The Utility of Refined $\delta^{13}C$ Values in Hominin Paleoecology

by

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(Under the Direction of Elizabeth Reitz)

ABSTRACT

The ‘‘Habitat Theory’’ by Elisabeth S. Vrba offers an insightful perspective on the connection between paleoclimate and hominin evolution. However, approaches to test this theory precisely using faunal evidence are lacking. Refined $\delta^{13}C$ values offer promising grounds to test this theory. This thesis refines (normalizes and corrects) $\delta^{13}C$ values from modern African Great Apes, and demonstrates the efficacy of stable carbon isotope ecology to test postulates of the ‘‘Habitat Theory.’’ The mean for all refined $\delta^{13}C$ values is -14.8‰. This reflects a predominantly C_3 feeding and forest-adapted lineage. Habitat patterns explain 88% of the variation in refined $\delta^{13}C$ values; genus explains 5%; species level explains 51%; and subspecies explains 55% of the variation. Refined $\delta^{13}C$ values also show that most populations are significantly different from each other. Tracing $\delta^{13}C$ value patterns from fossil fauna promises to provide insights on the connection between paleoclimate and hominin evolution.

INDEX WORDS: ‘‘Habitat Theory’’; Paleoclimate; Hominin Evolution; African Great Apes; Refined $\delta^{13}C$ Values

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DEDICATION

To my parents, Partison Nakaya and Florence Nthenya Iminjili who imbued in me a hardworking and ‘‘never say die’’ spirit that has brought me this far,

Thure Cerling and Meave Leakey who enthused me to join stable isotopes and primate evolution studies,

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CHAPTER 1

INTRODUCTION

Of all the potential studies on the East Turkana monkeys which can be done in the future, a few stand out as most pressing and interesting. The first of these would be a comprehensive study of the stable isotope composition of the dental enamel of as many of the monkey species from the region as possible.

-Jablonski and Leakey (2008b, p 411)

The milestone achievements realized in paleoanthropological studies during the last two centuries point to the potential of more intriguing achievements being made during the 21st century (Behrensmeyer et al., 2007; Ciochon and Fleagle, 2006; Darwin, 1859; Grant and Grant, 2008; Jablonski and Leakey, 2008a; Sponheimer and Lee-Thorp, 2007; Vrba et al., 1995; Werdelin and Sanders, 2010). Stable carbon isotope ecology promises to provide intriguing insights into the connections between paleoclimate and hominin evolution (Cerling et al., 1998; Cerling et al., 1997a; Cerling et al., 1999; Cerling et al., 2010a; Cerling et al., 1997b; Cerling et al., 2004; Cerling et al., 2011a; Cerling et al., 2011b).

Our current understanding of hominin evolution is mainly based on achievements made during the last two centuries. Darwin wrote ‘‘*The Origins of Species by Means of Natural Selection*’’ during the 19th century (Darwin, 1859). The 20th

century witnessed landmark hominin discoveries that have transformed our understanding of the emergence, and subsequent evolution of our early hominin ancestors. Major sahelanthropine, orrorine, australopithecine, paranthropine, kenyanthropine, ardipithecine, and early *Homo* fossil discoveries were made during this period (Maclatchy et al., 2010). Owing to these discoveries we now know that hominins evolved in a bushy, non-linear pattern.

During the last two decades of the 20th century, palaeoanthropological investigations at subtropical African fossil sites were focused on recovering hominin remains and mapping evolutionary patterns within this lineage (Behrensmeyer et al., 2007; Maclatchy et al., 2010). Major contributions that track trends in orbital forces and connect them to global climatic trends and hominin evolution were made during these last two decades (deMenocal, 2011; Feakins and deMenocal, 2010; Patridge, 2010; Vrba et al., 1995). Paleoecological studies became core components of palaeoanthropological studies during this same time (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Bobe et al., 2002; Bobe et al., 2007; Frost, 2007). Studies aimed at reconstructing hominin ecologies focused on tracking ecological changes over time in line with Orbital Forcing Timescale (OFT) climatic cycles during this period (Behrensmeyer et al., 2007; Bromage and Schrenk, 1999; Vrba et al., 1995). The ‘‘Habitat Theory’’ was formulated and became a central theory in hominin paleoecology during this time.

