et al., 2004) although they are not common. The tribe Alcelaphini today includes wildebeest, topi, hirola and kongoni, all are variable to obligate grazers (Gagnon and Chew, 2000), inhabiting open woodland or edaphic and secondary grasslands (Estes, 1991). $\delta^{13}\text{C}_{\text{enamel}}$ values of the three samples from Asbole average $1.3 \pm 1.1 \text{‰}$ (n=3). Our isotopic data suggest that the dietary strategies of the Alcelaphini were grazing and fed exclusively on C₄ grass (*i.e.* 100% C₄ grass), like their modern relatives (Cerling et al., 2003c; Sponheimer et al., 2003) although Kingston and Harrison (2007) indicate that early lineages or individual taxa of small-sized alcelaphines may not have been as committed to specialized grazing niches as their modern-day counterparts.

The fossil Reduncini from Asbole are represented by *Kobus kob* (the most common species in Asbole) and *Redunca* sp. (Geraads et al., 2004) but molars of these species are almost of the same size and could not be identified below tribal level. $\delta^{13}\text{C}_{\text{enamel}}$ values of the samples analyzed have an average of $0.1 \pm 2.5 \text{‰}$. (n=13). These isotopic data suggest that the dietary strategies of the Reduncini were generally C₄ grazers, (*i.e.* 93% C₄

grasses) as do most modern reduncines (Levin et al., 2008). One of our samples has a $\delta^{13}\text{C}_{\text{enamel}}$ value of -5.7 ‰, suggesting the presence of C_3 plants in its diet, but we note that one species of *Redunca redunca* (Bohor reedbuck) sampled from the Bale Mountains in Ethiopia had a $\delta^{13}\text{C}_{\text{enamel}}$ value of -7.1‰, suggesting that some reduncines in less arid environments may consume C_3 vegetation (Levin et al., 2008).

Hippotragini are represented in Asbole solely by the genus *Oryx* (Geraads et al., 2004). $\delta^{13}\text{C}_{\text{enamel}}$ values of the samples analyzed have an average of $0.6 \pm 0.7\text{‰}$. (n=2). These isotopic data suggests that the dietary strategies of Hippotragini were generally grazing and fed primarily on C_4 grass, like modern representatives of this tribe (Kingston & Harrison, 2007).

Antilopini from Asbole are represented by *Gazella* cf. *thomsoni* and *Gazella* aff. *granti* (Geraads et al., 2004). $\delta^{13}\text{C}_{\text{enamel}}$ values of the samples analyzed here, have an average of $-5.7 \pm 1.7\text{‰}$ (n=8), but individual specimens could not be identified to species. The isotopic data suggest that Antilopines were adapted to a wide range of diets more preferably browsing with significant arid-adapted C_4 vegetation and/or some C_4 biomass (i.e. 52% C_4 grasses). Modern gazelles, dibatag, and gerenuk inhabit desert, grassland, savanna and open woodland biomes (Gentry, 1992), and have diets ranging from variable grazers dominated by C_4 grass for Thomson's gazelle (*G. thomsoni*) to greater emphasis on browsing (*G. granti*), while the gerenuk (*Litocranius walleri*) is an essentially pure C_3 browser. Studies of fossils from Eastern and Southern Africa (Lee-Thorp, 1989; Sponheimer et al., 1999; Gagnon and Chew, 2000; Cerling et al., 2003c) have indicated a

similar range of some of the Antilopine diets. Some had mixed feeding strategies with emphasis on browsing (*i.e.*, Grant's gazelle), others had a variable isotopic signature, but one dominated by C₄ grass (*i.e.*, Thomson's gazelle) while others had $\delta^{13}\text{C}_{\text{enamel}}$ values corresponding to a diet of essentially pure C₃ browse (*i.e.*, gerenuk).

Table 2.2 Daily food consumption and C4 proportion in the diet of Asbole Fauna used in the calculation of $\delta^{13}\text{C}_{\text{ecosystem}}$

Fauna	Fauna Abundance %	Average $\delta^{13}\text{C}_{\text{enamel}}$ (‰)	C4 proportion in the diet (%)	Weight of animal (kg)	Average Food consumption (kg/day)
Elephantidae	1	-1.4	82.9	3500-6500	41.6
Rhinocerotidae	4	-0.89	86.5	800-1400	14
Equidae	2	0.71	97.9	270-400	4.6
Suidae	17	-0.19	91.5	45-100	2.3
Hippopotamidae	3	-1.32	83.4	510-3200	17.7
Giraffidae	0.3	-8.71	30.6	1180-1930	19.6
<i>Theropithecus</i>	4	-0.9	86.4	13-21	0.51
<i>Colubus</i>	12.5	-9.6	24.3	5.0-14.0	0.56
<i>Papio</i>	1.7	-7.6	38.6	13-21	0.65
<i>Chlorocebus</i>	1.7	-8.93	29	4.0-8.0	0.01
Alcelaphini	2.6	1.28	102	140-260	2.9
Tragelaphini	3.6	-7.21	41.4	30-80	1.1
Reduncini	28.6	0.05	93.2	43-65	1.1
Hippotragini	1.04	0.57	96.9	400-500	6.0
Bovini	10.9	0.87	99.07	250-850	8
Antilopini	5.2	-5.68	52.3	38-67	1.1

Note: Average weight of animals (kg) and average food consumption (kg/day) of Elephantidae, *Hippopotamus amphibus*, *Syncerus caffer*, *Gazella granti*, *Gazella thomsoni*, *Aepyceros melampus* and *Connochaetes taurinus*) are from Delany and Happold (1979). These data are used to calibrate a relationship between body mass and average food consumption used for the rest of the taxa.

2.6 Paleoenvironmental interpretations based on faunal abundance

The faunal composition of the Asbole fauna, in and of itself allows drawing some paleoecological inferences. Figure 2.4 shows the relative abundances of the various

mammalian families, based upon all identifiable specimens, collected and uncollected (n = 642). Although comparable quantitative data are badly lacking in Eastern Africa, two significant points stand out about the Asbole fauna: the scarcity of hippos and the high proportion of cercopithecids represented by five species, with colobines as the dominant primate group. The abundance of arboreal primates is an indicator of high tree cover (Reed, 1997), and this is especially true at Asbole where the primates mostly consist of colobines, an arboreal group specialized in leaf eating (almost 2/3 of the total primates are colobines; Frost & Alemseged, 2007). The low frequency of hippos contrasts with their abundance in most other eastern African vertebrate fossil sites; it can perhaps be explained by the absence of perennial streams or lakes large enough for these animals.

The relative abundance of the various bovid tribes (Figure 2.5) is often used as a paleoecological indicator (Vrba, 1980), as it is very informative. Here, the very high proportion of reduncines (mostly *Kobus*) very likely points towards the dominance of a seasonally inundated open environment, such as a floodplain or even swamp that would also suit the bovines which are also quite common. In contrast, indicators of drier grasslands in uplands, such as alcelaphines and antilopines, are rare. We may also note the low frequency of tragelaphines and the absence of the impala; this might suggest poor representation of a suitable ecotone between forest and grassland, but is consistent with the interpretation of narrow gallery forest or wooded environment with a sharp boundary to a widespread open environment.

The other mammals provide less clear ecological indications, but support the previous ones. Among rhinos, the browser or mixed-feeder *Diceros* is more common than the

grazer *Ceratotherium*. Although there was certainly a size bias in the collection of rodents, the common, *Thryonomys*, is a mesic-adapted genus found in swamps and other moist habitats, and similar conditions may suit the other taxa, *Tachyoryctes*, *Otomys*, and *Arvicanthis*. Although they are rare and not very good ecological indicators, the carnivores at Asbole do not contradict these interpretations.

2.7 Faunal-abundance-weighted $\delta^{13}\text{C}_{\text{ecosystem}}$ value

In general, our carbon isotopic results shows that C_4 grasses were a significant components of the total diet of the Asbole fauna, but to better account for the average carbon isotopic value of the ecosystem we calculate a weighted average $\delta^{13}\text{C}_{\text{ecosystem}}$ value using the average $\delta^{13}\text{C}_{\text{enamel}}$ of each taxon weighted by faunal abundance and the estimated daily food intake of each large vertebrate (>50 kg) taxon (Table 2). This value approximates the $\delta^{13}\text{C}$ value of the total vegetation present in an ecosystem, or at least that consumed by large vertebrates. Using the data in Table 2, the $\delta^{13}\text{C}_{\text{ecosystem}}$ value for the Asbole faunal zone was -14.7‰, which underscores the near-absolute dominance of C_4 vegetation in the region sampled by the total large vertebrate fauna (C_4 vegetation ranges from -19 to -9‰ with a mean of -13‰). Using these end member isotopic compositions of vegetation, the proportion of C_3 vegetation at Asbole is estimated as 12%. Sensitivity tests were done to check the effect on the calculated $\delta^{13}\text{C}_{\text{ecosystem}}$ value by categorically including/excluding primates, which are comparatively abundant but consume little biomass in comparison to large vertebrates, including primates in this analysis shows little effect (i.e. -0.3‰ change in $\delta^{13}\text{C}_{\text{ecosystem}}$), which contributes an additional 2% to the estimated C_3 vegetation cover.

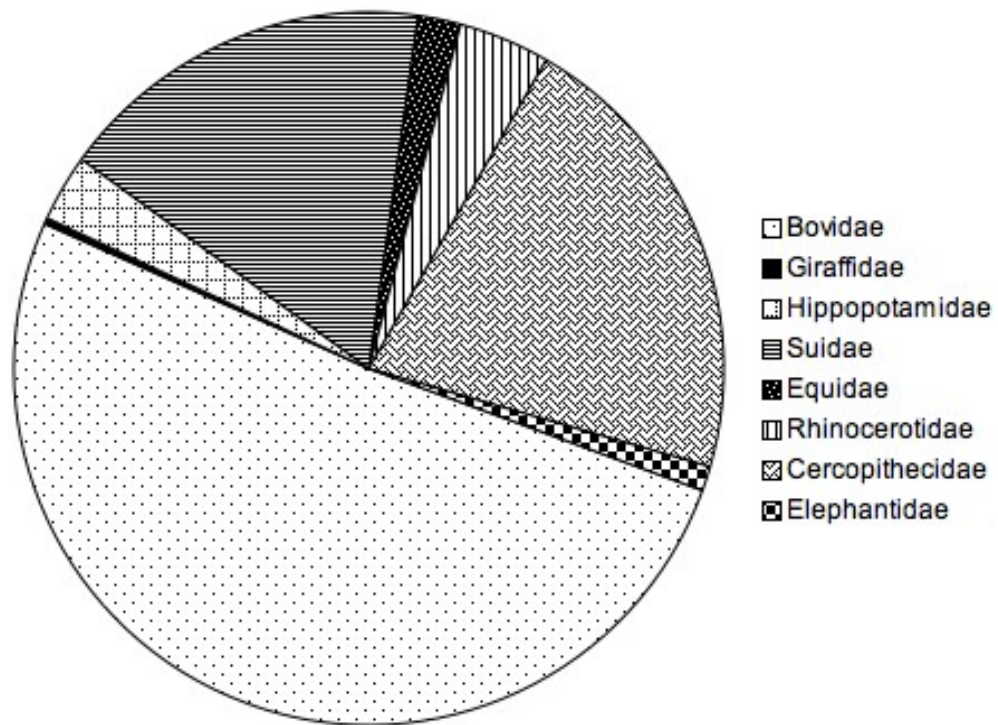


Figure 2.4 Relative abundances of the mammalian families from the Asbole fauna, excluding rodents and carnivores.

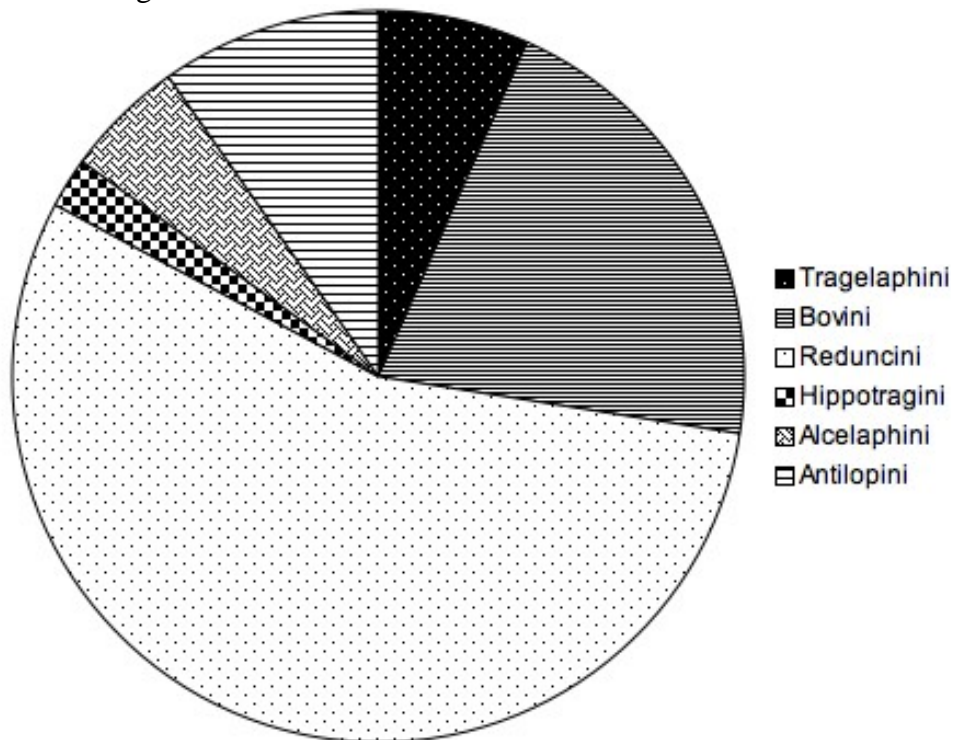


Figure 2.5 Relative abundances of the bovid tribes from Asbole.

The faunal abundance weighted average $\delta^{13}\text{C}_{\text{ecosystem}}$ values in this study remains to be calibrated with the modern analogs and studies are under progress. To better calibrate the data and obtain a representation of all the species a range of environments should be considered.

2.8 Oxygen isotopic composition of tooth enamel

2.8.1 Observed $\delta^{18}\text{O}_{\text{enamel}}$ values

The wide range of $\delta^{18}\text{O}$ values of tooth enamel from the Asbole fauna (-6.3 to +8.4‰) indicates significant variation in the oxygen isotope composition of animal water sources, food, and thermophysiological adaptations (*e.g.*, Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999b). Given the theoretical constraints on $\delta^{18}\text{O}_{\text{enamel}}$, we can distinguish “obligate drinkers” that get water from river or lakes, and thus track $\delta^{18}\text{O}$ of meteoric water most faithfully (*e.g.*, Reduncini, *Equus* and suids) from other “non-obligate drinkers” that obtain most of their water from leaves in which ^{18}O is enriched compared to the local meteoric water (*e.g.*, *Giraffa*). Still others are aquatic, in which ^{18}O is significantly depleted in relation to other herbivores (*e.g.*, *Hippopotamus*; Levin et al., 2006). $\delta^{18}\text{O}_{\text{enamel}}$ values of the Asbole fossils range between -6.3 and +8.4‰ (Figure 2.6) reflecting all drinking habits of animals from non-obligate drinkers (*i.e.*, *Giraffa*, Antilopini and Tragelaphini) through intermediates (*i.e.* Hippotragini and Bovini) to obligate drinkers (*i.e.*, Reduncini, Alcelaphini, hippopotamids, rhinocerotids, elephantids and to less extent equids, and suids). The range of $\delta^{18}\text{O}_{\text{enamel}}$ values also differs between taxa, which may be explained by the degree of adaptation of the animal, specialization of different taxa in different ecotone or differences in seasonal migrations. The largest range

of $\delta^{18}\text{O}_{\text{enamel}}$ within individual taxon occurs in Bovini, Antilopini and *Giraffa* (8.0, n= 12), 7.2 (n=8) and 7.2‰ (n=2) respectively), while the rest of the fauna shows lower ranges of $\delta^{18}\text{O}_{\text{enamel}}$ values between 0.7-5.8 (n between 1 and 13) ‰ *Hystrix*, *Elephas*, *Chlorocebus*, *Theropithecus* and *Diceros* are represented by a single value). The narrow range of the $\delta^{18}\text{O}$ of the Asbole rodentia would indicate its potential to provide localized paleoenvironmental signals at a finer scale than other lines of evidence (Reed, 2007)

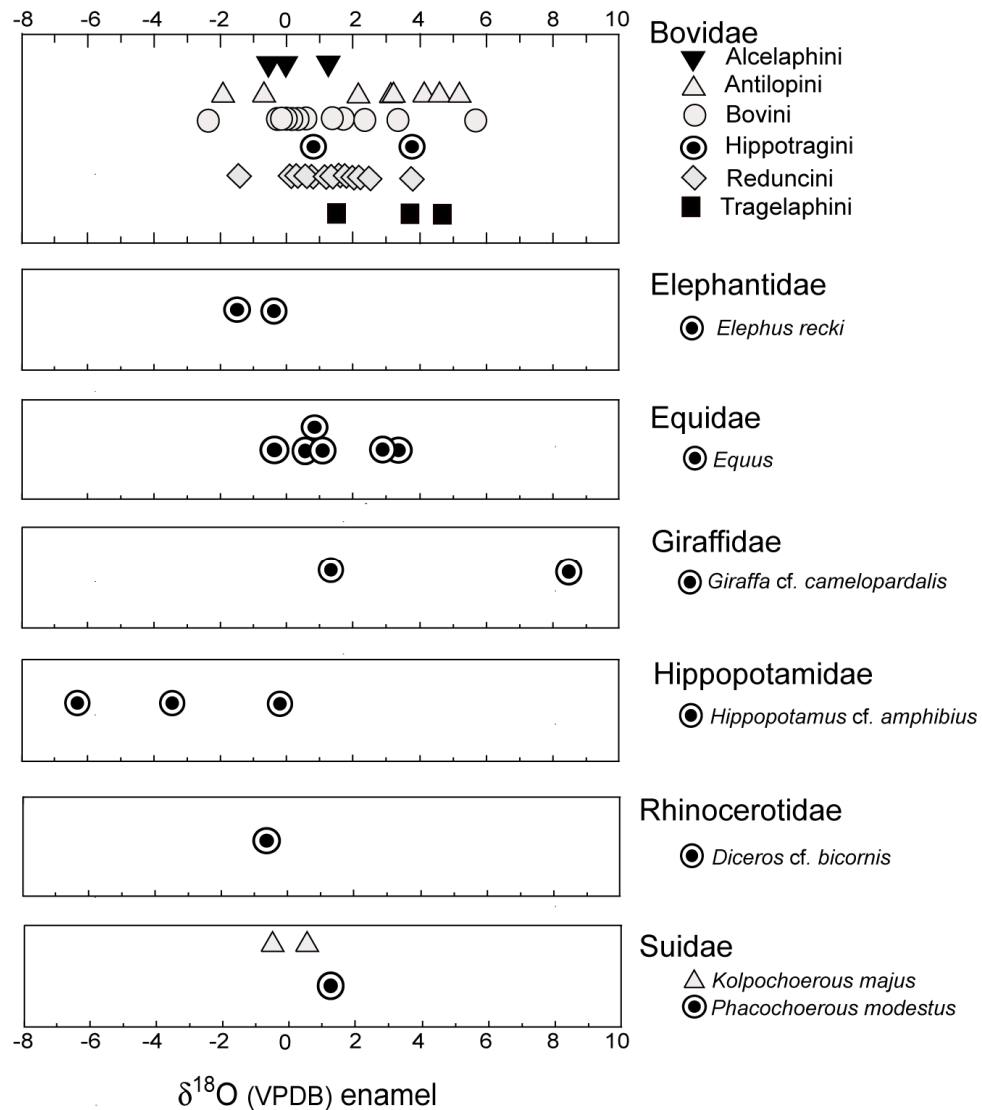


Figure 2.6 $\delta^{18}\text{O}_{\text{enamel}}$ of herbivores teeth from Asbole fauna.

2.8.2 Estimating paleo-aridity using $\delta^{18}\text{O}_{\text{enamel}}$

We applied the novel method of Levin et al. (2006) to estimate the paleo-aridity at Asbole based on interpretation of the $\delta^{18}\text{O}_{\text{enamel}}$ values of evaporation sensitive (ES) and evaporation insensitive (EI) taxa. EI taxa are those that are obligate drinkers, and thus track the $\delta^{18}\text{O}$ value of local meteoric water as their main source of oxygen in body water. Meanwhile ES taxa are the non-obligate drinkers whose main source of oxygen is from the evaporatively ^{18}O -enriched water in leaves. Because the $\delta^{18}\text{O}$ value of leaf water increases by evaporation and this increase is proportional to aridity, the oxygen isotopic enrichment between ES and EI taxa ($\epsilon_{\text{ES-EI}}$) also increases with aridity, and is an independent of the isotopic composition of local meteoric water, making it an ideal paleoaridity index in terrestrial environments. Water deficit (WD) values are used to characterize environmental aridity, which is the difference between potential evapotranspiration (PET) and the mean annual precipitation (MAP). Figure 2.7 shows the calibration data set from Levin et al. (2006) of $\epsilon_{\text{ES-EI}}$ to water deficit from a range of climates in East Africa. Based on this calibration, and our estimate of the $\epsilon_{\text{ES-EI}}$ determined from the Asbole fauna, the mean annual water deficit of the Middle Pleistocene at Asbole is calculated to be 1470 mm. Thus the paleoclimatic condition of Asbole is similar to that near the most arid end members of the modern calibration data set: Olorgesailie (Magadi station; 1341 mm) and the Turkana Basin (Lodwar station; 1588 mm). We also calculated WD for climate stations near Asbole in Ethiopia for comparative modern analogs (Table 2.3).

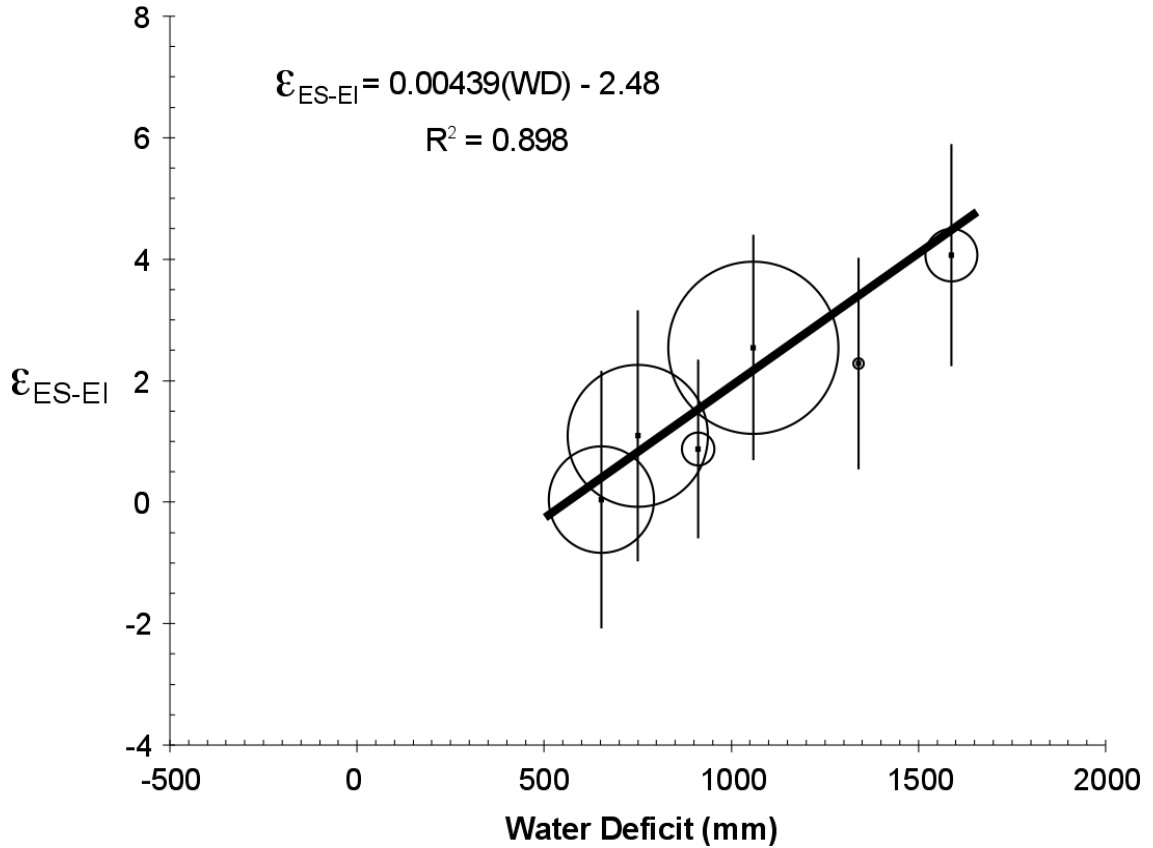


Figure 2.7 Relationship between aridity (measured as water deficit, WD) and the oxygen isotopic enrichment between evaporation sensitive (ES) and evaporation insensitive (EI) taxa (ϵ_{ES-EI}), based on the calibration data in Levin et al. (2006). From this data set, we chose only the clearly identified taxa for the ES (*Syncerus caffer*, *Oryx beisa*, *Giraffa camelopardalis*, *Madoqua kirkii*, *Gazella granti*) and EI (*Loxodonta africana*, *Hippopotamus amphibius*, *Equus burchelli*, *Aepyceros melampus*, *Potamochoerus larvatus*, *Diceros bicornis*, *Phacochoerus africanus*, *Papio anubis*) categories. Each point represents a location, with climate determined from East African Meteorological Department data. Based on the suggestion of minimum sample size required, only locations from this calibration data set with > 10 combined ES and EI samples are used in the regression, which is weighted to the total number of ES and EI samples from each location. The size of the circle surrounding each point is proportional to the total number of samples from that location, while the error bars represent the average of the standard deviations for ES and EI samples from each location. The regression slope here (0.00439/mm) corresponds well to the suggested value based on the pooled or common slope of individual regressions from Levin et al., (2006; 0.00501/mm).

Table 2.3 Calculated Water Deficit (WD) from the highlands and lowlands of the Rift Valley of Ethiopia, compared to the estimated value for the Middle Pleistocene at Asbole based on ϵ_{ES-EI} .

Location	MAP	PET	WD	Elevation (m)
<i>Based on modern climate data</i>				
Desse	1230	721	-509	2510
Bati	916	960	44	1502
Ziway	740	930	191	1643
Gewane	417	1906	1435	618
Dubti	195	3143	2948	503
<i>Fossil locality based on ϵ_{ES-EI}</i>				
Asbole			1470	

Note: MAP- Mean annual precipitation, PET- potential evapotranspiration, WD-Water deficit. (where $WD = PET - MAP$). Meteorological data of Gewane, Bati, Dubti, Ziway and Desse are adopted from the Ethiopian National Meteorological Agency.

WD values from Gewane, Bati, Dubti, Ziway and Desse indicate a wide variation in environmental aridity between Ethiopian Rift Valley, highland and the lowlands. Of these data, the paleo-water deficit for Asbole is most similar to the nearby Gewane station, which might indicating little change in aridity in this part of the Ethiopian Rift since the Middle Pleistocene. This interpretation is also supported by the dominance of arid-adapted C_4 vegetation evident from the $\delta^{13}C_{ecosystem}$ value discussed above.

2.9 Conclusions

Isotopic analyses of mammalian herbivore taxa from the “Asbole faunal zone” (0.8 - 0.64 Ma) including multiple samples of 15 taxa representing 9 different families, were sampled to analyze dietary adaptations and reconstruct the range of paleoenvironmental conditions in which the fauna lived. The Asbole carbon isotopic data indicate a wide range of foraging strategies, across the entire spectrum of pure C_4 to C_4 -dominated diet, mixed C_3/C_4 diet and C_3 -dominated diet.

The stable oxygen isotope data signifies that most of the species are evaporation insensitive which track the meteoric water faithfully, while a few species such as (*Giraffa*, Antilopini and Tragelaphini) are evaporation sensitive and track the isotopic composition of vegetation consumed. Our estimate of the oxygen isotopic enrichment between these two groups (ϵ_{ES-EI}) determined from representative samples of the Asbole fauna is 3.7‰. This value provides an estimate of the mean annual water deficit of the Middle Pleistocene at Asbole to be 1470 mm, which is similar to the present day water deficit at the climate station of Gewane in an arid climate.

Although no hominin remains have been found at Asbole thus far, the presence of abundant MSA archeological remains at Asbole (Alemseged and Geraads, 2000) shows that hominins were present in the area between 0.6 and 0.8 Ma. The very diverse nature of mammalian species at the site is rather unique and not common for the Middle Pleistocene (*i.e.*, five primate species are encountered and overall primates are very abundant, while hippos are much less abundant than at many similarly-aged sites). Based

on previous study, Alemseged and Geraads (2000) suggested that overall, the ecological implications of the bovid assemblage recalls more some Pliocene sites than Pleistocene ones.

Based on carbon isotopic analysis of the large vertebrate fauna, combined with faunal abundance and dietary intake data, we interpret the overall environment at Asbole between 0.64 and 0.8 Ma to be an arid, C₄-dominated open vegetation region, with an abundance of forest dwelling primates indicating the presence of isolated gallery forests flanking tributary streams (~12 % C₃ biomass). So, with these combined methodologies, we can elucidate a more detailed character of the “mosaic” of environments. By combining the stable isotopes, which emphasize the widespread open and xeric condition, with faunal abundance data, which indicated the presence of wooded environment as gallery forests along the main river (Geraads et al., 2004), we are able to obtain a more detailed picture than with a single proxy alone. More stable isotopic studies, specifically of the diverse primate fauna from Asbole, will be the next platform to better quantify the abundance and specific nature of the gallery forest environments.

It is generally accepted that environmental conditions in East Africa became more open and xeric through time in the Plio-Pleistocene, with cooler and drier conditions in the late Early Pleistocene (Coppens, 1975, Vrba, 1985, 1988 and 1995). The stable carbon and oxygen isotope data presented here, in the context of similarly analyzed African Plio-Pleistocene sites, lends support to this hypothesis. Previous work at Asbole based on faunal abundance combined with the current study demonstrate that though major trends

in environmental changes could be true, regional and local environmental variations were equally important. A good example is the abundant remains of water loving (reduncini) and forest dwelling (colobines) species at the Middle Pleistocene site of Asbole compared to Andale in the Middle Awash Region, located not far from Asbole and with the same geological age, documents a similar fauna, but with very different proportions (Kalb et al., 1982). For example, among the bovids at this site, Reduncini is not the most common as this tribe is over taken by Tragelaphini, probably showing some local environmental distinction among the two proximal sites. These findings caution against oversimplification of Pleistocene environmental reconstructions, based on single proxies at isolated localities.

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CHAPTER THREE

DIETARY AND PALEOENVIRONMENTAL RECONSTRUCTION USING STABLE ISOTOPES OF HERBIVORE TOOTH ENAMEL FROM MIDDLE PLIOCENE DIKIKA, ETHIOPIA: IMPLICATION FOR *AUSTRALOPITHECUS AFARENSIS* HABITAT AND FOOD RESOURCES

3.1 Introduction

Exploring the paleoenvironmental and paleoclimatic conditions as well as available food resources and habitats of early hominins has been a key issue in answering major questions pertaining to the origin, evolution, and extinction of hominin species in addition to understanding their morphological and behavioral adaptations (Dart, 1925; Robinson, 1954; Vrba, 1985; Reed, 1997; Alemseged and Bobe, 2009). Paleoenvironmental reconstruction of hominin fossil localities in Africa has been based on paleosol carbonate (*e.g.*, Levin et al., 2004; Aronson et al., 2008), taxonomic uniformitarianism (*e.g.*, Vrba, 1980) faunal abundance (*e.g.*, Reed, 1997, 2008), ecomorphology (*e.g.*, Plummer et al., 2008), and palynologic analysis (*e.g.*, Bonnefille et al., 2004). The use of carbon and oxygen stable isotopes of mammalian tooth enamel has proven a successful tool in the study of paleodietary and habitat reconstruction of both hominin and non-hominin species (Lee-Thorp, 1989; Bocherens et al., 1996; Kohn et al.,

1996; Kingston, 1999; Sponheimer et al., 1999; Zazzo et al., 2000; Cerling et al., 2003a; Levin et al., 2008; White et al., 2009; Bedaso et al., 2010). However, compared to the other Pliocene fossil localities in Africa, previous stable isotope studies of mammalian tooth enamel from the Awash Valley of Ethiopia have been sparse.

This study uses stable isotopes of carbon and oxygen from tooth enamel to reconstruct dietary adaptations of herbivorous ungulates, assess shifts in the relative abundance of C₄ grasses, reconstruct the oxygen isotopic composition of meteoric water and interpret the environmental context, habitat structure, and climatic conditions between 4–3 Ma at Dikika Ethiopia. It has direct relevance to the understanding of the paleoenvironmental context and available food resources of the only known middle Pliocene hominin in the region: *Australopithecus afarensis*.

3.2 Background

The Dikika Research Project (DRP) area is perhaps best known for the juvenile early hominin skeleton “Selam,” (*A. afarensis*), and the earliest evidence of stone-tool-assisted consumption of ungulates by hominins (Alemseged et al., 2005; Alemseged et al., 2006; Wynn et al., 2006; Geraads, 2005; McPherron, et al., 2010). Dikika is surrounded by the Hadar, Middle Awash, Gona and Ledi-Geraru paleontological research areas in the Afar Depression (Figure 3.1). The area represents one of the key paleontological and paleoanthropological sites in East Africa and the project seeks to address key

evolutionary questions pertaining to various aspects of early hominins paleobiology as well as their cultural evolution over the past ca. 4 Ma.

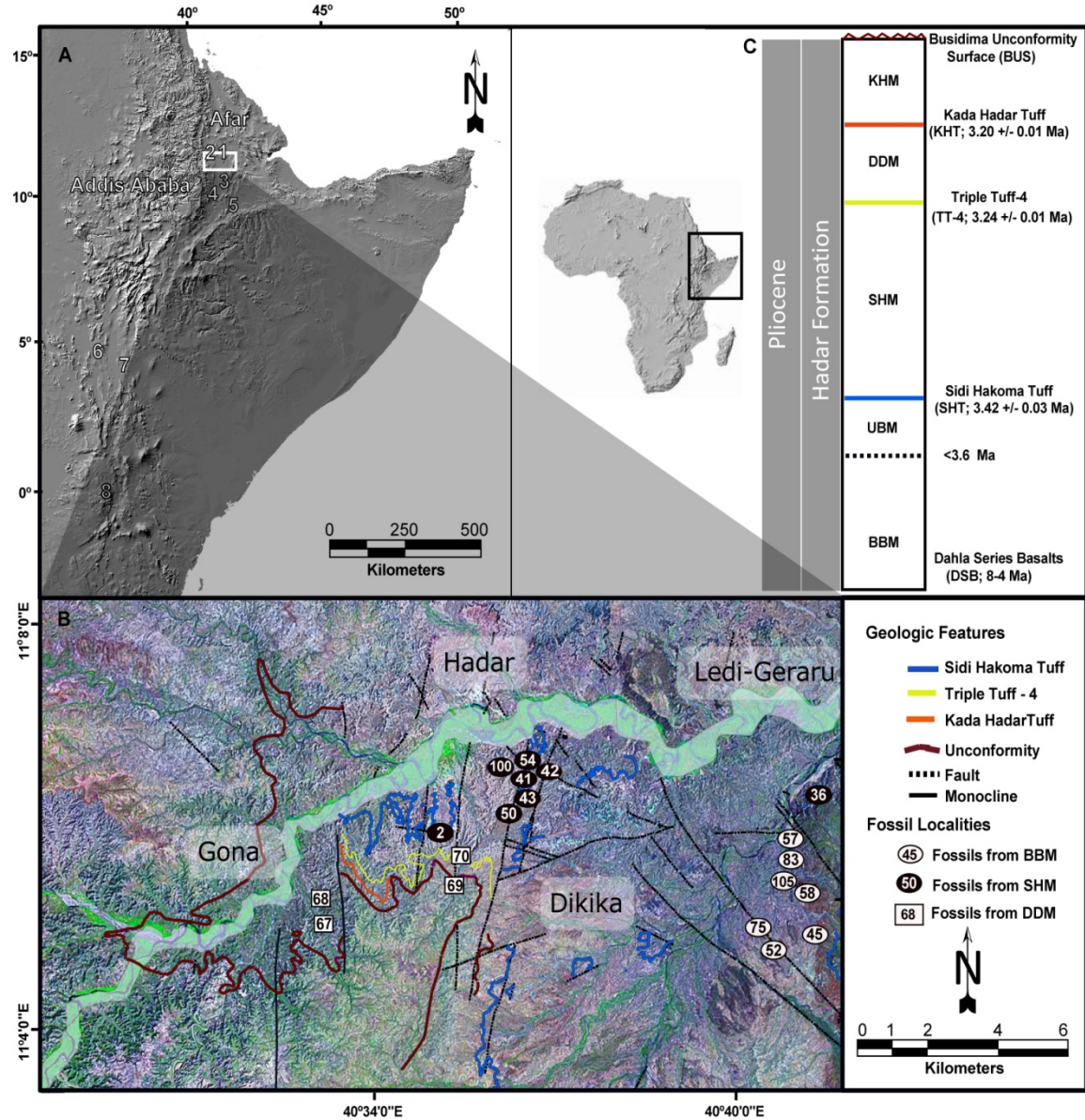


Figure 3.1 Location map of the Dikika Research Project area **a**, A map showing fossil sites which bear *Australopithecus afarensis* (1-Hadar, 3-Maka, 6-Turkana 7-Koobi Fora and 8-Laetoli) and other sites with published tooth enamel isotope data (2-Gona, 4-Aramis and 5-Chorora) **b**, Detailed map showing the eastern portion of DRP area (*i.e.* fossil localities representing the Hadar Formation, marker beds and geological structures) and adjacent fossil sites (Hadar, Gona and Ledi-Geraru) **c**, Generalized composite stratigraphic column of the Hadar Formation showing age of sampling intervals used in this study.

Fluvial and lacustrine sediments exposed in the DRP area date from the Pliocene to the Middle Pleistocene (Wynn et al., 2008). Middle Pleistocene sediments are exposed on the west side of the Awash River at Asbole (Alemseged & Geraads, 2000; Frost & Alemseged, 2007), whereas Pliocene sediments are found in the east at Dikika (Alemseged et al., 2005; Wynn et al., 2008). The interval between 4–3 Ma has yielded diverse faunal assemblages that include over 60 species of large mammals as well as the remains of reptiles, fish, birds, amphibians, molluscs, ostracods and plants (see Wynn et al., 2006). Eight hominin-bearing localities have been found at Dikika (see Alemseged et al., 2005, Alemseged et al., 2006, also a pelvis and several mandibular and maxillary fragments have been discovered from other unpublished localities).

3.3 Geological context

The DRP area is approximately 500 km northeast of Addis Ababa within an active tectonic setting that is commonly referred to as the triple junction between the Nubian, Somalian and Arabian Plates (Beyene and Abdelsalam, 2005; Figure 3.1). The composite stratigraphy of the DRP area encompasses what has classically been assigned to the Hadar Formation (Basal, Sidi Hakoma, Denen Dora and Kada Hadar Members), as well as disconformably overlying sediments of the Busidima Formation (Wynn et al., 2008; Quade et al., 2008). The sequence begins with the Basal Member of the Hadar Formation (below the Sidi Hakoma Tuff (SHT) 3.42 ± 0.03 Ma), which was deposited on a dissected and deeply weathered surface of the uppermost flow of the Dahla Series Basalt (8–4 Ma; Taieb et al., 1976). The Basal Member has a total thickness of 80 m, which is divided here into the Base of Basal Member (BBM) and the Upper Basal member (UBM)

separated by a diatomite layer ~40 m below the SHT. The SHT is overlain by the Sidi Hakoma Member (between SHT & Triple Tuffs (TT-4) 3.24 ± 0.018 Ma), Denen Dora Member (between TT-4 and Kada Hadar Tuff (KHT) 3.20 ± 0.01 Ma), and Kada Hadar Member (above KHT and below the unconformity, 2.9–2.7 Ma; Campisano and Feibel, 2008). Sediments of the Hadar Formation indicate a repeated transgression and regression of the Hadar Lake and are deposited in deltaic, fluvial and lacustrine depositional environments (Wynn et al., 2008).

3.4 Methods

3.4.1 Sample collection

Fossil tooth enamel was primarily sampled from specimens collected during 2009 and 2010 field seasons and supplemented by previously collected fossils housed in the National Museum of Ethiopia in Addis Ababa. Almost all of the fossils materials are surface collections from different stratigraphic levels. The age of the fossils was determined in the field using the exposed stratigraphic section. We analyzed a total of 210 samples (*i.e.*, 140, 17, and 53 from the Sidi Hakoma (SHM), Upper Basal (UBM), and Base of the Basal (BBM) members, respectively) from 15 different mammalian taxa (Table 3.1).

The surface of each tooth was cleaned of adhering sediment and secondary or nonstructural carbonate. Then a bulk enamel sample was taken by drilling down the tooth along the growth axis with a 0.5 mm diamond-impregnated drill bit, cleaning the drill bit between sampling. Care was taken to avoid dentine, cementum and/or matrix in the

sample powder. To avoid juvenile dietary signals in teeth formed in the early developmental stage, in most cases, molars, preferably the M3, were sampled. Approximately 15–20 mg of powdered enamel was extracted from each tooth.

3.4.2 Sample treatment and isotopic analysis

The powder produced was pretreated with 3% H₂O₂ followed by a 1 M acetic acid-calcium acetate buffer to remove organic matter and secondary carbonates, and thoroughly rinsed with deionized water following standard procedures for the treatment of tooth enamel of Lee-Thorp and Van der Merwe (1987) and Koch (1998). 5–7 mg of the pretreated powder was reacted with 103% H₃PO₄ at 25°C in He-flushed exetainer vials for 24 hrs to produce CO₂ for analyses of carbon and oxygen isotopic composition. Isotope ratios were measured on a Thermo Fisher Scientific (Finnigan) Delta V 3 keV Isotope Ratio Mass Spectrometer and results are reported using the standard per mil notation:

$$\delta^{13}\text{C} \text{ or } \delta^{18}\text{O} = \left(\frac{R_{\text{sample}}}{R_{\text{Standard}}} - 1 \right) * 1000\text{‰}$$

where R_{sample} and R_{standard} are the ¹³C/¹²C ratios in the sample and standard, respectively, for δ¹³C and the ¹⁸O/¹⁶O ratios in the sample and standard, respectively, for δ¹⁸O. The reference standard is the international reference scale VPDB, which was normalized using replicate analyses of IAEA reference materials NBS-18 and NBS-19. The average within-run standard deviations for both δ¹³C and δ¹⁸O were <0.1‰.

The isotopic enrichment between two materials A and B is reported as:

$$\varepsilon_{A-B} = \left(\frac{R_A}{R_B} - 1 \right)$$

Statistical analyses on the isotope data were performed using SAS 9.2. All tests of hypothesis were two tailed and significance (α) for statistics was set at 0.05. For pair wise comparison the Wilcoxon Rank Sum test, which is also referred as Mann-Whitney U test, was used.

3.5 Interpretation of carbon and oxygen isotopes

The $\delta^{13}\text{C}$ values of most C_3 plants range between about -25‰ and -29‰ and average approximately -26‰. However, the total observed range in $\delta^{13}\text{C}$ values for C_3 plants is from about -22‰ to -35‰. These variations among C_3 plants are attributed to environmental factors including canopy density, light intensity, water availability, nutrient levels, temperature and partial pressure of CO_2 , which produce predictable variations in $\delta^{13}\text{C}$ values (Ehleringer & Monson, 1993, Koch, 1998). C_4 plants have an average $\delta^{13}\text{C}$ value of -13‰ with a range between -19‰ to -9‰. C_4 plants show little environmental variability in $\delta^{13}\text{C}$ values due to their efficient method of carbon fixation under low CO_2 concentration (Marino & McElroy, 1991). Field studies of large herbivores from different habitats estimate the average ^{13}C -enrichment between diet and tooth enamel ($\varepsilon_{\text{diet-tooth enamel}}$) at ~14‰ (Cerling and Harris, 1999). Following Cerling et al. (2003c), we use $\delta^{13}\text{C}_{\text{enamel}}$ values to classify the herbivores into three categories: browsers ($\delta^{13}\text{C}_{\text{enamel}} \leq -8\text{‰}$), mixed feeders ($-2\text{‰} > \delta^{13}\text{C}_{\text{enamel}} > -8\text{‰}$) and grazers ($\delta^{13}\text{C}_{\text{enamel}} \geq -2\text{‰}$) (Figure 3.2 and 3.3).

The oxygen isotopic composition of mammalian tooth enamel is directly related to that of body water, which in turn reflects that of drinking water and from other, largely dietary sources. These source effects are further modified by the physiology of the animal, diet, and climatic conditions (Longinelli, 1984; Luz et al., 1984, Kohn, 1996). As mammals larger than 1 kg have a constant body temperature near 37 °C, enamel hydroxyapatite ($\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$) is precipitated in these species at a virtually constant temperature. This allows the oxygen isotopic signature of the ingested material to be recorded without the effect of temperature dependence of the fractionation factor or of changes in external temperatures (Longinelli and Nuti, 1973). Thus, for large mammals, there is a constant ^{18}O -enrichment between $\delta^{18}\text{O}$ of body water (bw) and that of the PO_4 fraction of bioapatite ($\epsilon_{\text{PO}_4\text{-bw}} = \sim 18\text{‰}$, Luz and Kolodny, 1985) and between the PO_4 and CO_3 fraction of bioapatite ($\epsilon_{\text{CO}_3\text{-PO}_4} = \sim 8\text{‰}$, Bryant et al., 1996). This implies constant ^{18}O -enrichment between the CO_3 fraction of bioapatite and body water, which can be used to calculate the $\delta^{18}\text{O}$ meteoric water, and thus serve as proxy for $\delta^{18}\text{O}$ meteoric water and for reconstructing pale-moisture sources.

3.6 Results

3.6.1 Carbon isotopic composition by taxa

$\delta^{13}\text{C}_{\text{enamel}}$ values of the Dikika fossils between 4–3 Ma ranges between -11.5 and +0.3‰ in the base of the Basal Member (BBM; > 3.8–< 3.6 Ma), -14.0 and +0.8 ‰ in the Upper Basal Member (UBM; < 3.6 – 3.42 Ma), -14.3 and +3.1‰ in the Sidi Hakoma Member (SHM; 3.42–3.24 Ma) and -1.8 and +2.4‰ in the Denen Dora Member (DDM; 3.24–3.20

Ma). Thus, the values span the entire C₃–C₄ range of dietary adaptation in all units, except DDM, but this may reflect the relatively few specimens analyzed (Table 3.1).