The ‘‘Habitat Theory’’ provides a comprehensive theoretical perspective on the connection between faunal evolutionary patterns and habitat changes associated with OFT climatic cycles and orogenic disruptions (Vrba, 1992; 1995a; b; 1999; 2000; Vrba et al., 1995). Major faunal speciation, migration, and extinction patterns are interpreted

as a product of these two phenomena. Faunal lineages are viewed as being adapted to either warm/wet or cold/dry climatic cycles, which are products of OFT shifts. Variations in solar insulation reaching the earth over time as a result of orbital precession, axis of rotation, and orbital eccentricity cycles are cited as the main orbital forces driving climatic trends and hominin evolution (Bromage and Schrenk, 1999; Vrba et al., 1995).

Orogenic disruptions, primarily, plate tectonic and volcanic activity, cause perturbations in the OFT climatic cycles (deMenocal, 2011; deMenocal and Bloemendal, 1995; Feakins and deMenocal, 2010; Patridge, 2010; Patridge et al., 1995a; Patridge et al., 1995b; Vrba, 2000). The development of the East African Rift System (EARS) and orogenic events in other continents interfered with the global current circulation and led to an expansion of grassland habitats in eastern Africa. Records from continental dust show that subtropical African climatic patterns are in line with the OFT climatic cycles (deMenocal, 2004; 2011; deMenocal and Bloemendal, 1995). Evidence shows that subtropical Africa has experienced multiple cycles of first, expansion of forests and contraction of grasslands, followed by expansion of grasslands and contraction of forests (Bonnefille, 2010; Kingdon, 1984). There were periods when forests extended to the interior of eastern Africa (Ethiopia, Kenya, and Tanzania), and periods when grasslands expanded to the interior of the Congo Basin. During the last 5 Ma the forest-grassland expansion and contraction cycles have tilted towards more numerous, and longer duration grassland and shorter forest expansion cycles in eastern Africa (Fig. A1.1).

Patterns of primate evolution in subtropical African fossil sites mirror the paleoclimatic cycles associated with OFT (Jablonski and Leakey, 2008a; Kingdon, 2001; Werdelin and Sanders, 2010). Before 5 Ma the fossil record shows that subtropical Africa had the largest diversity of apes ever recorded in primate history. Monkey taxa were extant but not as numerous as ape taxa. During the last 5 Ma the trend has shifted. Monkey taxa diversified and became more numerous all through the African fossil record. Ape taxa disappeared from the eastern Africa fossil record, though noted briefly around 300 Kyr (Harrison, 2010; McBrearty and Jablonski, 2005). Today, apart from regions around Lake Tanganyika in Tanzania, the Virunga volcanoes in Rwanda, and Kibale region in Uganda apes are not found in eastern Africa (Fig. A1.2) (Campbell et al., 2006; Kingdon, 2001). Monkeys have continued to be present and diverse in eastern Africa from the Plio-Pleistocene to the present time (Jablonski and Leakey, 2008a). During the last 5 Ma, the speciation patterns evident in the fossil record of monkeys mirrors the speciation patterns seen in early hominins: an increase and decrease in number of species overtime.

Understanding the connections between speciation patterns evident in the fossil archives, and the finer details of OFT climatic cycles, is of great significance to paleoecologists. Hominin paleoecologists use the basic assumptions that natural laws were the same in the past as they are today and that organisms with structures similar to those in organisms living today had similar patterns of behavior and similar ecological characteristics (Odum and Barrett, 2005). The ecological indicator taxa approach, a core investigative tool in hominin paleoecology is built on these assumptions (Behrensmeyer et al., 2007). This approach use modern mammalian communities, and extrapolations

based on taxonomic relations to reconstruct paleoecology. This is based on the assumptions: (1) that the range of modern examples covers the range of ancient adaptations and community structure, and (2) that it is valid to apply ecomorphic characteristics of modern taxa to their extinct relatives. Are these assumptions appropriate? Are they effective? Are they exhaustive?