The $\delta^{13}\text{C}_{\text{enamel}}$ values of some of the mammals indicate a consistent consumption of pure C₄ vegetation between 4–3 Ma, while pure C₃ dietary preferences are represented only in the UBM and SHM. Generally the dietary adaptation of the species considered in this study did not show major change through the entire period (4–3 Ma), but there are slight changes in adaptation and the range of incorporation of C₄ vegetation and total range of $\delta^{13}\text{C}_{\text{enamel}}$ in each member (Table 3.1). Most of the taxa including Alcelaphini, Reduncini, *Notochoerus*, Equidae and Elephantidae consumed predominantly C₄ vegetation, while Deinotheriidae and Giraffidae consistently consumed predominantly C₃ vegetation. The rest of the taxa (Bovini, Hippotragini, Tragelaphini, *Kolpochoerus*, *Nyanzachoerus* and Hippopotamidae) had mixed C₃/C₄ feeding strategies.

3.6.1.1 Proboscidea

The fossil Proboscidea from Dikika include elephantids from BBM, UBM, SHM, and *Deinotherium* from UBM and SHM. Most of the proboscidean teeth from the BBM are very fragmentary and collected for isotope analysis and are difficult to identify to a more precise taxonomic level, but fossils collected from DIK-1 are attributed to *Elephas* cf. *recki brumpti* and *E.* cf. *ekorensis* (see Wynn et al., 2006). The $\delta^{13}\text{C}_{\text{enamel}}$ value of elephantids averages -2.2 ± 1.6 ‰ (n=16), -0.3 ± 0.2 ‰ (n=2) and -2.1 ± 1.1 ‰ (n=10) from BBM, UBM and SHM respectively. The $\delta^{13}\text{C}_{\text{enamel}}$ value of relatively rare

deinotheres averages -14.1‰ (n=1) from UBM and -12.1 ± 0.4 ‰ (n=2) from the SHM (Table 3.1, Figure 3.2A).

Table 3.1 Stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of fossil tooth enamel collected from Hadar Formation at Dikika.

Sample number	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
ZK-EN 355	Bovidae	Aepycerotini	SHM	-6.56	-6.21
ZK-EN-D291	Bovidae	Aepycerotini	SHM	-2.21	-4.52
ZK-EN-D294	Bovidae	Aepycerotini	SHM	-5.40	0.14
ZK-EN-D300	Bovidae	Aepycerotini	SHM	-2.02	-5.29
ZK-EN-D272	Bovidae	Aepycerotini	SHM	-1.36	-4.46
ZK-EN-D275	Bovidae	Aepycerotini	SHM	-3.38	-1.61
ZK-EN-D18	Bovidae	Alcelaphini	SHM	-3.38	3.27
ZK-EN-D36	Bovidae	Alcelaphini	SHM	-1.99	5.03
ZK-EN-D37	Bovidae	Alcelaphini	SHM	0.73	1.44
ZK-EN-D44	Bovidae	Alcelaphini	SHM	0.08	-6.07
ZK-EN-D55	Bovidae	Alcelaphini	SHM	1.76	2.49
ZK-EN-D57	Bovidae	Alcelaphini	SHM	1.15	2.90
ZK-EN 327	Bovidae	Alcelaphini	SHM	-5.22	2.23
ZK-EN 333	Bovidae	Alcelaphini	SHM	-0.18	-0.32
ZK-EN-D279	Bovidae	Alcelaphini	SHM	1.82	3.37
ZK-EN-D283	Bovidae	Alcelaphini	SHM	-2.79	4.64
ZK-EN-D284	Bovidae	Alcelaphini	SHM	-0.89	0.57
ZK-EN-D286	Bovidae	Alcelaphini	SHM	2.07	-6.85
ZK-EN-D296	Bovidae	Alcelaphini	SHM	0.01	3.74
ZK-EN-D293	Bovidae	Alcelaphini	SHM	-0.54	3.78
ZK-EN-D295	Bovidae	Alcelaphini	SHM	1.43	2.93
ZK-EN-D298	Bovidae	Alcelaphini	SHM	-0.18	2.65
ZK-EN-D304	Bovidae	Alcelaphini	SHM	3.06	2.15
ZK-EN-D306	Bovidae	Alcelaphini	SHM	1.04	3.53
ZK-EN-D269	Bovidae	Alcelaphini	SHM	-1.19	-6.05
ZK-EN-D273	Bovidae	Alcelaphini	SHM	1.40	3.91
ZK-EN-D17	Bovidae	Bovini	SHM	-8.41	-5.78
ZK-EN-D281	Bovidae	Bovini	SHM	-5.12	-6.09
ZK-EN-D73	Bovidae	Bovini	SHM	-0.69	0.10
ZK-EN-D74	Bovidae	Bovini	SHM	-1.40	-1.79
DIK 8-2	Bovidae	Bovini	SHM	-1.06	-3.43
ZK-EN-D59	Bovidae	Bovini	SHM	-5.39	-6.00
ZK-EN 353	Bovidae	Bovini	SHM	-5.38	-1.96
ZK-EN-D276	Bovidae	Bovini	SHM	-2.94	-6.44
ZK-EN-D277	Bovidae	Bovini	SHM	-5.69	-0.91
ZK-EN-D289	Bovidae	Bovini	SHM	-2.73	-5.76

Sample number	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
ZK-EN-D297	Bovidae	Bovini	SHM	-2.83	0.66
ZK-EN-D301	Bovidae	Bovini	SHM	-5.39	-5.49
ZK-EN-D302	Bovidae	Bovini	SHM	-2.59	-7.46
ZK-EN-D303-1	Bovidae	Bovini	SHM	-0.33	-5.34
ZK-EN-D303	Bovidae	Bovini	SHM	-4.08	-4.14
ZK-EN-D305	Bovidae	Bovini	SHM	-2.74	-6.27
ZK-EN-D307	Bovidae	Bovini	SHM	-4.02	-4.90
ZK-EN-D271	Bovidae	Bovini	SHM	-0.34	-6.70
ZK-EN-D274	Bovidae	Bovini	SHM	-5.02	-7.56
ZK-EN 320	Bovidae	Bovini	SHM	-2.30	-0.62
ZK-EN-D278	Bovidae	Hippotragini	SHM	-7.25	3.59
ZK-EN-D280	Bovidae	Hippotragini	SHM	-3.63	0.83
ZK-EN-D56	Bovidae	Hippotragini	SHM	-7.43	-5.57
ZK-EN 350	Bovidae	Reduncini	SHM	1.03	-1.32
DIK 22-1	Bovidae	Tragelaphini	SHM	-3.78	-3.10
DIK 22-4	Bovidae	Tragelaphini	SHM	-6.02	-2.26
ZK-EN-D35	Bovidae	Tragelaphini	SHM	-5.79	0.03
ZK-EN-D66	Bovidae	Tragelaphini	SHM	-5.04	-6.55
ZK-EN 337	Bovidae	Tragelaphini	SHM	-6.37	-0.29
DIK 22-3	Bovidae	Tragelaphini	SHM	-7.63	-3.89
ZK-EN 357	Bovidae	Tragelaphini	SHM	-0.30	4.57
ZK-EN-D1	Elephantidae		SHM	-3.79	-2.36
ZK-EN-D2	Elephantidae		SHM	-2.99	-6.86
ZK-EN-D26	Elephantidae		SHM	-2.16	-6.01
ZK-EN-D27	Elephantidae		SHM	-2.48	-1.13
ZK-EN-D28	Elephantidae		SHM	-2.19	-5.16
ZK-EN-D3	Elephantidae		SHM	-0.95	-5.64
ZK-EN-D102	Elephantidae		SHM	-2.13	-1.45
ZK-EN-D4	Elephantidae		SHM	-1.43	-3.26
ZK-EN-D5	Elephantidae		SHM	-2.65	-5.75
ZK-EN-D54	Elephantidae		SHM	-0.09	-1.89
ZK-EN-D285	Equidae		SHM	-5.08	-0.89
ZK-EN-D270	Equidae		SHM	-1.34	-0.31
DIK 1-7	Equidae		SHM	-2.65	-2.16
ZK-EN-D32	Equidae		SHM	-1.58	0.93
ZK-EN-D33	Equidae		SHM	-2.41	-0.99
ZK-EN-D48	Equidae		SHM	-2.61	-4.15
ZK-EN-D9	Equidae		SHM	-2.11	-7.43
Dik 11-1	Equidae		SHM	-4.18	-5.39
ZK-EN 317	Equidae		SHM	-2.00	-6.81
ZK-EN 318	Equidae		SHM	-1.70	-6.83
ZK-EN-D332	Equidae		SHM	-3.12	-1.07
ZK-EN 334	Equidae		SHM	-1.28	0.49
ZK-EN 380	Equidae		SHM	-4.03	-6.56
ZK-EN-D308	Equidae		SHM	-0.39	1.88
ZK-EN-D309	Equidae		SHM	-2.08	-6.39

Sample number	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
ZK-EN-D310	Equidae		SHM	-2.86	-6.32
ZK-EN-D311	Equidae		SHM	-1.76	-6.28
ZK-EN-D312	Equidae		SHM	-0.46	-7.60
ZK-EN-D313	Equidae		SHM	-1.47	-5.84
ZK-EN-D314	Equidae		SHM	-1.69	-0.50
ZK-EN-D316	Equidae		SHM	-1.41	-6.53
ZK-EN-D314A	Equidae		SHM	0.68	0.77
ZK-EN-D314B	Equidae		SHM	0.64	0.62
ZK-EN-D314C	Equidae		SHM	0.67	1.00
ZK-EN-D314D	Equidae		SHM	0.32	1.03
ZK-EN-D314E	Equidae		SHM	0.29	1.58
ZK-EN-D314F	Equidae		SHM	0.07	1.49
ZK-EN-D314G	Equidae		SHM	-0.18	1.50
ZK-EN-D314H	Equidae		SHM	-0.39	1.77
ZK-EN-D314I	Equidae		SHM	-0.69	1.55
ZK-EN-D314J	Equidae		SHM	-1.42	0.17
ZK-EN-D330	Equidae		SHM	-4.29	-3.08
ZK-EN-D78	Giraffidae		SHM	-10.81	-4.39
ZK-EN-D79	Giraffidae		SHM	-9.46	-5.19
ZK-EN 321	Giraffidae		SHM	-13.19	-3.63
ZK-EN 322	Giraffidae		SHM	-9.05	-0.73
ZK-EN-D321A	Giraffidae		SHM	-13.46	-1.37
ZK-EN-D321B	Giraffidae		SHM	-14.30	-1.80
ZK-EN-D321C	Giraffidae		SHM	-12.77	-2.36
ZK-EN-D321D	Giraffidae		SHM	-14.23	-1.40
ZK-EN-D31	Hippopotamidae		SHM	-10.32	-9.92
ZK-EN-D6	Hippopotamidae		SHM	-5.23	-8.27
ZK-EN-D7	Hippopotamidae		SHM	-0.79	-5.64
ZK-EN-D8	Hippopotamidae		SHM	-2.06	-7.20
ZK-EN-D84	Hippopotamidae		SHM	-6.14	1.69
ZK-EN-D262	Hippopotamidae		SHM	-7.81	-7.78
ZK-EN-D264	Hippopotamidae		SHM	-7.93	-9.82
ZK-EN-D265	Hippopotamidae		SHM	-0.06	-8.74
ZK-EN-D266	Hippopotamidae		SHM	-2.59	-7.55
ZK-EN-D267	Hippopotamidae		SHM	-3.93	-8.20
ZK-EN-D268	Hippopotamidae		SHM	-3.94	-7.53
ZK-EN-D101	Deinotheriidae		SHM	-12.32	-3.42
ZK-EN 352	Deinotheriidae		SHM	-12.46	-3.85
ZK-EN-D51	Deinotheriidae		SHM	-11.81	-2.19
ZK-EN-D105	Rhinocerotidae		SHM	-4.63	-0.86
ZK-EN-D107	Rhinocerotidae		SHM	-3.40	-2.89
ZK-EN-D108	Rhinocerotidae		SHM	-4.13	-3.29
ZK-EN-D331	Rhinocerotidae		SHM	-5.34	-5.60
ZK-EN-D263	Suidae	<i>Kolpochoerus</i>	SHM	-4.07	-7.85
DIK 1-8	Suidae	<i>Kolpochoerus</i>	SHM	-3.94	3.77
ZK-EN-D261	Suidae	<i>Kolpochoerus</i>	SHM	-4.39	-6.59

Sample number	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
ZK-EN-D258	Suidae	<i>Kolpochoerus</i>	SHM	-6.25	-7.45
ZK-EN-D91	Suidae	<i>Kolpochoerus</i>	SHM	-4.04	-7.63
ZK-EN-D10	Suidae	<i>Notochoerus</i>	SHM	-0.83	-6.00
ZK-EN-D11	Suidae	<i>Notochoerus</i>	SHM	-3.48	-4.49
ZK-EN-D12	Suidae	<i>Notochoerus</i>	SHM	-0.89	-6.07
ZK-EN-D14	Suidae	<i>Notochoerus</i>	SHM	-1.19	-6.01
ZK-EN-D41	Suidae	<i>Notochoerus</i>	SHM	-2.52	-5.36
ZK-EN-D255	Suidae	<i>Notochoerus</i>	SHM	-1.33	-6.57
ZK-EN-D257	Suidae	<i>Notochoerus</i>	SHM	-7.14	-6.58
ZK-EN-D260	Suidae	<i>Notochoerus</i>	SHM	-0.87	-6.07
ZK-EN-D282	Suidae	<i>Notochoerus</i>	SHM	-3.19	-1.49
ZK-EN-D256	Suidae	<i>Nyanzachoerus</i>	SHM	-1.60	-0.66
ZK-EN-D19	Bovidae	Aepycerotini	UBM	-3.07	1.25
ZK-EN-D20	Bovidae	Alcelaphini	UBM	-3.93	-1.35
ZK-EN-D336	Bovidae	Alcelaphini	UBM	0.79	-1.53
ZK-EN-D21	Bovidae	Bovini	UBM	-5.25	-1.44
ZK-EN-D45	Bovidae	Tragelaphini	UBM	-10.93	-1.68
ZK-EN-D25	Elephantidae		UBM	0.14	-0.71
ZK-EN-D29	Elephantidae		UBM	0.38	0.08
ZK-EN 328	Equidae		UBM	0.20	-1.77
ZK-EN-D30	Hippopotamidae		UBM	-5.75	-7.39
ZK-EN-D100	Deinotheriidae		UBM	-14.08	-5.05
ZK-EN 323	Rhinocerotidae		UBM	-4.75	-0.21
ZK-EN-D15	Suidae	<i>Kolpochoerus</i>	UBM	-3.99	-7.06
ZK-EN-D22	Suidae	<i>Kolpochoerus</i>	UBM	-4.60	-4.95
ZK-EN-D23	Suidae	<i>Kolpochoerus</i>	UBM	-1.53	-4.94
ZK-EN-D24	Suidae	<i>Kolpochoerus</i>	UBM	-2.50	-3.42
ZK-EN-D16	Suidae	<i>Notochoerus</i>	UBM	-0.28	-4.07
ZK-EN-D42	Suidae	<i>Notochoerus</i>	UBM	-1.11	-4.49
ZK-EN 362	Bovidae	Aepycerotini	BBM	-2.25	-3.55
ZK-EN 363	Bovidae	Aepycerotini	BBM	-2.50	-4.04
ZK-EN 364	Bovidae	Aepycerotini	BBM	-3.80	-4.43
ZK-EN 365	Bovidae	Aepycerotini	BBM	-0.56	-3.16
ZK-EN-D290	Bovidae	Alcelaphini	BBM	-2.49	-0.03
ZK-EN 354	Bovidae	Bovini	BBM	-5.50	-4.82
ZK-EN 346	Bovidae	Bovini	BBM	-2.70	-4.84
ZK-EN-D234	Elephantidae		BBM	-1.05	-0.59
ZK-EN-D237	Elephantidae		BBM	-3.75	-5.82
ZK-EN-D241	Elephantidae		BBM	-2.59	-1.45
ZK-EN-D242	Elephantidae		BBM	-3.37	-4.82
ZK-EN-D243	Elephantidae		BBM	-1.59	-5.11
ZK-EN-D206	Elephantidae		BBM	-2.17	-5.60
ZK-EN-D209	Elephantidae		BBM	-1.50	-1.69
ZK-EN-D213	Elephantidae		BBM	-0.57	-5.99

Sample number	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
ZK-EN-D214	Elephantidae		BBM	-2.92	-4.29
ZK-EN-D223	Elephantidae		BBM	-0.83	-5.60
ZK-EN-D228	Elephantidae		BBM	-3.32	-4.77
ZK-EN-D230	Elephantidae		BBM	-2.74	-5.53
ZK-EN-D232	Elephantidae		BBM	-0.81	-1.68
ZK-EN-D233	Elephantidae		BBM	-0.18	-4.97
ZK-EN-D204	Elephantidae		BBM	-0.58	-4.83
ZK-EN-D224A	Equidae		BBM	-0.63	-6.15
ZK-EN-D224B	Equidae		BBM	-0.63	-6.61
ZK-EN-D224C	Equidae		BBM	-1.24	-6.23
ZK-EN-D224D	Equidae		BBM	-1.42	-5.63
ZK-EN-D224	Equidae		BBM	-2.07	-6.01
ZK-EN-D224E	Equidae		BBM	-1.75	-5.57
ZK-EN-D224F	Equidae		BBM	-2.04	-5.55
ZK-EN-D224G	Equidae		BBM	-2.15	-5.91
ZK-EN-D224H	Equidae		BBM	-2.40	-6.28
ZK-EN-D224I	Equidae		BBM	-2.39	-6.29
ZK-EN-D224J	Equidae		BBM	-2.77	-6.62
ZK-EN-D224K	Equidae		BBM	-2.70	-6.81
ZK-EN 351	Equidae		BBM	-1.67	0.44
ZK-EN-D224-1	Equidae		BBM	-11.50	-7.04
ZK-EN 361	Giraffidae/Sivatherium		BBM	-9.03	1.14
ZK-EN-D240	Hippopotamidae		BBM	-7.25	-7.05
ZK-EN-D212	Hippopotamidae		BBM	-3.56	-7.89
ZK-EN-D215	Hippopotamidae		BBM	-2.41	-7.30
ZK-EN-D221	Hippopotamidae		BBM	-0.92	-4.84
ZK-EN-D226	Hippopotamidae		BBM	-0.30	-7.59
ZK-EN-D227	Hippopotamidae		BBM	-5.01	-7.16
ZK-EN 349	Rhinocerotidae	<i>Ceratotherium</i>	BBM	-2.50	-6.16
ZK-EN-D235	Rhinocerotidae	<i>Ceratotherium</i>	BBM	0.30	-1.29
ZK-EN 358	Suidae	<i>Kolpochoerus</i>	BBM	-6.31	0.37
ZK-EN 360	Suidae	<i>Notochoerus</i>	BBM	-2.41	-1.06
ZK-EN 366	Suidae	<i>Notochoerus</i>	BBM	-8.59	-1.54
ZK-EN-D239	Suidae	<i>Notochoerus</i>	BBM	-1.68	-4.52
ZK-EN-D239-1	Suidae	<i>Notochoerus</i>	BBM	-1.62	-4.10
ZK-EN 359	Suidae	<i>Nyanzachoerus</i>	BBM	-5.47	-5.40
ZK-EN-D259	Suidae	<i>Nyanzachoerus</i>	BBM	-2.97	-1.94
ZK-EN-D203	Suidae	<i>Nyanzachoerus</i>	BBM	-4.68	-4.39
ZK-EN-D205	Suidae	<i>Nyanzachoerus</i>	BBM	-3.12	-5.87

The $\delta^{13}\text{C}_{\text{enamel}}$ values of Elephantidae from both the SHM and BBM indicate that their diet was dominated by C_4 grasses and did not show any shift in dietary adaptation between 4–3 Ma (Mann–Whitney, $p=0.7234$). The deinotheres, on the other hand,

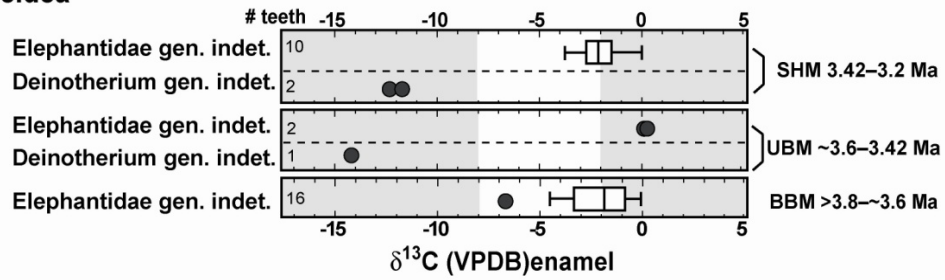
exclusively fed on C₃ vegetation and we agree with Harris' (1983) interpretation that they most likely inhabited woodland habitats, such as wooded grassland or gallery forest, to meet the dietary requirement of such an exceptionally large-bodied, pure browser. Isotopic studies of tooth enamel from Miocene to Pleistocene elephantids and deinotheres in the Afar Depression and elsewhere in East Africa also indicate consistently distinct grazing and browsing feeding adaptations, respectively (Cerling et al., 1999; Zazzo et al., 2000; Kingston and Harrison, 2007; Levin et al., 2008; White et al., 2009; Bedaso et al., 2010). Cerling et al. (1999) indicate that elephantids had a predominantly grazing diet from ~ 7 to < 1 Ma while deinotheres maintained a C₃ diet from their earliest record until their extinction in the Early Pleistocene.

3.6.1.2 *Rhinocerotidae*

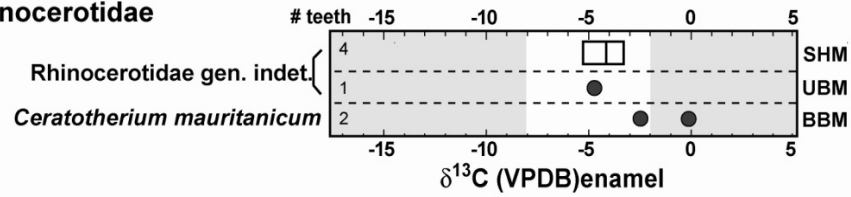
In the middle Pliocene deposits of the Hadar Formation, fossil representatives of the two African rhinoceros lineages, *Ceratotherium* and *Diceros*, coexisted and both arose from *C. neumayri*, which is morphologically and ecologically intermediate between the two genera (Geraads, 2005). Although both genera are represented in the Hadar Formation, only *C. mauritanicum* is positively identified at Dikika (Wynn et al., 2006).

The average $\delta^{13}\text{C}_{\text{enamel}}$ value of rhinocerotids from the BBM is -1.1‰ (n=2), while the $\delta^{13}\text{C}_{\text{enamel}}$ values are more negative in the UBM, -4.6‰ (n=1) and SHM, -4.4‰ (n=4; Table 3.1, Figure 3.2B). In the BBM, the diets of these large bodied herbivores were dominated by C₄ grasses (*i.e.*, 85% C₄ grasses), while in the UBM and SHM, the carbon isotopic values indicate a mixed C₃/C₄ dietary adaptation with an emphasis on

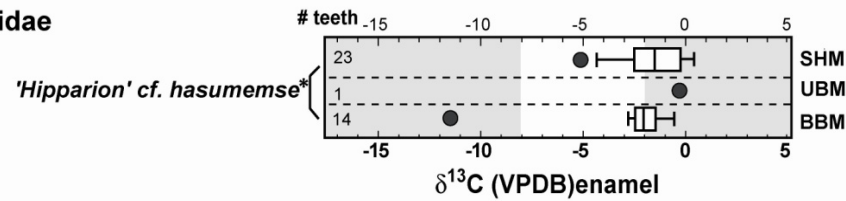
A Proboscidea



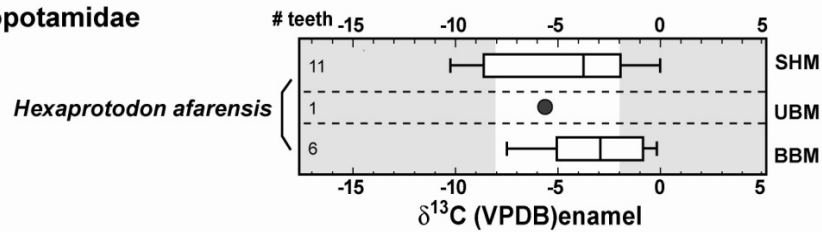
B Rhinocerotidae



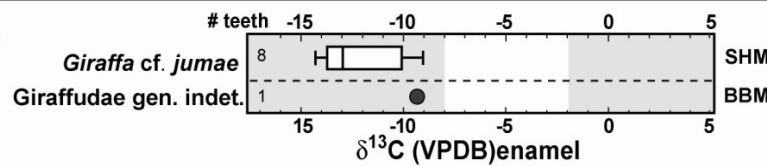
C Equidae



D Hippopotamidae



E Giraffidae



F Suidae

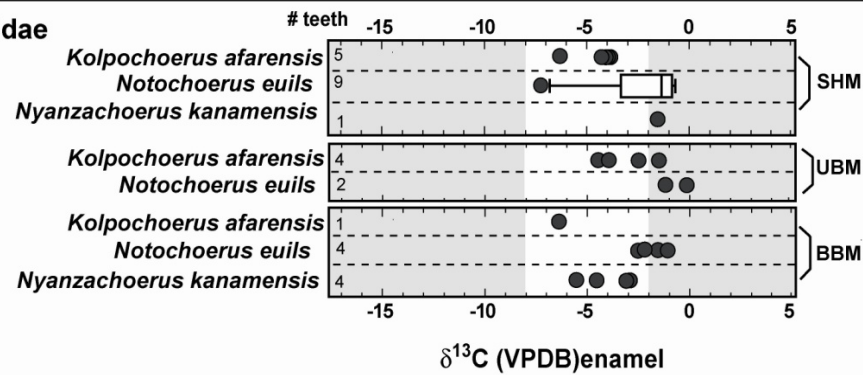


Figure 3.2 Box and whisker plots of stable carbon isotopic composition of mammals ($\delta^{13}\text{C}_{\text{enamel}}$) from the Hadar Formation at Dikika from three different sampling intervals (*i.e.*, base of the Basal Member, upper Basal Member, and Sidi Hakoma Member). The box is bounded by first quartile (25%) and the third quartile (75%) of the variable population. Each box encloses 50% of the data with the median value represented by a vertical line in the box. The horizontal line extending from the sides of the box represents the acceptable range of data. Outliers are displayed as individual points outside of the acceptable range of the data. Taxa represented by less than five individuals are plotted as individual points. The herbivores are grouped into predominantly C_4 -diet ($\delta^{13}\text{C}_{\text{enamel}} \geq -2\text{‰}$), mixed C_3/C_4 diet ($\delta^{13}\text{C}_{\text{enamel}} -2\text{‰}$ to -8‰) and a predominantly C_3 diet ($\delta^{13}\text{C}_{\text{enamel}} \leq -8\text{‰}$) based on (Cerling et al., 2003). Pure C_4 grasses and C_3 closed resources are indicated in dark gray bars. (* equids identified at Dikika as “hipparion” (= *Eurygnathohippus*, Bernor et al., 2005).

grazing, consisting of 59% and 62% C_4 grasses respectively. As Geraads (2005) suggested, the two lineages split soon after the Miocene-Pliocene boundary, deriving from an ancestral mixed feeder, to a lineage of grazers (*Ceratotherium*) and a lineage of browsers (*Diceros*). Although the isotopic signatures from UBM and SHM do not indicate an exclusively browsing habit, it shows a significant C_3 component in the diet and more importantly, higher $\delta^{13}\text{C}_{\text{enamel}}$ values in the BBM clearly indicate the emergence of the grazer *Ceratotherium mauritanicum* from the Late Miocene mixed feeder ancestor *Ceratotherium neumayri*, which is ecologically intermediate between the two genera.

Although the habitat and dietary preferences of *Ceratotherium* and *Diceros* are expected to be much less distinct during the middle Pliocene than today, isotopic and morphological studies of both modern and fossil species of rhinocerotids clearly reflect dietary partitioning (Lee-Thorp, 1989; Bocherens et al., 1996; Cerling and Harris, 1999; Cerling et al., 2003b; Geraads, 2005; Kingston and Harrison, 2007; Levin et al., 2008; Bedaso et al., 2010). Kingston and Harrison (2007) suggested that Pliocene

Ceratotherium was more of an opportunistic feeder, rather than an obligate or variable grazer, and tracking the diet of this lineage through the Pliocene may provide a useful tool to document environmental and habitat change.

3.6.1.3 Equidae

The fossil Equidae from the Hadar Formation at Dikika is represented by '*Hipparion*' cf. *hasumense* (Wynn et al., 2006). In the same time interval, Eisenmann (1976, 1983) indicated the presence of hipparion species at Hadar, and Bernor and Armour-Chelu (1997) and Bernor et al. (2005) suggest *E. hasumense* was the sole “hipparion” (= *Eurygnathohippus*) at Hadar until the appearance of *E. afarensis*.

$\delta^{13}\text{C}_{\text{enamel}}$ values of the equids from Dikika were obtained from four different stratigraphic levels within the Hadar Formation (*i.e.*, BBM, UBM, SHM and DDM; Table 1). The isotopic data in the different stratigraphic levels signifies a similar average carbon isotopic composition and a narrow range of values except a single outlier value ($\delta^{13}\text{C}_{\text{enamel}} = -11.5\text{‰}$) in the BBM and three values that range between -4.0 and -5.1‰ in the SHM. The data clearly indicate that the equids at Dikika generally had similar diet and show no evidence of major shift in dietary adaptation through time (Mann–Whitney, $p=0.2218$). The average $\delta^{13}\text{C}_{\text{enamel}}$ values from the BBM, UBM, SHM and DDM are -2.5‰ (n=14), 0.2‰ (n=1), -1.6 ‰ (n=32) and -1.8‰ (n=2) respectively (Table 3.1, Figure 3.2C). So, the Dikika equids were generally grazers and relied heavily on C₄ grasses throughout the Hadar Formation (4–3 Ma). The serial samples collected from a single tooth both from the BBM and the SHM shows a range of $\delta^{13}\text{C}_{\text{enamel}}$ values of 2.2‰ and 2.1‰,

respectively, indicating a slight seasonal change in the diet within the C₄ range and suggests the presence of C₄ grasses year round rather than on a seasonal basis. Cerling et al. (1997) found that the diet of tropical and subtropical Africa equids shifted from C₃-dominated to C₄-dominated diet in conjunction with a global expansion of C₄ biomass during the Late Miocene. A more mixed C₃/C₄ dietary strategy was reported from Chorora, -7.5‰ to -4.6‰ (~10 Ma; Bernor et al., 2004), Samburu, -3‰ to -5‰ (Namurungule Fm., ~9 Ma), and Lothagam, ≥-2‰ (lowest Lower Nawata, ~7.5 Ma; Cerling et al., 2005). Later C₄-dominated diet was reported from Gona: Adu-Asa Formation (6.5—5.2 Ma, average $\delta^{13}\text{C}_{\text{enamel}} = -1.2\text{‰}$) and Sagantole Formation (4.6–4.2 Ma, average $\delta^{13}\text{C}_{\text{enamel}} = -0.6\text{‰}$) excluding two significantly lower values, which average -6.1‰ (Levin et al., 2008). White et al. (2009) identified *Eurygnathohippus* as a pure grazer with an average $\delta^{13}\text{C}_{\text{enamel}}$ of 0.6‰ from Aramis (~4.4 Ma). In addition to isotopic studies, Gray (1980) describe the equids from Hadar as grazers based on the dental morphology which was sufficiently hypsodont with complex enamel folding to exploit grass, although not as hypsodont as later *Equus*.

3.6.1.4 Hippopotamidae

Hippopotamids are one of the most abundant herbivores in the Hadar Formation at Dikika, where they are represented by *Hexaprotodon afarensis* (Wynn et al., 2006). The family Hippopotamidae at Hadar is represented by two different genera (*Hexaprotodon* and *Trilobophorus*) with one species each, the dominant being *Trilobophorus afarensis* (Gèze, 1980).

The average $\delta^{13}\text{C}_{\text{enamel}}$ value of hippos at different stratigraphic levels from the Hadar Formation at Dikika shows no significant change (Mann–Whitney, $p=0.4043$) but does show wide range of variation within each member except UBM, which is represented by a single value. In the BBM, the $\delta^{13}\text{C}_{\text{enamel}}$ values of hippos range from -0.3‰ to -7.3‰ with an average of $-3.2 \pm 2.6\text{‰}$ ($n=6$). At the UBM, the $\delta^{13}\text{C}_{\text{enamel}}$ value from a single individual is -5.8‰ and in the SHM, the $\delta^{13}\text{C}_{\text{enamel}}$ values show a wide range of variation between -0.1‰ and -10.3‰ , the average $\delta^{13}\text{C}_{\text{enamel}}$ being $-4.6 \pm 3.2\text{‰}$ ($n=11$; Table 3.1, Figure 3.2D). In the respective members of the Hadar Formation, the isotopic data reflects a mixed C_3/C_4 diet with no dietary shift between 4–3 Ma but some of the specimens were entirely C_4 grazers while others consumed significant C_3 vegetation. Harris et al. (2008) indicate that hippos were more versatile in their dietary adaptation than is generally thought, and were opportunistic feeders that sample available vegetation within a relative short distance from their source of aquatic shelter.

Harris et al. (2008) also indicate that isotopic analysis of fossil hippopotamids from Turkana Basin in Kenya document a variation in the proportion of dietary C_3 and C_4 vegetation with a trend towards a C_4 diet. A transitional C_4 -dominated diet to C_3/C_4 mixed feeding strategies of Hippopotamidae have also been observed from Late Miocene and early Pliocene sites of the Awash Valley (Levin et al., 2008; White et al., 2009) and a C_4 -dominated diet from Pleistocene sites at Asbole (Bedaso et al., 2010). Elsewhere in Africa, with the exception of the diet of early Pliocene hippopotamids from Langebaanweg, which was clearly dominated by C_3 plants (Franz-Odenaal, et al., 2002), Miocene and Pliocene hippos dominantly fed on C_4 vegetation but with significant a C_3

component (Boisserie et al., 2005; Cerling et al., 2008; Harris et al., 2008, Levin et al., 2008, White et al., 2008, Zazzo et al., 2000).

3.6.1.5 Giraffidae

The fossil Giraffidae from the Hadar Formation at Dikika is represented by *Giraffa* cf. *jumae* and *Sivatherium maurusium* (Wynn et al., 2006). The $\delta^{13}\text{C}_{\text{enamel}}$ value of a single giraffid from the BBM is -9.0‰ (n=1), while the average $\delta^{13}\text{C}_{\text{enamel}}$ value of giraffids from the SHM is $-12.2 \pm 2.1\text{‰}$ (n=8; Table 3.1, Figure 3.2E), indicating a C_3 -dominated diet. Serial sampling shows no significant seasonal dietary change (*i.e.*, $<1.5\text{‰}$) and probably indicates feeding on vegetation at different height or slightly different C_3 vegetation. A similar isotopic signature is documented from the Adu-Asa Formation (6.5–5.2 Ma, average $\delta^{13}\text{C}_{\text{enamel}}$ -10.9‰) and the Sagantole Formation (4.6–4.2 Ma, average $\delta^{13}\text{C}_{\text{enamel}}$ -9.8‰) at Segala Noumou in Gona (Levin et al., 2008) and for giraffids and sivatheres at Aramis in the Middle Awash (-12.1‰ and -11.9‰, respectively, White et al., 2009).

Modern giraffids generally feed on C_3 -dominated diet and are considered browsers, but isotopic data indicate that there is a range of variation in the $\delta^{13}\text{C}_{\text{enamel}}$ value within C_3 feeders, which is caused by change in environmental conditions and water availability (Ehleringer and Monson, 1993). Kingston and Harrison (2007) also showed that carbon isotopic analysis did not differentiate feeding niches in the Laetoli giraffids and indicated that this might be because of the complexity of browsing strategies of the taxa or the limited resolution of carbon isotopic composition of tooth enamel in differentiating the various C_3 vegetation and presence of microhabitats. On the other hand, stable isotope

data, combined with evidence of tooth morphology, size (larger and more hypsodont teeth) and of Sivatherium's short neck, may indicate that they incorporated C₄ graze into their diet and would perhaps be classified as a low-level mixed feeder (or even grazer) in more open habitats compared to other giraffids (Gray, 1980; Geraads, 1985).

3.6.1.6 Suidae

The fossil Suidae from the Hadar Formation at Dikika are represented by three genera: *Kolpochoerus*, *Notochoerus*, and *Nyanzachoerus*, each represented by a single species: *K. afarensis*, *No. euilus* and *Ny. kanamensis* (Wynn et al., 2006). Here, $\delta^{13}\text{C}_{\text{enamel}}$ of *Kolpochoerus* and *Notochoerus* is presented from BBM, UBM and SHM, while *Nyanzachoerus* data are limited to BBM and SHM.

The $\delta^{13}\text{C}_{\text{enamel}}$ value of *Kolpochoerus* from BBM is -6.3‰ (n=1) and averages $-3.2 \pm 1.4\text{‰}$ (n=4) and $-4.5 \pm 1.0\text{‰}$ (n=5) from UBM and SHM respectively (Table 3.1, Figure 3.2F). The $\delta^{13}\text{C}_{\text{enamel}}$ values of *Kolpochoerus* at Dikika indicate a C₃/C₄ mixed diet and show no trend in dietary adaptation between 4–3 Ma. Although no published isotopic data is available for comparison with *K. afarensis*, dental morphology and ecomorphological studies of other species indicate a complex adaptive strategy (Bishop 1999; Kullmer, 1999; Harris and Cerling, 2002). Based on postcranial adaptations, Bishop (1999) indicates a gradual change in habitat preference of *Kolpochoerus* from woodland to habitats with a mix of woodland and grassland. On the other hand, Bedaso et al. (2010), based on isotopic data from Asbole indicate an exclusively grazing diet for *K. majus* in the Middle Pleistocene, and isotopic studies from the Sagantole Formation at

Gona on *K. deheinzeli* show a large range in carbon isotopic values, which suggest a wider range of dietary adaptation (Levin et al., 2008). So, the result of the above studies indicates a general trend of dietary adaptation of *Kolpochoerus* towards an increased dependence on C₄ vegetation from the Miocene to the Pleistocene.

The $\delta^{13}\text{C}_{\text{enamel}}$ values of *Notochoerus* averages $-3.6 \pm 3.4\text{‰}$ (n=4), $-0.7 \pm 0.6\text{‰}$ (n=2) and $-2.4 \pm 2.1\text{‰}$ (n=9) from BBM, UBM and SHM respectively (Table 1, Figure 2F). The $\delta^{13}\text{C}_{\text{enamel}}$ value of *Notochoerus* at Dikika indicates a mixed C₃/C₄ diet with a significant C₄ component in the BBM and a C₄-dominated diet in both UBM and SHM. Single values of -8.6‰ and -7.1‰ reported from BBM and SHM respectively indicate a significant C₃ component in the diet, and they might indicate the range of adaptation of opportunistic taxa. The habitat preference and dietary adaptation of *N. euilus* has been interpreted from wooded to forested habitat (Kullmer, 1999; Bishop, 1999), to C₄ to mixed C₃/C₄ diet (Bobe, 1997; Kingston and Harrison, 2007), or savanna grassland habitat adapted to dedicated grazing (Zazzo et al., 2000). The present analysis confirms the mixed-feeder interpretation.

The $\delta^{13}\text{C}_{\text{enamel}}$ value of *Nyanzachoerus* averages $-4.1 \pm 1.2\text{‰}$ (n=4) from the BBM and -1.6‰ (n=1) from the SHM (Table 3.1, Figure 3.2F). The $\delta^{13}\text{C}_{\text{enamel}}$ value of *Nyanzachoerus* at Dikika indicates a mixed C₃/C₄ diet with significant C₄ component in the BBM and a C₄-dominated diet in the SHM. Although SHM is represented by a single value, it is more positive than all samples from BBM. Similar to *Notochoerus*, habitat preferences and dietary adaptations of *Nyanzachoerus* have been variously estimated.

Harris (1983b) and Kullmer (1999) suggested a generalized omnivorous or browsing diet in a wooded savanna and forest-fringe habitat, whereas Bishop (1999), Levin et al. (2008) and White et al. (2009) suggest a preference for an intermediate habitat and mixed C₃/C₄ and C₄-dominated diet.

All three suid genera, *Nyanzachoerus*, *Notochoerus* and *Kolpochoerus* were characterized by increase in hypsodonty, size and the complexity of the third molar, which is interpreted to indicate dietary shift from a browsing to a grazing diet (Cerling et al., 2005). Harris and Cerling (2002) also indicate that suids show a gradual increase in the proportion of C₄ grass in their diets over several million years and became exclusively grazers by about 3 Myr. Here, the change in the dietary adaptation from mixed C₃/C₄ diet to C₄ grazing observed in *Notochoerus* and *Nyanzachoerus* is in a good agreement with these previous studies. However, stable isotope values in the UBM indicate a slight higher $\delta^{13}\text{C}_{\text{enamel}}$ values while *Kolpochoerus* did not show any change of the dietary adaptation in this part of the Hadar Formation.

3.6.1.7 Bovidae

Analyses of fossil bovids have been one of the most widely utilized sources of paleoenvironmental information and central to reconstruction of the habitat present on the landscape where they coexisted with early hominins (Reed, 2008, Bobe and Eck, 2001; Sponheimer et al., 1999; Vrba 1985). Different approaches to habitat and diet reconstruction of extinct bovids in Africa include relative abundance of bovid tribes (Vrba, 1980, 1985), ecomorphology based on postcranial indices (Kappelman et al.,

1997; DeGusta and Vrba, 2003), and stable isotopes from tooth enamel (Cerling et al., 2003c; Sponheimer and Lee-Thorp, 2003; Levin et al., 2008; White et al., 2009; Bedaso et al., 2010). Despite the success of each of these methodologies, there are some limitations: (1) taxonomic uniformitarianism assumes that extant mammals occupy the same general habitat today as their fossil relatives did millions of years ago, but this assumption is not always warranted, and (2) in stable isotope studies of tooth enamel it is sometimes difficult to make taxonomic identification of specimens to the required level.

As in most comparable sites, bovids are the most abundant mammalian taxa in the Hadar Formation. In the Dikika faunal assemblage, bovids are 37% of the total fauna and 35% of the SHM (Z.A., unpublished data). Seven bovid tribes are represented at Dikika: Tragelaphini, Bovini, Hippotragini, Alcelaphini, Aepycerotini, Reduncini, and Antilopini. Isotopic analyses were done from the four levels (BBM, n=8, UBM, n=5, SHM, n=57 and DDM, n= 3), but because of limited number of analysis from some of the taxa and members, general interpretation and comparison of the environment are done only when applicable.

Tragelaphini in the Hadar Formation at Dikika is mostly represented by *Tragelaphus* aff. *nakuae* (Wynn et al., 2006). The average $\delta^{13}\text{C}_{\text{enamel}}$ value of Tragelaphini from the SHM is $-5.0 \pm 2.4\text{‰}$ (n=7) and it is represented in the UBM by a single value of -10.9‰ . No tragelaphines, however, were analyzed from the BBM (Table 3.1, Figure 3.3A–B). The isotopic data from Dikika indicate that Tragelaphini exhibit a wide range of dietary adaptations ranging from generally browsing in the UBM to mixed C_3/C_4 diet in the

SHM. Modern tragelaphines inhabit diverse environments ranging from forest to semi-arid, seasonal bushland (Kingdon, 1982). In the same way, different studies indicate that tragelaphines were adapted to a wide range of dietary adaptation and habitat preferences. Based on postcranial morphology, Plummer et al. (2008) suggest that fossil tragelaphines lived under heavy cover. Whereas Kappelman et al. (1997) suggests light to heavy cover environments. Isotopic studies of extant Tragelaphini from East and South Africa indicate a C₃-dominated diet with evidence of mixed C₃/C₄ diet (Lee-Thorp, 1989; Gagnon and Chew, 2000; Cerling et al., 2003a), which agrees with dietary adaptation in the SHM, but Levin et al. (2008) reported a more ¹³C-enriched $\delta^{13}\text{C}_{\text{enamel}}$ values up to -0.1‰ from Sagantole Formation.

The tribe Alcelaphini is one of the most common bovids in the Hadar Formation at Dikika. Alcelaphines are mainly represented by *Damalops* sp. (Wynn et al., 2006). The $\delta^{13}\text{C}_{\text{enamel}}$ value of Alcelaphines from the BBM from a single analysis is -2.5‰ and averages $-1.6 \pm 3.3\text{‰}$ (n=2) and $-0.1 \pm 2.1\text{‰}$ (n=20) from UBM and SHM respectively (Table 3.1, Figure 3.3A–C). The isotopic data suggests that the dietary strategies of Alcelaphini in the BBM and UBM were grazing and fed exclusively on C₄ grass and inhabited open-wooded or savanna grasslands. Similarly, in the SHM, the average carbon isotopic composition indicates a grazing dietary adaptation with a wider range of values indicating significant C₃ vegetation in the diet of some of the specimens analyzed.

Bovidae

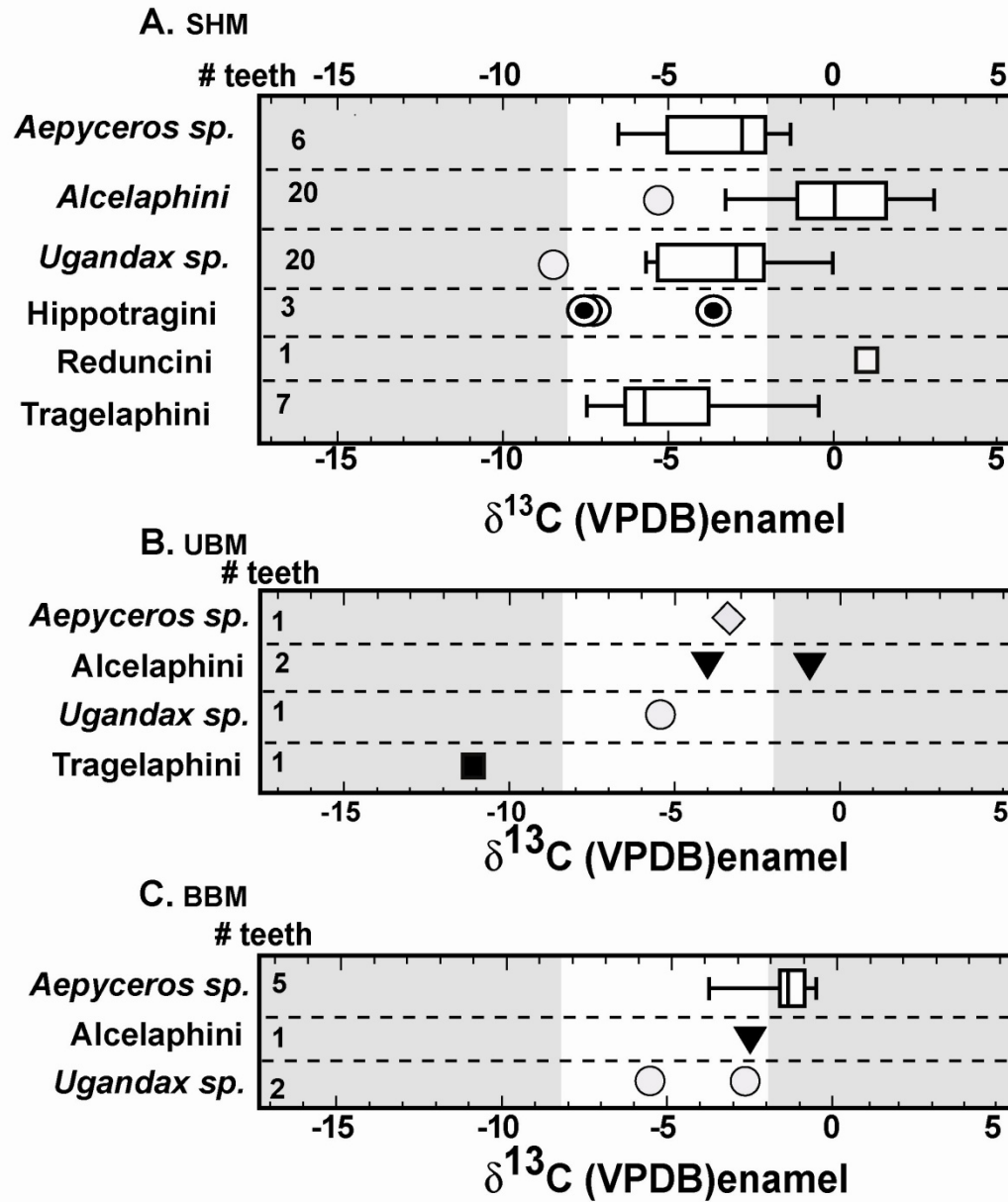


Figure 3.3 Box and whisker plots of stable carbon isotopic composition of bovids. ($\delta^{13}\text{C}_{\text{enamel}}$) from the Hadar Formation at Dikika (See Figure 3.2 for explanation).

This variation is possibly an effect of the larger sample size compared to the Basal Member and/or the presence of more than one species with slightly different diet in the SHM. Similar results were obtained from both modern and fossil specimens studied and analyzed elsewhere in East Africa. Plummer et al. (2008) suggest an open habitat from astragalus morphology, while Cerling et al. (2003c) and Sponheimer et al. (2003) suggest a diet dominated by C₄ grasses. Using isotopic profiles of extant taxa, Bedaso et al. (2010) indicated a C₄-dominated diet from Pleistocene Alcelaphines. On the other hand, Kingston and Harrison (2007) reported a $\delta^{13}\text{C}_{\text{enamel}}$ value of an Alcelaphini up to -8.6‰ , which indicates a significant C₃ contribution in the diet, in addition to several specimens with $\delta^{13}\text{C}_{\text{enamel}}$ values greater than 0‰ .

Bovini are also abundant at Dikika. They are represented by *Ugandax coryndonae* (Wynn et al., 2006). The $\delta^{13}\text{C}_{\text{enamel}}$ value of *Ugandax* from the BBM averages $-4.1 \pm 2.0\text{‰}$ (n=2) and -5.3‰ (n=1) from UBM. In the SHM the $\delta^{13}\text{C}_{\text{enamel}}$ value averages $-3.2 \pm 2.1\text{‰}$ (n=20) and has a range between -8.1‰ and -0.3‰ (Table 3.1, Figure 3.3A–C). The isotopic data from Dikika indicate that Bovini were generally adapted to a mixed C₃/C₄ diet with a significant consumption of C₄ grasses, moreover the wider range of isotopic values in the SHM strengthens the dietary breadth and adaptation to different environments, as suggested by Boe (1997). $\delta^{13}\text{C}_{\text{enamel}}$ values from Pliocene fossils at Middle Awash and Gona (Levin et al., 2008; White et al., 2009) indicated C₄-dominated and mixed C₃/C₄ diet respectively while Middle Pleistocene isotope data from *Syncerus caffer* at Asbole indicated an exclusively C₄ diet (Bedaso et al., 2010).

The tribe Aepycerotini in the Hadar Formation at Dikika is represented by *Aepyceros* sp. and is the second most abundant mammal found in association with the *Australopithecus afarensis* juvenile skeleton described from Dikika (*i.e.*, “Selam”; Wynn et al., 2006). The $\delta^{13}\text{C}_{\text{enamel}}$ values range from -0.6‰ to -3.8‰ (average $-2.2 \pm 1.2\text{‰}$) in the BBM and from -1.4‰ to -6.6‰ (average $-3.5 \pm 2.1\text{‰}$) in the SHM, while it is represented by a single value of -3.1‰ in the UBM (Table 3.1, Figure 3.3A–C). The stable isotopic data from Aepycerotini at Dikika indicate a C_4 -dominated diet in the BBM and a mixed C_3/C_4 diet in the UBM and SHM. Although there is a relatively wider range of isotopic values obtained in the SHM, the range is narrower than reported from other studies in the Awash Valley (Levin et al., 2008; White et al., 2009). On the other hand, isotopic studies of extant impala from East Africa and fossils from South Africa indicate an average of 50% C_4 biomass with a range between 20-90% (Sponheimer et al., 2003; Cerling et al., 2003c). So the C_4 -dominated diet at Dikika is in agreement with those studies, moreover Kingdon (1982) and Gagnon and Chew (2000) indicate that Aepycerotini predominantly graze while grasses are green, and browse on foliage, forbs, shoots and seedpods at other times which ensures a varied, abundant, and reliable food supply.

3.6.2 Oxygen isotopes

3.6.2.1 Observed $\delta^{18}\text{O}_{\text{enamel}}$ variation

A wide range of $\delta^{18}\text{O}_{\text{enamel}}$ values are documented at different stratigraphic levels in the Hadar Formation at Dikika, with minimum and maximum values of -9.9‰ and 5.0‰ obtained from Hippotamidae and Alcelaphini, respectively. $\delta^{18}\text{O}_{\text{enamel}}$ values in the BBM range from -7.9‰ (Hippopotamidae) to 1.1‰ (Giraffidae) and in the SHM from -9.9‰

(Hippopotamidae) to 5.0‰ (Alcelaphini). The wide range of $\delta^{18}\text{O}_{\text{enamel}}$ values from the Hadar Formation could indicate variation in the isotopic composition of animal drinking source water, animal drinking habit, thermophysiological adaptations, migration, seasonality and paleoclimatic condition (atmospheric temperature, relative humidity and other climatic variables). A wide range of variation in $\delta^{18}\text{O}_{\text{enamel}}$ value is also observed within individual taxa from the SHM. The highest range of $\delta^{18}\text{O}_{\text{enamel}}$ within individual taxon occurs in Alcelaphini, Tragelaphini, Hippopotamidae and *Kolpochoerus* (11.9‰ [n=20], 11.1‰ [n=7], 11.6‰ [n=11] and 11.6‰ [n=5], respectively; Table 3.1, Figure 3.4), while the range is approximately 3-9‰ in the rest of the fauna.

Terrestrial animals have different drinking habits. Some drink water directly from surface water sources (*i.e.*, rivers, ponds, lakes and spring). The $\delta^{18}\text{O}_{\text{enamel}}$ of those animals tracks $\delta^{18}\text{O}_{\text{meteoric water}}$ and serves as a proxy of climatic effects on the isotopic composition of local meteoric water. Others obtain a significant amount of water from the food they consume. Liquid water obtained from plants has a wider range of values depending on the part of the plant consumed. Water in plant roots, stems and fruit has a similar isotopic composition to that of meteoric water, unlike leaf water which is ^{18}O -enriched due to preferential evapotranspiration of H_2^{16}O (Sternberg, 1989; Ehleringer and Dawson 1992). The enrichment is greatest under hot and dry conditions (Dongmann et al., 1974), especially for C_3 plants that retain their leaves throughout the dry season. Thus, animals which obtain most of the water from these plants have higher $\delta^{18}\text{O}_{\text{enamel}}$ values. At Dikika, giraffids, deinotheres, and Tragelaphini are grouped as evaporation sensitive (ES) or non obligate drinkers whereas hippopotamids, rhinocerotids, equids, elephantids,

Notochoerus and *Kolpochoerus* are grouped as evaporation insensitive (EI) or obligate drinkers. The rest of the taxa are intermediate between the two groups.

3.6.2.2 Estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ from $\delta^{18}\text{O}_{\text{enamel}}$

Large mammal tooth enamel is formed at constant body temperature in equilibrium with body water (Longinelli and Nuti, 1973, Luz & Kolodny, 1985). As a result, there is a predictable offset between $\delta^{18}\text{O}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{drinking water}}$ values, where oxygen isotopic composition of body water largely reflects the oxygen isotopic composition meteoric water, especially for obligate drinking animals. To be able to compare the estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ with previous estimates in the region, we convert the $\delta^{18}\text{O}_{\text{enamel}}$ from VPDB to VSMOW scale using ($\delta^{18}\text{O}_{\text{VSMOW}} = 1.03091(\delta^{18}\text{O}_{\text{VPDB}}) + 30.91$; Sharp, 2007). We then apply the enrichment factor (ϵ) reported by Luz and Kolodny (1985) and Bryant et al. (1996) to calculate $\delta^{18}\text{O}_{\text{drinking water}}$ of obligate drinker taxa. We calculate $\delta^{18}\text{O}_{\text{drinking water}}$ for the Dikika herbivores by taking the most negative value of a taxon from each stratigraphic level, to minimize the effect of evaporation from surface water that would contribute to higher $\delta^{18}\text{O}$ values. This most negative $\delta^{18}\text{O}_{\text{drinking water}}$ value is an estimate of the isotopic composition of meteoric water ($\delta^{18}\text{O}_{\text{meteoric water}}$). The average $\delta^{18}\text{O}_{\text{meteoric water}}$ value from the Hadar Formation is estimated as $-4.0 \pm 1.3\text{‰}$ (VSMOW), while the $\delta^{18}\text{O}_{\text{meteoric water}}$ values from BBM, UBM and SHM estimated as -3.6‰ (VSMOW), -3.0‰ (VSMOW), and -5.6‰ (VSMOW) respectively. We consider these values the most positive estimate of the $\delta^{18}\text{O}_{\text{meteoric water}}$ value as the drinking water sources were subjected to evaporation and would have been somewhat ^{18}O -enriched compared to precipitation.

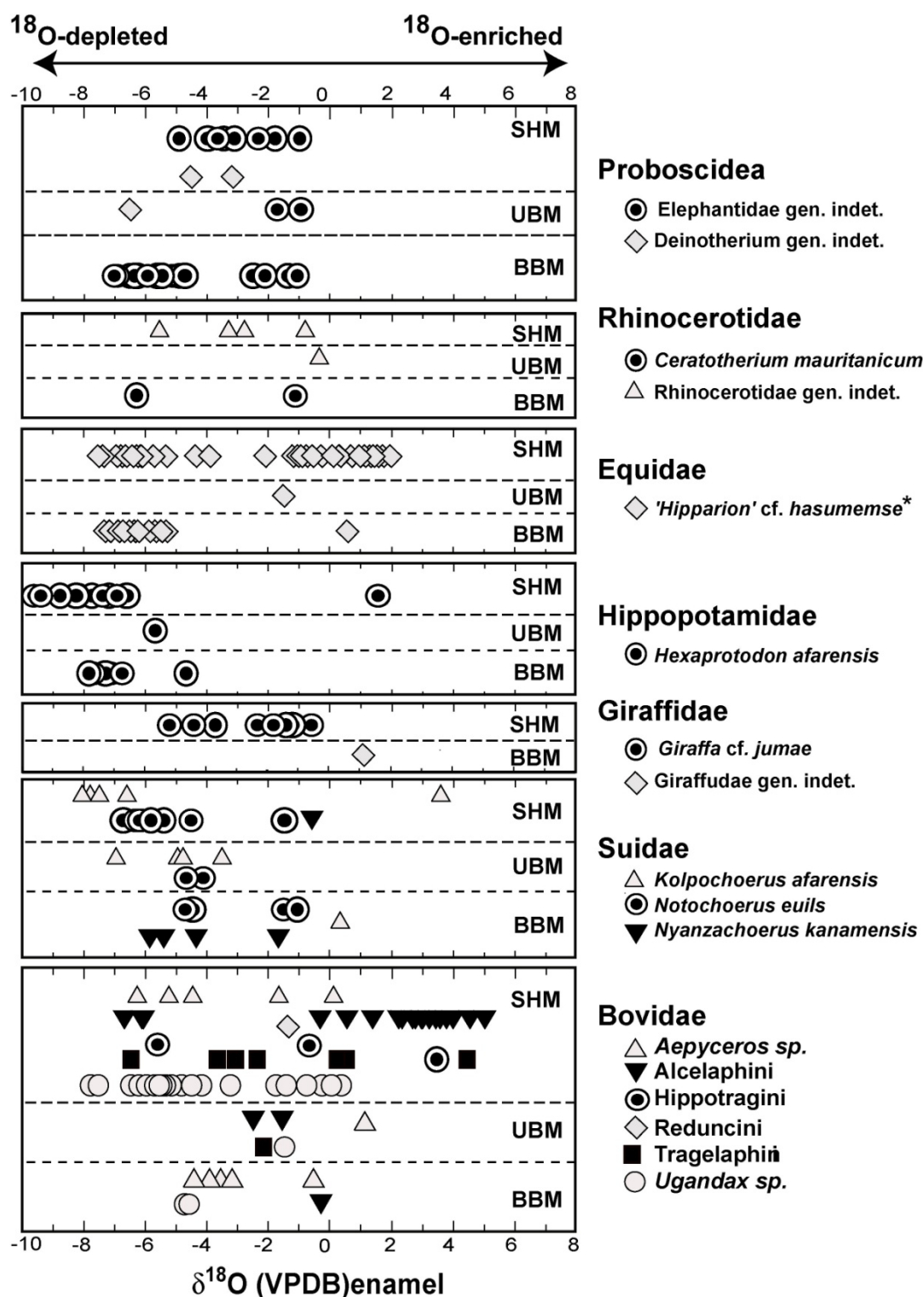


Figure 3.4 Stable oxygen isotopic composition of mammals tooth enamel ($\delta^{18}\text{O}_{\text{enamel}}$) from the Hadar Formation at Dikika (See Figure 3.2). (* equids identified at Dikika as “hipparion” (= *Eurygnathohippus*, Bernor et al., 2005).

Similarly, Aronson et al. (2008) estimated the oxygen isotopic composition of meteoric water from paleosol carbonates from the Hadar Formation at Hadar. They estimated the $\delta^{18}\text{O}_{\text{meteoric water}}$ as $-4.1 \pm 1.5\text{‰}$ (VSMOW) by assuming a fractionation factor for an average soil temperature of 25 °C. In the Middle Pleistocene Asbole Faunal Zone, we also estimated average $\delta^{18}\text{O}_{\text{meteoric water}}$ values of meteoric water of -1.9‰ (VSMOW; using data from Bedaso et al., 2010). The increase in the estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ value from the Pliocene to the Pleistocene could be attributed to any of the factors which affect the $\delta^{18}\text{O}_{\text{meteoric water}}$ (*i.e.*, rainfall amount, altitude effect, moisture source, humidity change (Dansgaard, 1964). This shift in $\delta^{18}\text{O}_{\text{meteoric water}}$ coupled with similar shift in the $\delta^{18}\text{O}_{\text{enamel}}$ for both ES and EI taxa lends confirmation to the interpretation of that some of this $\sim 2\text{‰}$ change is due to a change in the isotopic composition of precipitation rather than an increase in the amount of evaporation from surface waters. Levin et al. (2004) also attributed low estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ values in the early Pliocene to a regional change in the moisture source.

3.6.2.3 Reconstructed paleo-aridity using $\delta^{18}\text{O}_{\text{enamel}}$

Reconstructed paleo-aridity from the Dikika fauna is based on the interpretation of $\delta^{18}\text{O}_{\text{enamel}}$ for both ES and EI taxa. $\delta^{18}\text{O}_{\text{enamel}}$ values of EI taxa track the $\delta^{18}\text{O}$ values of source water, whereas $\delta^{18}\text{O}_{\text{enamel}}$ value of ES taxa tracks the additional evaporative ^{18}O -enrichment of the source water in leaves, as those animals obtain water from ^{18}O -enriched tree leaf water. Thus, the oxygen isotopic enrichment between ES and EI taxa ($\epsilon_{\text{ES-EI}}$) increases with environmental aridity, and is independent on the isotopic composition of local meteoric water (Levin et al., 2006). Environmental aridity can be

characterized by the annual water deficit (WD), which is the difference between mean annual potential evapotranspiration (PET) and the mean annual precipitation (MAP) amounts. Figure 3.5 shows the relationship of ϵ_{ES-EI} to water deficit based on Levin et al.'s. (2006) calibration data set from a range of climates in eastern Africa, but limited to those taxa represented at Dikika. Likewise, only locations with at least 10 ES and 10 EI taxa are used and the regression is weighted to the total number of taxa used in each location. To calculate the WD at Dikika for SHM, we use all EI taxa except equids as they exhibited a very wide range of variation in the oxygen isotopic composition. Similarly, all ES taxa except deinotheres are used since we do not know their drinking water behavior by comparison to modern related taxa, and their $\delta^{18}\text{O}_{\text{enamel}}$ value is relatively higher than expected in comparison to modern *Loxodonta*, despite their pure C_3 diet. The water deficit for the SHM is calculated as 1217 mm based on the oxygen isotopic enrichment between ES and EI taxa of the SHM ($\epsilon_{ES-EI} = 3.2$). Thus, the reconstructed water deficit from the Dikika fauna in the SHM indicate a wetter climate as compared to both the Middle Pleistocene site at Asbole (WD=1490 mm, Bedaso et al., 2010, Figure 3.5) and to the Pliocene site of Aramis in the Middle Awash (WD=1500 mm, White et al., 2009).

Similar results are obtained using different calibrations data but due to small number of giraffe fossils available in each member at Dikik, water deficit estimate is given using all specimens from the Hadar Formation. The reconstructed water deficit from the Dikika fauna in the Hadar Formation using the hippo-giraffe calibration gives an average of 1200 mm.

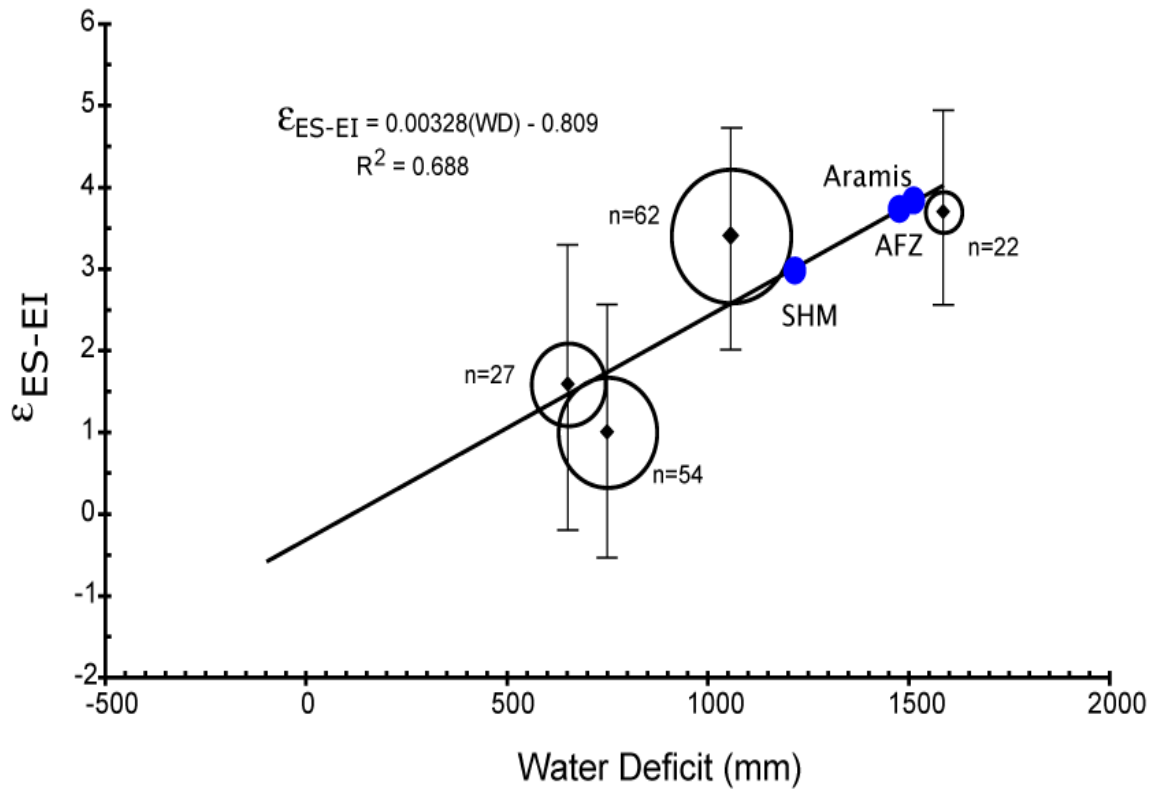


Figure 3.5 Oxygen isotope enrichment in tooth enamel between evaporation sensitive (ES) and evaporation insensitive (EI) sympatric taxa (ϵ_{ES-EI}) and aridity (expressed as water deficit, WD) based on the calibration data in Levin et al. (2006). To develop the relationship applicable to the taxa from the Hadar Formation, only those represented in Dikika collection or closely related taxa are used, ES (*Syncerus caffer*, *Oryx beisa*, *Giraffa camelopardalis*) and EI (*Loxodonta africana*, *Hippopotamus amphibius*, *Aepyceros melampus*, *Potamochoerus larvatus*, *Diceros bicornis*, *Phacochoerus africanus*). Following the suggestion of minimum samples size and to minimize standard error, only sites with combined ≥ 10 ES and ≥ 10 EI samples are used in the regression, which is weighted to the total number of ES and EI samples from each location (Athi, Mpala, Tsavo and Turkana). The filled circles are calculated values of WD from SHM, Asbole Fauna Zone (AFZ, Bedaso et al., 2010) and Aramis, (White et al., 2009).

3.7 Discussion

3.7.1 Paleoenvironments and diet of the Dikika fauna

The purpose of this study is to reconstruct the dietary adaptations and paleoenvironments of herbivores and infer the relative proportion of C_3 and C_4 vegetation of the paleolandscape where *Australopithecus afarensis* lived and foraged. Badgley et al. (2008) indicated that in modern terrestrial ecosystems, climate is an important factor that determines the timing and amount of food resources available and habitat structure, which in turn govern the type of herbivores supported in the ecosystem. Similarly, from the Middle Pleistocene site at Asbole, Bedaso et al. (2010) estimated the ecosystem $\delta^{13}C$ value and reconstruct the relative proportion of C_3 and C_4 vegetation using herbivore tooth enamel. Although there are many approaches to reconstruct the environmental and climatic conditions at the fossil localities, it is obvious that there are certain advantages and limitations associated with each method. Here, we use stable isotopic composition of carbon to retrieve environmental information, which has an advantage of being derived empirically and it is relatively assumption free (*i.e.*, dietary uniformitarianism, Sponheimer and Lee-Thorp, 2003).

The Dikika stable isotopic data indicate that the herbivores were adapted to a wide range of foraging strategies, characterized in general by mixed C_3/C_4 to C_4 -dominated diets in wet wooded grassland setting, although there is a difference in the relative proportion of C_3 and C_4 vegetation and range of variability within each member (Figure 3.6 A–C). Using the average $\delta^{13}C_{\text{enamel}}$ value, the fauna at Dikika between ~3.8–3.24 Ma include grazers, which consistently fed on C_4 grasses with no apparent trends or statistically

significant shifts throughout the middle Pliocene (Alcelaphini, Mann–Whitney, $p=0.3810$; Reduncini, insufficient sample size; equids, $p=0.2218$; elephantids, $p=0.7234$ and *Notochoerus*, insufficient sample size for Mann-Whitney test). Similarly, mixed feeders exhibited consistent mixed C_3/C_4 diet with no significant shift in the dietary adaptation but exhibited different proportion of C_3 and C_4 vegetation in the diet (Aepycerotini, small sample size; Bovini, $p=0.2218$; hippopotamids, $p=0.4043$; *Kolpochoerus*, insufficient sample size; *Nyanzachoerus*, $p=0.2218$ and Tragelaphini, insufficient sample size). Meanwhile, giraffids ($p=0.2220$) and deinotheres (insufficient sample size) showed a consistent browsing habit throughout the middle Pliocene. The dietary adaptations of the Dikika herbivores clearly indicate the presence of mixed C_3 and C_4 vegetation on the landscape. Although no significant dietary shift is documented in the Dikika fauna, it is evident that the proportion of C_3 and C_4 vegetation in the mixed feeders varies by up to 40% in the middle Pliocene. These variations in the relative proportions of C_3 and C_4 vegetation in the diet of herbivores imply change in the vegetation cover, which is determined by the climate. It also worth exploring further the use of $\delta^{13}C_{\text{enamel}}$ values of large samples of mixed feeders as a track log of ecological variability and habitat structure through time.

3.7.2 $\delta^{13}C_{\text{ecosystem}}$ estimate based on faunal abundance and $\delta^{13}C_{\text{enamel}}$

Paleoenvironmental reconstruction in paleontological sites has been previously done by analyzing relative changes in faunal abundance (*e.g.*, Vrba, 1974, 1980; Bobe and Behrensmeyer, 2003) and carbon isotopic composition of tooth enamel (*e.g.*, Cerling et al., 2003c, Levin et al., 2008, Bedaso et al., 2010). To better reconstruct the general

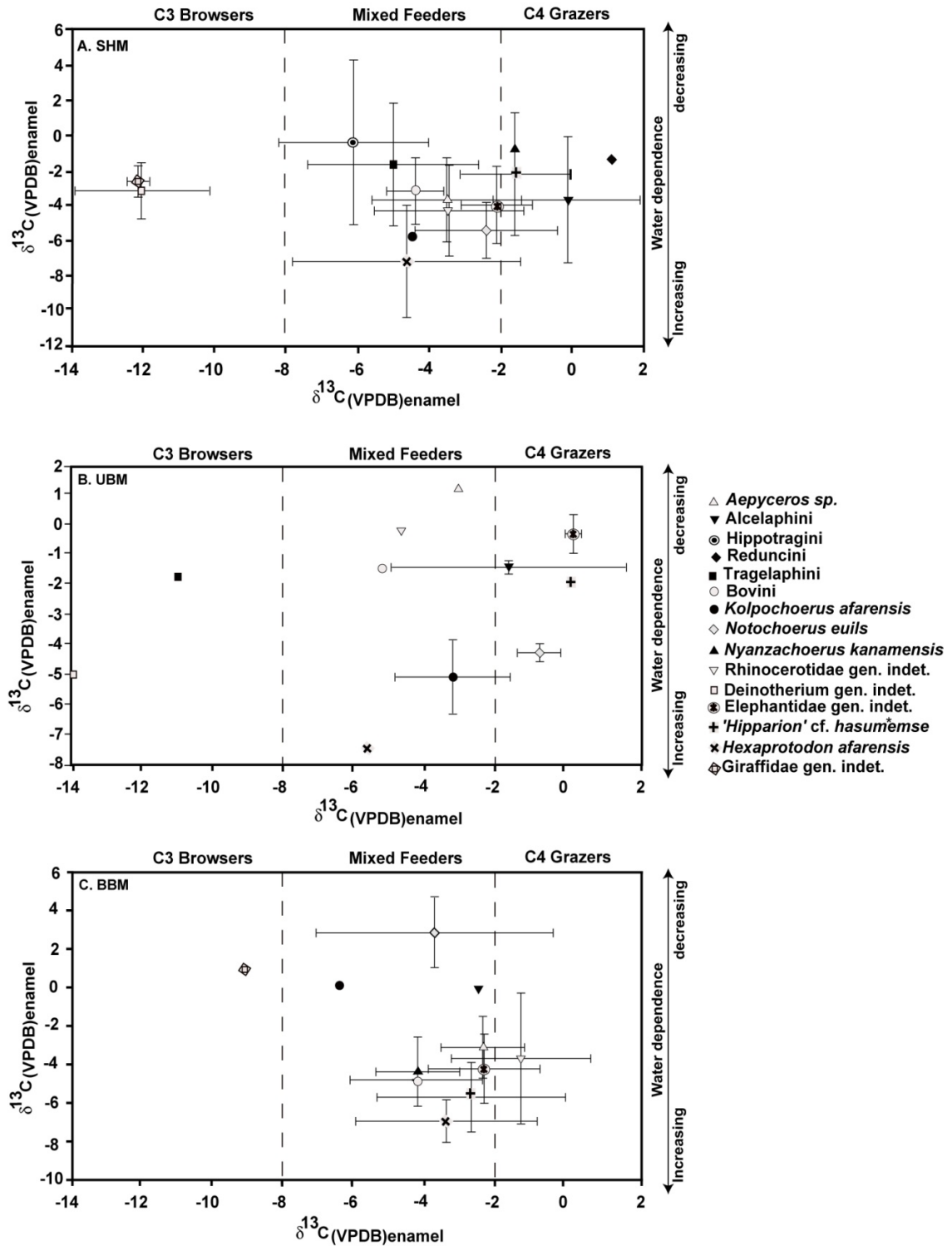


Figure 3.6 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic values of tooth enamel, the points represent the mean with standard deviation **a**, Sidi Hakoma Member **b**, base of the Basal Member **c**, upper Basal Member. (* equids identified at Dikika as “hipparion” (= *Eurygnathohippus*, Bernor et al., 2005).

paleoenvironmental condition, we combine the faunal abundance and average $\delta^{13}\text{C}_{\text{enamel}}$ values to estimate ecosystem carbon isotope ($\delta^{13}\text{C}_{\text{ecosystem}}$) value of the total vegetation consumed. A weighted average $\delta^{13}\text{C}_{\text{ecosystem}}$ value for each faunal collection is calculated using the average $\delta^{13}\text{C}_{\text{enamel}}$ of each taxon weighted by faunal abundance in respective members and the estimated daily food intake of each large vertebrate (>50 kg) taxon (Table 3.2; method described in detail in Bedaso et al., 2010). At Dikika, the average $\delta^{13}\text{C}_{\text{ecosystem}}$ signifies an environment dominated by wooded grasslands in both the SHM and BBM.

As emphasized by Behrensmeyer et al. (2007), there is often a general conception that paleoecological reconstructions are equivalent to ecological snapshots of modern landscapes. However one must consider that ecological information obtained from stratigraphic and faunal samples cover a very long period and are hence time averaged. Fossils collected from different surfaces could represent different time intervals based on the nature of the deposit, erosional and tectonic history and geomorphology of the basin, so it is critical to define the time interval for a particular fossil collection surface. The average carbon isotopic values signify the general paleoenvironmental condition, but it is difficult to elucidate changes that might have occurred at a temporal resolution higher than the time-averaged surface (Figure 3.7). In order to determine the entire range of habitats present on the landscape, we considered individual $\delta^{13}\text{C}_{\text{enamel}}$ values of each taxon (in 1‰ bins) and weighted these values by the faunal abundance and amount of biomass consumption of each taxa. The histogram produced is normalized to unity to show the relative proportion of habitats present (Figure 3.8, Appendix II).

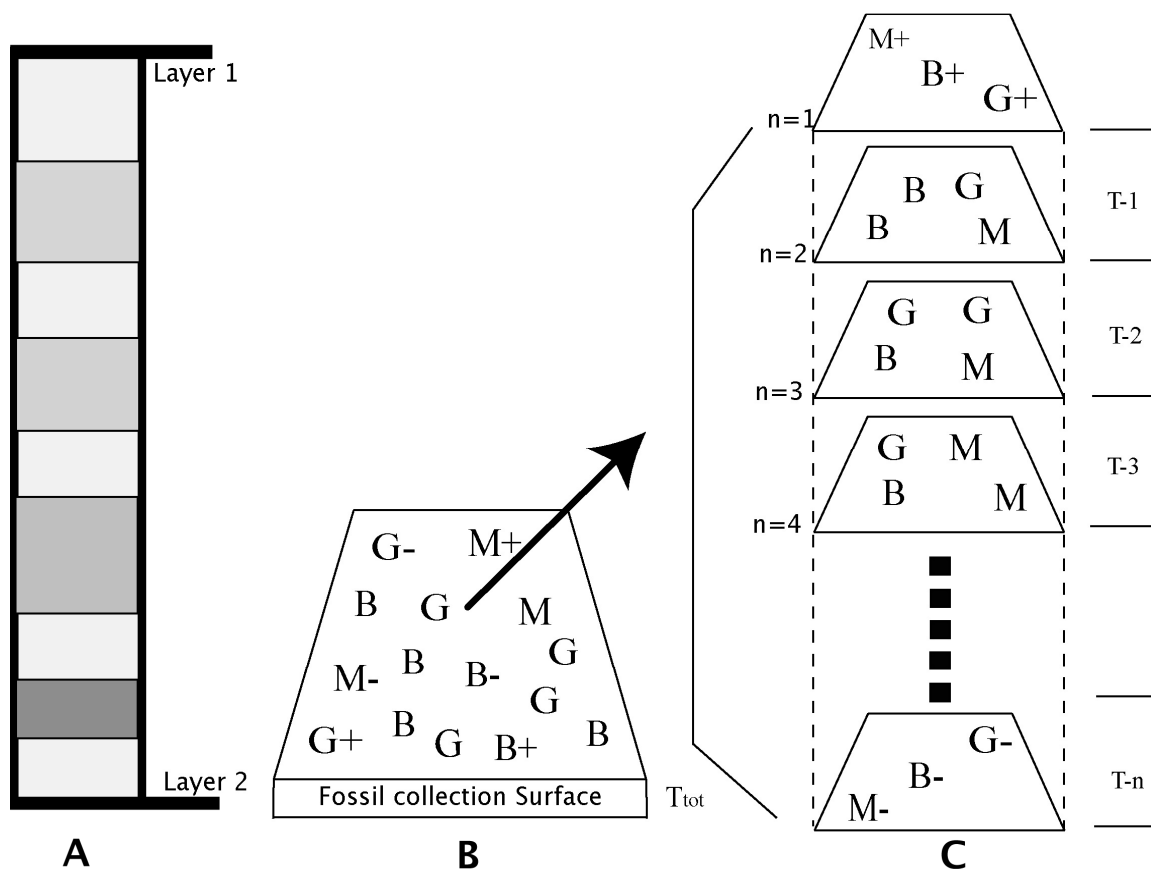


Figure 3.7 Diagram showing **a**, stratigraphic column bracketed with well dated layers, layer 1 and 2, provenance of fossils **b**, time averaging surface where fossils are collected for isotopic study. **c**, Possible depositional surfaces representing different time intervals from the stratigraphic column if we can resolve or breakdown the time-averaged surface and combine the isotope result in n different ways, where n is the number of layers. The letters represent isotopic values of grazer (G), browser (B), mixed feeder (M) and the + and – signs are used to indicate the most positive and negative values from respective groups and T represents the time averaged in between successive surfaces. T_{tot} is a total time averaged from fossil collection surface and in turn is the time between layer 1 and layer 2 [$T_{tot} = (T-1) + (T-2) + (T-3) + \dots + (T-n)$].

In the Basal Member, the calculated $\delta^{13}\text{C}_{\text{ecosystem}}$ value is -17‰. This indicates that the total large vertebrate fauna sampled a mixed C_3/C_4 to C_4 -dominated vegetation, which can be interpreted as wooded grassland with 73% C_4 biomass. In the same time interval, the estimated proportion of grasses on the landscape varies between 45%-89% based on

the most negative and positive $\delta^{13}\text{C}_{\text{enamel}}$ value (Table 3.2). Thus, in this time interval, the general paleoenvironmental condition at Dikika ranges between grassy woodland to open grassland based on the entire range of carbon isotope values of tooth enamel from each taxon (Figure 3.7). Likewise, the $\delta^{13}\text{C}_{\text{ecosystem}}$ value in the Sidi Hakoma Member, calculated by weighting the average $\delta^{13}\text{C}_{\text{enamel}}$ values of each taxon, is -18.4‰. This indicates mixed C_3/C_4 vegetation in the region and the ecosystem can be interpreted as wooded grassland with 61% C_4 vegetation cover (Table 3.2). For this time interval, the general paleoenvironmental condition ranges may have ranged between wooded grassland with 35% C_4 grasses and open grassland with 82% C_4 grasses on the landscape (Figure 3.8).

Isotopic data of tooth enamel from Dikika between ~3.8–3.24 Ma indicate a general wooded grassland to grassland dominated ecosystem with different relative proportion of C_3 and C_4 vegetation in each member, where all possible ranges of habitats from grassland to closed woodland may be represented (Figure 3.8). The oxygen isotopic compositions of fossil herbivore teeth from the Hadar Formation at Dikika are consistent with the overall ranges documented at other fossil localities (*e.g.*, Levin et al., 2008; White et al., 2009). Throughout the middle Pliocene there was no significant difference in the $\delta^{18}\text{O}_{\text{enamel}}$ values of all the taxa except equids, where the values are significantly ^{18}O -depleted in the BBM compared to the SHM ($p=0.0091$). The oxygen isotopic compositions of tooth enamel generally indicate a wetter condition at Dikika compared to early Pliocene and Middle Pleistocene sites in the region (White et al., 2009; Bedaso et al., 2010).

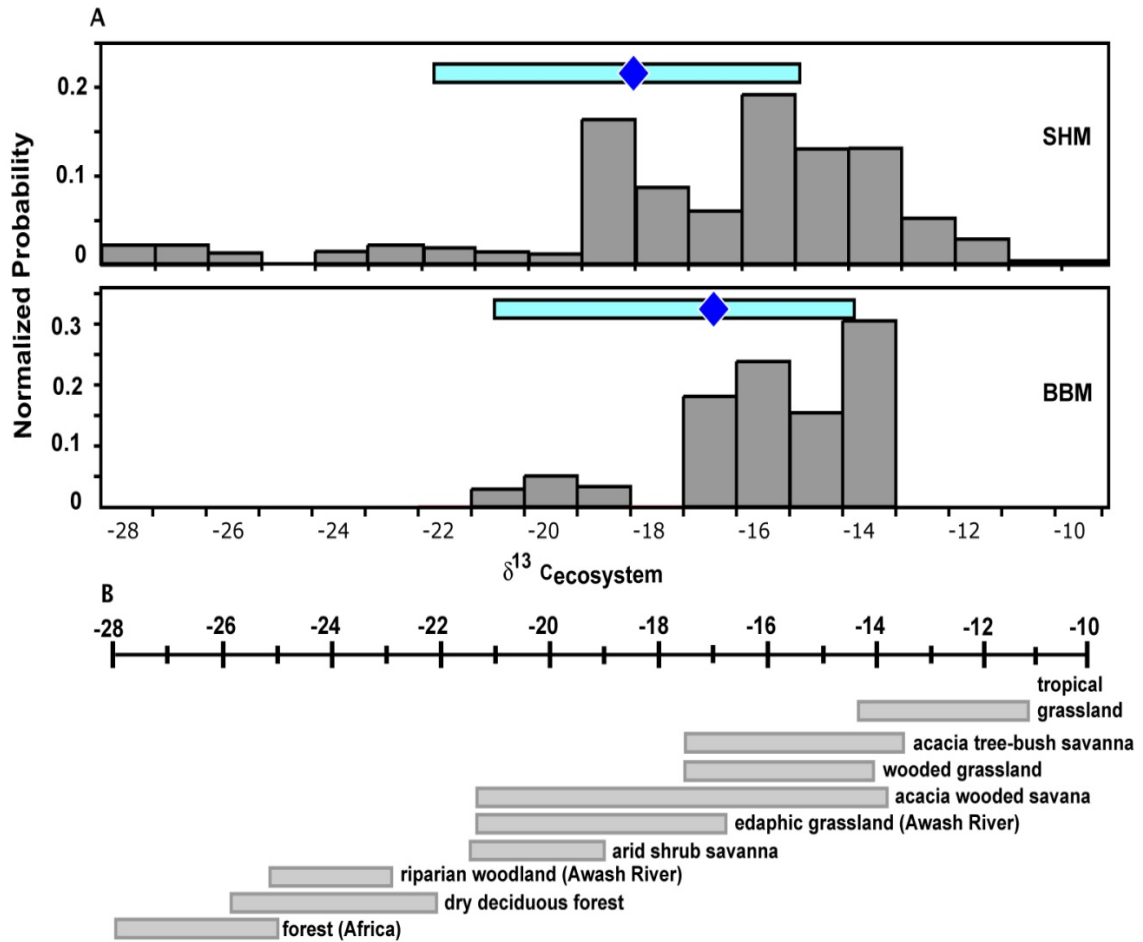


Figure 3.8 Interpretation of the habitat structure of at Dikika based on the $\delta^{13}\text{C}_{\text{ecosystem}}$ value derived from the faunal $\delta^{13}\text{C}_{\text{enamel}}$, faunal abundance and the estimated amount of food intake per day of each taxon from each member. SHM= Sidi Hakoma Member and BBM =Base of Basal Member. **a**, Histogram of the proportion of different habitats. The horizontal bar and the diamond symbol represent the range and average paleoenvironmental conditions based on estimates of the combined most positive and negative $\delta^{13}\text{C}_{\text{enamel}}$ values. **b**, Adapted from Cerling et al. (2010), but only ecosystems, which are common in the modern tropical Africa, are considered.

Table 3.2 Estimates of C₄ grasses in the diet and $\delta^{13}\text{C}_{\text{ecosystem}}$ values for SHM and BBM.

Fauna by Member	Faunal Abundance	Average $\delta^{13}\text{C}_{\text{enamel}}$ (‰)	Most (-Ve) $\delta^{13}\text{C}_{\text{enamel}}$ (‰)	Most (+Ve) $\delta^{13}\text{C}_{\text{enamel}}$ (‰)	C4 % (average)	C4 % (most -ve)	C4 % (most +ve)
Aepycerotini	10.3	-3.5	-6.6	-1.4	68	46	83
Alcelaphini	8.5	-0.1	-5.2	3.1	92	56	115
Bovini	12.3	-3.4	-8.4	-0.3	68	33	90
Hippotragini	1	-6.1	-7.4	-3.6	49	40	67
Reduncini	1	1.0	1.0	1.0	100	100	100
Tragelaphini	3	-5.0	-7.6	-0.3	57	38	91
Equidae	7.9	-1.6	-5.1	0.7	82	57	98
Elephantidae	3.5	-2.1	-3.8	-0.1	78	66	92
Deinotheriidae	0.3	-12.1	-12.3	-11.8	7	5	8
Giraffidae	2.9	-12.2	-14.3	-9.1	6	-9	28
Hippopotamidae	17.8	-4.6	-10.3	-0.1	60	19	92
Rhinocerotidae	5.4	-4.4	-5.3	-3.4	62	55	69
Kolpochoerus	10.2	-4.5	-6.3	-3.9	60	48	65
Notochoerus	2.6	-2.4	-7.1	-0.8	76	42	87
Nyanzachoerus	3.6	-1.6	-1.6	-1.6	81	81	81
SHM	$\delta^{13}\text{C}_{\text{ecosystem}}$	-18.4	-22.1	-15.5			
	C₄ estimates				61	35	82
Aepycerotini	9.7	-2.2	-3.8	-0.6	77	66	89
Alcelaphini	0.7	-2.5	-2.5	-2.5	75	75	75
Bovini	3	-4.1	-5.5	-2.7	64	54	74
Equidae	2.2	-2.5	-11.5	-0.6	75	11	88
Elephantidae	14	-2.2	-6.5	-0.2	77	46	92
Giraffidae	3.4	-9.0	-9.0	-9.0	28	28	28
Hippopotamidae	19	-3.2	-7.3	-0.3	70	41	91
Rhinocerotidae	1.1	-1.1	-2.5	0.3	85	75	95
<i>Kolpochoerus</i>	8	-6.3	-6.3	-6.3	48	48	48
<i>Notochoerus</i>	8.7	-3.6	-8.6	-1.6	67	31	81
<i>Nyanzachoerus</i>	8	-4.1	-5.5	-3.0	64	54	72
BBM	$\delta^{13}\text{C}_{\text{ecosystem}}$	-16.8	-20.7	-14.6			
	C₄ estimates				73	45	88

3.7.3 Regional environments and climatic condition of *Australopithecus afarensis*

Australopithecus afarensis is known to have existed in eastern and central Africa and persisted at Hadar between 3.7-3.0 Ma despite temporal climatic and environmental variability in the region (Brunet et al., 1995; Kimbel, 2007; Bonnefille, 2010). Previous reconstruction of the ecosystem from the Basal Member at Dikika, where *A. afarensis* was found, indicated a relatively open environmental condition in the proximity of water (Alemseged et al., 2005). Pollen analysis from Meshellu/Dikika, in lacustrine sediment in the Basal Member show predominantly pollen from grasses, cattails and sedges, indicating a mesic swampy condition close to a shallow lake (Bonnefille, 2010). From the same stratigraphic level at Hadar, Reed (2008) indicates that the habitat was likely a mosaic of woodland and shrubland. Our interpretation of the environmental and climatic condition in Basal Member at Dikika using isotopic composition of tooth enamel generally agrees with these previous interpretations based on the fauna and pollen analysis at Dikika and Hadar. In the SHM, based on the associated fauna with the juvenile hominin, “Selam” at DIK-1, Wynn et al. (2006) suggested a mosaic of mesic habitats. At Hadar, the SHM is divided into four sub-members and interpreted as an ecotone, woodland-shrubland and scrub woodland and grassland from the base to the top of the SHM (Reed, 2008). Meanwhile, fossil pollen assemblages in the SHM at Hadar indicate subaquatic reeds, sedges, and grasses indicating fresh water swamps or lakes with fluctuating lake level and floristic affinity with mixed deciduous/evergreen forest or woodland (Bonnefille, 2010). In the SHM isotopic composition of tooth enamel at Dikika indicate wet wooded grassland environment with significant C₄ grasses and a variety of habitats ranging from closed canopy forest to open grassland. Generally, our

interpretation agrees with both the pollen data (Bonnefille, 2010) and faunal data (Reed, 2008) from Hadar. However the latter did not indicate closed woodland habitat, and this might be attributed to the differences in the depositional environment between Dikika and Hadar. Elsewhere in East Africa, a wide range of ecosystems has been reconstructed for *A. afarensis*, mainly using the associated fauna. For example, at Maka (3.4 Ma), White et al. (1993) suggested that the habitat was a bushland or woodland with floodplain grassland. Harris (1991) suggested the habitat of Koobi Fora between 3.36 and 3.0 Ma was gallery forests along with floodplains, wet grasslands, and woodlands. Reed (1997) reconstructed the ecology during deposition of the Tulu Bor Member (3.36–3.0 Ma), as scrub woodland on a riverine floodplain. Here, from the environmental and climate data alone it is difficult to make any conclusion whether *A. afarensis* was adapted to the wide range of habitats reconstructed at different sites or whether they lived in a habitat that persisted throughout the middle Pliocene. However, it is evident that the species lived in a mosaic of landscape where variable shelter and food resources were available within a short distance.