During the last two decades, the ecological indicator taxa approach has dominated paleoecological studies in eastern Africa (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Bobe et al., 2002; Bobe et al., 2007). The ecological indicator taxa approach (index taxa approach) is a paleoecological perspective that uses specific fossil taxa (indicator taxa) as biomarkers for habitat types (Kingston, 2007, p 34). This approach assumes that indicator taxa have specific habitat preferences and that this habitat(s) is well established, typically on the basis of analogy with extant-descendant lineages or highly derived morphology (Kingston, 2007, p 34). Although this approach provides good evidence for speciation patterns in line with climatic changes, its support for the ‘‘Habitat Theory’’ is questionable (Bobe et al., 2007; Frost, 2007). This approach is also marred by inherent challenges that remain unresolved (Behrensmeyer et al., 2007; Bobe, 2006; Bobe and Behrensmeyer, 2004; Bobe et al., 2002; Bobe and Eck, 2001; Iminjili et al., 2009). These include: (1) assigning fossil specimens to genus, species, subspecies, and population taxonomic categories using morphological traits is still controversial and leads to differences in interpretation that may affect measures of faunal diversity, provinciality, and timing of appearances and extinctions; and (2) taphonomic processes, sampling, identification, and analytical protocols (collection methods) affecting the quality and space/time resolution of paleoecological information

have not been resolved. For example, many fossils were not collected or documented with paleoecological questions in mind, thus population data for these fossils are not adequate for paleoecological reconstruction (Iminjili et al., 2009). These challenges call for both the theory and the method to be tested further.

To improve our understanding of the connection between paleoclimate and hominin evolution, we need to have alternative approaches that will enable testing of the ‘‘Habitat Theory’’ more precisely. Stable carbon isotope ecology offers a promising ground for this adventure (Cerling et al., 1999; Cerling et al., 2010a; Cerling et al., 2011a; Uno et al., 2011). Preliminary work during the last two decades demonstrate the efficacy of stable carbon isotope ecology to provide insightful information that other approaches used in hominin paleoecology do not capture (Behrensmeyer et al., 2007; Cerling et al., 1999; 2005; Cerling et al., 2010a; Cerling et al., 1997b; Cerling et al., 2004; Cerling et al., 2011a; Uno et al., 2011). Further, due to technological advances over the last four decades, stable carbon isotope ecology has been refined and promises to test postulates of the ‘Habitat Theory’’ more precisely than earlier methods (Cerling et al., 2010a; Ehleringer et al., 2002; Lee-Thorp et al., 2003; Sponheimer et al., 2009; Sponheimer et al., 2005; Sponheimer and Lee-Thorp, 2007). This perspective is based on the biogeochemistry of stable carbon isotopes.

Stable carbon isotope ecology is different from the ecological indicator taxa approach in a number of ways. While both approaches indicate ecological characteristics, stable carbon isotope ecology is not taxa dependent, but is based on $\delta^{13}C$ values which can be from plant, animal or soil samples (Cerling, 1992b; Cerling et al., 2010a; Cerling et al., 2011b; Passey et al., 2010). While the ecological indicator taxa

approach infers ecology based on a species modern representative's physical traits, stable carbon isotope ecology uses $\delta^{13}C$ values to define the ecological attributes of a species (Cerling et al., 2010a). Further, the ecological indicator taxa approach as applied by hominin palaeoecologists studying fossil fauna is restricted to faunal evidence and assumes that the ecology of modern species is similar to closely related fossil species (Behrensmeyer et al., 2007).

There are three photosynthetic pathways utilized by plants: C_3, C_4, and CAM. The C_3 pathway is the least advanced (Cerling et al., 1998; Ehleringer et al., 1997). It was mainly used by the earliest plants from the early history of the earth when CO_2 was more abundant. The C_4 and CAM pathway evolved more recently in response to lower atmospheric CO_2 levels. C_3 plants make up most of the global biomass. C_4 plants make up about 18% of the global terrestrial productivity. CAM plants have a lower global productivity than both C_3 and C_4 plants. Most of the vegetation in subtropical Africa utilize either C_3 or C_4 photosynthetic pathways. The $\delta^{13}C$ values of a biome are recorded in the soil and enamel of animals that feed and live in that biome. The $\delta^{13}C$ values capture the speciation, dietary, and habitat patterns of a lineage at the population level and thus offer a precise way of reconstructing hominin paleoecology.

This thesis lays groundwork for developing an approach based on refined $\delta^{13}C$ values that will be used to reconstruct speciation patterns connected to dietary and habitat changes, postulated by the ‘‘Habitat Theory.’’ Two approaches based on refined $\delta^{13}C$ values from modern African Great Apes demonstrating the utility of $\delta^{13}C$ values in paleoanthropological studies are presented.

Three main objectives are addressed: (1) solve the normalization and correction conundrum in stable carbon isotope ecology; (2) use refined $\delta^{13}C$ values to shed light on the connection between dietary and speciation patterns among modern African Great Ape subspecies; and (3) use refined $\delta^{13}C$ values to reconstruct the habitats of modern African Great Ape subspecies.

The ability of refined $\delta^{13}C$ values to differentiate the dietary and habitat patterns of a lineage in line with cold/dry (glacial) and warm/wet (interglacial) climatic patterns and thus test postulates of the ‘‘Habitat Theory’’ will be demonstrated. African Great Apes represent a warm-adapted species (forest adapted C_3 feeders group), thus they offer a good analogue for an interglacial lineages' speciation and habitat patterns (Campbell et al., 2006; Fleagle, 1999; Kingdon, 2001).

Two hundred and seventy two $\delta^{13}C$ values from modern African Great Apes were normalized and corrected. They were analyzed using measures of central tendency and dispersion, and ANOVA. The analyses were used to test the connection between modern African Great Ape lineage speciation, dietary and habitat patterns. Two main hypotheses guided the study:

1) The connection between dietary and speciation patterns among subspecies of the modern African Great Apes (common chimpanzees, bonobos, and gorillas) can be derived from their refined $\delta^{13}C$ values.

2) The connections between speciation patterns and habitats for different modern African Great Apes can be verified from their refined $\delta^{13}C$ values.

For this study, diet refers to the food matter that an organism consumes (Fleagle, 1999). The habitat of an organism is the place where it lives, or the place where one

would go to find it (Odum and Barrett, 2005, p 311). Biome is a large regional or subcontinental system characterized by a particular major vegetation type (Odum and Barrett, 2005, p 513). Biomes are distinguished by the predominant plants associated with a particular climate. Ecosystem is a biotic community and its abiotic environment functioning as a system: a discrete unit that consists of living and nonliving parts interacting to form an ecological system (Odum and Barrett, 2005, p 516).

CHAPTER 2

LITERATURE REVIEW

The model I propose here predicts that lineages in contrasting habitat categories have new species starting up (by speciation) at displaced times and old species ending (by extinction) at differing times, rather like runners in a relay race.

-Vrba (1995b, p 29)

Understanding the processes that shaped hominin evolution over the last 5-10 Ma is complex (Behrensmeyer et al., 2007; Bonnefille, 2010; Bromage and Schrenk, 1999; Cerling et al., 2010a; Vrba et al., 1995; Werdelin and Sanders, 2010). The ‘‘Habitat Theory’’ provides a concrete theoretical perspective that connects paleoclimate with hominin evolution (Vrba, 1995b; 1999). Planetary investigations provide data on the connection between Orbital Forcing Timescale (OFT) and climatic cycles (deMenocal, 2011). Investigations on orogenic events provide information on plate tectonic and volcanic activities that influence the OFT climatic cycles (Patridge, 2010). Investigations of terrestrial life forms provide evidence on the connections between OFT climatic cycles, orogenic events, and faunal evolution (Behrensmeyer et al., 2007; Werdelin and Sanders, 2010). During the last four decades these approaches have provided overwhelming evidence that supports the connection between OFT climatic cycles and hominin evolution. Despite this success, we still do not have finer

details on the connection between OFT climatic cycles and hominin evolution at the population and habitat levels.