Temporal variation of $\delta^{18}\text{O}_{\text{enamel}}$ values within a given taxon as well as differences among sympatric taxa document different aspects of environment and climate (Kohn, 1996). In the SHM, the $\delta^{18}\text{O}$ values of the evaporation insensitive taxa show a large range of variation while some taxa even show a bimodal distribution (Figure 3.4). Both equids and Alcelaphini show two populations with an average $\delta^{18}\text{O}$ of $(-6.3 \pm 0.4\text{‰}, 2.8 \pm 1.3\text{‰})$ and $(-6.1 \pm 1.2\text{‰}, 0.6 \pm 1.1\text{‰})$ respectively. The variation in $\delta^{18}\text{O}$ values may indicate variable sources of drinking water with different oxygen isotopic composition, or strong

seasonality, or the samples may come from different stratigraphic horizons within a single member where the drinking water could have different $\delta^{18}\text{O}$ values under different climatic conditions. The other possibility may be that these changes were associated with the change in the size of the Hadar Lake with time, which affected the $\delta^{18}\text{O}$ value of drinking water, especially evident in evaporation insensitive taxa such as the hippopotamids. The ^{18}O -enriched value of the lake water would increase as the lake contracts whereas the ^{18}O -depleted values would indicate a large lake with continuous supply of fresh water from perennial river. Hailemichael et al. (2002) reconstructed the $\delta^{18}\text{O}$ of paleo-Lake Hadar approximately between -4‰ and -5‰ (VSMOW) using $\delta^{18}\text{O}$ values in fossil mollusk shells from the SHM at Hadar assuming the mean temperature of the Pliocene Lake Hadar was 25–30 °C. This is in a general agreement with our reconstructed value from the Hadar Formation using hippopotamid tooth enamel at Dikika ($-4.0 \pm 1.3\text{‰}$ VSMOW).

3.8 Conclusion

Isotopic analyses of a collection of mammalian herbivore taxa from the Hadar Formation at the middle Pliocene site of Dikika, including multiple samples of 15 taxa representing eight families, were used to reconstruct the relative proportion of C_3 and C_4 vegetation and the change in this proportion through time. $\delta^{13}\text{C}_{\text{enamel}}$ documented a wide foraging strategies and the presence of both C_3 and C_4 vegetation throughout the Hadar Formation. Carbon isotopic composition of the fauna reveals that some of the mammals consistently grazed and browsed while others had variable and flexible foraging patterns. Most of the species including Alcelaphini, Reduncini, *Notochoerus*, equids and elephantids consumed

dominantly of C₄ vegetation while deinotheres and giraffids, consumed predominantly C₃ vegetation. Bovini, Hippotragini, Tragelaphini and *Nyanzachoerus*, *Kolpochoerus*, hippopotamids, had mixed C₃/C₄ feeding strategies. The middle Pliocene paleoenvironmental condition at Dikika is generally interpreted as wooded grassland with C₄ grasses ranging between 73% of the biomass in the BBM to 61% in the SHM. The habitat structure at the Dikika hominin sites in the middle Pliocene could be as diverse as open grassland, wooded grassland, woodland to forest between 3.42–3.24 Ma and wooded grassland, woodland to grassland between 3.8–3.42 Ma. In both time intervals, it is clear that although all the habitats except closed woodland and forest were persistent throughout the middle Pliocene, their proportion changes with time. These changes could have affected fauna in terms of the available preferred food resources and shelter. Hence, given the climatic and environmental variability documented in the region, the existence of *A. afarensis* throughout the middle Pliocene indicate the species might have adapted to a wide range of habits or their preferred habitat might not have been affected by otherwise-documented paleoclimatic changes.

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CHAPTER FOUR

CARBON AND OXYGEN ISOTOPIC SIGNATURE OF TOOTH

ENAMEL AS A PROXY FOR THE PLIOCENE

PALEOENVIRONMENT AND PALEOCLIMATE FROM MOUNT

GALILI FORMATION, ETHIOPIA

4.1 Introduction

The Galili PaleoAnthropological Research (GPAR) area is the southernmost Pliocene early hominin site in the Afar Depression (Figure 4.1). Since 2000, more than 1500 fossil specimens of more than 50 vertebrate taxa were collected and hominids are represented by several teeth (Macciarelli et al., 2004), and a femur of *Australopithecus* sp.. The early Pliocene vertebrate fauna from Galili includes large mammals (Equidae, Rhinocerotidae, Deinotheriidae, Elephantidae, Bovidae, Suidae, Hippopotamidae, Giraffidae, Carnivora, Cercopithecidae, reptiles (Crocodylia, Chelonia), and various species of fish (Urbanek et al., 2005; Kullmer et al., 2008).

Stable carbon and oxygen isotopic composition of tooth enamel have been used for paleoenvironmental and paleoclimatic reconstruction at paleontological sites from stratigraphic horizons that are closely associated with hominids in space and time (*e.g.*, Lee-Thorp et al., 1989; Sponheimer and Lee-Thorp, 2003; Bocherens et al., 1996;

Cerling et al., 2003c; Levin et al., 2008, Bedaso et al., 2010). This successful approach is based on establishing dietary consumption of individual taxa as reflection of the presence, absence and proportion of C₃ and C₄ vegetation on the paleolandscape (Lee-Thorp and Sponheimer, 2007). Despite the useful paleoenvironmental information obtained from carbon isotopes, little has been done to explicate vegetation or habitat structure. Reconstructing habitat structure is necessary to understand the availability and distribution of resources for early hominins, and has been a key issue in answering questions related to the origination, adaptation and extinction of our ancestors (Reed, 1997).

The present study uses stable isotopes of mammalian tooth enamel to assess the paleoenvironmental and paleoclimatic conditions and reconstruct habitat structures at four different time intervals between >5.29 Ma and ~3.6 Ma at Galili. It has a direct relevance to the understanding of the paleoenvironmental contexts of *Ardipithecus ramidus*, and *Australopithecus*. In addition to the environmental reconstruction at Galili, we compare fossil tooth enamel isotopic results from *Ardipithecus* and *Australopithecus*-bearing time intervals in the Awash Valley. For *Ardipithecus* comparable data are obtained from the As Duma and Segala Noumou Members of the Sagantole Formation at Gona (Levin et al., 2008) and Aramis Member of the Sagantole Formation at Middle Awash (White et al., 2009). Likewise, for *Australopithecus* we use isotope data from the base of Basal Member and Sidi Hakoma Member of the Hadar Formation at Dikika (Bedaso et al., in review). Previous studies have indicated that *Ardipithecus* may have inhabited a variety of landscapes within less than 100 km of each other in the Awash

Valley. So, the Galili tooth enamel isotope data will provide an opportunity to widen the spatial scale beyond a single sedimentary basin, and assess large-scale lateral variation of vegetation and habitat structure on the landscapes where early hominins lived.

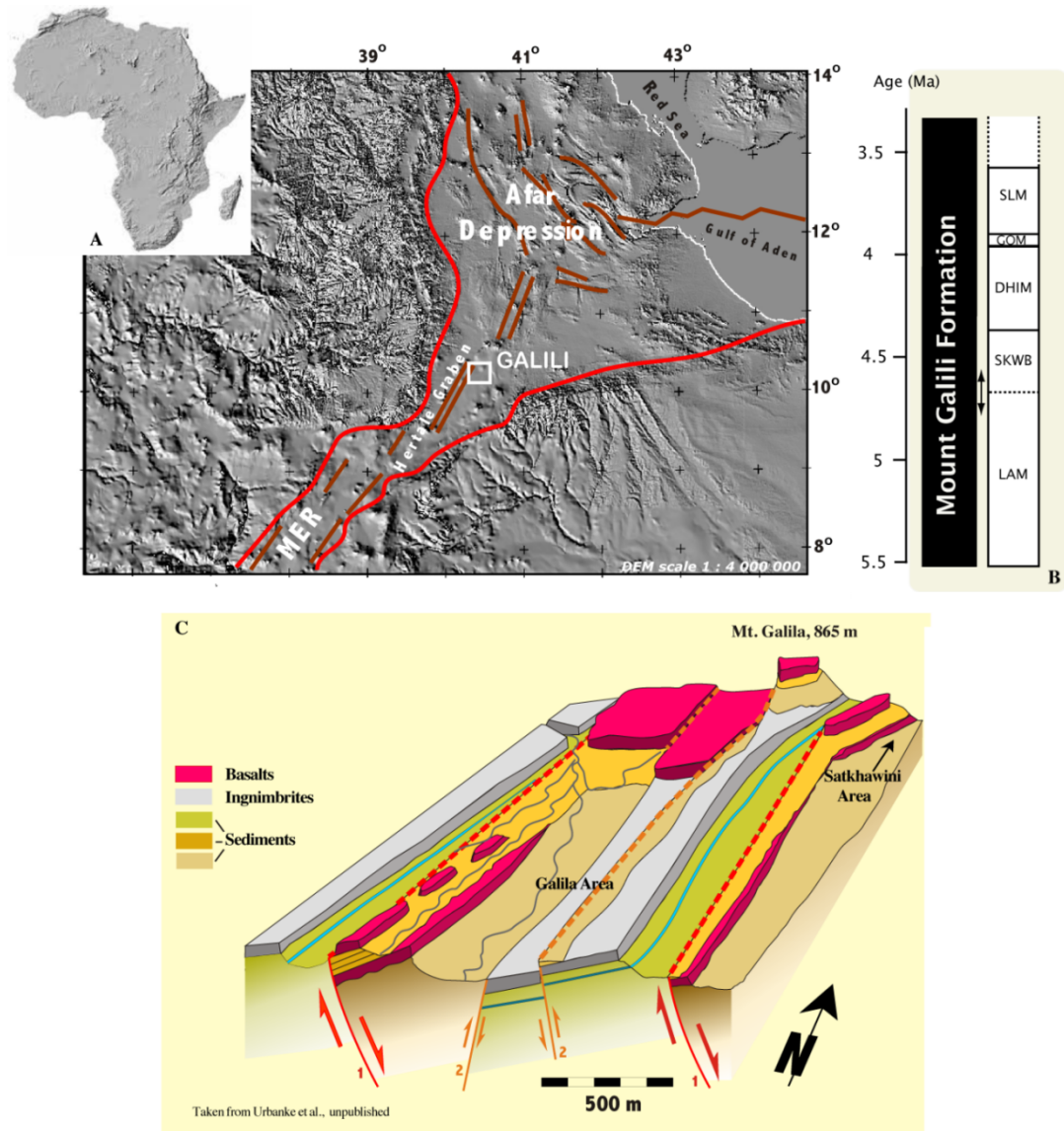


Figure 4.1 **A.** Location map of the Galili Research Project area. **B.** Simplified stratigraphic section of the Mount Galili Formation showing members only with between 5.29 and >3.6 Ma. **C.** A simplified geological model of Galili area, adapted from Urbanek et al., unpublished)

4.2 The geologic context of the Galili fauna

The volcano-sedimentary succession of the GPAR area is exposed on the eastern rift shoulder of the northernmost Miocene rift-in rift basin, N-S striking Sabure-Hertale-Adado graben (Figure 4.1, Urbanek et al., 2003). The graben is situated in the transition zone between the northern Main Ethiopian Rift and the southern Afar Depression (Beyene and Abdelsalam, 2005). In general, the region is faulted by N-S oriented normal faults and exposed sedimentary successions of lacustrine and fluvial origin intercalated with volcanic marker beds, where these deposits are assigned to Mount Galili Formation (Urbanek et al., 2005, Figure 4.1). Similarly at Galili the area is faulted by N-S striking faults, where the blocks are mainly tilted and generally dips NW, 5-15° (Figure 4.1). As a result sediments are mainly exposed along, and between the fault blocks. Due to the NW tilting of the block, the general younging direction is from east to west, where the oldest sediments are exposed in the western part of the research area while the youngest sediments are exposed in the eastern part of the research area.

The composite thickness of the Mount Galili Formation is approximately 230 m (Figure 4.1). The Mount Galili Formation is divided into six members, separated by volcanic layers: Lasdanan Member (LAM), Dhidinley Member (DHIM), Godiray Member (GOM), Shabeley Laag (SL), Dhagax Member (DXM) and Caashacado Members (CAM) (Urbanek et al., 2005). Here we only will summarize the age of the sediments and depositional environment of the members where tooth enamel was collected. The succession begins with LAM, which is bracketed by two basalt flows. Based on $^{40}\text{Ar}/^{39}\text{Ar}$ dates and Paleomagnetic measurements, LAM is dated as between $>5.296 \pm 0.05$ and 4.38 ± 0.02 Ma. The sediments deposited in this member indicate a shallow lake

environment cut by fluvial channels (W.H., unpublished data). DHIM is bracketed by the Lasdanan fissure basalt at the bottom and grayish ignimbrite at the top. $^{40}\text{Ar}/^{39}\text{Ar}$ dates and paleomagnetic measurements date this member between 4.38 ± 0.02 and 3.92 ± 0.01 Ma. The sediments deposited in this member indicate a flood plain deposit and shallow lake margin with multiple brief transgressions. SLM is exposed between a white Lapilli tuff at the bottom and unnamed basalt flow at the top. The base of SLM is dated with a paleomagnetic measurements as 3.92 ± 0.02 Ma, and the top is >3.6 Ma using biostratigraphy (*i.e.*, *Notochoerus jageri*). The sedimentary succession in this member indicates a range of environments from fluvial to lake margin and permanent lake with multiple transgression and regression cycles (W.H., unpublished data).

No fossils were recorded from DHX and CAM. For this study, all the tooth enamel samples were collected from the LAM, DHIM and SLM in different localities at Galili. Additional samples were also collected from the Satkawhini area, a locality northeast of Mount Galili (Figure 4.1) where the sediments are not yet attributed to a formal stratigraphic member. However based on geological observations and biostratigraphic evidences the sediments exposed at Satkawhini area, here after Satkawhini Beds (SKWB) are time equivalent to the upper part of the LAM (Kullmer et al., 2008; W.H and B.V, personal communication).

4.3 Methods

We collected and analyzed tooth enamel samples from 15 different mammalian taxa subsampled in 2008 and 2010 (Table 4.1). Most of the fossils are surface collections from

different fossil localities defined in the research area. The age of the fossils were defined in the field during locality delineation using the exposed stratigraphic section, drainage patterns and the topography. Samples were mainly collected from the late erupting teeth (*e.g.*, third molars) in order to avoid the effect of additional fractionation during the weaning period evident in the juvenile teeth (DeNiro and Epstein, 1978). Bulk enamel samples were taken by drilling down the tooth along the growth axis with a 0.5 mm drill bit, and cleaning the drill bit between sampling. Care was taken to avoid dentine, cementum and matrix in the sample powder. About 10 - 20 mg of powder enamel was extracted from each tooth and homogenized to average out intra-tooth variability.

The powder produced was pretreated with 3% H₂O₂ followed by a 1 M acetic acid-calcium acetate buffer to remove organic matter and secondary carbonates, respectively. Samples then more thoroughly rinsed with deionized water and dried (following standard procedures for the treatment of tooth enamel of Lee-Thorp and Van der Merwe, 1987; Quade et al., 1992; Koch, 1998). Approximately 5-7 mg of the pretreated powder was reacted with 103% H₃PO₄ in He flushed exetainer vials at 25°C for 24 hrs. to produce the CO₂ analyte gas for analyses of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Isotope ratios were measured on a Thermo Fisher Scientific (Finnigan) Delta V 3 keV Isotope Ratio Mass Spectrometer and results are reported using the standard per mil notation.

$$\delta^{13}\text{C} \text{ or } \delta^{18}\text{O} = \left(\frac{R_{\text{sample}}}{R_{\text{Standard}}} - 1 \right) * 1000$$

Where, R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios in the sample and standard, respectively, for $\delta^{13}\text{C}$ and the $^{18}\text{O}/^{16}\text{O}$ ratios in the sample and standard, respectively, for

$\delta^{18}\text{O}$. The reference standard is VPDB, to which samples were normalized using replicate analysis of IAEA reference materials NBS-18 ($\delta^{13}\text{C} = -5.04\text{‰}$, $\delta^{18}\text{O} = -23.05\text{‰}$, and NBS-19 ($\delta^{13}\text{C} = +1.95\text{‰}$, $\delta^{18}\text{O} = -2.20\text{‰}$, NIST, 1992). The average standard deviations for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were $<0.1\text{‰}$. We report the isotopic enrichment between groups of taxa is the difference between the two groups, which may or may not be in equilibrium, using the enrichment between taxa A and B.

$$\varepsilon_{A-B} = \left(\frac{R_A}{R_B} - 1 \right)$$

Statistical analyses on the isotope data were performed using SAS 9.2. All tests of hypothesis were two tailed and significance (α) for statistics was set at 0.05. For pair wise comparison Wilcoxon Rank Sum test, which also referred as Mann-Whitney test, are used (see Appendix I for taxa by taxa carbon and oxygen isotope statistical result).

4.4 Carbon and oxygen isotopic variation in tooth enamel

The interpretation of carbon isotopic composition of tooth enamel is based on differences in discrimination of carbon isotopes among plants, which is controlled by enzymes and the “leakiness” of cells (Kohn and Cerling, 2002). Terrestrial plants use three types of metabolic pathways to fix CO_2 from the atmosphere: the C_3 photosynthesis pathway (the Calvin Cycle), the C_4 photosynthesis pathway (Hatch-Slack cycle) and the CAM (Crassulacean Acid Metabolism) pathway (see, Ehleringer et al., 1991). Most trees and shrubs, as well as some herbs and most grasses in regions with cool growing seasons use the C_3 photosynthetic pathway, and have $\delta^{13}\text{C}$ values (mean -26‰ , range -22‰ to -35‰) that are much lower than those of atmospheric CO_2 (-7.7‰ ; O’Leary, 1988). C_4 plants,

on the other hand, have $\delta^{13}\text{C}$ values (mean -12‰, range -9‰ to -19‰) that are more similar to those of the atmosphere. C_4 photosynthesis is less common and occurs in some grasses, sedges, and herbs, but only those that grow under sufficiently dry and/or warm climatic conditions (Ehleringer & Monson, 1993). The CAM plants (*e.g.*, succulent plants) are mostly adapted to arid climates and known to follow either of the C_3 or C_4 pathways, and have intermediate isotopic values (Ehleringer & Monson, 1993). Although in general the average separation between average C_3 and C_4 plants is ~14‰, in different ecosystem the value has been reported as high as ~17‰ in some mesic environments and as low as ~11‰ in certain xeric environments (Cerling et al., 2003c). In this study we use the ~14‰ spacing between C_3 and C_4 vegetation. The average enrichment factor between diet and tooth enamel ($\epsilon_{\text{diet-tooth enamel}}$) is estimated as ~14‰ (Cerling and Harris, 1999).

The essence of using oxygen isotopic composition of herbivore tooth enamel as a paleoclimatic proxy relies on the fact that tooth enamel carbonate forms at equilibrium with body water, which in turn reflects drinking water and oxygen from the food and water they consume coupled with animal physiology, and climatic conditions (Longinelli, 1984; Luz et al., 1984; Kohn, 1996). In general, animals that drink water more frequently from lakes, ponds, and streams (such as hippopotamids, rhinocerotids, Equus, *Phacochoerus*, and Reduncini), tracks meteoric water more closely than animals that obtain water from leaves (such as such as *Giraffa*, Tragelaphini and Antilopini). Sternberg (1989) indicated that leaf water is relatively ^{18}O -enriched as compared to liquid water in plant stems, fruits and underground storage organs, which has a similar oxygen isotopic composition as the available drinking water. Although very little is known about

the oxygen isotope bond in food, Helliker and Ehleringer (2002) show that $\delta^{18}\text{O}$ values of leaf water directly translated to $\delta^{18}\text{O}$ value of cellulose, which is also indirectly affected by relative humidity and serve as a proxy for relative humidity changes.

Table 4.1 Stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) fossil tooth enamel collected from Mount Galili Formation of Galili.

Cat-No	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
GLL 0360	Bovidae	Aepycerotini	SLM	-2.7	-1.0
GLL 0614	Bovidae	Aepycerotini	SLM	-2.3	-2.7
GLL 0178	Bovidae	Alcelaphini	SLM	2.1	-2.4
GLL 0438	Bovidae	Alcelaphini	SLM	1.1	-0.4
GLL 0014	Bovidae	Bovini	SLM	-5.1	-6.1
GLL 0217	Bovidae	Bovini	SLM	-6.8	-5.3
GLL 0325	Bovidae	Bovini	SLM	-3.1	-5.0
GLL 1079 a-b	Bovidae	Bovini	SLM	-2.0	-5.7
GLL 0375	Bovidae	Bovini	SLM	-4.2	-6.9
GLL 0425	Bovidae	Bovini	SLM	0.9	-4.1
GLL 0825	Bovidae	Reduncini	SLM	0.3	0.1
GLL 0212	Bovidae	Reduncini	SLM	-8.0	-6.7
GLL 0420	Bovidae	Tragelaphini	SLM	-4.2	-2.5
GLL 1430	Bovidae	Tragelaphini	SLM	-8.7	-1.5
GLL 1485	Bovidae	Tragelaphini	SLM	-11.3	-0.4
GLL 1814	Bovidae	Tragelaphini	SLM	-9.7	-7.3
GLL 0410	Bovidae	Tragelaphini	SLM	-6.2	-3.7
GLL 0460	Bovidae	Tragelaphini	SLM	-1.3	-4.9
GLL 0602	Bovidae	Tragelaphini	SLM	-2.6	1.8
GLL 0187	Equidae		SLM	-0.8	-3.6
GLL 0274	Equidae		SLM	-1.7	-6.0
GLL 0301	Equidae		SLM	-0.1	-1.4
GLL 0338	Equidae		SLM	-4.2	-5.5
GLL 0506	Equidae		SLM	-6.0	-2.7
GLL 1078	Equidae		SLM	-4.5	-6.2
GLL 1256	Equidae		SLM	-0.6	-1.0
GLL 1539	Equidae		SLM	-0.4	-3.6
GLL 0307	Hippopotamidae		SLM	-10.9	-6.8
GLL 0320	Hippopotamidae		SLM	-8.7	-6.1
GLL 0605 ab	Hippopotamidae		SLM	-5.9	-6.0
GLL 0349	Hippopotamidae		SLM	-3.6	-7.4
GLL 0389	Hippopotamidae		SLM	-8.7	-8.1
GLL 0390	Hippopotamidae		SLM	-7.1	-7.4
GLL 1815	Hippopotamidae		SLM	-5.1	-7.9

Cat-No	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
GLL 0498	Hippopotamidae		SLM	-2.4	-6.5
GLL 0499	Hippopotamidae		SLM	-4.9	-6.2
GLL 1436	Hippopotamidae		SLM	-3.6	-7.0
GLL 0323	Proboscidea		SLM	-9.4	-1.7
GLL 0007 a-d	Proboscidea	Elephas	SLM	-0.4	-5.6
GLL 0335	Proboscidea	Elephas	SLM	-3.0	-6.6
GLL 0366	Proboscidea	Elephas	SLM	-0.1	-0.9
GLL 0426	Proboscidea	Elephas	SLM	-3.2	-4.6
GLL 0445	Proboscidea	Loxodonta	SLM	-0.7	-4.0
GLL 0303	Suidae	Notochoerus	SLM	-0.8	-2.7
GLL 1076 a-b	Suidae	Notochoerus	SLM	-5.0	-6.0
GLL 1075	Suidae	Notochoerus	SLM	-4.4	-6.5
GLL 0297	Suidae	Notochoerus	SLM	-0.1	0.9
GLL 0351	Suidae	Notochoerus	SLM	-1.6	-4.4
GLL 0760	Suidae	Notochoerus	SLM	-0.4	-2.6
GLL 0328	Suidae	Nyanzachoerus	SLM	-3.8	-4.9
GLL 0430	Suidae	Nyanzachoerus	SLM	-2.7	-5.7
GLL 0477	Suidae	Nyanzachoerus	SLM	-6.2	-5.2
GLL 1240	Suidae	Nyanzachoerus	SLM	-0.6	-1.4
GLL 1798	Suidae	Nyanzachoerus	SLM	-4.1	-5.4
GLL 0076	Bovidae	Bovini	DHIM	-0.2	-1.3
GLL 0270	Bovidae	Bovini	DHIM	1.7	-0.3
GLL 0067	Bovidae	Bovini	DHIM	-9.6	-5.9
GLL 0986	Bovidae	Bovini	DHIM	-1.8	-1.5
GLL 1699	Bovidae	Bovini	DHIM	-7.3	-2.6
GLL 0267	Bovidae	Hippotragini	DHIM	-4.7	-2.7
GLL 0932	Bovidae	Reduncini	DHIM	-10.3	-5.4
GLL 1216	Bovidae	Reduncini	DHIM	-11.1	-1.8
GLL 1224	Bovidae	Reduncini	DHIM	-7.2	-2.6
GLL 1383	Bovidae	Reduncini	DHIM	-7.9	-3.5
GLL 0250	Bovidae	Tragelaphini	DHIM	-10.8	-0.6
GLL 0145	Bovidae	Tragelaphini	DHIM	-10.7	-6.6
GLL 0835	Bovidae	Tragelaphini	DHIM	0.0	2.0
GLL 0990	Bovidae	Tragelaphini	DHIM	-11.8	-3.4
GLL 0991	Bovidae	Tragelaphini	DHIM	-10.1	-3.3
GLL 0845	Bovidae	Tragelaphini	DHIM	0.4	-0.2
GLL 0157	Equidae		DHIM	-0.3	-2.8
GLL 0220	Equidae		DHIM	-2.6	-4.4
GLL 0231	Equidae		DHIM	-3.7	-3.4
GLL 0733	Equidae		DHIM	-1.6	-3.1
GLL 0777	Equidae		DHIM	-2.3	0.2
GLL 1217	Equidae		DHIM	-1.6	-2.6
GLL 1833	Equidae		DHIM	-1.9	-1.7
GLL 0689	Giraffidae		DHIM	-10.2	-2.7
GLL 0981	Giraffidae		DHIM	-9.1	-1.2

Cat-No	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
GLL 0234	Hippopotamidae		DHIM	-8.0	-6.3
GLL 0131	Hippopotamidae		DHIM	-9.9	-8.8
GLL 0132	Hippopotamidae		DHIM	-7.6	-9.5
GLL 0261	Hippopotamidae		DHIM	-9.9	-4.5
GLL 0846	Hippopotamidae		DHIM	-6.1	-6.4
GLL 0961	Proboscidea	Loxodonta	DHIM	-3.3	-1.5
GLL 0259	Proboscidea		DHIM	0.5	-4.4
GLL 0266	Suidae		DHIM	-2.9	-7.6
GLL 0540	Suidae		DHIM	-3.8	-1.9
GLL 0900	Suidae		DHIM	-5.1	-3.2
GLL 0997	Suidae		DHIM	-1.3	-1.3
GLL 1695b	Suidae		DHIM	-5.7	-6.3
SKW 079	Bovidae	Bovini	SKWB	-7.5	-3.6
SKW 086	Bovidae	Bovini	SKWB	-4.0	3.8
SKW 136	Bovidae	Bovini	SKWB	-0.4	3.4
SKW 138	Bovidae	Bovini	SKWB	-1.3	-0.8
SKW 154	Bovidae	Bovini	SKWB	-0.2	2.1
SKW 184	Bovidae	Bovini	SKWB	-1.6	1.8
GLL 1208	Bovidae	Reduncini	SKWB	-11.2	-1.8
GLL 1223	Bovidae	Reduncini	SKWB	0.9	1.2
GLL 1227	Bovidae	Reduncini	SKWB	-2.2	1.5
SKW 144	Bovidae	Reduncini	SKWB	-0.6	-3.5
SKW 206	Bovidae	Reduncini	SKWB	0.6	2.7
SKW 248	Bovidae	Reduncini	SKWB	0.4	-0.4
SKW 191	Bovidae	Tragelaphini	SKWB	1.8	3.3
GLL 1501	Bovidae	Tragelaphini	SKWB	-2.8	4.4
GLL 1514	Bovidae	Tragelaphini	SKWB	-2.8	3.4
SKW 167	Bovidae	Tragelaphini	SKWB	-5.5	3.0
SKW 183	Bovidae	Tragelaphini	SKWB	2.1	-2.0
SKW 208	Bovidae	Tragelaphini	SKWB	-0.1	3.4
GLL 1620	Equidae		SKWB	-3.3	-5.2
GLL 1655	Equidae		SKWB	-0.5	-3.1
GLL 1673	Equidae		SKWB	-2.6	-4.6
GLL 1689	Equidae		SKWB	-4.3	-6.7
GLL 1319	Equidae		SKWB	-1.3	-0.8
GLL 1327	Equidae		SKWB	-1.6	1.2
GLL 1604a	Equidae		SKWB	-1.5	-4.1
GLL 1631	Equidae		SKWB	-1.0	-0.4
SKW 177	Equidae		SKWB	-1.3	-1.5
SKW 213	Equidae		SKWB	-2.4	1.0
SKW 225	Equidae		SKWB	-0.1	-0.3
SKW 228	Equidae		SKWB	-0.6	-2.1
SKW 232	Equidae		SKWB	0.3	2.6
SKW 204	Giraffidae	Sivatherium	SKWB	-10.5	0.8
SKW 016	Hippopotamidae		SKWB	-5.5	-2.9

Cat-No	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
SKW 094	Hippopotamidae		SKWB	-2.4	-1.2
SKW 113	Hippopotamidae		SKWB	-4.1	0.1
GLL 1604b	Hippopotamidae		SKWB	-0.9	1.4
GLL 1627b	Hippopotamidae		SKWB	-0.9	-2.3
GLL 1649	Hippopotamidae		SKWB	-5.4	-4.6
SKW 105	Hippopotamidae		SKWB	-6.0	-3.7
SKW 141	Hippopotamidae		SKWB	-1.2	-2.0
SKW 143	Hippopotamidae		SKWB	-1.5	-6.2
GLL 1627a	Proboscidea	Anancus	SKWB	0.4	-3.7
SKW 161	Suidae	Notochoerus	SKWB	-0.7	-0.3
SKW 226	Suidae	Notochoerus	SKWB	1.0	-1.8
GLL 1308	Suidae	Notochoerus	SKWB	-0.7	-1.9
SKW 093	Suidae	Notochoerus	SKWB	0.0	-1.7
SKW 229	Suidae	Notochoerus	SKWB	-2.8	-2.2
SKW 110	Suidae	Nyanzachoerus	SKWB	-3.8	-2.6
GLL 1302	Suidae	Nyanzachoerus	SKWB	-0.8	-2.5
GLL 1590	Suidae	Nyanzachoerus	SKWB	-0.5	-0.5
SKW 140	Suidae	Nyanzachoerus	SKWB	-0.5	-2.3
SKW 152	Suidae	Nyanzachoerus	SKWB	-2.4	0.8
SKW 178	Suidae	Nyanzachoerus	SKWB	-2.0	-0.4
SKW 186	Suidae	Nyanzachoerus	SKWB	0.2	-1.8
GLL 1043	Bovidae	Alcelaphini	LAM	-0.3	-2.7
GLL 0914	Bovidae	Bovini	LAM	-4.5	-4.0
GLL 1146	Bovidae	Bovini	LAM	-6.4	-1.6
GLL 1168	Bovidae	Bovini	LAM	-1.2	-1.7
GLL 1548	Bovidae	Bovini	LAM	-4.5	-1.0
GLL 1011	Bovidae	Hippotragini	LAM	-5.3	-3.6
GLL 0885	Bovidae	Hippotragini?	LAM	-2.0	-3.4
GLL 0850	Bovidae	Reduncini	LAM	-1.9	-2.5
GLL 0867	Bovidae	Reduncini	LAM	-0.8	-5.3
GLL 0894	Bovidae	Reduncini	LAM	-1.7	-4.0
GLL 0907	Bovidae	Reduncini	LAM	0.6	-4.2
GLL 0909	Bovidae	Reduncini	LAM	-10.6	-2.3
GLL 1008	Bovidae	Reduncini	LAM	-4.9	4.8
GLL 1174	Bovidae	Reduncini	LAM	-3.8	-4.3
GLL 1175	Bovidae	Reduncini	LAM	-1.9	-2.2
GLL 1469	Bovidae	Reduncini	LAM	-5.3	-0.3
GLL 0294	Bovidae	Tragelaphini	LAM	-8.1	-4.4
GLL 0897	Bovidae	Tragelaphini	LAM	1.9	2.5
GLL 1060	Bovidae	Tragelaphini	LAM	-7.2	4.4
GLL 0860	Bovidae	Tragelaphini	LAM	-9.3	-3.5
GLL 1009	Bovidae	Tragelaphini	LAM	-6.4	1.3
GLL 1391	Bovidae	Tragelaphini	LAM	-2.2	-4.4
GLL 1916	Bovidae	Tragelaphini	LAM	-11.3	-1.7
GLL 0899	Equidae		LAM	-4.6	-2.3

Cat-No	Family	Taxon	Stratigraphy	$\delta^{13}\text{C}_{\text{enamel}}$	$\delta^{18}\text{O}_{\text{enamel}}$
GLL 1041	Equidae		LAM	-0.1	-1.4
GLL 1193	Equidae		LAM	-0.9	1.2
GLL 1282	Equidae		LAM	-2.4	-2.5
GLL 1283h	Equidae		LAM	-3.7	-3.2
GLL 1565	Equidae		LAM	-2.0	1.3
GLL 1643	Equidae		LAM	-4.4	-3.2
GLL 1671	Equidae		LAM	0.2	-2.3
GLL 1676	Equidae		LAM	-4.7	-2.8
GLL 0834	Giraffidae	Giraffa	LAM	-11.5	2.7
GLL 1045	Giraffidae		LAM	3.2	-0.8
GLL 0738	Hippopotamidae		LAM	-6.3	-2.9
GLL 1046	Hippopotamidae		LAM	-3.8	-4.3
GLL 1404	Hippopotamidae		LAM	-5.1	-6.0
GLL 1431	Hippopotamidae		LAM	-4.6	-5.5
GLL 1672	Hippopotamidae		LAM	-7.5	-5.3
GLL 1720	Hippopotamidae		LAM	-3.3	-2.4
GLL 1793	Hippopotamidae		LAM	-4.7	-7.8
GLL 1809	Hippopotamidae		LAM	-10.4	-6.3
GLL 0926	Suidae	Notochoerus	LAM	-1.2	-5.2
GLL 1623	Suidae	Notochoerus	LAM	-3.4	-3.9
GLL 1850	Suidae	Notochoerus	LAM	-2.8	-4.5
GLL 1941	Suidae	Notochoerus	LAM	-6.0	-1.0
GLL 1039b	Suidae	Notochoerus	LAM	-0.3	-5.0
GLL 0880	Suidae	Nyanzachoerus	LAM	-0.3	-3.8
GLL 0843	Suidae	Nyanzachoerus	LAM	-2.8	-5.3
GLL 0865	Suidae	Nyanzachoerus	LAM	-4.9	-4.8
GLL 0886	Suidae	Nyanzachoerus	LAM	-2.7	-5.7
GLL 1068	Suidae	Nyanzachoerus	LAM	-6.6	-3.1

4.5 Results

4.5.1 Carbon isotopic composition of tooth enamel by taxa

Over 200 representative tooth enamel samples of 15 herbivore taxa were analyzed for stable isotopes of carbon and oxygen from multiple members within the Mount Galili Formation (Table1, Figure 2 –4). $\delta^{13}\text{C}_{\text{enamel}}$ values of the Galili fossils range between -11.5‰ to +3.2‰ in the LAM, -11.2‰ to +2.1‰ in the SKWB, -11.8‰ to +1.7‰ in the DHIM and -11.3‰ to +2.1‰ in the SLM. The ranges of values from each member represents a wide range of dietary adaptation of the mammals (*i.e.*, pure C_3 diet $\leq -13\text{‰}$,

C₃-dominated diet ($\delta^{13}\text{C}_{\text{enamel}} -13 < \delta^{13}\text{C}_{\text{enamel}} -8\text{‰}$), mixed C₃/C₄ diet ($-2\text{‰} > \delta^{13}\text{C}_{\text{enamel}} > -8\text{‰}$), and Pure C₄-dominated diet ($\delta^{13}\text{C}_{\text{enamel}} \geq -2\text{‰}$; Figure 4.2). The prevalence of taxa in these categories signify the presence of different types of vegetation and hence the mosaic nature of the paleolandscape at Galili.

The $\delta^{13}\text{C}_{\text{enamel}}$ data from Galili indicate a wide range of variation of values within a single taxon with substantial difference in the degree of incorporation of C₃ and C₄ vegetation. This variation might be explained by fossils, which come from different horizons in a single member, difference in the seasonal availability of vegetation, migration of larger mammals and/or the presence of two or more species with a slightly different dietary adaptation. In general, Alcelaphini, Equidae, *Notochoerus*, Elephantidae and Gomphotheriidae show dominantly grazing diet, while Deinotheriidae and Giraffidae were exclusively browsers, and the rest of the taxa exhibited grazing to mixed dietary adaptations with varying percent C₃ and C₄ vegetation. Most of the taxa considered here did not show major shifts in the dietary adaptation with time.

4.5.1.1 Proboscidea

Proboscideans belong to two taxa, which are well studied from the Galili collection for biostratigraphy purposes. The fossil Proboscidea at Galili is represented by Deinotheridae (*Deinotherium bozasi*), Gomphotheriidae (*Anancus kenyensis*) and Elephantidae (*Loxodonta* cf. *exoptata*, *Loxodonta* cf. *adaurora*, *Elephas recki brumpti* and *Elephas* cf. *ekorensis*) (Kullmer et al., 2008). The $\delta^{13}\text{C}_{\text{enamel}}$ value of Gomphotheriidae (*Anancus* sp.) in the SKWB and DHIM from single specimens is 0.4‰ and 0.5‰, respectively showing

that they dominantly fed on C₄ grasses. A single isotopic value of Elephantidae from the DHIM has a value of -3.3‰ showing a mixed C₃/C₄ diet, while the average $\delta^{13}\text{C}_{\text{enamel}}$ value from the SLM is $-1.5 \pm 1.5\text{‰}$ (n=5) indicating a C₄-dominated dietary adaptation. Deinotheres are only analyzed from the SHM with $\delta^{13}\text{C}_{\text{enamel}}$ value of -9.4‰, which signifies a C₃-dominated diet (Figure 4.2A). Based on average $\delta^{13}\text{C}_{\text{enamel}}$ values, the Pliocene Elephantidae at Galili show a range of C₄ dietary contribution between 69% and 82% in different stratigraphic levels but based on individual isotope measurements C₄ dietary contributions could be as high as 92%. Similarly, Gomphotheriidae show a high degree of incorporation of C₄ vegetation up to 96% in both SKWB and DHIM. Deinotheridae, on the other hand, incorporated only 26% (n=1) C₄ vegetation in the diet. These results are consistent with isotopic data of Proboscidean from Late Miocene and early Pliocene sites in the Awash Valley and elsewhere in east and central Africa (Cerling et al., 1999; Zazzo et al., 2000; Semaw et al., 2005; Kingston and Harrison, 2007; White et al., 2009; Levin et al., 2008; Bedaso et al., in review)

4.5.1.2 Equidae

The fossil Equidae at Galili is represented by *Eurygnathohippus* sp. (Urbanek et al., 2005). *Eurygnathohippus* sp. is common in Lasdanan Member, Dhidinley Member, Godere Member and Shebele Laag Member (Kullmer et al., 2008).

Isotope analyses were done on 37 specimens from LAM, DHIM, SLM and SKWB and the $\delta^{13}\text{C}_{\text{enamel}}$ values are reported in Table 4.1 and Figure 4.2B. The isotope analyses at the different stratigraphic levels signify similar average and ranges of carbon isotope

values. The maximum range documented is 5.9‰ in SLM and the minimum range of 3.6‰ in the DHM. In general, the equids at Galili during the Pliocene exhibited a similar dietary adaptation with little to no C₃ vegetation in the diet and no major shift in the dietary adaptation. The average $\delta^{13}\text{C}_{\text{enamel}}$ values from the LHM, SKWB, DHIM and SLM are $-2.5 \pm 1.9\text{‰}$ (n=9), $-1.6 \pm 1.3\text{‰}$ (n=13), $-2.0 \pm 1.0\text{‰}$ (n=7) and -2.3 ± 2.3 (n=8) respectively (Table 4.1). The isotopic data suggest that the dietary strategies of Pliocene equids at Galili were grazing primarily on C₄ grasses with some incorporation of C₃ vegetation. The percent C₄ contribution in the diet ranges between 75% and 82%. These results are consistent with isotopic data of equid enamel from the Awash Valley and elsewhere in tropical and sub-tropical African Plio-Pleistocene and modern samples. The $\delta^{13}\text{C}_{\text{enamel}}$ values reported are in the range of 0‰ to -3‰ indicating a C₄-dominated and pure C₄ diet (Morgan et al., 1994; Bocherens et al., 1996; Cerling et al., 1997b, 2003a, 2003b; Kingston and Harrison, 2007; Levin et al., 2008; White et al., 2009; Bedaso et al., 2010).

4.5.1.3 Hippopotamidae

Hippopotamids are one of the most common large mammals at Galili and obviously, because of their aquatic mode of life, hippos are often the most common mammals in Pliocene and Pleistocene terrestrial assemblages of Africa (*e.g.*, Boisserie et al., 2005; Harris et al., 2008). The fossil Hippopotamidae at Galili is represented by two genera, namely *Hexaprotodon* and *Hippopotamus*, where *Hexaprotodon* sp. are common in the LAM, while *Hippopotamus* sp. are common in DHIM, and SLM (Urbanek et al., 2005; Kullmer et al., 2008).

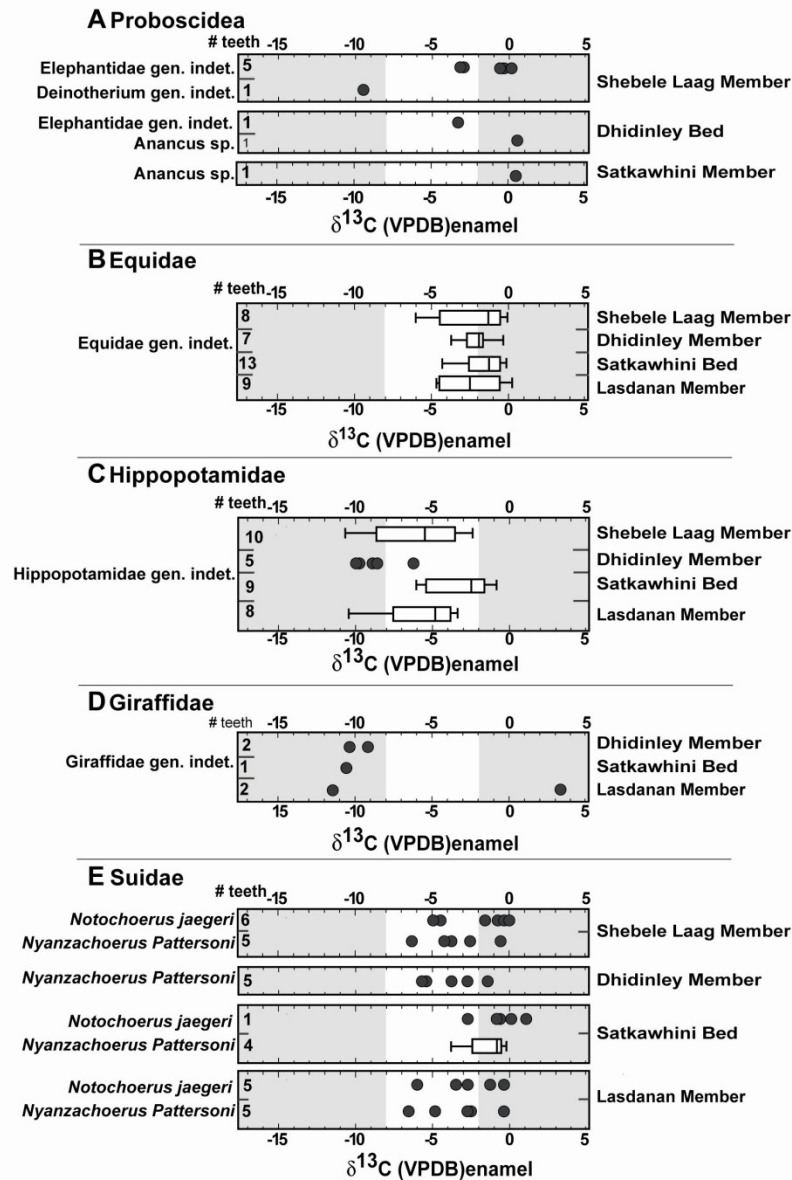


Figure 4.2 Box and whisker plots of stable carbon isotopic composition of mammals tooth enamel ($\delta^{13}\text{C}_{\text{enamel}}$) from the Mt. Galili Formation from four different sampling intervals (*i.e.*, Lasdanan, Satkawhini beds, Dhidinley and Shebele Laag Members). The box is bounded by first quartile (25%) and the third quartile (75%) of the variable population and each box encloses 50% of the data with the median value represented by a vertical line in the box. The horizontal line extending from the sides of the box represents the acceptable range of data. Outliers are displayed as individual points outside of the acceptable range. The herbivores grouped into predominantly C_4 -diet ($\delta^{13}\text{C}_{\text{enamel}} \geq -2\text{‰}$), mixed C_3/C_4 diet ($\delta^{13}\text{C}_{\text{enamel}} -2\text{‰}$ to -8‰) and a predominantly C_3 -diet ($\delta^{13}\text{C}_{\text{enamel}} \leq -8\text{‰}$) based on (Cerling et al., 2003c)

Isotope analyses of the hippos in different members indicate a wide range of dietary adaptations stretching between pure C₃ to C₄ diets in the LAM and SLM but a relatively narrow range is documented in the SKWM and DHIM (Figure 4.2C). The average $\delta^{13}\text{C}_{\text{enamel}}$ values of hippos through the Pliocene at Galili show a statistically significant increase in C₄ contribution in the diet between SKWB and DHIM (Mann Whitney, $p < 0.001$) and between SKWB and SLM (Mann Whitney, $p = 0.0435$). Despite the fact that the Pleistocene and extant hippos diet is dominated by C₄ vegetation, the average percent C₄ contribution to diet of the Pliocene hippos at Galili varied between 33% in DHIM and 70% in the SKWB, while based on individual values the C₄ contribution could vary between 21% and 86%. Although the C₃-dominated dietary adaptation in DHIM is not common in East African Pliocene, Franz-Odenaal, et al. (2002) reported an average carbon isotopic values of -12 ± 1.5 , $n=15$, from an early Pliocene hippopotamids at Langebaanweg, South Africa. On the other hand, C₃/C₄ mixed diet has been documented in many Plio-Pleistocene sites in the Awash Valley and elsewhere in eastern Africa (Zazzo et al, 2000; Boissarie et al., 2005; Cerling et al., 2008; Harris et al., 2008; Levin et al., 2008; White et al., 2009; Bedaso et al., in review).