The challenges inherent in the ecological indicator taxa approach calls for a revision of both the method and theory (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Bobe et al., 2002; Bobe et al., 2007; Frost, 2007). Due to these challenges, studies utilizing this approach are contradictory. The study by Frost (2007) on fossil monkeys does not support postulates of the ‘‘Habitat Theory.’’ Other studies do not differentiate cold/dry and warm/wet-adapted speciation patterns (Bobe and Behrensmeyer, 2004; Bobe et al., 2002; Bobe et al., 2007). Although the Bobe et al. (2007) approach supports postulates of the ‘‘Habitat Theory,’’ this approach assumes that fossil bovid tribe members reflect dietary and habitat patterns similar to modern members of these tribes. Similar assumptions are used to reconstruct hominin paleoecology. *Paranthropus boisei* is a classic example (Cerling et al., 2011a; Maclatchy et al., 2010; van der Merwe et al., 2008). Due to its robust morphology, *P. boisei* has been interpreted as having dietary patterns similar to modern chimpanzees (browsing C_3). *P. boisei*’s flared zygomatic arches, massive sagittal crest, post-canine megadontia, and robust appearance have been interpreted to mean that *P. boisei* was feeding on nuts similar to modern chimpanzees. Nuts are found in forested and closed woodland biomes (C_3 vegetation) and so it is expected that $\delta^{13}C$ values from a habitual nut feeder will reflect a C_3 signature. Stable carbon isotope investigations show *P. boisei* was a predominantly C_4 feeder (grazer). Stable carbon isotope ecology investigations on modern and fossil proboscids from eastern and central Africa discussed below and

results of this thesis show that members of a lineage at the population/habitat level can have diametrically different diet/habitat patterns.

Stable carbon isotope ecology promises to replicate speciation and habitat patterns of lineages and thus test postulates of the ‘‘Habitat Theory’’ more precisely than other methods have been able to do. This thesis uses refined $\delta^{13}C$ values from modern African Great Apes to demonstrate this utility. This chapter reviews the available literature on the connections between OFT climatic cycles, orogenic events, and faunal evolution during the late Cenozoic.

The first part of this chapter looks at paleoclimate and hominin evolution. The emergence and subsequent evolution of our early hominin ancestors is placed in the context of OFT climatic cycles. In the next section, a discussion of the ‘‘Habitat Theory’’ and its challenges followed by a section on Darwin’s finches are provided. Next, extensive reviews on the connections between late Cenozoic climatic patterns in subtropical Africa, OFT climatic cycles, plate tectonics, and volcanic activities in subtropical Africa are provided. Reviews of two leading studies that use the ecological indicator taxa approach to test postulates of the ‘‘Habitat Theory’’ are also provided. The main limitations of this approach for testing postulates of the ‘‘Habitat Theory’’ precisely are highlighted. In the next section, the theoretical basis of stable carbon isotope ecology is provided followed by a discussion of its utility in paleoanthropological investigations. The main challenges in stable carbon isotope ecology and how to approach them are reviewed. Debatable conclusions in stable carbon isotope ecology are also discussed in this part. A discussion on the prospects for a multi-proxy stable isotope studies in hominin paleoecology is provided in the next part. In the

last part of this chapter, a discussion that justifies the use of modern African primates in the refined $\delta^{13}C$ values approach is provided followed by a discussion of African Great Apes taxonomy, diet, and habitat patterns.

Paleoclimate and Hominin Evolution in Subtropical Africa

The emergence, radiation, and evolution of our hominin ancestors is closely connected to the OFT climatic cycles, and perturbations caused by orogenic events (Bonnefille, 2010; Bromage and Schrenk, 1999; deMenocal, 2011; Jablonski and Leakey, 2008a; Vrba, 1995b; 2000; Werdelin and Sanders, 2010).

Deep-sea records of aeolian dust from West and East Africa track the OFT climatic cycles in subtropical Africa during the Plio-Pleistocene (deMenocal, 2011; deMenocal and Bloemendal, 1995). Climatic perturbations near 2.8 Ma and again at 0.9 Ma coinciding with major changes in high-latitude climate are recorded. Intense dry periods are recorded in the eastern African region between 1.8 and 1.6 Ma. Aeolian variability prior to 2.8 Ma coincides with the 23-19 Kyr cycles associated with orbital precession. The 41 Kyr cycles associated with the tilt of axis (rotation) become dominant after 2.8 Ma, followed by the dominance of the 100 Kyr cycles associated with eccentricity after 0.9 Kyr.