4.5.1.4 Giraffidae

The fossil Giraffidae at Galili is represented by two genera and three species, *Sivatherium* sp., cf. *Giraffa pygmaea*, *Giraffa* aff. *Stilei* and *Giraffa* sp. (Urbanek et al., 2005; Kullmer et al., 2008). Giraffids are rare in all members and only a few specimens were subsampled for isotope studies except in the SLM. Unlike today, where there is only one species of *Giraffa* (*G. camelopardalis*), there were three different Plio-Pleistocene

Giraffa species (*G. jumae*, *G. pygmaea*, and *G. Stilei*) as well as *Sivatherium maurusium*. The coexistence of several paleospecies is most likely related to specific browsing height ranges (Kingdon, 1979). Two teeth samples were analyzed from LAM. $\delta^{13}\text{C}_{\text{enamel}}$ values represent two extreme values of -11.5‰ ($n=1$), which indicate a pure C_3 diet while the other specimen has a $+3.2\text{‰}$ ($n=1$) indicate a pure C_4 diet. A single tooth analyzed from the SKWB has $\delta^{13}\text{C}_{\text{enamel}}$ values of -10.5‰ indicating a pure C_3 -dominated diet. The average $\delta^{13}\text{C}_{\text{enamel}}$ value of $-9.6 \pm 0.7 \text{‰}$ ($n=2$) documented from the DHIM, which shows a C_3 diet with significant incorporation of C_4 vegetation (Figure 4.2D).

A similar isotopic signature is reported from other sites in the Awash Valley, which indicate that throughout the Pliocene Giraffids consistently relied on C_3 vegetation and show no changed in dietary adaptation. At Dikika, $\delta^{13}\text{C}_{\text{enamel}}$ values range between -9.0‰ and -12‰ in the Hadar Formation (Bedaso et al., in review), and values of -9.8‰ are reported from the Sagantole Formation and -10.9‰ from the Adu-Asa Formation at Gona (Levin et al., 2008), and -12.1‰ and -11.9‰ from giraffids and sivatheres respectively from Aramis Member of Sagantole Formation at Middle Awash (White et al., 2009). Early Pliocene giraffids from Tanzania (Kingston and Harrison, 2007) and Late Miocene giraffids from Chad (Zazzo et al., 2000) reported a dietary adaptation consistent with C_3 to C_3 -dominated diet.

4.5.1.5 Suidae

The fossil Suidae at Galili is represented by three genera and four species, *Nyanzachoerus pattersoni*, *Notochoerus jaegeri*, *Notochoerus euilus*, and *Kolpochoerus*

deheinzellini (Urbanek et al., 2005; Kullmer et al., 2008). Suids are also a well-studied group at Galili for biostratigraphic purposes. Of the four species represented at Galili, *Nyanzachoerus pattersoni* and *Notochoerus jaegeri* were sampled and analyzed. *Notochoerus euilus*, and *Kolpochoerus deheinzellini* are rare compared to the other species in the area, so only one *Notochoerus euilus* was collected from the SHM. The $\delta^{13}\text{C}_{\text{enamel}}$ value of *Notochoerus jaegeri* averages $-2.1 \pm 2.1\text{‰}$ (n=6), $-2.7 \pm 2.7\text{‰}$ (n=5) and $-0.63 \pm 1.4\text{‰}$ (n=5) in the SHM, LAM and SKWB respectively. The range of $\delta^{13}\text{C}_{\text{enamel}}$ values in the respective members is different with a maximum being in the LAM and the minimum in the SKW (Table 4.1, Figure 4.2E). The average $\delta^{13}\text{C}_{\text{enamel}}$ values of *Notochoerus* at Galili indicate a dominantly C₄ grazing diet with some incorporation of C₃ vegetation (up to 26%) in some of the specimens analyzed in the LAM, DHIM and SLM. However in the SKWB they were exclusively grazing on C₄ grasses with minor contribution from C₃ vegetation (*i.e.*, 12%). During early to middle Pliocene at Galili *Notochoerus* shows no significant change in the dietary adaptation except a change in the proportion and degree of incorporation of C₃ vegetation in the diet. The $\delta^{13}\text{C}_{\text{enamel}}$ value of *Nyanzachoerus pattersoni* at Galili averages $-3.5 \pm 2.0\text{‰}$ (n=5), $-3.8 \pm 1.8\text{‰}$ (n=5), $-3.5 \pm 2.4\text{‰}$ (n=5) and $-1.4 \pm 1.4\text{‰}$ (n=5) in the SLM, DHIM, LAM and SKWB respectively. Compared to the SKWB, the other members exhibit a wider range of $\delta^{13}\text{C}_{\text{enamel}}$ values (Table 4.1, Figure 4.2E). *Nyanzachoerus pattersoni* at Galili showed a change in dietary adaptation from mixed C₃/C₄ to C₄-dominated diet in the early Pliocene to exclusively C₄ grazing diet and back to the C₃/C₄ to C₄-dominated diet in middle Pliocene. However, the dietary changes in Pliocene at Galili are not statistically significant except between SKWB and DHIM (Mann Whitney, $p=0.048$). The Dietary

adaptation of suids at Galili has a general agreement with other isotopic studies within the Awash Valley and beyond (*e.g.*, Harris and Cerling, 2002)

4.5.1.6 Bovidae

Bovids are one of the most abundant mammalian taxa in all members of the Galili faunal assemblage; ~23% of the total fauna and 19%, 27%, 16% and 32% in the SLM, DHIM, LAM and SKWB respectively (B.V unpublished data). At Galili, six bovid tribes are represented in the faunal assemblage: Tragelaphini, Bovini, Hippotragini, Alcelaphini, Apeycerotini and Reduncini. Isotopic analyses were done from the four time intervals (SLM (n=19), DHIM (n=16), LAM (n=23) and SKWB (18)). To obtain a robust reconstruction of the paleoenvironment and habitat, tooth enamel samples were collected from all the tribes when possible (Table 4.1, Figure 4.3). Tragelaphini, Bovini, Alcelaphini, Apeycerotini and Reduncini are analyzed from SLM, Tragelaphini, Bovini, Hippotragini and Reduncini analyzed from DHIM, Tragelaphini, Bovini, Alcelaphini, Hippotragini, and Reduncini were analyzed from LAM while Tragelaphini, Bovini and Reduncini were analyzed from the SKWB (Figure 4.3).

Tragelaphini in the Mount Galili Formation at Galili are represented by *Tragelaphus* cf. *nakuae*, aff *Tragelaphus kyaloae* and *Tragelaphus* sp. (Urbanek et al., 2005; Kullmer et al., 2008). The average $\delta^{13}\text{C}_{\text{enamel}}$ value of Tragelaphini from the SLM is $-6.3 \pm 3.8\text{‰}$ (n=7) with a range of 10‰; the individual values spanning almost the entire range of C_3/C_4 dietary adaptations where the proportion of C_4 grasses varies between 12% and 84%. In the DHIM two different populations of Tragelaphini with the average $\delta^{13}\text{C}_{\text{enamel}}$

values separated by 11‰ are recognized (*i.e.*, $-10.8 \pm 0.87\text{‰}$ (n=4) and $-0.2 \pm 0.3\text{‰}$ (n=2), Figure 4.3). The $\delta^{13}\text{C}_{\text{enamel}}$ value of Tragelaphini from the LAM ranges between -10.6 and 0.6 ‰ with an average of $-6.1 \pm 4.5\text{‰}$ (n=7). The average $\delta^{13}\text{C}_{\text{enamel}}$ value of Tragelaphini in the SKWB is $-1.2 \pm 3\text{‰}$ (n=6) where the values are bracketed between -5.5‰ and 2.1‰. The isotope data from Galili indicate that Tragelaphini exhibit a very wide range of dietary adaptations within each member and throughout the early and middle Pliocene. In the SLM and LAM, the contribution of C₃ vegetation ranges between 0% and 88% but in the SKWB, the C₃ contribution to the diet is only between 0% and 52%. Although Tragelaphini show a wide range of dietary adaptations from pure grazing to pure browsing diet in each member and SKWB, there was no statistically significant change in diet throughout the early and middle Pliocene (See Appendix I). Isotopic studies of Tragelaphini from eastern and South Africa so far, indicated pure C₃ to C₃/C₄-dominated diet (Cerling et al., 2003c; Sponheimer and Lee-Thorp, 2003; Levin et al., 2008, White et al., 2009; Bedaso et al., 2010, in review). However, paleoenvironmental reconstruction based on the diet of extant taxa signifies a wooded environment. It is notable that the isotopic data presented here shows Tragelaphins had a predominantly C₃/C₄ diet with significant C₄ grasses and suggests a need for careful use of uniformitarian dietary assumption, which consider similar dietary adaptation and habitat preference of fossil taxa with their modern relatives (*e.g.*, Vrba, 1980).

Alcelaphini in the Mount Galili Formation at Galili are represented by Alcelaphini gen. sp. indet., *Damaliscus* sp. and *Parmularius* sp. (Urbanek et al., 2005; Kullmer et al., 2008). Alcelaphinis are rare at Galili and sampled only from the SLM and LAM.

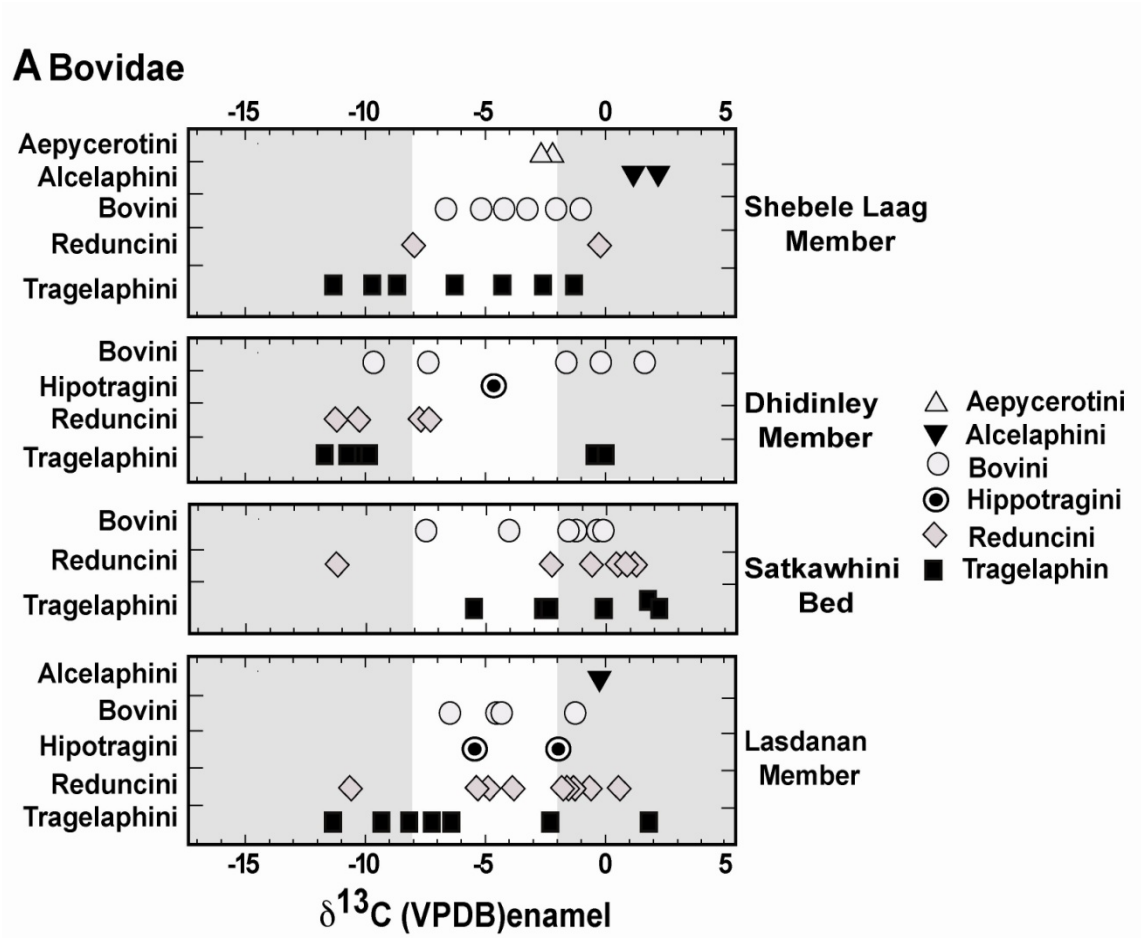


Figure 4.3 Box and whisker plots of stable Carbon isotopic composition of Bovid ($\delta^{13}\text{C}_{\text{enamel}}$) from the Mount Galili Formation (See Figure 4.2)

The average $\delta^{13}\text{C}_{\text{enamel}}$ value of Alcelaphini from the SLM is $1.6 \pm 0.8\text{‰}$ ($n=2$) and -0.3‰ from a single in the LAM. The isotope data from Galili indicate that Alcelaphini were exclusively C_4 grazers with 100% C_4 grasses in the SLM and 91% in the Lasdanan Member. Due to the small sample size, it is difficult to draw any conclusion on the long-term dietary adaptation of Alcelaphini. However, Alcelaphini $\delta^{13}\text{C}_{\text{enamel}}$ data from early Pliocene sites in eastern and South Africa indicated a consistent C_4 -dominated diet (Cerling et al., 2003c; Sponheimer et al., 2003; Bedaso et al., in review).

The tribe Bovini is one of the most common bovids in the Mount Galilia Formation and represented by cf. *Ugandax* sp., commonly in the SLM and DHIM and rarely in the LAM (Kullmer et al., 2008), and *Ugandax gauieri* (Urbanek et al., 2005). The average $\delta^{13}\text{C}_{\text{enamel}}$ values of Bovini are $-3.4 \pm 2.7\text{‰}$ (n=6), $-3.43 \pm 1.9\text{‰}$ (n=4), $-4.12 \pm 2.1\text{‰}$ (n=4) and $-2.51 \pm 2.1\text{‰}$ (n=6) in the SHM, DHIM, LAM and SKWB respectively. The isotope data indicate that at Galili Bovini, generally had a C₃/C₄ mixed dietary adaptation in the SLM, DHIM and LAM but C₄ dominated diet in the SKWB. In the Pliocene at Galili, the contribution of C₄ vegetation in the Bovini diet varies between 69% and 75% with no major shift in dietary adaptations. However referring the individual values, pure grazing diet is documented in all members and a browsing diet in the DHI Member (not statistically significant, Mann Whitney, $p=0.4848$). A C₃/C₄ mixed to C₄-dominated diet is also reported from the Awash Valley (Levin et al., 2008; White et al., 2009; Bedaso et al., in review)

The tribe Aepycerotini is rare in the Mount Galili Formation and so far found only in the SHM and DHIM. The tribe is represented by a single genus *Aepyceros* sp. (Urbanek et al., 2005; Kullmer et al., 2008). Isotopic analysis was done only on specimens collected from The SLM. The $\delta^{13}\text{C}_{\text{enamel}}$ value of Aepycerotini in the SLM averages $-2.53 \pm 0.3\text{‰}$ (n=2). The isotope data signifies that Aepycerotini dominantly fed on C₄ grasses which incorporate up to 73%-75% C₄ grasses in the diet. Isotopic studies of Aepycerotini in East and South Africa indicated a wider range of values while the amount of C₄ vegetation varies between 20% and 90% (Sponheimer et al., 2003; Cerling et al., 2003c, Levin et al., 2008).

The tribe Hippotragini is also a rare bovid in the Mount Galili Formation but reported from SHM, DHIM and LAM. The tribe is represented by *Hippotragus gigas* and *Hippotragus* sp. (Urbanek et al., 2005; Kullmer et al., 2008). Isotope analysis of Hippotragini was only done from DHI and LAM. The average $\delta^{13}\text{C}_{\text{enamel}}$ value of Hippotragini from LAM is $-3.64 \pm 2.3\text{‰}$ (n=2) and it is represented in the DHIM by a single value of -4.7‰ . The isotope data from Galili indicate that Hippotragini exhibit a mixed C_3/C_4 diet with an average of 60%-67% C_4 grasses in the diet, but the C_4 contribution from one specimen in the LAM indicate contribution of C_4 grasses up to 79%. Isotopic data from Aramis at Middle Awash indicate Hippotragini were exclusively grazing on C_4 grasses (White et al., 2009), while data from the Hadar and the Adu-Asa Formation show a mixed C_3/C_4 and C_3 -dominated diet at Dikika and Gona, respectively (Levin et al., 2008; Bedaso et al., in review).

Reduncini in the Mount Galili Formation is common in the LAM but rare in all the other members. Reduncinis at Galili are represented by Reduncini gen. sp. indet. and *Menelikia lyrocer* (Urbanek et al., 2005; Kullmer et al., 2008). The isotope data of Reduncini at Galili in the Pliocene hints at the coexistence of two different genera with different dietary preferences, possibly in different part of the paleolandscape where preferred food resources were available. In the SLM, the $\delta^{13}\text{C}_{\text{enamel}}$ value of Reduncini from two specimens measured have different values (*i.e.*, -8.0‰ and 0.3‰ , Table 4.1, Figure 4.3), which indicate different dietary adaptation with 36% and 95% contribution of C_4 grasses in the diet, respectively. The average $\delta^{13}\text{C}_{\text{enamel}}$ value of Reduncini from the DHIM is $-9.1 \pm 1.9\text{‰}$ (n=4) where the values range between -7.2‰ and -11.1‰ and possibly, in this

case, represent a single genus. The Reduncini from DHIM had a browsing dietary adaptation where the percent C₄ grasses in the diet varies between 13% and 41%. In the LAM, $\delta^{13}\text{C}_{\text{enamel}}$ value of Reduncini averages $-2.0 \pm 2.0\text{‰}$ (n=8) not including an outlier value (-10.6‰). This group signifies a C₃/C₄ mixed feeding to C₄ grazing dietary adaptation, with an outlier representing a C₃-end member. Similarly, the $\delta^{13}\text{C}_{\text{enamel}}$ value of Reduncini in the SKWB averages $-0.16 \pm 1.3\text{‰}$ (n=5) not including an outlier value (-11.2‰). The isotope data in the SKWB indicate that Reduncini fed on C₄-dominated diet and heavily relied on C₄ grasses, which contribute an average of 9% C₄ grasses to the diet. Carbon isotope studies of Reduncini so far signify a pure C₄ diet throughout the Pliocene and Pleistocene both in eastern and South Africa (Sponheimer et al., 1999; Cerling et al., 2003c; Levin, 2008; Bedaso et al., 2010). On the contrary, Spencer (1997) based on the cranio-mandibular remains suggests that *M. lyrocer* was not a grass feeder, but has most of the distinguishing characteristics of a mixed feeder. Similarly Alemseged and Bobe (2009) examine the geographic distribution of two fossil species of the tribe Reduncini, *Menelikia lyrocer* and *Kobus sigmoidalis*, across the Shungura paleolandscape and based on differences in their faunal abundance between these two bovids suggested possible differences in the paleoenvironmental context and diet. Here our isotope data supports this explanation.. In addition, at Galili compared to the LAM most of ¹³C-enriched values come from SKWB, indicating lateral changes in the vegetation type (C₃ and C₄), which could be attributed to different depositional environment.

4.5.2 Oxygen isotopic composition of tooth enamel

At Galili, oxygen isotope composition of tooth enamel was measured at four different stratigraphic levels. The $\delta^{18}\text{O}_{\text{enamel}}$ values in the Pliocene of the Mount Galili Formation ranges between -9.5‰ and 4.8‰ and show a wide variation within a single taxon, both in a single stratigraphic level and through different members (Table 4.1, Figure 4.4). Similarly, $\delta^{18}\text{O}_{\text{enamel}}$ values among sympatric taxa show a wide variation. In general the range of $\delta^{18}\text{O}_{\text{enamel}}$ values in different members are similar, but most of the taxa in LAM and SKWB show relatively ^{18}O -enriched values compared to same taxa in the SLM and DHIM. However the observed change is statistically significant only in Hippopotamids (Mann Whitney, $p < 0.001$), *Nyanzachoerus* (Mann Whitney, $p = 0.0303$) and Tragelaphini (Mann Whitney, $p = 0.0152$). The wide range of $\delta^{18}\text{O}_{\text{enamel}}$ value at Galili could indicate variation of the water isotopic composition of source water, drinking habit, thermophysiological adaptation, migration, seasonality and change in paleoclimatic condition with time (atmospheric temperature, relative humidity and other climatic variables).

Wide ranges of intra-taxon $\delta^{18}\text{O}_{\text{enamel}}$ variability were documented throughout the Mount Galili Formation. Equids and Hippopotamids in the SKWB show the maximum range of values while Tragelaphini show groups of ^{18}O -depleted and ^{18}O -enriched values. Assuming that each taxon has a similar drinking habit and thermophysiological adaptation in a single member, the wide range of $\delta^{18}\text{O}_{\text{enamel}}$ value could indicate a change in the drinking water source, seasonality and proportion of the water source from food and drinking water especially for mixed feeders. Bedaso et al. (in review) indicate that an

increase in the proportion of C₃ vegetation in the diet of mixed C₃/C₄ feeders increase ¹⁸O-enriched values of tooth enamel. The $\delta^{18}\text{O}_{\text{enamel}}$ of Hippopotamids are usually the most ¹⁸O-depleted compared to other taxa in the same member (*e.g.*, Bocherens et al., 1996; Bedaso et al., 2010), where their $\delta^{18}\text{O}_{\text{enamel}}$ closely track $\delta^{18}\text{O}$ of meteoric water. However, the wider range and ¹⁸O-enriched values in the SKWB in Hippopotamids is attributed to evaporated source water from shallow lake (Figure 4.4). Similarly, Reduncini are the most water dependant of the bovid tribes also had a wider range in the SKW and LA members, which could signify availability of ¹⁸O-enriched surface water and imply drier climatic conditions.

The $\delta^{18}\text{O}$ of enamel carbonate reflects the $\delta^{18}\text{O}$ of mammalian body waters because it precipitates in equilibrium with body water at a near constant body temperature of 37 °C, independent of external temperatures (Longinelli and Nuti, 1973a). Three main oxygen inputs for mammals include: ingested water (drinking water and water in food), solid food and atmospheric O₂ (Luz and Kolodny, 1985). In mammals that drink directly, enamel $\delta^{18}\text{O}$ values follow the local meteoric water $\delta^{18}\text{O}$ values. However, the $\delta^{18}\text{O}$ of mammalian body water does not track meteoric $\delta^{18}\text{O}$ values in a linear or direct manner. It is further complicated by each animal's thermoregulatory system, water dependence (obligate and non-obligate drinkers), diet, body size and behavior (Bryant and Froelich, 1995; Kohn, 1996; Longinelli et al., 2003). Here we use obligate drinkers to estimate the $\delta^{18}\text{O}$ of meteoric water.

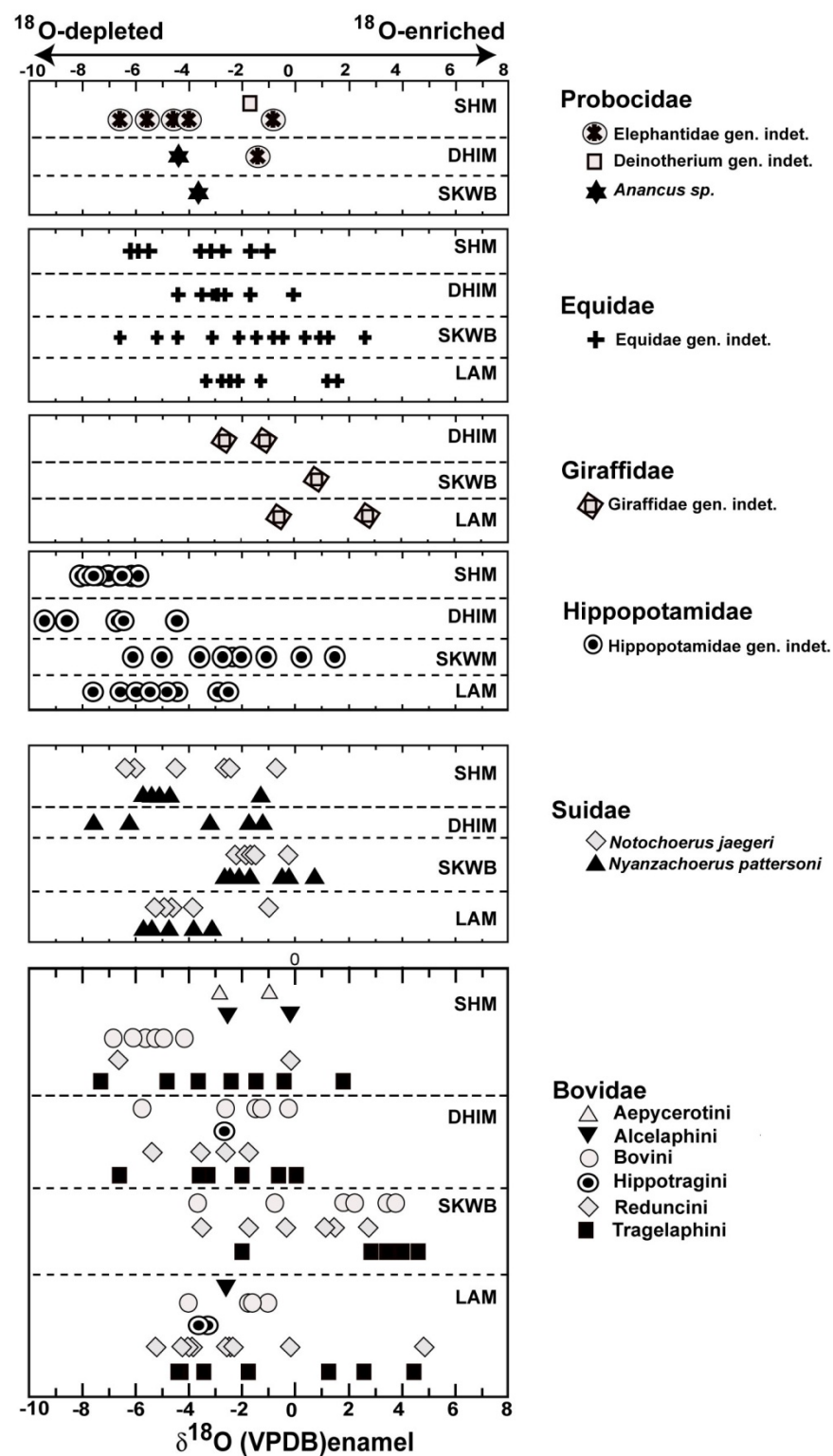


Figure 4.4 Stable oxygen isotopic composition of mammals tooth enamel ($\delta^{18}\text{O}_{\text{enamel}}$) from the Mount Galili Formation (See Table 4.1)

The most ^{18}O -depleted value from each stratigraphic level is used to calculate the most ^{18}O -enriched value of meteoric water that the animal drank. Luz and Kolodny (1985) estimated the fractionation factor (α), between body water (bw) and the phosphate (p) fraction of apatite as ($\alpha_{\text{p-BW}}=1.0178$), which is defined as $\alpha_{\text{A-B}}= (1000 + \delta_{\text{A}}/1000 + \delta_{\text{B}})$ where A and B are phases at equilibrium. Similarly, Bryant et al. (1996) estimated the fractionation factor between the phosphate fraction and structural carbonate (sc) as ($\alpha_{\text{sc-p}}=1.0086 \pm 0.0007$) and by combining the two equilibrium fractionation factors, a fractionation factor that relating $\delta^{18}\text{O}_{\text{sc}}$ to $\delta^{18}\text{O}_{\text{bw}}$ were estimated as ($\alpha_{\text{sc-bw}}=1.0263 \pm 0.0014$). To be able to compare the estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ with previous estimates in the region, we convert the $\delta^{18}\text{O}_{\text{enamel}}$ from VPDB to VSMOW scale using ($\delta^{18}\text{O}_{\text{VSMOW}}=1.03091(\delta^{18}\text{O}_{\text{VPDB}}) + 30.91$; Sharp, 2007). The $\delta^{18}\text{O}$ values of meteoric water from LAM, SKWB, DHIM and SLM were calculated as -3.5‰ (SMOW), -1.8‰ (SMOW), -5.2‰ (SMOW) and -3.8‰ (SMOW) respectively and as the meteoric water subjected to evaporation, the calculated $\delta^{18}\text{O}$ value from hippo can be considered as the most ^{18}O -enriched meteoric water.

Levin et al. (2006) suggest an approach that relates the $\delta^{18}\text{O}$ of herbivore values to aridity that bypasses the complex considerations of $^{18}\text{O}/^{16}\text{O}$ flux through animals. Instead, this aridity index relies on establishing an isotopic distinction between herbivores that are sensitive and insensitive to aridity. Although this method has not been yet widely used before, Bedaso et al. (2010) successfully applied to the Middle Pleistocene faunal assemblage in Asbole and systematically applied to Pliocene fossils at Dikika. Bedaso et al., (in review) also recommend additional points in order to consider to improve the

calibration curve for specific faunal assemblage at a given time. The calibration curve for the Pliocene Mount Galili faunal assemblage is similar to the calibration curve developed for Sidi Hakoma Member in the Hadar Formation (see Bedaso et al., in review). At Galili, giraffids, deinotheres, Tragelaphini and Aepycerotini are grouped as evaporation sensitive (ES) or non-obligate drinkers while hippopotamids, equids, elephantids, *Notochoerus* and *Nyanzachoerus* grouped as evaporation insensitive (EI) or obligate drinkers, but the rest of the taxa are intermediate between the two groups. The ^{18}O -enrichment between ES and EI taxa (ϵ_{ES-EI}) is obtained from the respective designated taxa and water deficit (*i.e.*, the difference between potential evaporation and mean annual precipitation) at Galili in the Pliocene is calculated using the calibration curve adopted (see Figure 4.5). The water deficits calculated from LAM, SKWB, DHIM and SLM are 1028 mm, 1530 mm, 890mm and 1042 mm respectively.

Thus, the paleoclimatic condition based on the water deficit and the $\delta^{18}\text{O}$ meteoric water derived from the hippo $\delta^{18}\text{O}_{\text{enamel}}$ value indicate drier conditions in the SKWB and LAM as compared to the younger SLM and DHIM, the most arid being SKWB. Elsewhere in the Awash Valley, the water deficit values indicate temporal change, Bedaso et al. (in review) reported a water deficit of 1218 mm in middle Pliocene at Dikika, whereas, White et al., (2009) reported water deficit of 1500 mm at Aramis in early Pliocene, which is comparable to the contemporaneous SKW bed at Galili. In general the Pliocene climate in the region shows long-trend from arid to humid conditions through the early and middle Pliocene, and latter shows a drier condition in the Pleistocene.

4.6 Discussion

4.6.1 Reconstruction of mammalian diet

In tropical ecosystems, the presence of both C_3 dicots and C_4 grasses is the basis for grouping animals as browsers, mixed feeders and grazers (Cerling et al., 2003c). The Pliocene Galili isotopic data indicate all ranges of foraging strategies, characterized by C_3 browsing, mixed C_3/C_4 and C_4 -dominated diet. Throughout the Pliocene, most of the taxa studied had a mixed C_3/C_4 diet to C_4 -dominated diet but the specimens analyzed from the middle Pliocene between 4.38 Ma and 3.92 Ma show mixed C_3/C_4 to C_3 -dominated diet (Figure 4.5). In general, Alcelaphini, *Notocherous*, equids, elephantids and gomphotheres were grazers with C_4 -dominated diet although there was a difference in the composition of the vegetation and range of variability within each member. Giraffids and deinotheres are the only dedicate browsers at Galili although Tragelaphini had occasional pure C_3 diet. Bovini, Hippotragini and *Nyanzachoerus* on the other hand had a mixed C_3/C_4 diet with significant difference in the proportion of C_4 grasses. Most of the taxa considered here, specially the pure C_3 browsers and C_4 grazers did not show major shifts in the dietary adaptation with time despite the change in the environmental condition, as long as their preferred diet is available on the landscape. Although the change in the dietary adaptation of some of the mixed feeds is not statistically significant, they track the environmental changes through time more closely. For example, Bovini show a change of dietary adaptation from exclusive C_4 grazing in the SKWB, to variable grazing to mixed C_3/C_4 diet in the other members, which reflect the relative proportion of C_3 and C_4 vegetation in respective members (Figure 4.5). Similarly, Tragelaphini also exhibited dietary shift from browsing in the DHIM to mixed feeding in all the other members, and

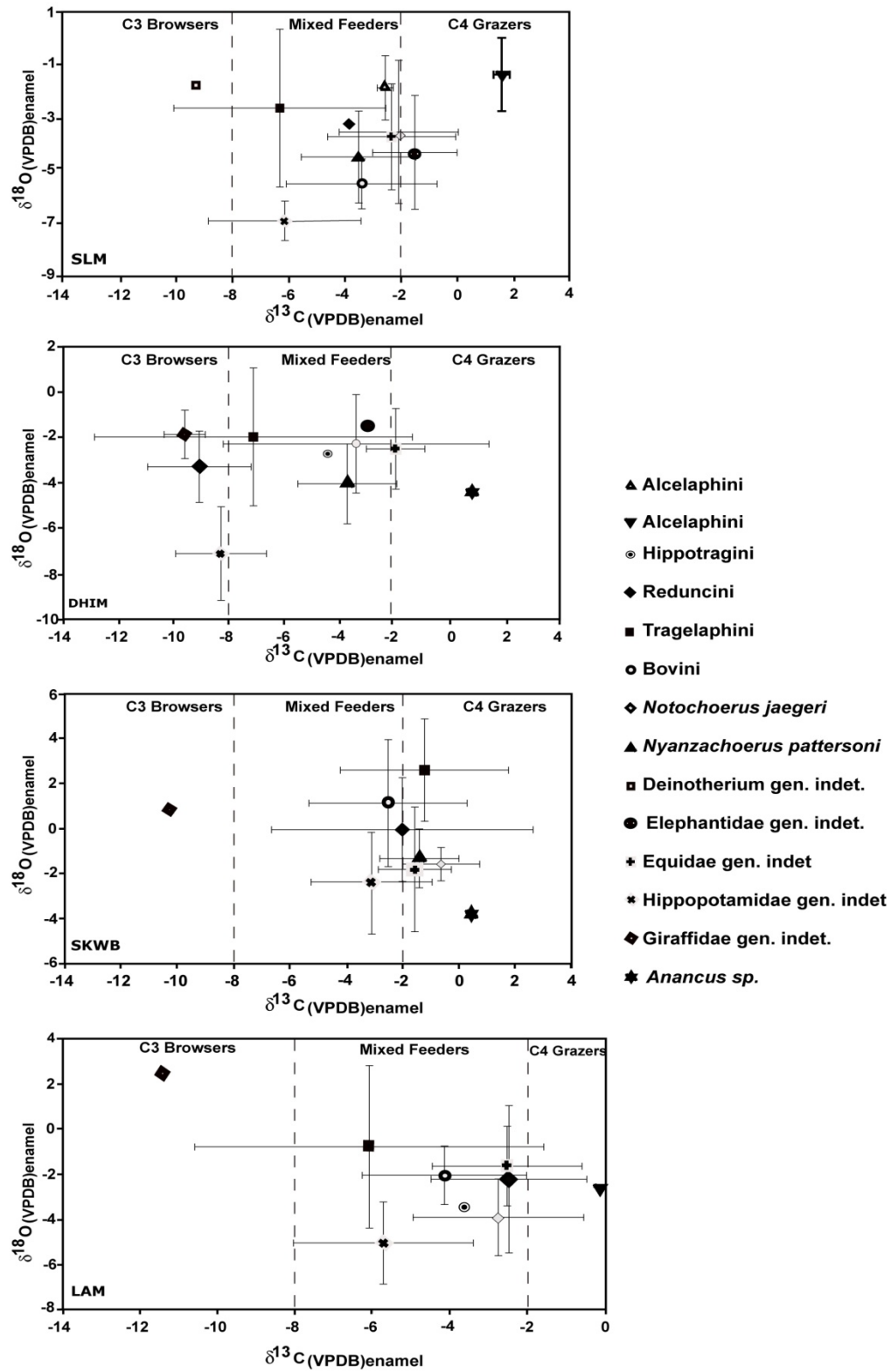


Figure 4.5 Bivariate $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic plot of tooth enamel; the points represent the mean with standard deviation (1σ) in respective stratigraphic members.

Nyanzachoerus were exclusively grazing on C₄ vegetation in the SKWB while variably grazes in the other members. These changes in the relative proportion of C₃/C₄ vegetation in the mixed feeder's diet faithfully follow the relative proportion of C₃ and C₄ vegetation on the landscape in the early to middle Pliocene at Galili and suggest the use of mixed feeders as environmental tracers.

4.6.2 Paleoenvironmental reconstruction

Stable carbon and oxygen isotopic composition of tooth enamel has provided information regarding the paleoenvironmental and paleoclimate change of the past (*e.g.*, Lee-Thorp et al., 1989; Kingston and Harrison et al., 2007; Levin et al., 2008; Bedaso et al., 2010). A combined plot of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tooth enamel (Figure 4.5) indicates that in the early and middle Pliocene the environmental and climatic condition at Galili was variable. In the early Pliocene at Galili between 5.29 Ma and 4.38 Ma, C₄ vegetation was significant on the landscape with less C₃ vegetation, indicating a relatively wooded grassland paleoenvironmental condition with up to 80% C₄ grasses. The oxygen isotope values, along with the estimated water deficit, at the site signify a change from a wet to dry climate in the early Pliocene. The upper part of the early Pliocene was evidently drier and with more open vegetation than the lower part. In the lower part of the middle Pliocene, between 4.38 Ma-3.92 Ma, C₃ vegetation was dominant over C₄ vegetation. Oxygen isotope values signify a wetter climatic condition than the rest of the early and middle Pliocene. The Paleoenvironment in this interval is interpreted as wet wooded grassland to grassy woodland. The landscape in the upper part of the middle Pliocene at Galili was dominated by C₄ grasses with some C₃ vegetation. The ecosystem carbon isotope coupled

with the oxygen isotope data is interpreted as wet wooded grassland. The general environmental and climate trend from early to middle Pliocene at Gallili shows a change from dry/open to a humid/closed environmental condition. The observed change in the abundance of C₄ grasses, reconstructed $\delta^{18}\text{O}_{\text{meteoric water}}$ values and calculated water deficit in respective members during the Pliocene indicate fluctuation of the climate and environmental condition in the region rather than uni-directional change, at least in the early to middle Pliocene.

4.6.3 Habitat structure

Habitat structure is a very important concept in ecology. We adopt the habitat structure definition verbatim from Byrne (2007), which is modified from McCoy and Bell (1990) and Beck (2000), “the amount, composition and three-dimensional arrangement of biotic and abiotic physical matter within a defined location and time; refers to complexity and heterogeneity of physical matter across horizontal and vertical physical space”. The heterogeneity and complexity of the Neogene landscape in Eastern Africa arises from the emergence and expansion of C₄ grasses, short and long-term climate variability in the region, and active tectonic, volcanism and changes in topography (Bobe and Behrensmeyer, 2004, deMenocal, 2004; Wynn, 2004; Kingston, 2007). Detailed reconstruction of habitat structure is then critical to understand the available resources including food, shelter and further morphological and behavioral adaptations of Plio-Pleistocene hominids (Spencer 1997). However, unlike the general paleoenvironmental reconstruction and proportion of C₃ and C₄ vegetation on the landscape, determining the habitat change with time has remained a challenge (Plummer et al., 2008). The following

section discusses the use of carbon isotopic composition of tooth enamel to reconstruct and estimate the relative proportion of the early and middle Pliocene habitat at Galili.

In general, the carbon isotopic results show that C₄ grasses were significant components of the total diet of the fauna at Galili and on the paleolandscape but this did not necessarily show that all grass was found in an open grassland habitat, instead this grass could be distributed over woodland or shrubland habitats. To assess the types of habitat that would have been present, individual isotopic values in each member are weighted by faunal abundance and biomass consumption per day of the respective taxa (See Bedaso et al., 2009) and normalized to unity to show the relative proportion of different habitats (Figure 4.6). The description and nomenclature vegetation and habitat used in this study follows the United Nations Scientific and Cultural Organization (UNESCO) definitions for classification of African vegetation (White et al., 1983). We use the ecosystem description of $\delta^{13}\text{C}$ values for soil organic matter from different tropical ecosystems compiled by (Cerling et al., 2010 and references therein).

The carbon isotope data in the early Pliocene at Galili between 5.29 Ma-4.38 Ma documented large variation in terms of the general paleoenvironmental conditions and type and proportion of paleohabitats present (Figure 4.6). In early Pliocene the habitat structure at Galili was dominated by wooded grassland and shrubland followed by grassland and riparian woodland (*i.e.*, ~ 35% wooded grassland, ~ 45% shrubland, ~12% grassland and ~8% riparian woodland, Figure 4.6) with $\delta^{13}\text{C}_{\text{ecosystem}} = -16.8\text{‰}$ indicating 63% C₄ grasses on the landscape. Later in this interval, the $\delta^{13}\text{C}_{\text{ecosystem}}$ value of -16.8‰ indicates an increase in the amount of C₄ grasses to 73% and a trend towards more open

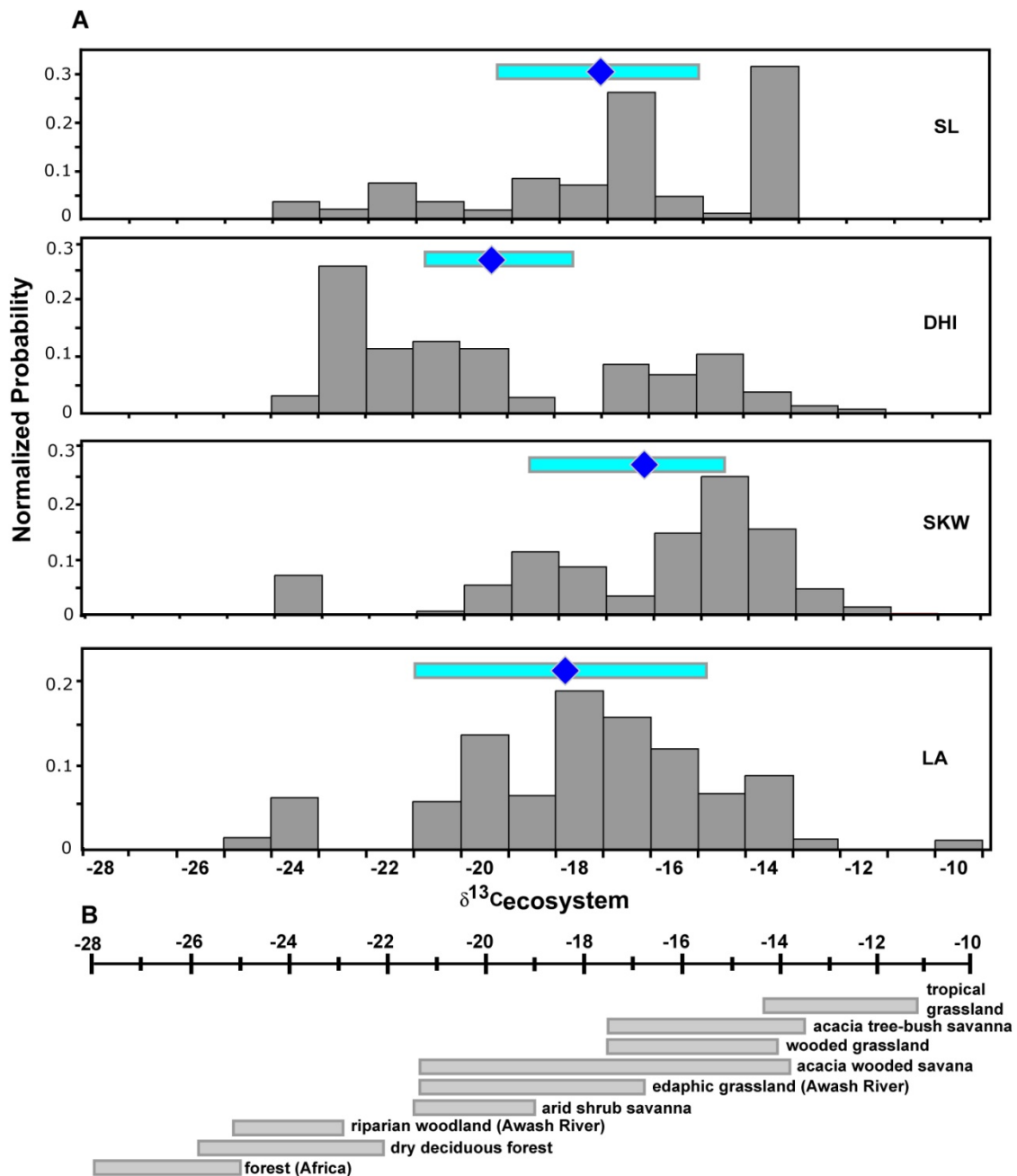


Figure 4.6 Interpretation of the habitat structure of Galili based on the ecosystem carbon isotope value derived from the $\delta^{13}\text{C}_{\text{enamel}}$, faunal abundance and the amount of food intake per day of each taxon from each member (LA= Lasdanan, SKW= Satkawhini, DHI=Dhidinleyand SL= Shabeley Laag). (A) Histogram showing the proportion of habitat in the paleolandscape and the horizontal bar and the diamond symbol represent the range and average paleoenvironmental conditions based on estimated ecosystem carbon isotope value. (B) Adopted from Cerling et al., (2010), but only ecosystems which are common in the modern tropical Africa are considered

environment with habitats dominated by wooded grassland, shrubland and grassland with subordinate riparian woodland (*i.e.*, ~ 43% wooded grassland, ~ 27% shrubland, ~ 23% grassland, and ~7% riparian woodland). In this time interval at Galili, grasses were more abundant compared to previous reconstructions from other Pliocene sites in the Awash Valley (*e.g.*, Levin et al., 2008; White et al., 2009), which elucidate spatial variation in vegetation structure over a short distance.

Similarly, the middle Pliocene at Galili between 4.38 Ma and >3.6 Ma was characterized by a wide range of variation in the proportion of C₄ grasses, habitat type and proportion. At the lower part of this interval, between 4.38 Ma- 3.92 Ma, the average $\delta^{13}\text{C}_{\text{ecosystem}}$ value of -19.1‰ (*i.e.*, 50% C₄ grass) indicate equal proportion of C₄ grasses and C₃ vegetation. The habitat structure also signifies the high proportion of C₃ vegetation, where the habitat was ranging from closed woodland/ riparian woodland to wooded grassland with minor grassland (*i.e.*, ~40% closed woodland/riparian woodland, ~29% wooded grassland, ~27% shrubland and ~2% grassland, Figure 4.6). While, the upper part, between 3.92 Ma and >3.6 Ma was characterized by a relative increase in the C₄ proportion, with an average $\delta^{13}\text{C}_{\text{ecosystem}}$ value of -17.6‰ indicating 67% C₄ grasses on the landscape (Figure 4.6). The habitats were ranging from riparian woodland/deciduous forest to grassland (*i.e.*, ~33% wooded grassland, ~32% grassland, ~21% shrubland, ~13% riparian woodland/deciduous forest, Figure 4 6).

4.6.4 Regional environments of the Pliocene

In early and middle Pliocene, the isotopic data from mammalian tooth enamel at Galili itself indicate a wide range of paleoenvironmental conditions on the landscape laterally and with time from open wooded grassland in the early Pliocene (*i.e.* 5.29 Ma–4.38 Ma) to more closed woodland in the middle Pliocene (*i.e.*, 3.92 Ma–4.38 Ma). Regionally, early Pliocene paleoenvironmental reconstructions were done from *Ardipithecus*-bearing deposits at Aramis in the Middle Awash (WoldeGabriel et al., 1994; White et al., 2009) and similar horizons at Gona (Levin et al., 2008). However they reported a contrasting environmental condition at respective locations. At Aramis WoldeGabriel et al. (1994) and White et al. (2009) have suggested humid and cooler conditions than it is today with habitats ranging from woodlands to patches of forest. They use stable isotopic composition of tooth enamel and paleosol. While, Levin et al. (2008) using the same proxy suggests a paleohabitat with abundant C₄ grasses on the landscape. Similarly, Cerling et al. (2010) found the environmental context of *Ar. ramidus* at Aramis to be tree or bush savanna with a habitat ranged from riparian forest to grassland. The tooth enamel isotopic data at Galili from the same level indicate a range of dry open woodland to grassland habitat, where C₄ grass was prominent on the landscape. This diversity in the paleoenvironment and habitat structure in spatial scale is attributed to a number of factors including but not limited to active tectonics, volcanism, availability of water and type of depositional environment in respective sedimentary basins. Regardless the heterogeneity of habitat within a short distance made diverse resources available to early hominins.

4.7 Conclusion

Stable carbon and oxygen isotopic composition of herbivores tooth enamel from the Galili PaleoAnthropological Research area (GPAR) provides a paleoenvironmental and paleoclimatic record of the early and middle Pliocene as far south in the Afar depression as possible. The result from this study increases the spatial scale, which could indicate the degree of variability in the environmental conditions among basins, that are distinct at least in terms of the local geology, soil type, geomorphology and the presence or absence water bodies and type of water bodies (*i.e.*, rivers and lake) present. The Pliocene Galili isotopic data indicate all ranges of foraging strategies, characterized by C_3 browsing, mixed C_3/C_4 and C_4 grazing diet. Throughout the early and middle Pliocene most of the taxa had a mixed C_3/C_4 to C_4 -dominated diet but the specimens analyzed from middle Pliocene between 4.38 Ma-3.92 Ma shows mixed C_3/C_4 to C_3 -dominated diet. These ranges of dietary adaptations indicate the presence of a variety of vegetation on the paleolandscape that includes gallery forest, closed woodland, open woodland and grasslands. The early to middle Pliocene habitats represented at Galili were heterogeneous, but with a general tendency towards more open habitat broadly similar to the modern African savanna (*i.e.*, grasses were a dominant cover, White et al., 1983) and would include grassland and wooded grassland (Cerling et al., 2010 and references therein). This clearly indicates the significance of C_4 grasses in the paleolandscape by Late Miocene or early Pliocene the latest, and could have an important implication to the morphological adaptation (*e.g.*, early bipedalism) and resources available for the early hominins. The oxygen isotopic composition of tooth enamel indicates a generally variable climatic condition in the early and middle Pliocene but with wetter condition in

the middle Pliocene compared to the early Pliocene although the lower part of early Pliocene is wetter than the later part, where, it is characterized by a high aridity index and estimated ^{18}O -enriched meteoric water.

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CHAPTER FIVE

PLIO-PLEISTOCENE PALEOCLIMATES OF AWASH VALLEY

5.1 Introduction

The degree to which human evolution has been shaped by past global climate changes has been a subject of considerable debate, especially with respect to adaptive or causal perspectives on the morphological and behavioral variability documented in the human fossil record (Vrba et al., 1995; Potts, 1998; Kingston, 2007). Human evolution has been linked and interpreted in a global climatic framework obtained from marine core sediments, which are in general characterized by an increase in aridity, seasonality, and environmental variability periodically punctuated by intervals of environmental changes (Potts, 2007; deMenocal, 2004). Although these marine records provide relatively continuous and well-dated global paleoclimatic framework, the temporal resolution of the hominid record is not sufficient to develop unambiguous causal links with human evolution (Kingston, 2007). Moreover, making a link between global and regional paleoclimate change has been a challenge and remains to be established. This is partly because of the fragmentary nature of the environmental evidence on land both in time and space, which is further hampered by dating uncertainties and preservation biases in the fossil record (deMenocal, 2004). Additionally climate is not the only influence acting on landscapes, rather it is coupled with local tectonic activity (Lee-Thorp and Sponheimer, 2007; Maslin and Christensen, 2007). To establish a link between regional and global

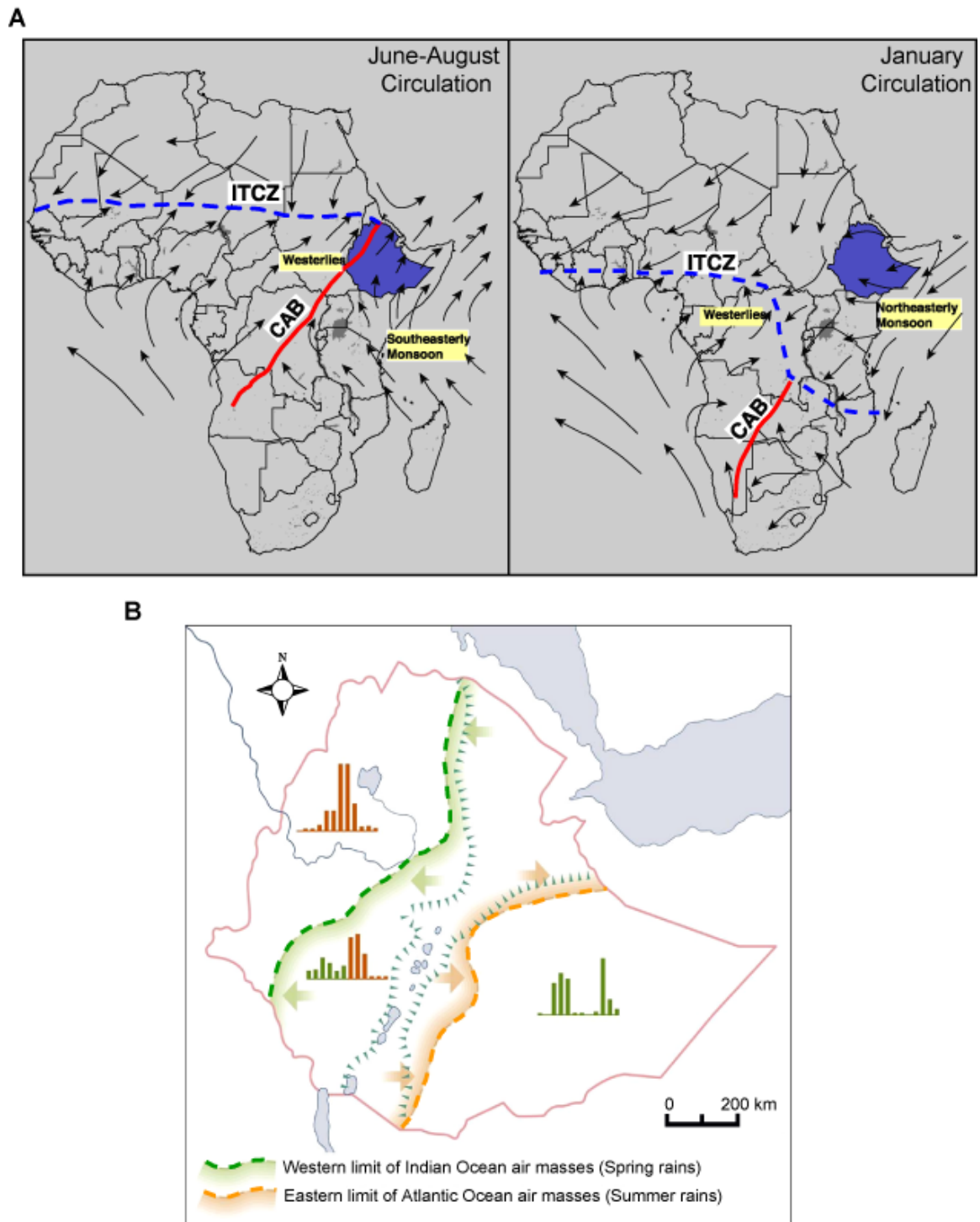
paleoclimatic change, and the causative role of climate change in human evolution, there is a need to integrate various lines of evidence from multiple localities across space and time. First, it is important to address questions at the scale of individual basins and then combine the results to compare spatial variation and build a regional environmental and climatic framework (Campisano and Feibel, 2007).

This chapter discusses tooth enamel stable oxygen isotope data compiled from four different sites in the Afar Rift: Chorora (11–10.5 Ma), Galili (>5.29–>3.6 Ma), Dikika (>3.8–3.24 Ma) and Asbole (0.8–0.64 Ma). The previous chapters (chapters 2, 3 and 4) discussed site-specific paleoenvironmental and paleoclimatic conditions for the respective time intervals and compared with contemporaneous sites in eastern Africa. Here, the focus is (1) to synthesize the regional Plio-Pleistocene paleoclimatic conditions, (2) to assess the link between global and regional climate conditions, (3) to determine the role of climate change in the ecosystem dynamics, and, finally, (4) to introduce a new proxy for paleotemperature estimates using stable oxygen isotopic composition of tooth enamel from hippopotamus and crocodile.

5.2 Global and regional climate change and human evolution

An understanding of the present African climate system lays a foundation for understanding how climate has varied through time, what factors governed the climate, and how it might have influenced human evolution. Equatorial East Africa is considered one of the more meteorologically complex regions of Africa (Nicholson and Entekhabi, 1987; Nicholson, 1996). Its climate is impacted primarily by moisture from the Indian

Ocean and Atlantic Ocean sources, where the northeasterly trade winds mostly bring dry air and the southeasterly trade winds supply moisture from the Indian Ocean, and converge at the Intertropical Convergence Zone (ITCZ). Atlantic-derived westerly African monsoon brings moisture to eastern Africa and converges with the easterly trade winds along the Congo Air Boundary (CAB) (Nicholson, 1996). The north-south seasonal migration of the ITCZ is one of the main controls on the timing of rainy seasons in eastern Africa (Griffiths, 1972; Nicholson, 1996). In addition, the movement of ITCZ controls the moisture sources and relative contribution of moisture from the Indian and Atlantic Oceans which varies locally, seasonally and annually. Figure 5.1A, B shows the seasonal distribution of rainfall in Ethiopia and the different moisture sources. In Ethiopia, the North Western Plateau (NWP) receives precipitation from Atlantic sources and has only one rainy season, whereas the South Eastern Plateau (SEP) has two rainy seasons both from the Indian Ocean. The Ethiopian Rift Valley (ERV) obtains moisture from both the Indian and Atlantic oceans, and has two rainy seasons. The two rainy season in Ethiopia are: “big rains” (locally known as *Kiremt*), that last from June through September and “small rains” (locally known as *Belg*), that last between March and May (Gamachu, 1977). Between June and September, the ITCZ is located in northern Ethiopia and the region is under the influence of the southwesterly and southerly monsoon flows, when the NWP, SEP and the MER get rain. Between October and March, the ITCZ is located south of Ethiopia, and the region is under the influence of northeasterly flow of dry, cold air. In spring, the ITCZ migrates northward, and moisture from northeasterly and easterly flows from the Northern Indian Ocean (Gamachu, 1977).



ITCZ is located south of Ethiopia where the country is under the influence of northeasterly dry air masses. **B.** Seasonal distribution of rainfall in different physiographic regions of Ethiopia. The histograms show monthly rainfall distribution starting from January. The western most sector of Ethiopia has only one rainy season in the months of JJAS. The central sector is characterized by bimodal rainfall distribution during the months of March to April and the main rainy seasons JJAS. While the eastern sector of Ethiopia has two rainy seasons with the main rainfall from March to May and in October. The green and orange dotted lines indicate the western limit of the Indian Ocean air masses and the eastern limit of the Atlantic Ocean air masses respectively (Figure source, Nicholson, 1996).

The change in seasonal moisture sources and proportion control the isotopic composition of precipitation. Based on surface and groundwater isotopic analyses, Kebede (2004) showed the relationship between the seasonal variations in isotopic composition of Ethiopian precipitation with changes in the moisture sources. In general, the summer rainfall is ^{18}O -depleted as compared to spring rainfall. In spring, the country receives moisture from the North Indian Ocean, which is geographically closer than the other moisture sources. As a result, the moisture that reaches the area represents the initial stage of condensation which did not undergo major rainout fractionation effects and is therefore relatively enriched in ^{18}O (Joseph et al., 1992).

Neogene climate variability has been documented in marine and terrestrial sediments and expressed on various timescales, each of which may have been important for human evolution. On long term, over millions of years, climate shows a general global cooling trend and intensification of polar ice sheets, which favors aridification and progressive replacement of C_3 vegetation by C_4 grasses, which in turn set preconditions for the overall hominin evolution (deMenocal, 1995, 2004; Wynn, 2004; Potts, 2007). On shorter term, tens of thousands of years, earth orbital processes was critical for controlling the

climate and aridification cycles in Africa (deMenocal, 2004), which could have influenced hominin geographic dispersal, adaptation, as well as water and food resource availability (Potts, 1998, 2007).

Marine sediment cores taken off the coast of Africa provide records of African climate changes for the Plio-Pleistocene time interval, where major global climate change phenomena are recorded. The major global climate changes include the onset and intensification of Northern Hemisphere glaciations, and shift in the dominance of Earth's orbital parameters (*i.e.*, precession, obliquity and eccentricity). deMenocal (1995) indicated that these shifts occur approximately at 2.8, 1.7, and 1.0 Ma simultaneously with changes in fluxes of aeolian sediment deposits in West and East Africa. Further, these shifts are associated with important hominin evolutionary changes including speciation, morphological and behavioral adaptation, and faunal shifts toward arid and more open vegetation (Wesselman, 1985; Vrba, 1995).

Although terrestrial records at fossil localities or nearby sites have the potential to provide long-term climate trends directly relevant to hominin evolution as well as other faunal elements, continuous paleoclimatic records are rare from East African terrestrial deposits, where active tectonics, change in basin hydrology, erosion and non-deposition play significant roles in diminishing spatiotemporal resolution (Maslin and Christensen, 2007; WoldeGabriel et al., 2000). However, multiple lines of evidences combined from terrestrial deposits broadly indicate a change of climate in East Africa from warmer, wetter conditions in the Late Miocene and early Pliocene to cooler, drier and more

variable climate during the late Pliocene and Pleistocene (Bonnefille et al., 2004; Aronson et al., 2008). Similarly, progressive replacement of closed forest and woodland by open grasslands initiated Middle Miocene with further increases after 1.8 Ma, 1.2 Ma, and 0.6 Ma as indicated by stable isotopic analysis of soil carbonate (Cerling, 1992; Hailemichael et al., 2002; Levin et al., 2004; Wynn, 2004). More recently, hominin environments are being reconstructed from the Awash Valley by using stable isotopes on associated mammalian tooth enamel (Levin et al., 2008; White et al., 2009, Bedaso et al., 2010; in press). To this end, new isotopic measurements on herbivore tooth enamel were made from the Chorora, Mount Galili, Hadar and Busidima formations, which provide stand-alone paleoenvironmental and paleoclimatic record, potentially used to reconstruct the habitat structure and available food resources for early hominins. In general, this combined data set shows a similar trend in the increase of open vegetation on the landscape, an increase in the proportion of C₄ grasses in most of the mammalian diet and progressively drier climatic condition from the Late Miocene through the Pliocene to Pleistocene. But it is also evident that this trend was not a steady, uniform process. For example, middle Pliocene data from Dikika and Galili indicate wetter climatic conditions compared to early Pliocene and Pleistocene periods, and a rebound of closed vegetation at least some time between ~ 4.38 Ma and ~ 3.24 Ma.

5.3 Mammalian tooth enamel from Awash Valley

Mammalian tooth enamel has been analyzed from multiple sites in the Awash Valley. The Pliocene and Pleistocene fossil bearing sediments at Dikika are formally attributed to the Pliocene Hadar and the Pleistocene Busidima formations (Taieb et al., 1972; Quade et

al., 2004), while sediments at Galili are designated as Mount Galili Formation and are time equivalent to the Pliocene Sagantole Formation (Urbanek et al., 2005). In addition, new data is presented from the Chorora Formation, which is the oldest unit in the Afar Depression and was deposited along its southeastern escarpment. It is composed of fluvial and lacustrine diatomaceous sediments with pumice and tuffs initially dated between 9 Ma and 10.5 Ma (Kunz et al., 1975). Later, based on various geologic and paleontologic data, along with a biochronologic assessment of the fauna, Geraads et al. (2002) reassigned the Chorora fauna to between 10.6 and 10.3 Ma. The data presented here significantly increase the spatio-temporal data of tooth enamel isotopes in the Awash Valley.

All of these stratigraphic records except the upper Busidima Formation, where the Asbole fossils were collected, are part of a complex history of lake migration in conjunction with subsiding axial rift basins from that southeast part of Afar, near Chorora towards the northeast, where the triple junction is presently located (Kalb, 1995; Tesfaye et al., 2003). Within individual basins, the lake experienced multiple transgression-regression cycles, intercalating among intervals of fluvial and deltaic sedimentation as well as soil formation (Hailemichael et al., 2002; Wynn et al., 2008). The Busidima Formation on the contrary shows intermittent deposition in a predominantly fluvial environment with periods of erosion and non-deposition (Geraads et al., 2004; Wynn et al., 2008). These changes in the depositional environment, erosion and non-deposition signify the change in the paleohydrology of the basin with time and availability of drinking water from various sources.

Drinking water source for the fauna and early hominin includes perennial rivers, ephemeral streams, ponds, closed evaporative lakes, and lakes with continuous supply of fresh water from perennial rivers. The $\delta^{18}\text{O}$ of the water was affected by evaporation. River water is sourced from either direct precipitation as run-off or via groundwater from springs. River water, however, only tracks $\delta^{18}\text{O}$ if the surface run-off predominates, as groundwater is isotopically constant, at least in the relatively short term, and reflects the average annual isotopic composition of precipitation (Kebede et al., 2007). These differences in the $\delta^{18}\text{O}$ composition of water source coupled with seasonality and drinking habits of various faunal elements (i.e., obligate versus non-obligate drinkers), and other climate factors which affect the oxygen isotopic composition of meteoric water could be reflected in the variation of oxygen isotopic composition of tooth enamel within a single taxon and among sympatric taxa.

In the Plio-Pleistocene of the Awash Valley, a very wide range of mammalian tooth enamel oxygen isotope values have been documented (Figure 5.2). The maximum range of $\delta^{18}\text{O}_{\text{enamel}}$ values observed within a taxon ranges between 8‰ in the AFZ and 11.6‰ in the SHM, while the differences between the average $\delta^{18}\text{O}_{\text{enamel}}$ of sympatric taxa range between 5.0‰ and 8.5‰ in different members. These isotopic variations in respective members could be attributed to evaporation of the source water and seasonal differences in the oxygen isotope composition of rainwater over the short term. However, over the long term, it could be attributed to changes in the moisture source or proportion of moisture sources and change in the isotopic composition of ocean (Dansgaard, 1964).

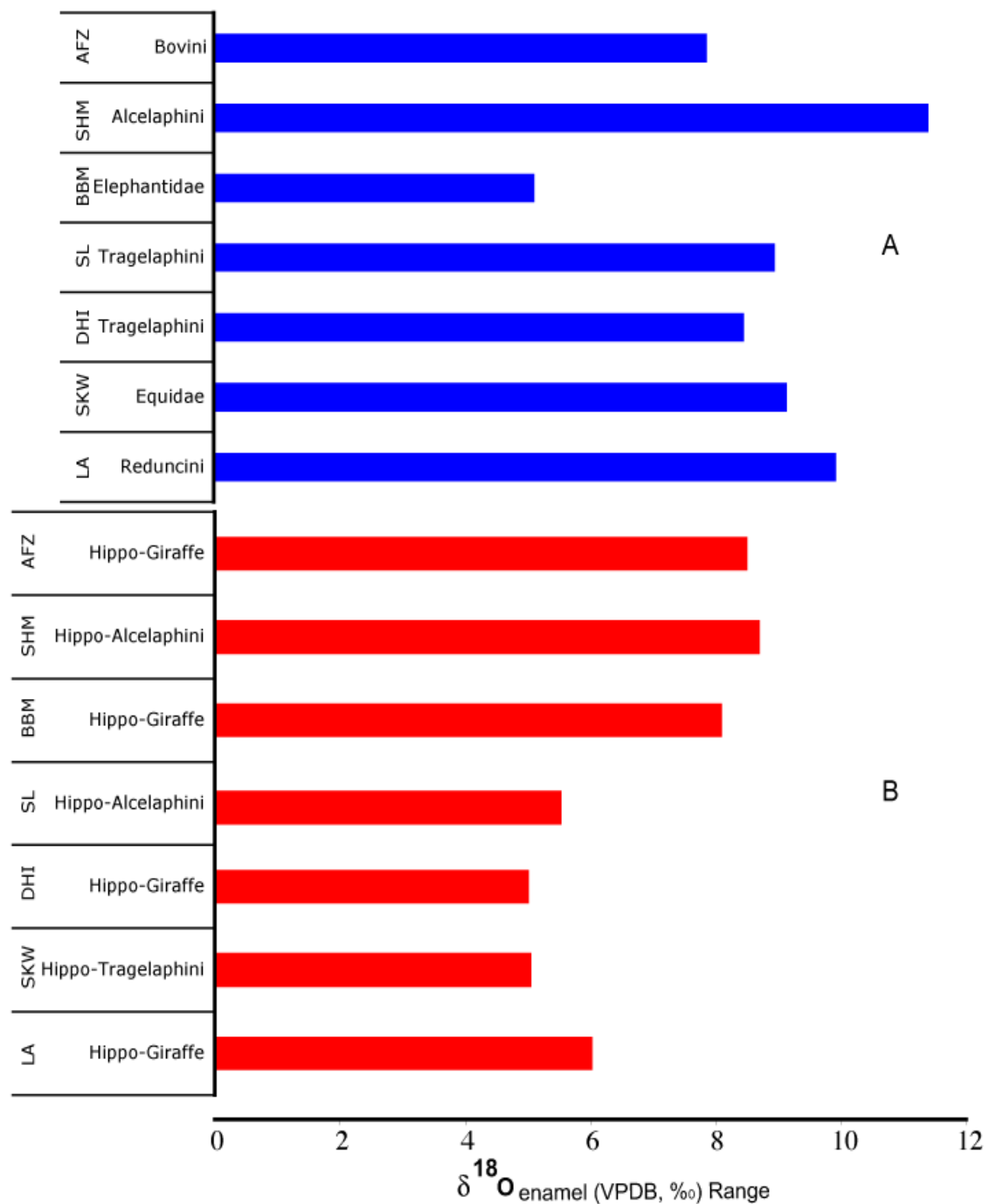


Figure 5.2 $\delta^{18}\text{O}_{\text{enamel}}$ variations by member **a**: Variation within taxon **b**: Variation across the palelandscape between taxa where the range is calculated as a difference between average values of taxa with highest and lowest values.

On the other hand, it is indicated that diet, physiology, and drinking habit affect the oxygen isotopic composition of tooth enamel. Bocherens et al. (1996) and Kohn (1996) used modern taxa within limited areas of similar climate but with different dietary adaptation and reported as much as 9‰ variation in $\delta^{18}\text{O}_{\text{enamel}}$ sympatric taxa. In comparing the $\delta^{18}\text{O}_{\text{enamel}}$ values of sympatric taxa, results from previous studies are in a general agreement that browsing herbivores tend to be enriched in ^{18}O compared to grazing herbivores whereas mixed-feeding herbivores are intermediate between the two groups (e.g. Kohn, 1996; Cerling et al., 1997; Levin et al., 2008; Bedaso et al., 2010). In contrast, Bocherens et al. (1996) reported that browsing rhinos and mixed-feeding elephants were depleted in ^{18}O compared to other sympatric taxa. In the SHM (Chapter 3 Figure 3.4), also the Alcelaphini, which were exclusively grazers, have the most ^{18}O -enriched values as compared to the other taxa. Alcelaphini in the SHM member also show values which are clustered around +3.0‰ and -7.0 ‰, where the variation could be explained by one or a combination of factors explained above but it is equally important to emphasize that the samples might come from different levels within the SHM.

5.4 Short-term variation in $\delta^{18}\text{O}$ of tooth enamel

5.4.1 Seasonality

Stable isotopes of tooth enamel provide information on animals' diet consumed over the time of tooth formation. Once enamel is formed as the skeletal material is not re-absorbed and modified, it preserves the signal recorded during tooth formation unlike bone, which are characterized by re-absorption and precipitations throughout a mammal's life, and provides information about average diet (Koch, 1998). Tooth enamel mineralizes starting

from the crown to the root over a limited period, which varies among animals and even between different teeth of a single individual. The $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ values along a tooth growth axis represent a time succession of isotopic variations relating to dietary changes and available drinking water (Zazzo et al., 2005). Furthermore, Kohn et al. (1998) indicated that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variation reveals seasonal changes in climate elements including rainfall, humidity, and temperature, which affect the availability of forage as well as drinking water compositions.

Eight equid and giraffid fossil teeth from BBM, SHM, AFZ and one modern tooth from Dikika were serially sampled. These teeth are represented by intra-tooth profiles, with each tooth consisting of 4-6 samples in the case of giraffids, and 11-13 samples from equids with profile length ranging between 12 -21.5 mm and 50 -53.5 mm from occlusal surface to root respectively. Each sample was approximately 2 mm long with ~0.5 millimeter between sequential samples. The size of the equid tooth allows successive samples of sub-seasonal resolution. Hoppe et al. (2004) indicated that in modern equids it takes up to ~1.5 to ~2.8 years to mineralize enamel completely. All sampling was done on M3, and samples were removed from the teeth using a Dremel high-speed rotary tool with a 0.5 mm drill bit. Sample pretreatment and preparation were done following the standard procedures for the treatment of tooth enamel (Lee-Thorp and Van der Merwe 1987; Koch 1998). Figure 5.3 shows $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tooth enamel from fossil equids sampled from BBM,

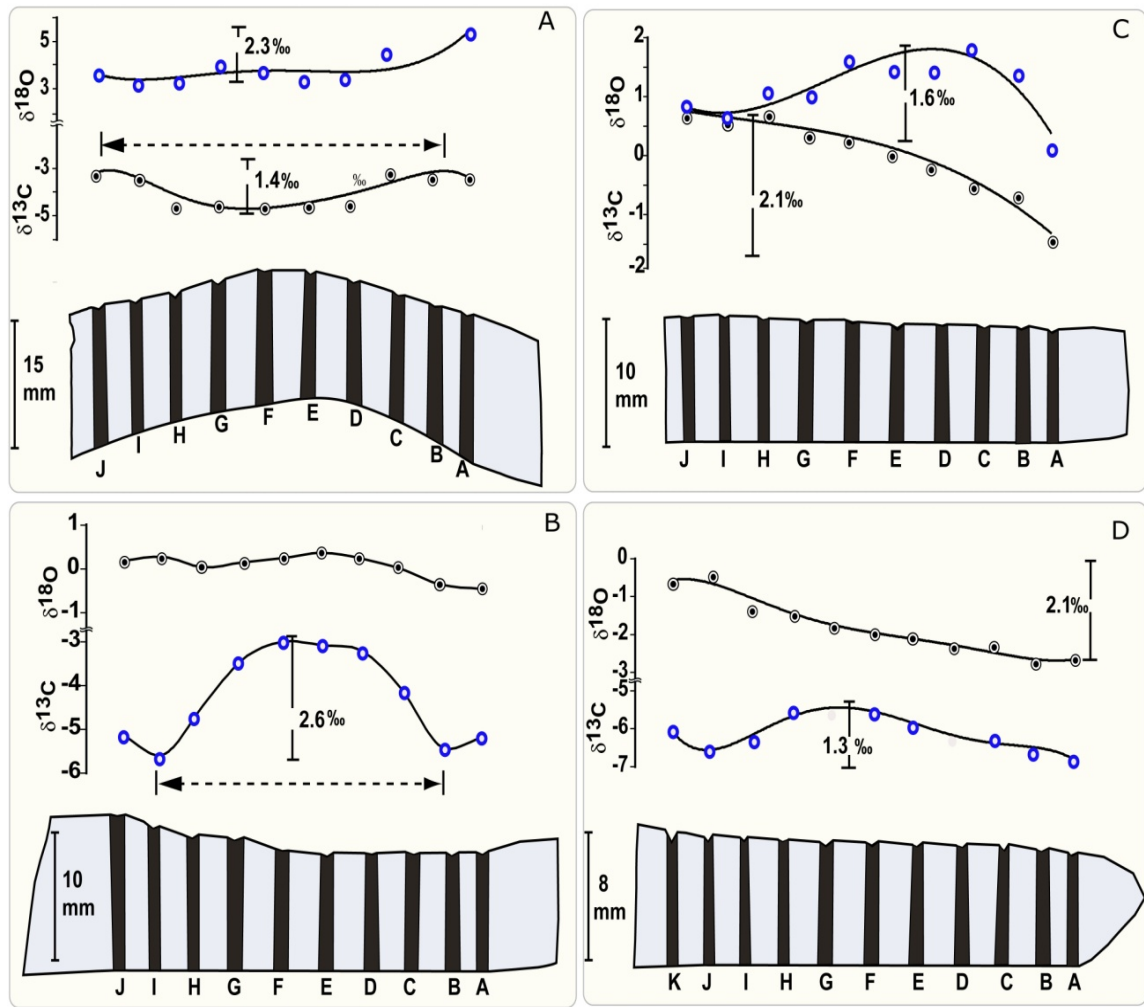


Figure 5.3 Carbon and oxygen isotopic profiles of equids from fossil and modern tooth sample from A to J cervix to apex **a**: Modern **b**: Asbole fauna zone (0.8–0.64 Ma) **c**: Sidi Hakoma Member (3.42–3.24 Ma) and **d**: Base of Basal Member (>3.8–3.6 Ma).

SHM, AFZ and modern samples from Dikika. The interpretations of the sinusoidal patterns of intra-tooth $\delta^{18}\text{O}$ values assign the more ^{18}O -enriched values to summer and the less ^{18}O -enriched values to winter (Fricke et al., 1998; Kohn et al., 1998). In the same way, more ^{13}C -enriched values indicate more C_4 grasses in the diet than less ^{13}C -enriched values.

5.4.2 Intra-tooth Isotopic variations

Intra-tooth enamel $\delta^{18}\text{O}$ values of the middle Pliocene equids from the BBM and SHM of the Hadar Formation display isotopic variation ranging from 1.3 ‰ to 1.6‰ respectively. In the Middle Pleistocene equids at the AFZ in the Busidima Formation and in a modern equid tooth sampled from the Dikika the range is 2.6 and, 2.3‰, respectively. Relatively small intra-tooth enamel $\delta^{18}\text{O}$ variation of 1.0‰ and 0.9‰ were documented in the giraffids from middle Pliocene SHM and middle Pleistocene AFZ, respectively. The difference in the intra-tooth $\delta^{18}\text{O}$ values between equids and giraffids in a single member could be attributed to differences in the range of dietary adaptation and use of the different drinking water sources available on the landscape. Because giraffes are non-obligate drinkers and get most of their water from leaves, they are unlikely to drink directly from evaporative lakes and rivers. Given minimum variation in humidity throughout the year, the seasonal variation of $\delta^{18}\text{O}$ of leaf water would be insignificant. On the contrary, equids access both ^{18}O -depleted and ^{18}O -enriched open drinking water sources. In tropical and subtropical grasslands, seasonality of rainfall is strong and determines the available water, and after rainy season ends soil dry out at the top layer first and progressively dry out downward. This progressive drying out first affects the shallow rooted-grasses community, while water is still available for deep-rooted C_3 plants (Flanagan and Ehleringer, 1991). Moreover, seasonal grazing on dry grasses and green grasses along with possible migration could contribute to observed seasonal variation in $\delta^{18}\text{O}$ of tooth enamel (Flanagan and Ehleringer, 1991). Although here drinking habit, dietary adaptation, and migration of animals are considered to explain the oxygen isotope variation within a single taxon and sympatric taxa, there are a number of other ecological,

physiological, geographical and climatic factors, which have effects on oxygen isotope composition of tooth enamel and drinking water source.

5.5 Long-term variation in $\delta^{18}\text{O}$ of tooth enamel

The variation of oxygen isotopic composition of tooth enamel for a given taxon and the difference among sympatric taxa document different aspects of the environment and climate (Kohn, 1996). Taxa which are obligate drinkers, track the drinking water, and provide information on change in the isotopic composition of precipitation, whereas non-obligate drinkers track evaporative ^{18}O enrichment of leaf water, which is also a proxy for relative humidity (Levin et al., 2006). During the Plio-Pleistocene, a significant change in the oxygen isotopic composition of tooth enamel is documented in Bovini, Tragelaphini, Reduncini, equids, hippopotamids, and to less extent elephantids and *Nyanzachoerus* while there was no significant change in Alcelaphini, Hippotragini and giraffids (see Appendix I, for statistical tests).

Although there are some differences between taxa in the timing of the observed changes in the oxygen isotope values, in general shows generally ^{18}O -enriched values occur in the SKWM (~ 4.5 Ma) and later post unconformity in the AFZ (~0.7 Ma)(Figure 5.4). The oxygen isotopic composition of tooth enamel shows an average of 4.0‰ variation between 5.29 and ~3.0 Ma) and an average of 6.0‰ difference between pre- and post-unconformity assemblages at Dikika. Likewise, similar variations are documented between Galili and the AFZ except between 4.6 Ma to ~4.38 Ma, where there is no statistically significant difference ($p= 0.600$).

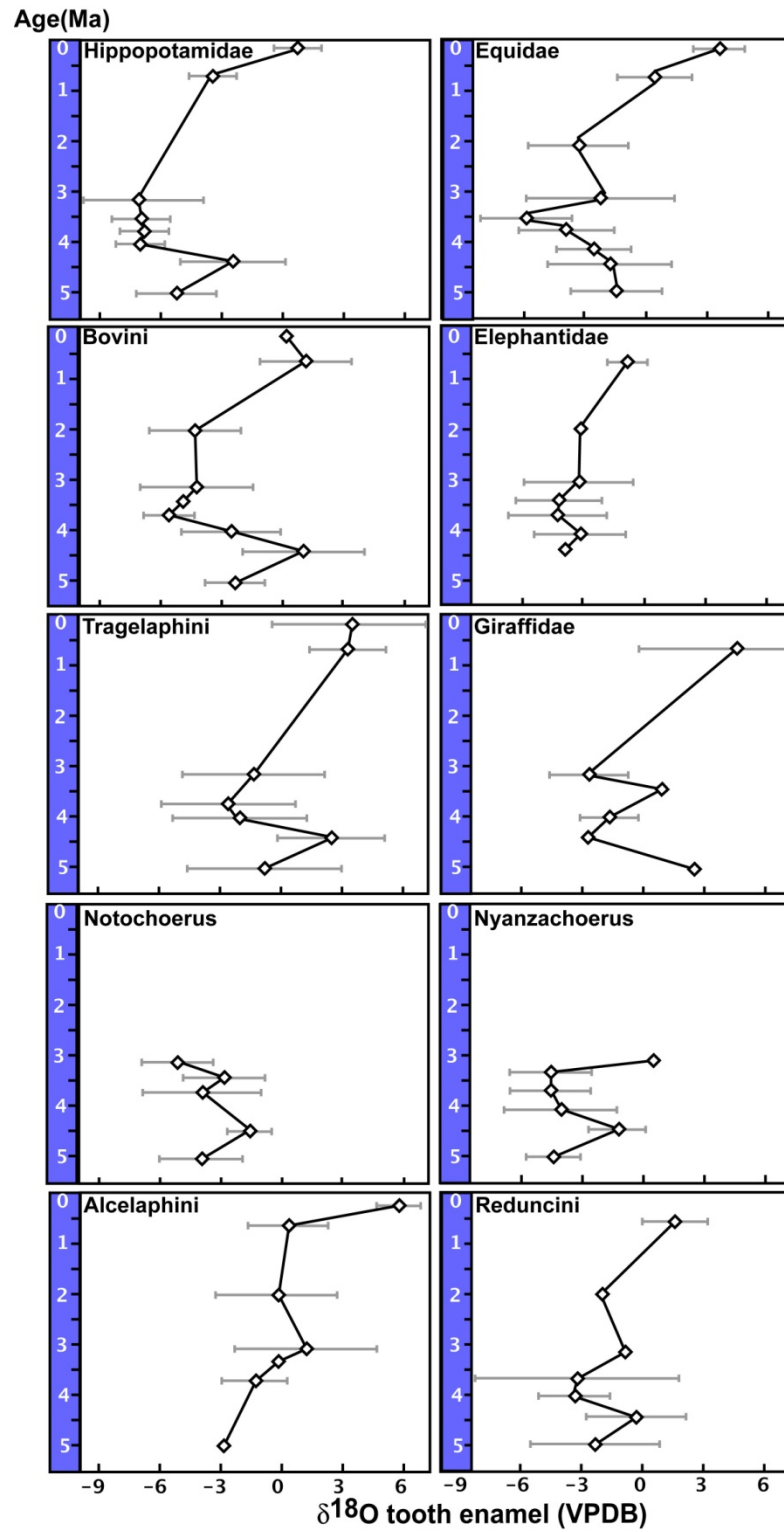


Figure 5 4 $\delta^{18}\text{O}_{\text{enamel}}$ of taxa with time, the diamonds represents average values with error bars of $\pm 1\sigma$ and each point represent different members from Galili, Dikika and Asbole.

Inter-basin comparison of oxygen isotopic compositions of tooth enamel is further complicated by additional factors including, but not limited to differences in surface and groundwater hydrology, catchment sizes, vegetative cover, and degree of evaporation (Kebede et al., 2007). However, in the absence of continuous sedimentary records from a single basin, integrating records from adjacent basins provides a regional perspective of temporal changes (Campisano and Feibel, 2007). To this end, analyzing the changes in the oxygen isotopic composition of tooth enamel in a single taxon both in space and time, difference between obligate and non-obligate drinking taxa signify the nature of controlling factors of those variations. In the Plio-Pleistocene there are similar trends in the variation $\delta^{18}\text{O}_{\text{enamel}}$ within Hippopotamidae and Bovin, where both are obligate drinkers; this indicate a change in the $\delta^{18}\text{O}$ of drinking water through this interval (Figure 4). Temporal changes in the $\delta^{18}\text{O}_{\text{enamel}}$ of obligate drinkers track isotopic composition of precipitation, which in turn is sensitive to climatic variables such as, mean annual temperature, rainfall seasonality, rainfall amount, and vapor transport paths and altitude (Dansgaard, 1964). On the other hand, changes in $\delta^{18}\text{O}_{\text{enamel}}$ of non-obligate drinkers with time accompanied by no change in their sympatric obligate drinkers indicate less humid or arid conditions. Thus, the $\delta^{18}\text{O}$ of tooth enamel can be used as a proxy for paleoclimate, and track moisture sources, change in the proportions of moisture from different source and ultimately reflect the $\delta^{18}\text{O}$ of ocean water.

5.6 Plio-Pleistocene $\delta^{18}\text{O}$ meteoric water reconstruction

Oxygen stable isotopic composition of precipitation can be used to track moisture sources and meteorological processes as the distribution of a heavy or light isotope in water

depends on equilibrium and kinetic processes associated with water-phase transitions (Dansgaard, 1964). $\delta^{18}\text{O}_{\text{enamel}}$ of obligate drinkers has been used to track $\delta^{18}\text{O}_{\text{meteoric water}}$ and serve as a proxy for local meteoric water (Kohn, 1996). In the Awash Valley and elsewhere in East Africa, the $\delta^{18}\text{O}_{\text{enamel}}$ of hippopotamuses (*Hippopotamus amphibius*) are significantly ^{18}O -depleted compared to remaining, coeval herbivores; as a result, they better approximate the $\delta^{18}\text{O}_{\text{meteoric water}}$ (Bocherens et al., 1996; Cerling et al., 1997, Bedaso et al., in press). The $\delta^{18}\text{O}$ data in Table 2.1, 3.1 and 4.1 of chapter 2, 3 and 4 shows that in most members the values of hippos clustered relatively tightly, but the wide-ranging temporal shifts in these values could reflect differences in the isotopic composition of the water bodies they lived in. For example, smaller bodies of water, such as ephemeral drinking pools, experience rapid water replacement, thereby reducing the effect of evaporation. Meanwhile larger, buffered bodies of water from springs and rivers would yield evaporated signal, the former reflect $\delta^{18}\text{O}$ values of precipitation more accurately (Koch et al., 1989). To better approximate $\delta^{18}\text{O}_{\text{meteoric water}}$, the most negative $\delta^{18}\text{O}$ of tooth enamel from hippos at each interval is used. Luz and Kolodny (1985) estimated the isotopic fractionation between body water (bw) and the phosphate (p) fraction of apatite as ($\epsilon_{\text{p-bw}} = 17.8\text{‰}$). Similarly, Bryant et al., (1996) estimated the isotopic enrichment between the phosphate fraction and structural carbonate (sc) as ($\epsilon_{\text{sc-p}} = 8.6\text{‰}$). By combining the two the isotopic fractionation between $\delta^{18}\text{O}_{\text{sc}}$ to $\delta^{18}\text{O}_{\text{bw}}$ was estimated as ($\epsilon_{\text{sc-bw}} = 26.3\text{‰}$). Reconstructed Plio-Pleistocene $\delta^{18}\text{O}_{\text{meteoric water}}$ from the most negative $\delta^{18}\text{O}_{\text{enamel}}$ value of hippos within each member ranges between -5.6‰ (VSMOW) in the middle Pliocene and -1.9‰ (VSMOW) in the Middle Pleistocene.

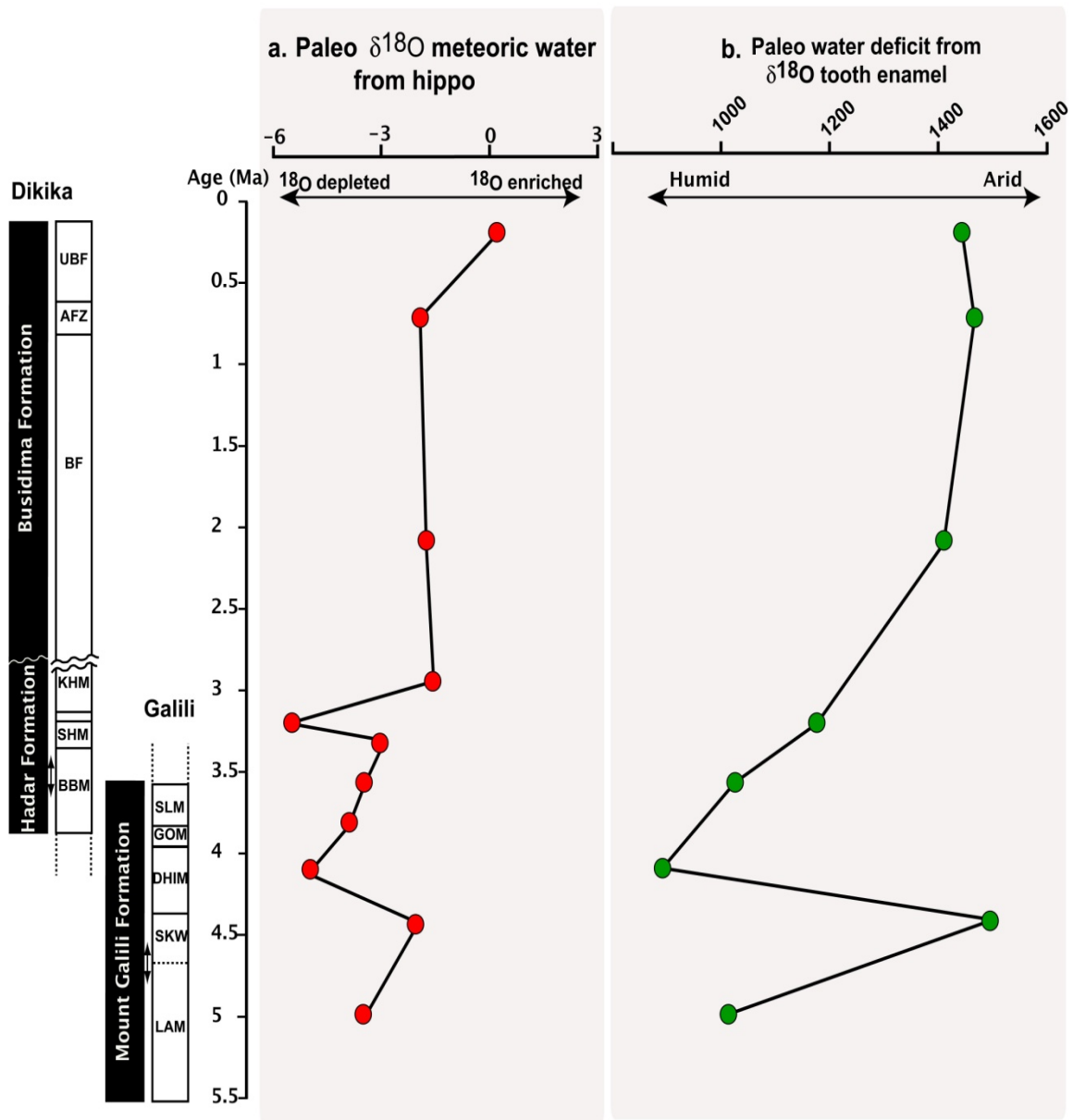


Figure 5.5 Plio-Pleistocene reconstructed isotopic composition of meteoric water and aridity index **a:** Estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ using the most ^{18}O depleted values of hippopotamids tooth enamel to minimize the effect of evaporation from surface water in each member. **b:** Estimated paleoaridity using $\delta^{18}\text{O}_{\text{enamel}}$, the aridity is expressed in terms of water deficit (WD), which is the difference between potential evapotranspiration (PET) and the mean annual precipitation (MAP).