Orogenic events significantly affected the subtropical African climatic patterns (Feakins and deMenocal, 2010; Patridge, 2010; Patridge et al., 1995a; Patridge et al., 1995b; Vrba, 1999; 2000). African climate was independent of high-latitude climate prior to 2.8 Ma, when ice sheets were small and invariant build-up of the northern hemisphere ice sheets after 2.8 Ma led to the dependence of African climate upon the high-latitude glacial and interglacial cycles. The formation of the East African Rift

System (EARS) led to aridity and expansion of grasslands in eastern Africa over the last 5 Ma. These changes coincide with several major steps in hominin evolution (deMenocal, 2011).

Major hominin extinction, speciation, and behavioral patterns are associated with changes in African climate during the Plio-Pleistocene (deMenocal, 2011; Feakins and deMenocal, 2010; Vrba, 1988; 1992; 1995a; 1999; 2000). Identifiable first appearance and extinction events, and key behavioral milestones, cluster between 2.9 and 2.6 Ma, and again between 1.9 and 1.6 Ma. *Australopithecus afarensis* goes extinct near 2.9 Ma, and paranthropines appear near 2.7 Ma. The large-brained *Homo* lineage appears after 2.6 Ma. First evidence of the Oldowan stone tool assemblage also appears around 2.6 Ma. Between 1.9 and 1.6 Ma *Homo erectus* appears as do more developed and refined Acheulian stone tools. Hominins migrate out of Africa around this time.

The fact that the emergence and subsequent evolution of our hominin ancestors is closely tied to OFT climatic cycles makes paleoecological studies significant to paleoanthropologists. The ‘‘Habitat Theory’’ provides a robust theoretical framework to look at the connections between paleoclimate and hominin evolution.

The ‘‘Habitat Theory’’

The ‘‘Habitat Theory’’ links faunal evolutionary patterns to environmental changes brought about by OFT climatic cycles and orogenic events (Vrba, 1988; 1992; 1995b; 1999; 2000; Vrba et al., 1989; Vrba et al., 1995). This theory postulates that species differ in habitat preferences and therefore in vicariance and speciation during the OFT climatic cycles. The theory predicts that lineages in contrasting habitat categories (warm and cold habitats) experience speciation and extinction at displaced times. This

relay model proposes that species turnover is characterized by particular sequential and frequency patterns. Long-term warming is accompanied by successive events roughly in the following order: (1) extinction of some cooler-adapted species; (2) speciation of surviving cooler-adapted species; (3) extinction of some warmer-adapted species; and (4) speciation of surviving warmer-adapted species. A higher proportion of warmer-adapted species should emerge as cooler-adapted species disappear. By contrast, long-term cooling triggers a turnover pattern in which warmer-adapted species turnover before cooler-adapted species; higher proportions of warmer-adapted species become extinct. The theory further argues for vicariance brought about by cyclic climatic changes driven by OFT as the major force driving faunal evolution. In addition, the theory claims that over the last few million years, glacial episodes have been dominant, thus favoring diversification of cool-adapted species.

Faunal evidence offers one of the best grounds to test postulates of the ‘‘Habitat Theory’’ precisely. Studies utilizing ecological indicator taxa approach to investigate hominin paleoecology arrive at conflicting conclusions over the ability of the ‘‘Habitat Theory’’ to explain evolutionary patterns. To be able to precisely map the connection between paleoclimate and hominin evolution over the last 5 Ma, a good background on speciation patterns at the subspecies, population and habitat levels is needed. Studies utilizing the ecological indicator taxa approach are not refined enough to capture subspecies and population variations within a species.

The ‘‘Habitat Theory’’: Challenges

Although the ‘‘Habitat Theory’’ offers an elaborate theoretical framework that connects hominin evolution and paleoclimate, it faces a number of challenges.

(Behrensmeyer et al., 1997; Kingston et al., 2007; McKee, 2001; Potts, 1998a; White, 1995).