A major shift in the isotopic composition of water at ~3.0 Ma was followed by a 6.0‰ increase from the middle Pliocene to the present (Mann Whitney, $p=0.0476$). Similarly, there were a 3.8‰ shift from the early to middle Pliocene, where the isotopic composition of meteoric water between 4.6 to 4.38 Ma was significantly enriched compared to the rest of the Pliocene (Mann Whitney, $p=0.0016$).

Although there are limited $\delta^{18}\text{O}$ measurements of rainfall in the Afar area, Wynn and Bedaso (2010) indicate a range of $\delta^{18}\text{O}$ values of rainfall from a single rainstorm event, which reflects rainfall intensity (*i.e.*, lower values for high intensity rain and vice versa). The $\delta^{18}\text{O}$ values rainfall measured from Asbole and Dikika ranges between -6.1‰ from high intensity rainfall collected during the 2003 fields season and +2.1‰ from light rain collected in the 2009 field season (Wynn and Bedaso, 2010, Table 1). Aronson et al. (2008) reported an average $\delta^{18}\text{O}$ rainfall measurement of +1.4 ‰ from Hadar collected in 1997. Modern mean annual $\delta^{18}\text{O}$ meteoric water values were also estimated from surface pond water, river water and shallow ground water samples by connecting the evaporation line to the Global Meteoric Water Line (GMWL), which is produced by regression through points representing the $\delta^{18}\text{O}$ values of water subjected to evaporation. These estimated values from Dikika ranges between 0.0‰ and -5.5‰ with a mean value of all the possible estimates of -2.0 ± 1.5 ‰ (Wynn and Bedaso, 2010), and estimates from Gona ranges from -2.9 ‰ to -0.8 ‰ (Levin et al., 2004). The $\delta^{18}\text{O}$ meteoric water estimate using the modern hippo tooth enamel data from Levin et al. (2008) (Figure 5.5a) is close to the modern $\delta^{18}\text{O}_{\text{meteoric water}}$ estimates but higher.

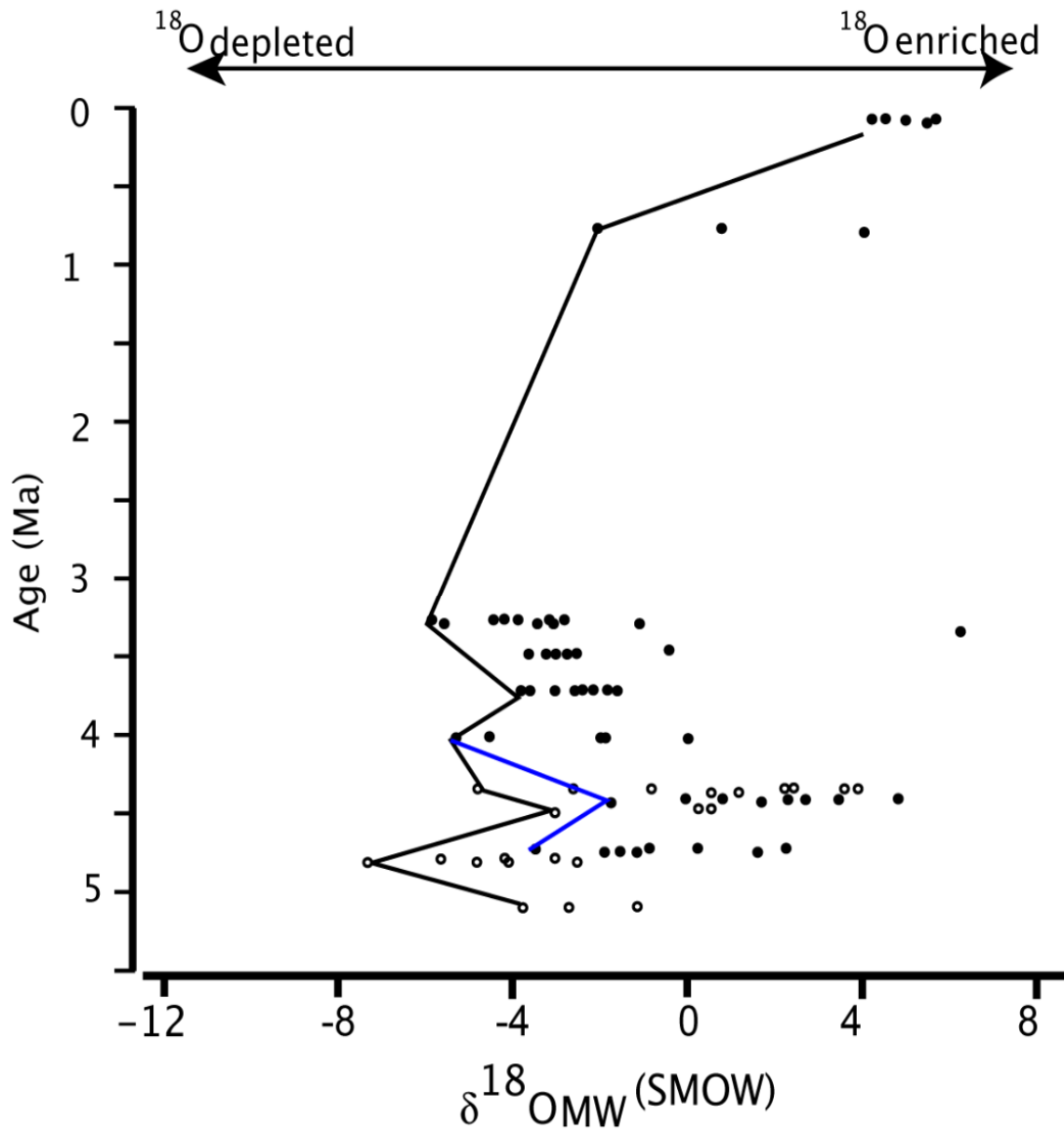


Figure 5.6 Estimated $\delta^{18}\text{O}_{\text{meteoric water}}$ from the Awash Valley using the hippo $\delta^{18}\text{O}_{\text{enamel}}$. Filled circles are data from Galili, Dikika and Asbole while open circles are data from Levin et al. (2008) and White et al. (2009). The black line connect minimum values for each time interval, and the blue line connect minimum values from Galili between ~4.6 and 4.4 Ma, which has a more positive values compared to data from Gona (Levin et al., 2008).

These ^{18}O -enriched values indicate slight evaporation and represent the most ^{18}O -enriched meteoric water estimates. Similarly, the paleo $\delta^{18}\text{O}_{\text{meteoric water}}$ estimates from fossil hippo give us the most ^{18}O -enriched values.

A large difference between reconstructed $\delta^{18}\text{O}$ values of Pliocene and modern meteoric water also have been reported from Hadar and Gona using different proxies. Hailemichael et al. (2002) calculated the $\delta^{18}\text{O}$ meteoric water using gastropod shells from the Hadar Formation, and reported values 6-7‰ lower in the Pliocene than the modern. Aronson et al. (2008) derived meteoric water values from paleosol carbonates from the Hadar Formation at Hadar as -4.1 ± 1.5 ‰. This reported value is 5.5‰ lower than their measured $\delta^{18}\text{O}$ of rainfall (average of five measurements). Likewise, Levin et al. (2004) using paleosol carbonate from Gona estimated a minimum of 6.5‰ increase in the $\delta^{18}\text{O}$ meteoric water since Pliocene. These similar changes in the oxygen isotope values of meteoric water in the Afar depression and elsewhere in East Africa suggest that regional variation was controlled by regional to global factors (Figure 5.6).

5.7 Controls on $\delta^{18}\text{O}$ meteoric water

The main factors that govern the isotopic composition of precipitation were first described by Dansgaard (1964). These factors include temperature, latitude, evaporation, rainfall amount, elevation, seasonality, distance from coastlines and water vapor transport path (Dansgaard, 1964). However, most isotopic variability at low latitudes correlates to the amount, altitude and continentality effects. These factors are commonly attributed to controlling $\delta^{18}\text{O}$ fractionation between vapor and condensate, where the heavier isotope

(^{18}O) is preferentially incorporated in the condensate as compared to the remaining pool of vapor. As vapor moves inland and condensation of water continues in a given storm, at higher elevation and towards the poles the remaining pool of vapor becomes progressively depleted in ^{18}O as well as successive precipitation (Dansgaard, 1964; Criss, 1999; Gat, 2000). In addition, moisture source, proportion of moisture from different sources and change in the amount of glacial ice accumulated at the poles with time are important for paleoclimate studies. This is because precipitation from different sources follows different transport paths, and the amount of ice present at the pole on the continent changes the $\delta^{18}\text{O}$ of the ocean water, which is an ultimate source of precipitation on land.

To explain the observed increase in the $\delta^{18}\text{O}_{\text{meteoric water}}$ and aridity throughout the early to middle Pliocene and from the Pliocene to the present, one or more of these factors had to have changed. The next section discusses various possible sources, including the position of the ITCZ, rearrangement of landmasses which change ocean circulation and changed both Sea Surface Temperature (SST), initiation and intensification of the Northern Hemisphere glaciations (NHG) and changed in the Earth's orbital parameters.

As indicated in the previous sections, today the East African climatic is controlled by the Atlantic and Indian Ocean monsoons and the rainfall is further influenced by the seasonal movement of the ITCZ and topography (Griffits, 1972; Gemechu, 1977). Likewise, Flohn (1965) indicated that the current East African aridity is primarily caused by the high topography that blocks Atlantic moisture sources. Seasonal variation in the $\delta^{18}\text{O}$ of

precipitation is also related to the seasonal shift of the ITCZ and the associated changes in sources of moisture from Atlantic and Indian Oceans. Recently, Levin et al. (2009) indicated that the $\delta^{18}\text{O}_{\text{meteoric water}}$ eastern Africa depends on the location of the Congo air boundary (CAB), which separate ^{18}O -depleted moisture sources from the Indian Ocean and transpired continental ^{18}O -enriched moisture from Congo Basin. They further implied change in the strength of moisture sources in the past would have affected the isotopic composition of water in the region. Haug et al, (2001) suggested a southward shift in the ITCZ between 5 Ma and 4 Ma. This shift in the position of ITCZ and any shift or change in the position of CAB and change in topography would explain at least some of the shift in the reconstructed $\delta^{18}\text{O}$ of meteoric water during Pliocene and through Pleistocene.

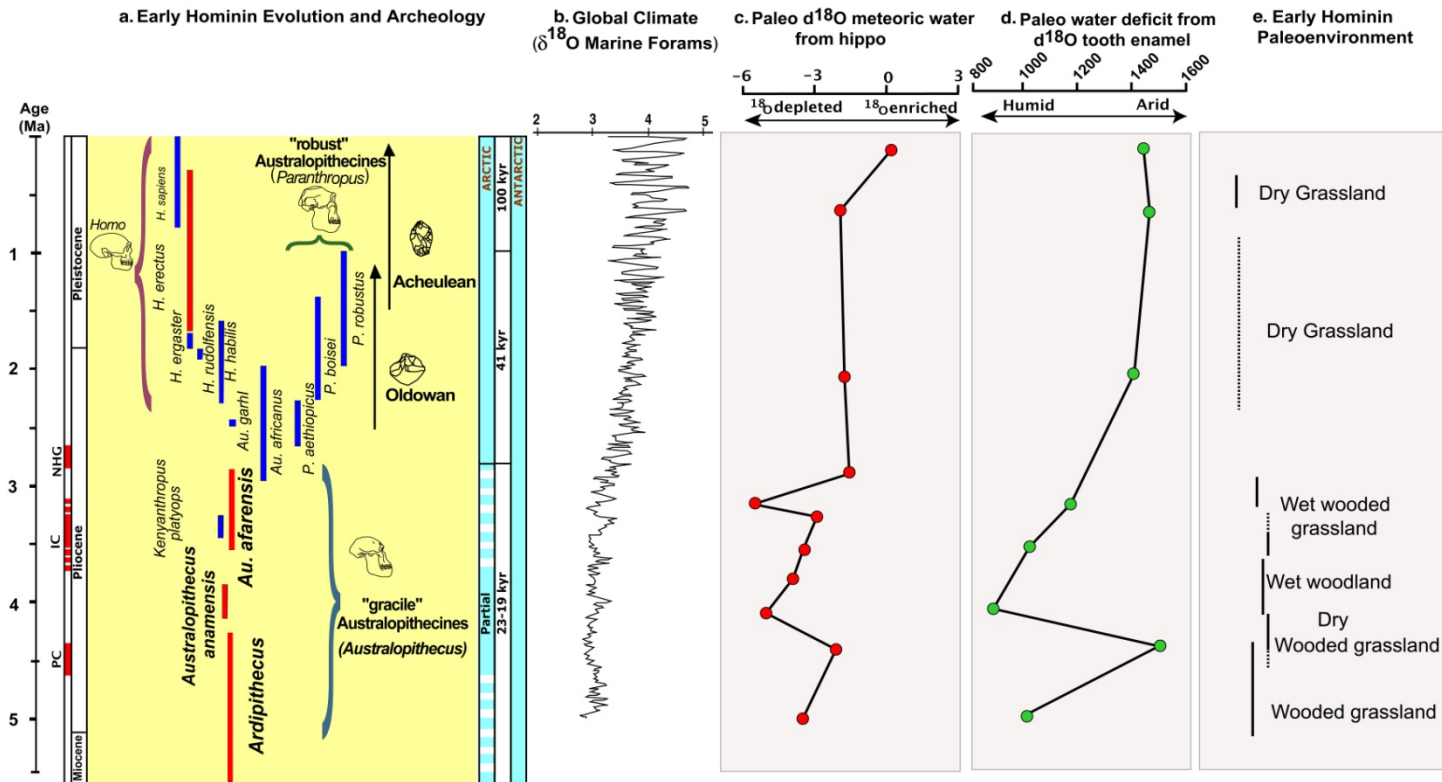


Figure 5.7 **a:** Record of hominin evolution and archeology in Africa, the phylogram adapted from Wood and Lonergan (2008), red color indicates the time interval covered by this study and has direct relevant to the respective hominins while the rest is blue. **b:** Global climate record derived from composite marine ^{18}O record of benthic foraminifera from ODP sites 588, 607, 659, 806, 846, 849, and 959 (Zachos et al., 2001). **c:** Reconstructed isotopic composition of meteoric water based on hippo $\delta^{18}\text{O}_{\text{enamel}}$ from Galili, Dikika and Asbole paleontological sites. **d:** Reconstructed water deficit based on herbivore $\delta^{18}\text{O}_{\text{enamel}}$ from Galili, Dikika and Asbole paleontological sites. **e:** Paleoenvironments of early hominin reconstructed using herbivore $\delta^{13}\text{O}_{\text{enamel}}$, and the nomenclature vegetation follows the United Nations Scientific and Cultural Organization (UNESCO) definitions for classification of African vegetation in (White et al., 1983)

During the Pliocene, tectonic processes such as closure of the Central America seaway and closure of the Indonesian seaway caused significant reorganization of tropical ocean circulation and drove long-term climate change (Molnar, 2008). Keigwin (1982) indicated that with the closure of the Central America seaway, North Atlantic Deep water was formed and the Atlantic thermohaline circulation strengthened, and evaporation in the Northern Atlantic favored increased precipitation in Northern Hemisphere high latitudes. Later, Haug and Tiedemann (1998) suggested a marked reorganization of ocean circulation at 4.6 Ma. This event coincides with increased aridity at Galili (Figure 5b). Furthermore, Haug et al. (2001) suggested that the isolation of the Atlantic Oceanic basin via the Isthmus of Panama and the following gradual intensification of NHG during the late Pliocene influenced the variability of African climate. Although no direct link between the early Pliocene aridity at Galili between 4.6 Ma and 4.3 Ma and this tectonic event, the reorganization of ocean circulation driving moisture to the high latitudes might have left the tropical Africa dry. Likewise, the closure of the sea way and associated changes could be partially responsible for higher $\delta^{18}\text{O}$ values meteoric water in the early Pliocene at Galili after 3.0 Ma.

Cane and Molnar (2001) suggest an alternative that the closure of the Indonesian seaway was a precursor to the East African aridification around 4-3 Ma instead of changes in the North Atlantic Ocean circulation due to closing of the Isthmus of Panama. The authors, using an ocean-circulation model, show the northward displacement of New Guinea-Australia, about 5 Ma ago, as a cause of switch of the source flow from warm South Pacific to relatively cold North Pacific waters through Indonesia, which would have

decreased the sea surface temperatures of the Indian Ocean and leading to reduced rainfall over eastern Africa. Furthermore, they argue that changes in the equatorial Pacific may have reduced atmospheric heat transport from the tropics to higher latitudes, initiating global cooling and eventually growth of ice. So, this predicted change in the Indian Ocean SSTs could be responsible for drying of the eastern Africa climate and the increase in the $\delta^{18}\text{O}$ values of meteoric water (Figure 5.7).

At local to regional scale, the formation of the East African Rift and the development of the highland might have influenced the local climate, surface hydrology, block depleted moisture sources and favor recycling of continental moisture sources (Maslin and Christensen, 2007). Bonnefille et al. (2004) using pollen indicated that the elevation at Hadar was a1000 m higher during the Pliocene than what is today. Thus, mountain building and associated changes are listed as some of the major driving force for enhanced variability of moisture availability in the region. So, in order to fully explain the 6.0‰ increase in the oxygen isotopic composition of meteoric water a combination of one or more of the factors should be accounted, for example the Plio-Pleistocene cooling at high altitude and the Northern Hemisphere Glaciations (NHG), explain only about 1.0‰ change in the $\delta^{18}\text{O}$ ocean water at most (Figure 5.7).

5.8 Paleotemperature estimate

5.8.1 Hippos

Hippos are one of the largest and most gregarious non-ruminant artiodactyls, but their origins have been greatly debated (Waston et al., 1979; Harris et al., 2008). In Africa

fossil hippos are known from late Miocene and due to their aquatic mode of life, hippos are the most common mammals in most of the African Pliocene and Pleistocene paleontological sites (Boisserie et al., 2005; Harris et al., 2008). Modern hippopotamuses, on the contrary, are represented only by two genera with one species each, *Hippopotamus* and *Hexaprotodon*, and are restricted to Africa (Jablonski, 2004). The larger and more widely distributed hippopotamus species of sub-Saharan Africa is *Hippopotamus amphibius*, which is referred to as the common hippo while the smaller and less common species *Hexaprotodon liberiensis*, is referred to as the pygmy hippo, and have limited geographical distribution (Eltringham, 1999). Hippos requires a permanent body of water (lake or river) deep enough to submerge during the day (Jablonski, 2004) and require fresh grass in the immediate surrounding area for grazing at night (Mackie, 1976) but generally 1-3 km (Smithers, 1971). But, it is also indicated that during dry season they migrate long distance in the river system and sometimes on land in search of sufficient depth and grazes (Viljoen and Biggs, 1998).

Hippos are endothermic animals (i.e. animals that maintain a constant body temperature, regardless of the outside temperature) (Cena, 1964). The body temperature of hippos shows a remarkable stability (35.4 ± 0.7 °C) with no obvious 24-h pattern (Luck and Wright 1959; Cena, 1964). The main reason hippos are dependent on permanent water body and submerge during the day is to protect their body from drying and cracking (Luck and Wright, 1964). In addition, due to the nature of the most superficial layer of the skin, they are subjected to higher water loss than has been observed for any other mammal (Luck and Wright, 1964). Like other mammals, fossil hippos are proven sources

of data for reconstructing the paleoenvironment in Asia (*e.g.*, Jablonski, 2004) and Africa (*e.g.* Bocherens et al., 1996; Boisserie et al., 2005; Harris et al., 2008; Levin et al., 2008; Bedaso et al., 2010).

5.8.2 Crocodile

Modern crocodilians are generally divided into three subfamilies: Alligatorinae (alligators and caimans), Crocodylinae (“true” crocodiles and the African dwarf crocodile), and Gavialinae (gharials and “false” gharials or *Tomistoma*) (Grenard, 1991). Crocodilians today are found in various part of the world and represented by 23 surviving crocodilian species of which seven species belong to Alligatorinae, thirteen to Crocodylinae, and two to Gavialinae and twelve extant species belonging to the genus *Crocodylus* , “true” crocodiles, that include the Nile crocodile, *C. niloticus*, (Njau, 2006). The upper jaw of an adult Nile crocodile has an average of 36 erupted teeth, while the lower jaw has an average of 30 teeth (Brazaitis, 1973). The Nile crocodiles are mostly aquatic and known to exist in a wide habitat (*e.g.* lakes, rivers, freshwater swamps brackish water), which is reflecting their success and distribution in most part of Africa (Njau, 2006).

Crocodiles are exothermic animals (*i.e.* animals that have a body temperature closely matches the outside water or air temperature and relay on external source of heat (Seebacher et al., 1999) and Fricke and Rogers (2000) indicated a daily to seasonal covariance between environmental and body temperatures. Exothermic animals regulate their body temperature, raising and lowering of body temperature, is often achieved by

behavioral adaptation (Seebacher et al., 1999). Crocodilians also show behavioral adaptation such as basking, moving between land and water, move between sun exposure and shade and stay inactive during the day (Ross et al., 1989; Seebacher et al., 1999) while some species, *Crocodylus palustris*, in particular use burrows as refugia during periods of temperature extreme (Ross et al., 1989). The Nile crocodiles, on the other hand, remained in water for longer periods (Pooley, 1982). Water serves as a heat source as well as a heat sink (Lang, 1987) depending on the difference in temperatures between the body and the water. Crocodile teeth continuously grow over several months by incremental layers with duration of complete tooth mineralization depending upon the size of the crocodile (Erickson, 1996). Oxygen isotopic composition of crocodile tooth enamel should thus reflect, the oxygen isotopic composition of their drinking water and their body temperature, which is most correlated to their immediate environment (Amiot et al., 2007) and seasonally track log the changes occur in the environment. But, in order to minimize possible seasonal variations in $\delta^{18}\text{O}$ values, the enamel should be sampled along the growth axis of the entire length from the cervix to the apex, and several teeth from each species.

Fossil crocodile teeth are abundant in most fossil localities but very little or no attention has been given compared to other vertebrate fossils, which contributed information about the past environmental and climatic conditions (Njau and Blumenschine, 2006 and references therein). However, previously crocodiles were used as an indication of the presence of marshes, lakes or larger rivers, at Dikika, crocodile fossils are found in the Basal and Sidi Hakoma Member, less so in the Denen Dora and Kada Hadar Members

(Alemseged et al., 2005; Wynn et al., 2006). At Asbole, on the other hand crocodile fossil are rare (D.G. personal communication). Elsewhere Jablonski (2004) suggests that the disappearance of other amphibians from the fossil record in the Plio-Pleistocene is directly related to dramatic changes in seasonal patterns of river flow, resulting from intensification of the summer and winter monsoons. Bedaso et al. (2010) similarly ties the low frequency of hippos to the absence of lakes or perennial streams deep enough for carry them and/or high seasonality, which is a reflection of the climatic condition.

5.9 Hippopotamus-crocodile Paleothermometry

As indicate above hippos and crocodile were commonly found in most Plio-Pleistocene fossil assemblages and coexist in modern lakes systems of Ethiopia and elsewhere in Africa. Using this advantage and the difference in the thermoregulation between the two animals, introduce a new technique to estimate the paleotemperature using tooth enamel from hippos, mineralized at $\sim 37^{\circ}\text{C}$, which tracks the drinking water and crocodile tooth enamel, mineralized at a variable body temperature, which tracks the ambient water temperature which in turn governed by atmospheric air temperature. The basic underling conditions and assumptions are:

1. The hippos and the crocodiles lived in the same water body (river, swamp, lake, etc.)
2. Atmospheric air temperature and water temperature are at equilibrium.
3. Body temperature and water/air temperature are at equilibrium at any time during tooth formation in crocodiles

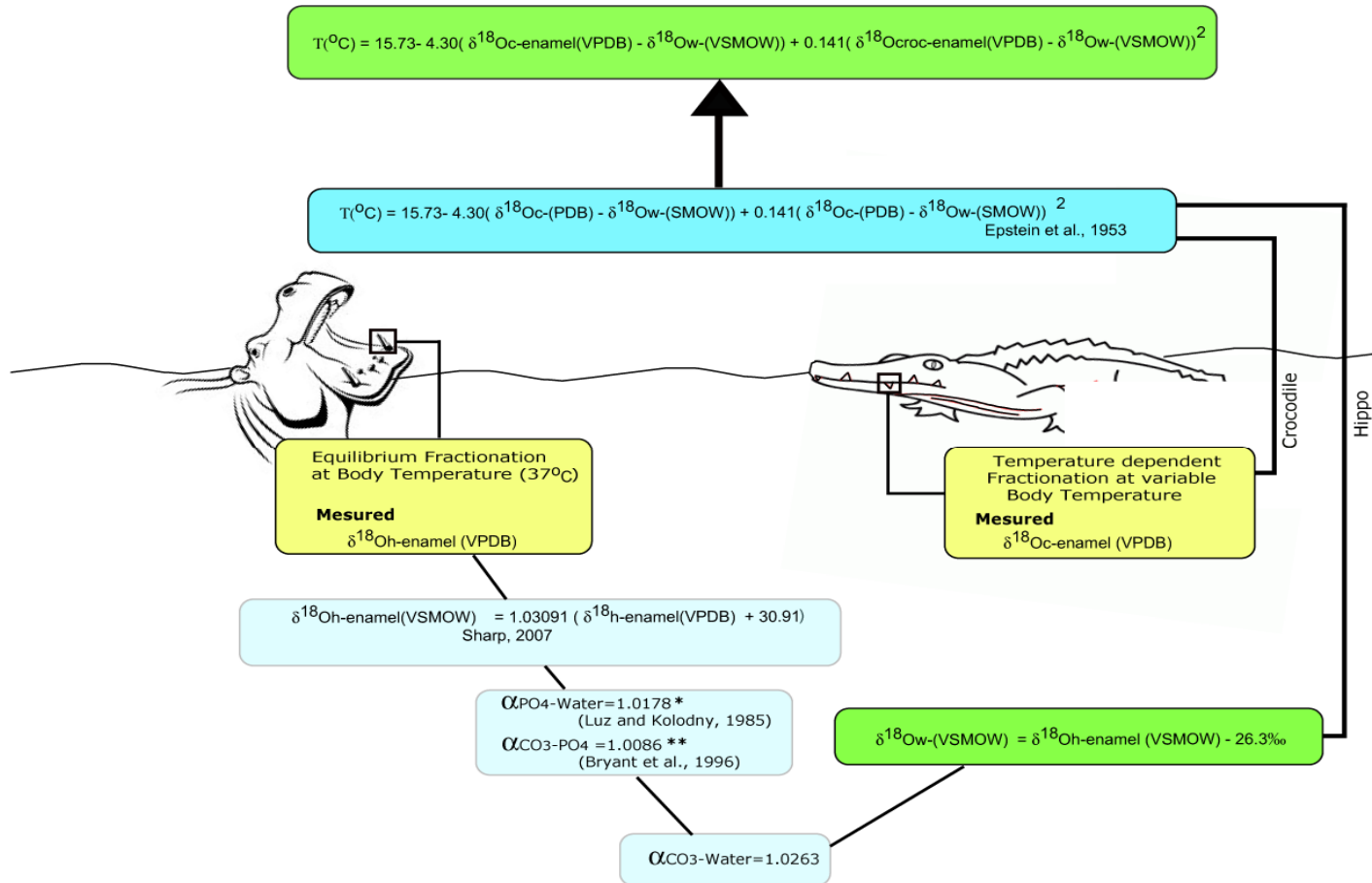


Figure 5.8 A conceptual model showing how oxygen isotope ratios from hippopotamus and crocodile living in a single lake environment can be used to estimate the lake temperature and local atmospheric temperature. First the $\delta^{18}\text{O}_{\text{lake water}}$ will be estimated using $\delta^{18}\text{O}_{\text{h-enamel}}$ of hippo, based on the equilibrium fractionation of oxygen at constant body temperature of $\sim 37^{\circ}\text{C}$ between the lake water and carbonate fraction of bioapatite ($\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$). Then the water temperature will be estimated using measured $\delta^{18}\text{O}_{\text{c-enamel}}$ of crocodile and the estimated $\delta^{18}\text{O}_{\text{w}}$ from $\delta^{18}\text{O}_{\text{h-enamel}}$ in the Epstein et al. (1953) classic paleotemperature equation, which assumed to be similar to atmospheric temperature.

In addition, this method acknowledges that in warm-blooded animals, $\delta^{18}\text{O}_{\text{enamel}}$ is independent of the environmental temperature while there is an equilibrium fractionation between body water and tooth apatite at their body temperature (i.e., 37 °C). Similarly, it is also reported that estimates of oxygen isotope fractionations between phosphate and water are similar across a phylogenetically various group of aquatic organisms, suggesting the fractionation is an equilibrium process and is not strongly affected by biological/kinetic effects (Longinelli & Nuti 1973).

In paleothermometry, an estimate of temperature using indirect geochemical approach has been based on the oxygen isotope composition ($\delta^{18}\text{O}$) of minerals such as calcite, aragonite, and apatite (Urey, 1947; Epstein, 1953; Longinelli and Nuti, 1973). However, the $\delta^{18}\text{O}$ values of these minerals depend on both mineralization temperature and the $\delta^{18}\text{O}$ of the water from which the mineral formed. Because water is normally rarely preserved in the geologic record, it is generally customary to assume a value for the $\delta^{18}\text{O}$ of water in order to calculate the biominerals growing temperature and hence atmospheric temperature (Eagle et al., 2010). The paleothermometry technique here after called – Hippo-Croc Paleothermometer – holds promise for overcoming some of the drawbacks of oxygen isotope paleothermometry that do not assume the $\delta^{18}\text{O}$ of the water the animals lived and provide body temperatures of extinct exothermic animals and hence the water and atmospheric air temperature of the past.

Figure 8, shows the conceptual model how the air/ water temperature is calculated from hippo and crocodile, which are living together in a lake. Based on the fractionation

factors listed above, the $\delta^{18}\text{O}$ of the lake water is calculated from the $\delta^{18}\text{O}$ -hippo tooth enamel formed at the body temperature of the hippo, $\sim 37^\circ\text{C}$ ($\Delta^{18}\text{O}_{\text{tooth enamel-water}} = 26.3\text{‰}$). Then, this value together with the measured $\delta^{18}\text{O}$ of tooth enamel from the co-existed crocodile is substituted in the Epstein et al. (1953) classic paleotemperature equation (Equation 1 and 2) to estimate the crocodile body temperature or the lake water temperature, which is similar to the atmospheric temperature (assumption 2).

$$T(^{\circ}\text{C}) = 15.73 - 4.30(\delta^{18}\text{O}_{\text{C-(PDB)}} - \delta^{18}\text{O}_{\text{W-(VSMOW)}}) + 0.141(\delta^{18}\text{O}_{\text{C-(PDB)}} - \delta^{18}\text{O}_{\text{W-(VSMOW)}})^2$$

Equ. 5.1 Epstein et al., 1953

$$T(^{\circ}\text{C}) = 15.73 - 4.30(\delta^{18}\text{O}_{\text{C-enamel-(VPDB)}} - \delta^{18}\text{O}_{\text{W-(VSMOW)}}) + 0.14130(\delta^{18}\text{O}_{\text{C-enamel-(VPDB)}} - \delta^{18}\text{O}_{\text{W-(VSMOW)}})^2$$

Equ.5. 2 modified from Equ. 5.1

Where:

$T(^{\circ}\text{C})$ – body temperature/ atmospheric or water temperature estimated from hippo and crocodile tooth enamel oxygen isotope values

$\delta^{18}\text{O}_{\text{C-enamel-(VPDB)}}$ – oxygen isotope measured from crocodile tooth enamel in VPDB scale

$\delta^{18}\text{O}_{\text{W-(VSMOW)}}$ – $\delta^{18}\text{O}$ of meteor water estimated from hippo tooth enamel

A total of 49 hippo and crocodile tooth enamel samples were collected from modern, Nech Sar National Park and fossils from the Hadar Formation (SHM and Base of Basal Member). The samples were pretreated and isotope values were measured following the method described in chapter 2, 3 and 4. To calculate the mean annual temperature

(MAT), the average $\delta^{18}\text{O}_{\text{enamel}}$ value of hippos is used to calculate the average $\delta^{18}\text{O}_{\text{lake water}}$, using this value and the crocodile $\delta^{18}\text{O}_{\text{enamel}}$ value, the water temperature is calculated using equation 5.1. Although the relationship between water and atmospheric temperature in different climatic zones, different elevation and rivers and lakes remains to be determined and calibrated in Ethiopia, elsewhere it is indicated that there exist a 1:1 relationship between average river water temperature and atmospheric MAT (Kothandarman and Evans, 1972). The advantage of using this method to estimate temperature over the traditional paleothermometer is that, it provides an independent temperature estimate that does not rely on present-day spatial relations between the $\delta^{18}\text{O}_{\text{meteoric water}}$ and MAT or the actual $\delta^{18}\text{O}$ value of the lake or river the animal lived. Thus, it is possible to calculate paleotemperature as long as both fossils found in the same stratigraphic interval.

The estimated temperature from SHM, BBM and Nech Sar National Park from coexisted hippo and crocodile are presented in Table 5.1. Where the temperature estimates are based on based on the average $\delta^{18}\text{O}$ values and reported uncertainties of 1σ . The Pliocene temperature at Dikika is estimated as 32.6 ± 4.0 °C between $>3.8 - \sim 3.6$ Ma and 33.8 ± 4.8 °C between 3.42-3.24 Ma. The relatively higher uncertainties with the Pliocene estimates is most likely due to the time averaging effect of the fossils, where fossils possibly came from a different horizons within a single members and have different $\delta^{18}\text{O}_{\text{enamel}}$ value, difference in the source water at different times, and partly due to seasonality. Likewise, the temperature estimated at Lake Abaya, Nech Sar National Park as 30.8 ± 2.5 °C. The uncertainties from the modern tooth enamel could be due to

seasonality reflected during tooth enamel formation. Overall, the temperature estimates are in good agreement with paleotemperature estimates from Turkana paleosol carbonate using clumped isotopes (^{13}C - ^{18}O), the principle focuses on bond ordering between rare isotopes within structural units of minerals, and the proportions of ^{13}C - ^{18}O bonds in carbonate minerals are sensitive to their growth temperatures (Passey et al., 2010), and the modern instrumental records respectively.

Table 5.1 Paleotemperature estimates of the middle Pleistocene from SHM and BBM, and modern from Lake Abey.

Member	Average $\delta^{18}\text{O}_{\text{hippo}}$ (VSMOW)	Average $\delta^{18}\text{O}_{\text{croc}}$ (VPDB)	T ($^{\circ}\text{C}$)
Modern	7.85	4.78	30.2 \pm 2.5
SHM	-2.85	-6.59	33.8 \pm 4.8
BBM	-2.64	-6.15	32.6 \pm 4.0

Paleotemperature estimates at hominin fossil bearing localities in East Africa are rare. As indicated by Passey et al., (2010) temperature estimates at the time relevant to human evolution could have implications for human thermophysiology. Furthermore, one of the most interesting and widely accepted explanations of why hominins became bipedal is the thermoregulatory hypothesis suggested by Wheeler (1991), which rests on reduction of thermal stress on early hominins to keep them active under hot climatic condition. So, better estimates of Plio-Pleistocene paleotemperature could enhance our understanding of some of the early hominin behavioral and morphological changes.

5.10 Summary

To sum up, the variation of oxygen isotopic composition of tooth enamel within a single species or among sympatric taxa in a given time interval and the change through time elucidate the range of variability in the source water, climatic and non-climatic factors controlling the $\delta^{18}\text{O}$ of tooth enamel. Tooth enamel is used in reconstructing the paleo- $\delta^{18}\text{O}$ of meteoric water using hippos and water deficit using obligate and non-obligate drinking animals. $\delta^{18}\text{O}$ of tooth enamel in the Awash Valley became more positive and the reconstructed $\delta^{18}\text{O}$ meteoric water shift to ^{18}O -enriched values after ~ 3.0 Ma. The increase in the ^{18}O enrichment of meteoric water and aridity in the region is in a general agreement and accommodated by both long-term global cooling and extensive local tectonic changes. However, to pin point the exact causes of the increase and make the link between local, regional and global factors controlling the climate change, a better understanding of water stable isotope (oxygen and hydrogen) in precipitation within modern system is critical. And, ultimately the reconstructed $\delta^{18}\text{O}$ of meteoric water and aridity in the region enhances our understanding of the availability, distribution and seasonality of water resources for early hominin which would have implication to the type of vegetation they lived in and potential source of food resources. The preliminary results of temperature estimated from modern and middle Pliocene fossils using the newly introduces hippo-croc paleothermometer shows the potential of the method for future use although the method remains to be calibrated across elevation gradients and different climatic zones.

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CHAPTER SIX

PLIO-PLEISTOCENE PALEOENVIRONMENTS OF AWASH VALLEY

6.1 Introduction

Palaeoenvironmental reconstruction is an integral part of palaeoanthropology as both human evolution as well as that of other faunal components is a result of their interaction with different abiotic and biotic environmental factors (Plummer et al., 2008; Reed, 2008). A firm knowledge of the environmental condition where hominins lived has been the basis to our understanding of the evolution and diversification of our ancestors (Vrba, 2007; Alemseged et al., 2007). Likewise, detailed reconstructions of palaeohabitats are necessary to understand the interrelationships between environmental factors and hominin morphological, biological, cultural, and behavioral adaptations as well as the origin and extinction of early hominins (deMenocal, 1995; Plummer, 2004; Kingston, 2007). Although there is general consensus on the timing of Neogene global climate cooling, increased aridification, climate fluctuation and changes in the mammalian behavior and morphology (Vrba, 2007), it does not demonstrate causality. Instead, assessing causality in human evolution ultimately requires clearly identifying the environmental factors, their interrelationship and the degree to which they were encountered by early hominins (Kingston, 2007).

Most East African Plio-Pleistocene paleontological sites have been reconstructed as a heterogeneous or as mosaics of paleolandscapes, which support the savanna hypothesis which suggest hominin have evolved in savanna mosaics that changed through time (Wynn, 2004; Kingston, 2007). Paleoenvironmental reconstructions of Late Miocene and early Pliocene eastern and central Africa early hominin sites indicate that hominins were associated with a range of environments, including shrubland, woodland, open woodland, forest, and riparian forest (*e.g.*, WoldeGabriel et al., 1994; Wynn, 2000 Semaw et al., 2005; Urbanek et al., 2005). Based on paleobotanical data, Bonnefille (2010) reconstructed a great variety of environments and ecosystems ranging from evergreen and deciduous forests to wet and dry woodland. Previous paleoenvironmental reconstructions indicated that *A. afarensis* occupied different types of ecosystems under various paleoenvironmental conditions in a wide range of habitats ranging from closed woodland through open woodland and shrubland (Boaz, 1977; Harris, 1991; White et al., 1993; Bonnefille et al., 2004; Reed, 2008). While, *Ar. Ramidus*' paleoenvironments were reconstructed as woodlands to patches of forest (WoldeGabriel et al., 1994; White et al., 2009) and bush savanna with a habitat ranging from riparian forest to grassland (Levin et al., 2008; Cerling et al., 2010). Generally, over the past 5.0 Ma the environment has been characterized by a change from forested to open grasslands, with different proportions of grasslands on the landscape (Cerling, 1992). However, the extent to which these spatial and temporal changes in the size of grasslands impacted human evolution remains to be answered.

Stable carbon isotopic composition of herbivore tooth enamel has been used as a reliable dietary indicator, which in turn reflects the relative proportion of C₄ (*i.e.*, grasses) to C₃ (*i.e.*, trees, shrubs and closed canopy resources). Plants in an animal's diet indicate potential food resources available for early hominin (Sponheimer and Lee-Thorp, 2007; Levin et al., 2008; Bedaso et al., 2010, in review). The isotopic approach of paleoenvironmental reconstruction used here relies purely on the link between the dietary adaptation of mammalian taxa as obtained from isotopic signals on the tooth enamel and the environment, rather than relying on the taxonomic uniformitarianism. The principle of taxonomic uniformitarianism, which assumes that the extant mammals inhabit the same habitat today as their relatives, did in the past, limits our prospective to explore the whole range of possibilities and understand how the past differs from the present, which is an integral goal of palaeoenvironmental research (Plummer et al., 2008). It is also evident that some mammals show a significant change in dietary and ecological adaptation through time (*e.g.* Cerling et al., 1999; Geraads, 2005). Although carbon isotopic composition of tooth enamel has been widely used for paleoenvironmental reconstruction, it has been limited to establishing dietary consumption and the presence and proportion of C₃ and C₄ vegetation in the paleolandscape (*e.g.*, Cerling et al., 2003; Levin et al., 2008; Bedaso et al., 2010). So far, carbon isotopes from tooth enamel do little to explicate vegetation or habitat structure, which is a primary associated with evolutionary change of early hominin (Spencer, 1997; Sponheimer and Lee-Thorp, 2003). However, Bedaso et al. (in review) used carbon isotopic composition of tooth enamel to reconstruct the proportion of various habitats present in the middle Pliocene at Dikika.

This chapter discusses stable carbon isotopic composition of tooth enamel from Chorora, Galili, Dikika and Asbole research areas and used to reconstruct mammalian dietary adaptation and dietary shift with time, and its implication for paleoenvironmental reconstruction and available food resources for early hominins. Then it discusses the paleoenvironmental reconstructions based on $\delta^{13}\text{C}_{\text{ecosystem}}$ estimates, which combine the carbon isotope of tooth enamel and faunal abundance, and reconstruct the range of possible environmental conditions (Bedaso et al., 2010). At the end, it devolves into a detailed reconstruction of habitat structure and its change with time on the paleolandscape where early hominins lived. This synthesis will provide a regional perspective of environmental changes over both temporal and spatial scales.

6.2 Mammalian Paleodiet

In most cases, dietary preferences of a species are closely linked to the habitat they live in and its surroundings (Kingston and Harrison, 2007). The ecological signal is then passed on to the animal tissue, but Behrensmeyer and Hook (1992) indicate that the diet of individual animals may or may not reflect the actual vegetation or habitat type that a particular animal lives in, but potentially indicates the presence of a certain habitat in the vicinity. Some of the factors, which amplify the problems associated with this approach include: selectivity of animals which biases interpretation of the environment, social behavior where some animals obtain their food outside of their habitat, migration of larger mammals and seasonal availability of vegetation (Cerling et al., 2004; Kingston and Harrison, 2007). To minimize the effect of these biases, a wide range of fossil herbivores sample can be used rather than rely on a single taxa. To this end, in this study

all large mammals except primates are used. Sensitivity tests were done to check the effects on $\delta^{13}\text{C}_{\text{ecosystem}}$ estimates by categorically including/excluding primates, which are comparatively abundant but consume little biomass than other large vertebrates and the result shows little effect (i.e., contribute additional 1–3% to the estimated C_3 cover).

The distinction between herbivore diets is based on the difference in the photosynthetic pathway C_3 and C_4 plants follow, which discriminate carbon isotopes differently (Koch, 1998). East Africa is considered one of the ideal locations for applying in $\delta^{13}\text{C}_{\text{enamel}}$ to make clear distinction between grazers and browsers, because in existing tropical regions almost all the C_3 and C_4 plants are dicots and grasses, respectively (Tieszen et al., 1979; Cerling and Harris, 1999). However, high elevation grasses are important exceptions as they follow the C_3 photosynthetic pathway reflecting cooler temperatures. As it is today, for the past 7-8 Myr, the C_3 and C_4 distinction in the tropics is between C_3 dicots and C_4 grasses, where both pedogenic and biogenic carbonate $\delta^{13}\text{C}$ recorded the emergence of C_4 grasses (Ségalen et al., 2007). Prior to 8 Ma Cerling et al. (1997) indicated that C_4 grasses were less common even in tropical and subtropical regions in contrast to what is found there today. However, in regions where the growing season temperature is cooler ($<20^\circ\text{C}$), C_3 grasses are dominant and as a result, distinguishing between browsers and grazers would be difficult. So, Prior to 8 Ma, the use of carbon isotopic composition of mammalian tooth enamel to estimate the proportion of C_3 contribution of browse versus grass in the diet could be misleading as the C_3 signature could be either of C_3 grasses or higher C_3 plants (Cerling et al., 2005).

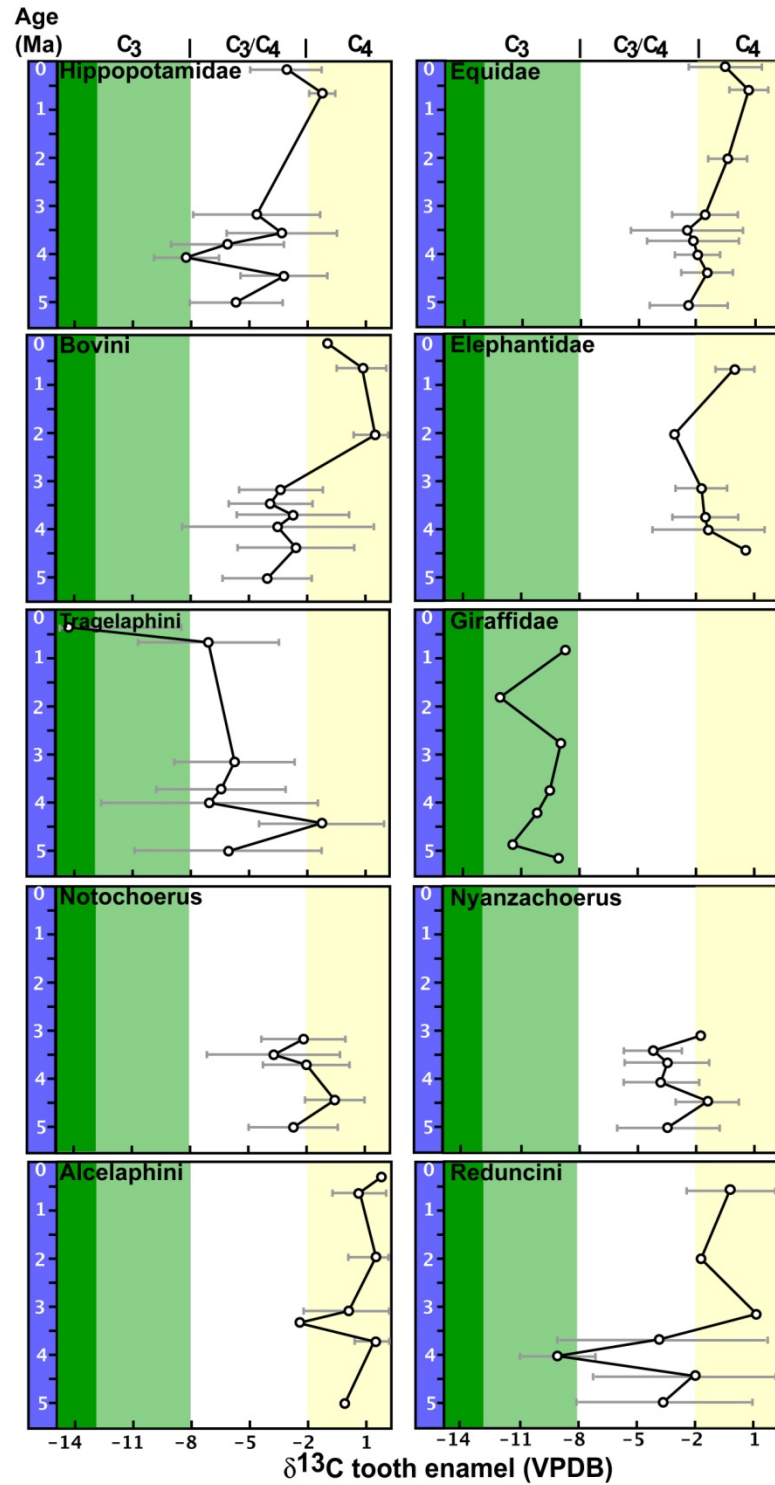


Figure 6.1 $\delta^{13}\text{C}_{\text{enamel}}$ of taxa with time, the open circles represent average values with error bars of $\pm 1\sigma$, The different colors indicate the ranges of diet, the pale orange= C₄, white=Mixed C₃/C₄, light green=C₃ diets and the Dark green= C₃ from closed-canopy forest.