Due to limited chronological control and the confounding effects of tectonic control on sedimentation patterns within the EARS, unequivocal evidence of climatic shifts at Pliocene hominin localities that can be directly linked to OFT climatic cycles is limited; this hampers attempts to develop causal relationships between hominin evolution and OFT climatic shifts (Kingston et al., 2007). A number of studies arrive at conclusions that contradict the ‘‘Habitat Theory’’ (Behrensmeyer et al., 2007; Behrensmeyer et al., 1997; Vrba et al., 1995). Despite purporting to support the ‘‘Habitat Theory’’, most of the articles published by Vrba et al (1995) show strong fluctuation between 2.8 and 2.5 Ma rather than a simple cooling or aridity shift (Potts, 1998a). Further, not all faunal taxa that have been studied support the ‘‘Habitat Theory.’’ African bovids, micromammals, and hominins are argued to support the theory (Vrba, 1995a; b; Wesselman, 1995), but according to some scholars, evidence from suids, monkeys, and hominins do not support the theory (Frost, 2007; White, 1995). Although the latest paleoecological studies based on fossil fauna from the Turkana Basin support postulates of the ‘‘Habitat Theory’’ (Bobe et al., 2007), earlier studies did not record statistically significant speciation patterns in either the first or last appearances at 2.5 Ma or between 2.8 and 2.5 Ma (Behrensmeyer et al., 1997). The work by Behrensmeyer et al. (1997) further shows that speciation patterns between 2.5 and 1.8 Ma was prolonged and a combination of warm and cold adapted species persisted from 3 to 2 Ma. It has been argued that this finding represents a prolonged turnover rather than pulse turnover (Behrensmeyer et al., 1997). The study by Frost

(2007) (discussed below) concludes that there is a relatively constant rate of turnover of cercopithecoids between 4 Ma and the Holocene (Frost, 2007).

In the next section, Darwin's finches are used to highlight the significance of looking at speciation patterns at population and habitat scales, and provide a bearing for this thesis.

Darwin's Finches and the ''Habitat Theory''

Using data from Darwin's finches, Grant and Grant (2008) demonstrate how 14 species of finches radiated from a single lineage as a result of climatic changes. When the ancestral species migrated to the Galapagos Islands, there were opportunities for the finches to make a living as seed eaters, cactus eaters, and so on. The new ecological niches available resulted in speciation patterns that led to the 14 finch species. During the late 1970s, Daphne Major Island experienced a severe drought. This drought led to food scarcity, and change in proportion of available food for finches on the Island. Small tender seeds became scarce while large, hard seeds increased in proportion. The finches with shallow beaks (adapted to feeding on small, tender seeds) experienced food scarcity more than those with deeper beaks (adapted to feeding on large, hard seeds). More of the shallow-beaked finches died. Within a span of two years, the number of finches on the island had decreased, but the proportion of finches with deeper beaks increased. More evidence from the Galapagos Islands tracks how the beak sizes of Darwin's finches change in response to habitat changes brought about by climatic cycles.

Dietary flexibility significantly contributes to a species ability to survive during times of environmental change (Grant and Grant, 2008). A lineages' physical structure

plays a significant role in shaping its dietary flexibility. A dietary switch is followed later by genetic and physical change in response to selection on any heritable character that would increase the efficiency of feeding on the available diet. The time taken for an emerging species to show distinct morphological traits from the parent species differs among lineages. Faunal groups with highly flexible morphology such as birds will show morphological changes faster than groups with less flexible morphology (elephants, bovids, and primates).

To capture the connection between speciation and OFT climatic cycles in the fossil record precisely, analysis at the population and habitat scales must be considered. Speciation, dietary, and habitat patterns among modern African Great Apes demonstrate this point (Campbell et al., 2006; Fleagle, 1999; Kingdon, 2001). Modern African Great Apes are divided into two species (*Pan troglodytes* and *Pan paniscus*) each with elaborate subspecies and populations in different habitats subsisting on varied diets. High resolution data that captures speciation patterns at the population and habitat scales for African primates and other faunal taxa in the fossil record are lacking (Cerling et al., 2010a; Frost, 2007; Jablonski and Frost, 2010; Jablonski and Leakey, 2008b).

Before looking at stable carbon isotope ecology, the next section gives a background on the connection between paleoclimate, OFT cycles, orogenic events, and faunal evidence for paleoecological change.