Over the long term, the reconstruction of atmospheric CO₂ concentrations using deep-sea cores signify that atmospheric composition had reached the low atmospheric CO₂ level favored by C₄ photosynthesis by the late Tertiary (Pagani et al., 2006). However, there is no agreement on the actual timing of the appearance of C₄ grasses on the landscape or when it became a significant component in tropical ecosystem. For instance, Kingston et al. (1994) and Morgan et al. (1994) indicate the appearance of C₄ grasses in the mid-Miocene (~14 Ma), while Bernor et al. (2004) suggest a significant proportion of C₄ grasses in equid diet at ~10.5 Ma, still others proposed a later expansion during the late Miocene (6-8 Ma; e.g., Cerling et al., 1997). Although the availability of continuous records are one of the limiting factor, Ségalen et al. (2007) attribute these varying scenarios to relatively minor differences in the interpretation of data. In addition, isotopic studies of tooth enamel from eastern Africa mammalian faunas hints that there are differences in the timing of change in the diet of some mammals to the emergence and expansion of grasslands, and there are some groups that show no response (Cerling et al., 2005; Ségalen et al., 2007).

To assess changes in the dietary adaptation of mammalian taxa with time carbon isotopic values of tooth enamel from multiple intervals are presented. Figure 6.1 show the carbon isotopic values of tooth enamel from some of the most common taxa represented in numerous faunal components from throughout the Plio-Pleistocene (see chapter 2–4 for details). In this section, a general summary of the dietary adaptations and an assessment of temporal changes in the diet of mammals from early Pliocene to present for most taxa and from late Miocene to the present for equids, giraffids and Tragelaphini. Statistical

analyses, Mann Whitney, are done to confirm the significance or non-significance of the changes in the $\delta^{13}\text{C}_{\text{enamel}}$. (See Appendix I, for statistical test result)

The carbon isotopic data of tooth enamel from Chorora, Galili, Dikika and Asbole indicate that the herbivores had a wide range of foraging strategies, including the entire range from pure C_3 , mixed C_3/C_4 and pure C_4 diets in a mosaic of environmental settings. Using the average $\delta^{13}\text{C}_{\text{enamel}}$ values, the fauna is grouped into grazers, which showed a consistent foraging strategy throughout the Plio-Pleistocene (Alcelaphini, Reduncini, equids, elephantids and *Notochoerus*). While deinotheres and giraffids showed a consistent browsing habit. The rest of the taxa (Aepycerotini, Hippotragini, hippopotamids and *Kolpochoerus*) exhibited consistent mixed feeding habits although the percentage of C_3 and C_4 vegetation in their diets was variable. None of these groups displayed a statistically significant change in their diet through time, except Bovini, which show a significant change from mixed C_3/C_4 diet to C_4 diet from middle Pliocene to Middle Pleistocene (Mann Whitney, $p < 0.001$). In addition, three different taxa, equids, giraffids and Tragelaphinis, were sampled from the Chorora Formation and it is evident that equids show a shift from mixed C_3/C_4 consumption to C_4 -dominated diet at least by the early Pliocene (Mann Whitney, $p < 0.001$). Likewise, Tragelaphini show a shift from significant C_3 vegetation consumption to mixed C_3/C_4 diet by early Pliocene but no dietary shift are observed for giraffids, which consistently browsed since the middle Miocene (Mann Whitney, $p = 0.0721$).

Equids are one of the taxa reported to change their diet from C₃ to C₄ and show the earliest evidence for a C₄-dominated (> 75%) diet (Cerling et al., 2005). All five Chorora equid teeth samples yield carbon isotopic values indicating a significant proportion of C₄ grasses in their diet, with $\delta^{13}\text{C}$ values ranging between -6.8‰ to -3.0‰ and averaging -5.6‰ . In equids, the exact timing of the transition from C₃ based to C₄ diet has yet to be elucidated due to lack of well-dated samples between 7.5 Ma and 10 Ma in the Awash Basin (Kalb, 1995) and elsewhere in Africa (Cerling et al., 2005). However, the Chorora data clearly indicate the incorporation of a significant amount of C₄ vegetation in the diet (45–71% C₄ grasses) by ~10.5 Ma. Bernor et al. (2004) also reported $\delta^{13}\text{C}$ values from Chorora ranging between -7.5 and -4.2‰ and based on serial samples on two different teeth suggested the presence of C₄ grasses year-round rather than being a seasonal component of the diet, and implied the $\delta^{13}\text{C}$ values are consistent with open, dry habitat exploitation by the Chorora equids. Levin et al. (2008) reported an exclusively grazing diet primarily on C₄ grasses with an average $\delta^{13}\text{C}_{\text{enamel}}$ values of $-0.6 \pm 0.5\text{‰}$ (n=8) from the Adu-Asa Formation (6.5–5.2 Ma) at Gona, which clearly indicates the transition from a C₃ to a C₄ diet in the Awash Valley by at least the late Miocene. Since then, equids show a consistent grazing diet through Pliocene and Pleistocene (Figure 6.1)

Elephantids from Galili, Dikika and Asbole exhibited a consistent grazing dietary adaptation with a predominantly C₄-dominated diet (Figure 6.1). The $\delta^{13}\text{C}_{\text{enamel}}$ values of elephantids in the Pliocene and Pleistocene ranges between -3.0 and 0.4‰ signifying up to 95% C₄ grasses in their diet. Whereas, deinotheres maintained a pure C₃ browsing diet with a $\delta^{13}\text{C}_{\text{enamel}}$ values ranging between -9.4‰ and -14.1‰ . Levin et al. (2008) from

Gona reported a similar dietary adaptation as old as 6.5 Ma for both elephantids and deinotheres. Elsewhere, Cerling et al. (1999) indicated that elephantids show a shift from C₃-dominated to C₄-dominated diet at ~7 Ma and dominantly were grazers until less than 1.0 Ma. Since then, elephantids show a C₃-dominated diet where today extant elephantids are predominantly browsers in almost all environments.

Suids from Galili, Dikika and Asbole include three genera: *Nyanzachoerus*, *Notochoerus* and *Kolpochoerus*. The $\delta^{13}\text{C}_{\text{enamel}}$ values in general indicate a mixed and C₄-dominated diet. *Nyanzachoerus* exhibited a consistent mixed C₃/C₄ diet from early to mid-Pliocene with the exception of samples from the SKWM (~4.6 Ma-4.38 Ma) at Galili with an average $\delta^{13}\text{C}_{\text{enamel}}$ value of 1.4‰ (~83% C₄ grasses), this enriched ¹³C value is statistically significant compared to the BBM at Dikika (Mann Whitney, $p=0.0242$) and DHIM at Galili (Mann Whitney, $p=0.0480$). The $\delta^{13}\text{C}_{\text{enamel}}$ value of *Notochoerus* in the Pliocene and Pleistocene indicate significant C₄ vegetation (~70%-80%) in the diet with no significant change although the sample size is small to back up the interpretation with statistics. *Kolpochoerus*, unlike the other suid genera shows a gradual change from mixed C₃/C₄ diet (~48% C₄ grasses) in middle Pliocene to exclusive C₄ diet (~92% C₄ grasses) in Middle Pleistocene. Cerling et al. (2005) indicate that suids, unlike, equids and elephantids, took longer to transition from a C₃ to C₄-dominated diet and became exclusive grazers by mid to late Pliocene.

Hippopotamids in the Plio-Pleistocene deposits of the Awash Valley show a general C₃/C₄ mixed diet with variable incorporation of C₄ grasses except in the DHIM (4.38

Ma–3.92 Ma) at Galili, where the average $\delta^{13}\text{C}_{\text{enamel}}$ value was -8.3‰ (~33% C_4 grass) and C_4 -dominated in the AFZ where the average $\delta^{13}\text{C}_{\text{enamel}}$ value is -1.3‰ (~84% C_4 grass). Figure 6.1 show a general shift in dietary adaptations from C_3/C_4 mixed feeding in the early to mid-Pliocene to exclusively grazing in the Middle Pleistocene (See appendix X, for statistical test result). Harris et al. (2008) indicated a variable proportion of C_3 and C_4 vegetation in the diet since Miocene but with a general trend towards C_4 -dominated diet for the Turkana basin in Kenya and southern Ethiopia.

Bovids represent a very common group of animals known to exist in a wide variety of habitats and adapted to a diverse diet. Evolutionary patterns and dietary adaptation of bovids have been linked specifically to environmental change and faunal turnover during the Miocene and Plio-Pleistocene of Africa (Vrba, 1985, 1995; Bobe and Eck, 2001). The $\delta^{13}\text{C}_{\text{enamel}}$ value of bovids from Galili, Dikika and Asbole clearly show a broad diet and a shift from Late Miocene to the Middle Pleistocene. In general, based on average $\delta^{13}\text{C}_{\text{enamel}}$ values and their temporal trends, the bovids are divided into three groups. (1) bovids which consistently grazed throughout the Pliocene and Pleistocene, *e.g.*, Alcelaphini; (2) bovids which were mixed feeders during most of the Pliocene and shift to a C_4 -dominated diet at the end of Pliocene or Early Pleistocene, *e.g.*, Bovini, Hippotragini, Reduncini and Aepycerotini; and (3) bovids with a C_3 -dominated diet in the Late Miocene but which shift to a mixed C_3/C_4 diet in the Plio-Pleistocene, *e.g.*, Tragelaphini.

Alcelaphini are the only bovid which show a consistent diet maintaining an exclusively grazing habit in both Pliocene and Pleistocene with average $\delta^{13}\text{C}_{\text{enamel}}$ values of 0.0 ‰ (> 90% C_4 grasses). Bovini, Hippotragini and Reduncini had a mixed C_3/C_4 diet with a variable proportion of C_3 and C_4 vegetation throughout the Pliocene. The average $\delta^{13}\text{C}_{\text{enamel}}$ values of Bovini vary between -3.4‰ and -4.1‰ (average C_4 grasses ~68%) in early and middle Pliocene (statistically not significant, Mann Whitney, $p=0.268$) and between -1.1‰ and 1.7‰ (average C_4 grasses ~68%) from mid-Pliocene to modern (statistically significant, Mann Whitney, $p<0.001$). The average $\delta^{13}\text{C}_{\text{enamel}}$ values of Hippotragini show a similar, statistically not significant trend in the diet with a shift in the late Pliocene but not statistically significant (Mann Whitney, $p=0.333$). Although it is not statistically supported due to the small sample size, the Hippotragini diet changed from C_3/C_4 mixed diet to a C_4 -dominated diet between the middle Pliocene and Middle Pleistocene. Similarly, the average $\delta^{13}\text{C}_{\text{enamel}}$ values of Reduncini show a general increase in the C_4 grass in the diet since early Pliocene to modern except in the DHIM where C_3 -dominated diet is documented. (See the discussion in chapter 4).

The average $\delta^{13}\text{C}_{\text{enamel}}$ value of Tragelaphini from the Chorora Formation signifies a C_3 -dominated diet. In Pliocene and Pleistocene the average $\delta^{13}\text{C}_{\text{enamel}}$ value, indicate a mixed C_3/C_4 diet except in the SKWM, where they had C_4 -dominated diet (*i.e.*, ~84% C_4 grasses) (statistically significant, Mann Whitney, $p=0.0221$). While, modern $\delta^{13}\text{C}_{\text{enamel}}$ values from Nech Sar National Park indicate a pure C_3 dietary adaptation.

6.3 Habitat structure

A comprehensive reconstruction of the Plio-Pleistocene vegetation and habitat structure is important to understand the biological, morphological and behavioral adaptations of hominin (deMenocal, 1995; Spencer, 1997; Reed, 1997). Despite a success in broadly reconstructing paleoenvironments using various proxies, determining the actual habitats present, relative proportion of individual habitats at a given place and time and the range of possible habitats for hominin for any particular locality, and the dynamic through time have been a challenge (Sponheimer et al., 1999; Plummer et al., 2008). The Plio-Pleistocene of eastern Africa was characterized by a diverse plant ecosystem, which was the result of climate change coupled with active tectonics, volcanism and changes in topography associated with the East Africa Rift formation (Sepulchre et al., 2006; Maslin and Christensen, 2007). Bonnefille (2010) suggested that the combination of a long history of climate change and the rift formation in the region could have contributed to the complexity of the distribution of vegetation and explain the observed range of vegetation from sub-desertic steppe to forests over a relatively short distance.

As described in the previous section, the general paleoenvironmental conditions are obtained using the average $\delta^{13}\text{C}_{\text{ecosystem}}$ values, which are estimated based on the carbon isotopic composition of tooth enamel, the faunal abundance, and amount of biomass the respective species consumed. In addition, in chapter three it is indicated that this methodology further investigates the range of possible variation in the paleoenvironmental condition by considering different combinations of isotopic values from all the taxa represented in respective member (see Table 3.2 in Chapter 3).

However, the $\delta^{13}\text{C}_{\text{ecosystem}}$ values give averages and cannot resolve all the habitats present on the landscape. To this end, the tooth enamel isotopic composition of each taxon for the entire pure C_3 to pure C_4 range with 1.0‰ increments were used and weighted by faunal abundance and food intake per day of the respective taxa and normalized to unity (Appendix II and Figure 6.2). The description of the habitats used in this study follows the United Nations Scientific and Cultural Organization (UNESCO) definitions for classification of African vegetation (White et al., 1983) and the interpretation of habitats is based on Cerling et al. (2010), a compilation of soil organic matter from different tropical ecosystems.

The habitats reconstructed from different stratigraphic levels will be discussed in three informally defined time intervals based on the timing relevant to the genus *Ardipithecus* (*Ar. ramidus* – ~4.4 Ma, White et al., 2009), *Australopithecus* (*A. anamensis*; 4.17 - 3.95 Ma; *A. afarensis*; 3.7–3.0 Ma, Kimbel, 2007) and *Homo* (*H. erectus*; 1.8- 30 ka, Wood and Lonergan, 2008). The time intervals are designated as “early Pliocene” between 5.26 and 4.38 Ma, “middle Pliocene” between 4.38 Ma – 3.24 Ma and “middle Pleistocene” between 0.8 and 0.64 Ma. Tooth enamel data were also collected from some of the horizons between 3.24 Ma and 0.8 Ma, but they are insufficient to make comprehensive environmental interpretation and habitat reconstruction, as a result they are not considered here.

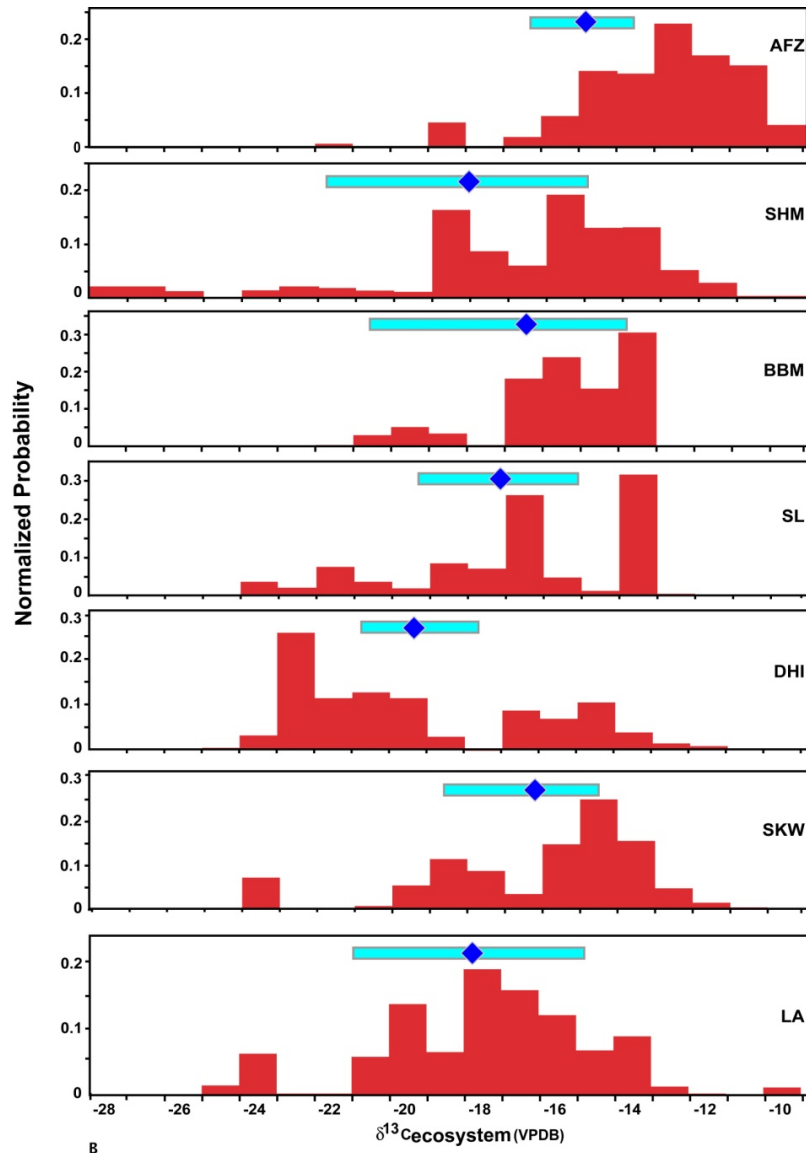


Figure 6.2 Reconstruction of the habitat structure based on the ecosystem carbon isotope value derived from the average $\delta^{13}\text{C}_{\text{enamel}}$, faunal abundance and the estimated amount of biomass consumption per day of each taxon using calibration data from Bedaso et al. (2010) based on the modern data of Delany and Happold (1979). **A.** The normalized probability (=the proportion of habitats normalized to one), of the different habitats where the histogram represent the proportion of the sum total of each taxon at 1.0 ‰ increment for entire C_3 to C_4 range, whereas the horizontal bar and the diamond symbol represent the range and average paleoenvironmental conditions. LA, Lasdanan, DHI, Dhidinley, SKW, Satkawhini, SL, Shabeley Laag, BBM, base of basal Member, SHM, Sidi Hakoma Member and AFZ, Asbole fauna zone **b.** Adopted from Cerling et al. 2010, but only ecosystems which are common in the modern tropical Africa are considered.

6.3.1 Early Pliocene (5.29 Ma–4.38 Ma)

The early Pliocene data comes from various localities within the Mt. Galili Formation namely: Galili, representing the older sediments, and Satkawhini, representing the younger sediments (see Figure 4.1, chapter 4).

This time interval shows considerable variation in terms of the general paleoenvironmental conditions, type and proportion of paleohabitats present and paleoclimatic conditions expressed from the water deficit calculations (Figure 6.2). The average ecosystem carbon isotope value in the early Pliocene ($\delta^{13}\text{C}_{\text{ecosystem}} = -16.8\text{‰}$, 63% C_4 grasses) signifies that in the lower part of the early Pliocene the paleoenvironmental conditions were dominantly wooded grasslands and grassy woodlands with C_4 grasses ranging between 40%–80% on the landscape (Figure 6.3). While, the habitat structure at Galili in this time interval was dominated by wooded grasslands and shrublands followed by grasslands and riparian woodlands (*i.e.*, ~35% wooded grassland, ~45% shrubland, ~12% grassland and ~8% riparian woodland, Figure 6.2 and 6.3). Later in this interval, the $\delta^{13}\text{C}_{\text{ecosystem}}$ value (-16.8‰ , 73% C_4 grasses) indicates a paleoenvironmental condition including wooded grassland, shrubland and grassland, where C_4 grasses range between 57% and 84%. At Galili, grasses were more abundant in the paleolandscape as compared to previous reconstructions from other Pliocene sites in the Afar region (*e.g.*, Levin et al., 2008; White et al., 2009), which elucidates spatial variation in the vegetation structure over a short distance. However, given the active tectonics, repeated volcanism and water resource variability depending on how far from lakes, rivers and presence or absence of lakes in different basins, this

range of variability is not surprising. Similarly, the habitat structure at Galili was dominated by wooded grasslands, shrublands and grasslands with subordinate riparian woodlands (*i.e.*, ~43% wooded grassland, ~27% shrubland, ~23% grassland, and ~7% riparian woodland).

Ar. ramidus fossils has been found at Aramis, Middle Awash, Ethiopia, where it is best described and dated as ~4.4 Ma (WoldeGabriel et al., 1994; White et al., 2009), and at As-Duma, in the Gona Western Margin of Ethiopia, where the fossil is dated between 4.51 Ma and 4.32 Ma (Semaw et al., 2005). Previous paleoenvironmental reconstructions using isotopic composition of tooth enamel on the associated herbivores fauna and paleosols from the same horizon where the fossil were collected at Aramis (*e.g.*, WoldeGabriel et al., 1994; White et al., 2009) suggest that *Ar. ramidus* lived in an environment that was humid and cooler than it is today in habitats ranging from woodlands to patches of forest. On the other hand, Levin et al. (2008) using the same proxy at As-Duma, Gona suggested a paleohabitat with abundant C₄ grasses on the landscape with a general woodland/bushland habitat. Similarly, Cerling et al. (2010) interpret the environmental context of *Ar. ramidus* at Aramis based on the paleosol and tooth enamel carbon isotope data presented in White et al. (2009) and WoldeGabriel et al. (2009) as bush savanna with a habitat ranging from riparian forest to grassland. Although *Ardipithecus* fossil has not reconstructions using isotopic composition of tooth enamel on the associated herbivores fauna and paleosols from the same horizon where the fossil were collected at Aramis been yet recovered at Galili, the isotopic data from the same

level indicate a range of dry open woodland to grassland habitat, where C₄ grasses were prominent on the landscape.

6.3.2 Middle Pliocene (4.38 Ma–3.24 Ma)

Combined data from middle Pliocene discussed here gives us the opportunity to characterize the paleoenvironmental condition in Afar region both in temporal and spatial scale. The lower part of the middle Pliocene between 4.38 Ma and ~3.6 Ma is represented by the Galili fauna while the upper part between >3.8 Ma and 3.24 Ma comes from Dikika. Inter-basin comparison between the SLM at Galili and BBM at Dikika, which are time equivalent members, provide information on the spatial distribution of habitat beyond a single sedimentary basin. As in the early Pliocene, this time interval was characterized by a wide range of variation in the proportion of C₄ grasses and habitat, but the average ecosystem carbon isotope values indicate a general wooded grassland environment (Figure 6.2). At the lower part of the middle Pliocene, between 4.38–3.92 Ma, the average $\delta^{13}\text{C}_{\text{ecosystem}}$ value (–19.1 ‰, 50% C₄ grasses) indicates wooded grassland with C₄ grasses ranging between 41% and 62% (Figure 6 3) where C₃ vegetation were significant on the landscape. This interval has the smallest proportion of C₄ grasses in the middle Pliocene. The habitat structure at Galili also signifies the high proportion of C₃ vegetation, where the habitat was ranging from closed woodland/ riparian woodland to wooded grassland with minor grassland on the landscape (*i.e.*, ~40% closed woodland/riparian woodland, ~29% wooded grassland, ~27% shrubland and ~2% grassland, Figure 6.2).

To date, *A. anamensis* has been found in Kenya and Ethiopia. In Kenya, the specimens were found in Pliocene deposits of Kanapoi and Allia Bay dated between 4.1 and 3.9 Ma (Leaky et al., 1995) and in Ethiopia at Asa Issie, Middle Awash dated between 4.2 and 4.1 Ma (White et al., 2006) and recently reported from Woranso-Mille (Haile-Selassie et al., 2010). Schoeninger et al. (2003) interpreted the paleoenvironments at Allia Bay based on the stable isotopic composition of herbivore tooth enamel as a mosaic of woodlands with open savanna. Likewise, Wynn (2000), using paleosol carbonates at Kanapoi, indicated a mosaic of environments ranging from forb-dominated edaphic grasslands to riparian woodlands. Whereas, White et al. (2008) placed *A. anamensis* from Middle Awash in a more wooded paleoenvironmental setting based on the associated fauna. Although no *A. anamensis* has been found from the Mt. Galili Formation at this time, the environment was wooded grasslands with significant C₃ plants and the habitat was dominated by closed woodland/riparian woodland with minor grassland.

The interval between 3.92 Ma and ~3.6 Ma was characterized by a relative increase in the proportion of C₄ plants. The average $\delta^{13}\text{C}_{\text{ecosystem}}$ value (-17.6‰, 67% C₄ grasses) signifies wooded grassland with C₄ grasses ranging between 51% and 81% (Figure 6.3). The reconstructed habitats at Galili were range from riparian woodlands/deciduous forests to grasslands (i.e. ~33% wooded grassland, ~32% grassland, ~21% shrubland, ~13% riparian woodland/deciduous forest, Figure 6.2). Similarly, the $\delta^{13}\text{C}_{\text{ecosystem}}$ value (-17.7‰, 71% C₄ grasses) from the BBM at Dikika indicates wooded grasslands and shrublands with C₄ grasses ranging between 44% and 85% (Figure 6.3). While, a diverse habitat dominated by wooded grassland covers ~57% of the total areas and open

grassland, shrubland and riparian woodland covers ~30%, ~11% and ~2% of the landscape respectively (Figure 6.2). The reconstructed paleoenvironment and paleohabitats of SLM at Galili and BBM at Dikika indicate a similar paleoenvironmental condition, wooded grassland, in either location with a slight difference in the habitat proportion signifying little spatial variation in the middle Pliocene compared to the temporal variation in the region.

Most of previous paleoenvironmental studies and habitat reconstructions for this time interval were done centered at *A. afarensis*. Reed (2008) suggests that the fauna from the Basal Member at Hadar indicates a mosaics woodland and shrubland, which agrees with the general interpretation at Dikika. Whereas, Haile-Selassie et al. (2010) from preliminary paleoecological interpretations based on faunal abundance at Woranso-Mille indicate a mosaic of habitats, primarily riverine gallery forests laterally extending to closed and open woodland and grassland. Although no hominins have been recovered at this interval at Hadar, *A. afarensis* at Dikika (Alemseged et al., 2005), Woranso-Mille (Haile-Selassie et al., 2010) and Galili (Macchiarelli et al., 2004) would have lived on the landscape, where there were wide range of habitat in a short distance and fed on the food resources available.

The upper part of the middle Pliocene (3.42 Ma-3.24 Ma) data comes from the SHM of Hadar Formation at Dikika. The average ecosystem carbon isotope value (-18.4‰ , 71% C_4 grasses) indicate wooded grassland similar to the rest of the middle Pliocene but a wider range of C_4 grasses between 35% and 82% (Figure 6.3). The habitat structure in

Figure 6.2 shows the presence of the entire range of habitat (*i.e.*, ~ 46% wooded grassland, ~22% open grassland, <20% shrubland, ~8% forest and ~4% riparian woodland/deciduous forest), which is not entirely indicated by the ecosystem carbon isotope values and closed canopy forest habitats are only represented in this time interval.

Hominin fossils have been recovered from SHM at both Dikika and Hadar (Alemseged et al., 2006; Kimbel, 2007), Matabaietu Formation at Maka, Middle Awash (White et al., 1993) and elsewhere in East Africa (Leaky et al., 1995). Analyses of pollen from Hadar (Bonnefille, 2004, 2010) suggest sub-aquatic reeds, sedges, grasses, trees and shrubs with pollens indicating a mosaic and changing environment throughout the Hadar Formation. Reed (2008) also suggests an ecotone habitat at the base of the SHM, followed by wooded shrubland in the middle and scrub woodland and grassland at the top. Unlike the faunal analysis (Reed, 2008), the pollen data (Bonnefille, 2004, 2010) and isotope data presented here show the presence of closed forest in the SHM. The fact that, the presence of closed woodland to forested habitats at Dikika would probably support the importance of arboreal behavior in the *A. afarensis* that has been argued by (Alemseged et al., 2006) in light of the scapula morphology, together with forelimb features such as the long and curved manual phalanges.

6.3.3 Middle Pleistocene (0.8 Ma-0.64 Ma)

At Asbole, although no hominins have been recovered from this time interval, the site is associated with an Acheulean industry (Geraads et al., 2004). The average ecosystem isotope value (−15.4‰, 83% C₄ grasses) indicating a wooded grassland to grassland

environment with C₄ grasses on the landscape ranges between 72% and 91%. Compared to the early and Middle Pliocene, the environment in the middle Pleistocene was open and dominated by C₄ grasses. The reconstructed habitats at Asbole were ranging from wooded grassland to grassland with minor shrubland and riparian forest (*i.e.*, ~73 grassland, ~21% wooded grassland, ~5% shrubland and ~1% riparian forest). Bedaso et al. (2010) based on $\delta^{13}\text{C}_{\text{ecosystem}}$ value and the presence of forest-dwelling primates indicated that the paleoenvironment at Asbole were open vegetation with a gallery forests flanking tributary streams to the paleo-Awash River. As the reconstruction of ecosystem value is only based on the mammals larger than 50 kg, all the primates and other small mammals are not included. But the sensitivity test performed using the most negative value for all the primates' shows that only a 3% increase in the riparian woodland habitat, and overall do not affect the paleoenvironmental and habitat reconstruction. Compared to the Pliocene sites in the Awash Valley the dominance of the grassland habitat is in general agreement with the expansion of grasslands in Africa over the past 3.0 Ma with further dominance after 2.0 Ma (Morgan et al., 1994, Cerling et al., 1997; Bobe and Behrensmeyer, 2007). As the reconstruction of ecosystem value is only based on the mammals larger than 50 kg, all the primates and other small mammals are not included. But the sensitivity test performed using the most negative value for all the primates' shows that only a 3% increase in the riparian woodland habitat, and overall do not affect the paleoenvironmental and habitat reconstruction.

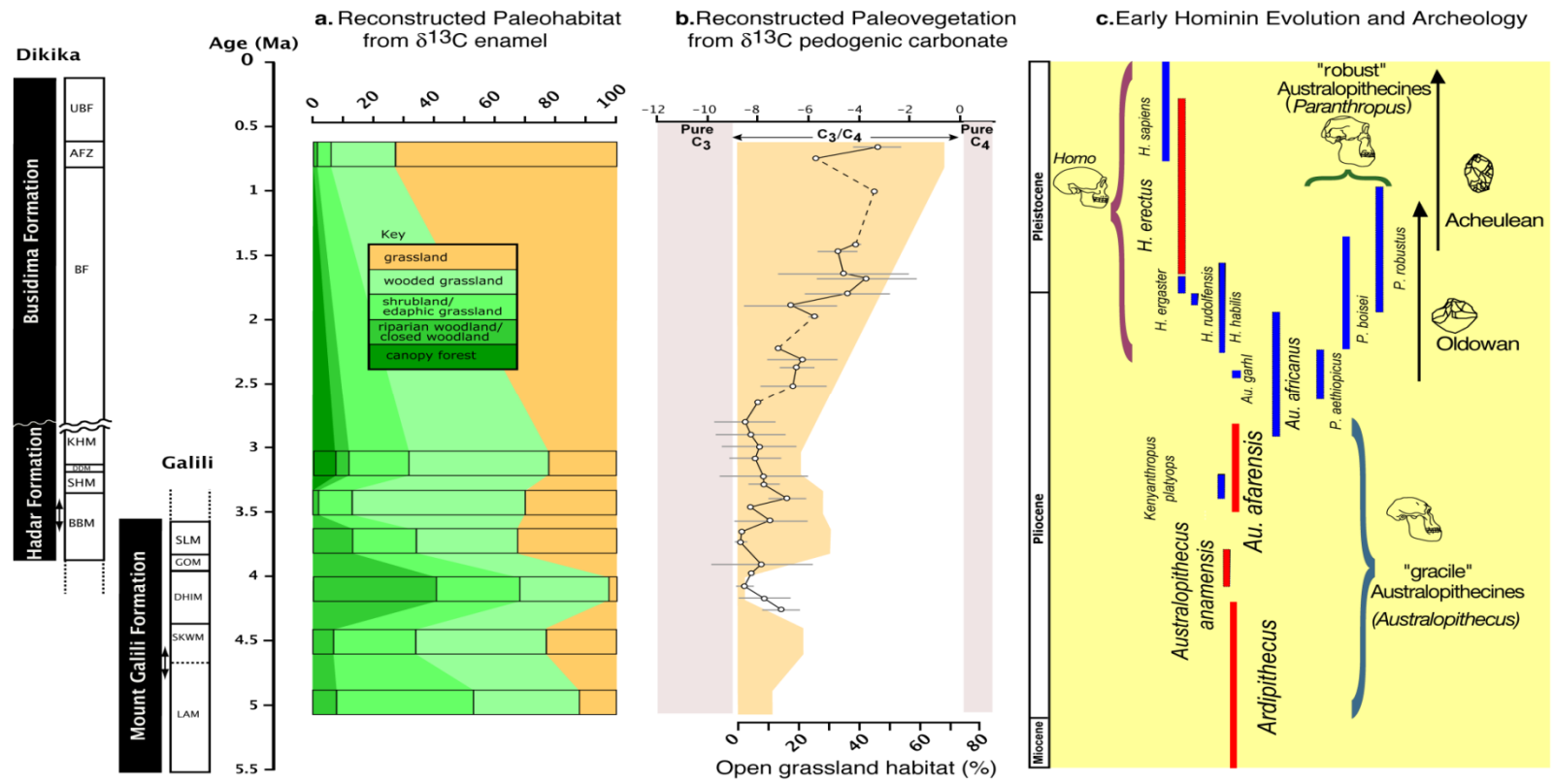


Figure 6.3 **a.** A simplified habitat structure (from Figure 6.2) in different members and change with time, the center of the rectangles represent approximate mid point in the respective members while the size of the do not signify age range. The nomenclature of vegetation follows the United Nations Scientific and Cultural Organization (UNESCO) definitions for classification of African vegetation in (White et al., 1983). **b.** Compiled stable carbon isotopic composition of pedogenic carbonate from Turkana (Cerling et al., 1988; Wynn 2000), the open circles represent the average calculated over a 100 ka with error bars of $\pm 1\sigma$, the pale orange shade superimposed is proportion of an reconstructed open habitat using carbon isotope composition of tooth enamel from Awash valley. **C.** Record of hominin evolution and archeology in Africa, the phylogram adapted from Wood and Lonergan (2008), red color indicates the time interval covered by this study and has direct relevant to the respective hominin while the rest is blue.

Compared to the Pliocene sites in the Awash Valley the dominance of the grassland habitat is in general agreement with the expansion of grasslands in Africa over the past 3.0 Ma with further dominance after 2.0 Ma (Morgan et al., 1994, Cerling et al., 1997; Bobe and Behrensmeyer, 2007). These paleoenvironmental changes have been used to suggest causation for morphological and behavioral changes during human evolution, including the origin of bipedalism since the earliest hominin, the development of megadont molars (Teaford and Ungar, 2000) and the origin of *Homo erectus* (Stanley, 1992, Bobe and Behrensmeyer, 2007).

6.4 Summary

Carbon isotope analysis from mammalian tooth enamel and the estimated ecosystem carbon isotope data, which is based on the average $\delta^{13}\text{C}_{\text{enamel}}$, faunal abundance, and weighted by the amount of biomass consumption, clearly shows that during the Plio-Pleistocene the proportion of C_3/C_4 vegetation substantially varied on the paleolandscape. In the Pliocene between 5.29 Ma and 3.24 Ma, the general paleoenvironmental condition was wooded grassland/shrubland with woodland between 4.38 Ma-3.92 Ma (Figure 6.2 and 6.3). While the paleoenvironmental reconstruction of the Middle Pleistocene between 0.8 Ma and 0.64 Ma indicate wooded grassland to grassland dominated landscape (Figure 6.2 and 6.3). Similarly, the Paleohabitat reconstructions indicate the presence of grassland, wooded grassland/shrubland and riparian woodland throughout the Pliocene and in Middle Pleistocene but canopy-forest was only found between 3.42 Ma and 3.24 Ma (Figure 6.2 and 6.3). Although these habitats were consistently found throughout the Pliocene, the relative proportions were considerably changed in respective members

(Figure 6 3). This shift from C₃-dominated vegetation in the Pliocene to C₄-dominated vegetation in the Middle Pleistocene is in a general agreement with previous reconstruction in the region, which indicates a shift from forest to open grassland since Late Miocene. However, the vegetation change documented here shows a rebound of closed habitat and C₃ canopy forest resources by middle Pliocene. These changes in the proportion of habitats could have put the fauna in competition for their preferred habitats and food resources, which could have forced migration, adaptation to other resources and/or extinction.

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APPENDIX I
MANN-WHITNEY STATISTICAL TEST USING SAS 9.2

APPENDIX I

Alcelaphini	AFZ	SHM	BBM	SLM	LAM	-	-
AFZ		0.3094	0.5	0.8	0.5	-	-
SHM	0.1152		0.381	0.2165	0.7619	-	-
BBM	1	0.4762		0.6667	-	-	-
SLM	0.4	0.1385	0.6667		0.6667	-	-
LAM	0.5	0.381	-	0.6667		-	-
Bovini	AFZ	SHM	BBM	SLM	DHIM	SKWB	LAM
AFZ		<0.001	0.022	0.0069	0.0485	0.0032	0.0022
SHM	<0.001		0.6234	0.9292	0.7173	0.2681	0.5249
BBM	0.022	0.7013		0.8571	0.8571	0.4286	1
SLM	<0.001	0.614	0.2857		0.9307	0.4848	0.7619
DHIM	0.0021	0.169	0.381	0.0519		0.9307	0.9048
SKWB	0.6659	0.0011	0.0714	0.0022	0.0823		0.3524
LAM	0.0071	0.1146	0.1333	0.0095	0.9048	0.6667	
Equids	AFZ	SHM	BBM	SLM	DHIM	SKWB	LAM
AFZ		<0.001	<0.001	0.0027	0.0023	<0.001	0.0016
SHM	0.0162		0.2218	0.5611	0.3981	0.9704	0.184
BBM	<0.001	0.0091		-	0.9131	-	-
SLM	<0.001	0.263	-		0.9551	0.6452	0.743
DHIM	0.0023	0.554	<0.001	0.281		0.3114	0.6065
SKWB	0.0125	0.8724	-	0.1213	0.5336		0.2349
LAM	0.0176	0.963	-	0.0745	0.2523	1	
Elephantids	AFZ	SHM	BBM	SLM	DHIB	-	-
AFZ		0.1818	0.2941	1	0.6667	-	-
SHM	0.0606		0.7234	0.5941	0.3636	-	-
BBM	0.0294	0.7647		0.4445	0.5	-	-
SLM	0.1905	0.6787	0.3949		0.3333	-	-
DHIM	0.6667	0.9091	0.625	0.6667		-	-
Giraffids	AFZ	SHM	BBM	DHIM	SKWB	LAM	-
AFZ		0.0444	0.6667	0.3333	0.6667	1	-
SHM	0.0444		0.222	0.2667	0.6667	0.2667	-
BBM	0.6667	0.2222		0.6667	-	1	-
DHIM	0.3333	0.2667	0.6667		0.6667	1	-
SKWB	0.6667	0.6667	-	0.6667		1	-
LAM	1	0.2667	1	1	1		-

APPENDIX I (CONTINUED)

Hippopotamids	AFZ	SHM	BBM	SLM	DHIM	SKWB	LAM
AFZ		0.1264	0.5476	0.007	0.0357	0.4818	0.0121
SHM	0.0604		0.4043	0.3494	0.0517	0.4119	0.492
BBM	0.0476	0.1802		0.0727	0.0087	1	0.1079
SLM	0.049	0.0845	0.7128		0.1292	0.0435	0.7618
DHIM	0.0714	0.6612	0.9307	0.953		<0.001	0.0653
SKWB	0.6	0.0016	<0.001	<0.001	0.004		0.0745
LAM	0.4973	0.0157	0.0593	0.0085	0.0932	0.0274	
Hippotragini	AFZ	SHM	DHIM	SKWB	LAM	-	-
AFZ		0.2	0.6667	-	0.333	-	-
SHM	0.8		1	-	0.4	-	-
DHIM	0.6667	1		-	1	-	-
SKWB	-	-	-		-	-	-
LAM	0.3333	0.8	0.6667	-		-	-
Nyanzachoerus	SHM	BBM	SLM	DHIM	SKWB	LAM	-
SHM		0.4	0.6667	0.6667	1	0.6667	-
BBM	0.4		0.7302	0.9048	0.0242	0.5556	-
SLM	0.3333	0.9048		1	0.0732	1	-
DHIB	0.3333	0.9048	1		0.048	0.6905	-
SKWB	1	0.0424	0.0303	0.1061		0.149	-
LAM	0.3333	0.9048	0.8413	0.7105	0.0025		-
Reduncini	AFZ	SHM	SLM	DHI	SKWB	LAM	-
AFZ		1	0.3619	<0.001	0.3132	0.0131	-
SHM	0.2857		0.6667	0.4	0.2857	0.2	-
SLM	0.0381	1		0.5333	0.6429	1	-
DHIM	0.0017	0.4	1		0.1143	0.0196	-
SKWB	0.2728	0.8571	0.4286	0.0667		0.2238	-
LAM	0.0018	0.6	0.9091	0.7105	0.0879		-
Tragelaphini	AFZ	SHM	SLM	DHIM	SKWB	LAM	-
AFZ		0.5167	0.6667	1	0.0476	0.8333	-
SHM	0.0667		0.535	0.366	0.0221	0.2593	-
SLM	0.0333	0.62		0.6282	0.0513	1	-
DHIM	0.0476	0.8357	0.6282		0.132	0.4452	-
SKWB	0.5476	0.0734	0.0082	0.0152		0.0734	-
LAM	0.1167	0.9015	0.4557	0.8357	0.1014		-

APPENDIX II
HABITAT PROPORTION

APPENDIX II

AFZ		
$\delta^{13}\text{C}$ ecosystem	Weighted frequency	Normalized Probability
-28	0	0
-27	0	0
-26	0	0
-25	3.96	0
-24	0	0
-23	0	0
-22	11.76	0.01
-21	0	0
-20	3.96	0
-19	87.46	0.05
-18	0	0
-17	35.42	0.02
-16	109.94	0.06
-15	270.7	0.14
-14	261.32	0.14
-13	438.82	0.23
-12	325.84	0.17
-11	290.34	0.15
-10	78.48	0.04
SUM	1918	1.0
SHM		
$\delta^{13}\text{C}$ ecosystem	Weighted frequency	Normalized Probability
-28	113.68	0.02
-27	113.68	0.02
-26	69.32	0.01
-25	12.48	0
-24	76.68	0.02
-23	113.68	0.02
-22	98.4	0.02
-21	74.82	0.01
-20	63.29	0.01
-19	833.06	0.16
-18	444.6	0.09
-17	309.7	0.06
-16	976.36	0.19

APPENDIX II (CONTINUED)

-15	663.23	0.13
-14	669.78	0.13
-13	267.15	0.05
-12	147.9	0.03
-11	24.65	0
-10	24.65	0
SUM	5097.11	1.0
BBM		
$\delta^{13}\text{C}$ ecosystem	Weighted frequency	Normalized Probability
-28	0	0
-27	0	0
-26	0	0
-25	10.12	0
-24	0	0
-23	15.4	0
-22	27.41	0
-21	342	0.03
-20	600.8	0.05
-19	391.6	0.03
-18	25.6	0
-17	2152.1	0.18
-16	2834.68	0.24
-15	1833.95	0.15
-14	3627.94	0.31
-13	15.4	0
-12	0	0
-11	0	0
-10	0	0
SUM	11877	1.0
SLM		
$\delta^{13}\text{C}$ ecosystem	Weighted frequency	Normalized Probability
-28	0	0
-27	0	0
-26	0	0
-25	4.84	0
-24	330.99	0.04
-23	192.64	0.02

APPENDIX II (CONTINUED)

-22	667.7	0.08
-21	330.99	0.04
-20	178.22	0.02
-19	750.26	0.09
-18	627.38	0.07
-17	2306.1	0.26
-16	424.89	0.05
-15	123.02	0.01
-14	2773.39	0.32
-13	56.08	0.01
-12	6.38	0
-11	6.38	0
-10	0	0
SUM	8779.23	1.0
DHIM		
$\delta^{13}\text{C}$ ecosystem	Weighted frequency	Normalized Probability
-28	0	0
-27	0	0
-26	0	0
-25	10.12	0
-24	0	0
-23	15.4	0
-22	27.41	0
-21	342	0.03
-20	600.8	0.05
-19	391.6	0.03
-18	25.6	0
-17	2152.1	0.18
-16	2834.68	0.24
-15	1833.95	0.15
-14	3627.94	0.31
-13	15.4	0
-12	0	0
-11	0	0
-10	0	0
SUM	11877	1.0
SKW		

APPENDIX II (CONTINUED)

$\delta^{13}\text{C}$ ecosystem	Weighted frequency	Normalized Probability
-28	0	0
-27	0	0
-26	0	0
-25	7.37	0.001
-24	290.04	0.07
-23	0	0
-22	0	0
-21	32.8	0.01
-20	219.48	0.05
-19	459.42	0.11
-18	351.64	0.09
-17	141.57	0.04
-16	593.12	0.12
-15	1001.36	0.25
-14	623.32	0.16
-13	193.89	0.05
-12	62.67	0.02
-11	20.46	0.01
-10	0	0
SUM	3997.14	1.0
LAM		
$\delta^{13}\text{C}$ ecosystem	Weighted frequency	Normalized Probability
-28	0	0
-27	0	0
-26	0	0
-25	41.35	0.02
-24	171.57	0.06
-23	8.03	0
-22	8.03	0
-21	158.48	0.06
-20	374.68	0.14
-19	178.17	0.07
-18	517.84	0.19
-17	432.16	0.16
-16	329.41	0.12
-15	185.06	0.07

APPENDIX II (CONTINUED)

-14	242.85	0.09
-13	36.76	0.01
-12	8.03	0
-11	0	0
-10	33.32	0.01
SUM	2725.74	1.0