Late Cenozoic Climatic Patterns in Subtropical Africa

Global climatic patterns have not been stable over the last 65 million years (Bonnefille, 2010; Cerling et al., 2005; Cerling et al., 1997b; deMenocal, 2004; 2011; Ehleringer et al., 2002; Vrba et al., 1995; Werdelin and Sanders, 2010). The fossil

record shows that, prior to the mid-Miocene, the global climate was dominated by warm, moist conditions and that subtropical Africa (from western to eastern Africa between 23.5° north and 23.5° south of the equator) was mostly covered by a thick band of mosaic forests and closed woodlands. Evidence from different sites shows that environmental conditions started changing beginning in the mid-Miocene (15 to 8 Ma). These changes intensified during the Plio-Pleistocene (5 to 1 Ma). The globe became cooler and dryer. The expansive, dense forests and closed woodlands that covered most of tropical Africa began to shrink. Notable changes in seasonal patterns and increased climatic variability are hypothesized for this period (Cerling et al., 2010a; Feakins and deMenocal, 2010; Jablonski and Frost, 2010; Jablonski and Leakey, 2008a; Jacobs et al., 2010; Potts, 1998a; b; Vrba, 1995b; 1999). This variability increased in intensity during the Plio-Pleistocene. These climatic changes are connected to OFT cycles and orogenic events.

Late Cenozoic Orogenic Events and Climate in Subtropical Africa

The mid-Miocene is marked by periods of significant orogenic events in the Earth's history that had immense impact on climatic patterns in subtropical Africa. Massive tectonic reorganization, volcanic eruptions, a fall in atmospheric $\delta^{13}C$ values, and dramatic cooling that plunged the globe from generally warm conditions to the cyclic glacial-interglacial sessions are noted (Cerling et al., 1998; Cerling et al., 1997b; Cerling et al., 1994; deMenocal, 2011; deMenocal and Bloemendal, 1995; Ehleringer et al., 2002; Feakins and deMenocal, 2010; Patridge, 2010; Patridge et al., 1995a).

Plate tectonics had profound impacts on the subtropical Africa climatic cycles from around the mid-Miocene (deMenocal, 2011; deMenocal and Bloemendal, 1995;

Patridge, 2010; Patridge et al., 1995a). The collision of the Indian subcontinent and the Asian continent and the subsequent rise of the Tibetan plateau are said to have led to fluctuations in the atmospheric $\delta^{13}C$ values. The rise of the Tibetan plateau also affected the circulation of air currents around the globe. Climatic changes linked to plate tectonics during the mid-Miocene are noted in atmospheric $\delta^{13}C$ values from around 8 Ma. These tectonic activities led to more cooling of the globe and ice sheets in the northern hemisphere during the Plio-Pleistocene.

The development of the EARS had significant impacts to the climatic patterns in subtropical Africa from the mid-Miocene (Bonnefille, 2010; deMenocal, 2011; Feakins and deMenocal, 2010; Patridge, 2010). Between 18 and 10 Ma, volcanism and faulting occurred south of the Ethiopian plateau. Further volcanic activities led to continued uplift of the rift shoulders around 5 Ma. Other global tectonic activities of significance to African climate at this time include the closure of the Panama seaway.

These tectonic and volcanic activities affected the circulation of moist air currents over subtropical Africa. Eastern Africa became more arid and dense forests retreated while C_4 vegetation expanded in this region from around 5 Ma (Bonnefille, 2010; Cerling, 1992a; Cerling et al., 2005; Cerling et al., 1997b; Cerling et al., 1994; Ehleringer et al., 2002; Patridge, 2010).

African Primates Evolutionary Dynamics: An Overview

The evolution of hominoids and cercopithecoids is complex (Jablonski, 1993a; 2002; Jablonski and Frost, 2010; Jablonski and Leakey, 2008a; Leakey et al., 2003; Leakey and Walker, 2003; Maclatchy et al., 2010; McBrearty and Jablonski, 2005). During the Miocene, apes were more diverse and abundant than monkeys. By the end of

the Miocene, the diversity and abundance of apes had declined and that of monkeys had increased. The Plio-Pleistocene marks an interesting period for both monkeys and hominins.

During this period, monkeys underwent major speciation. Baboons and colobus lineages diversified. In terms of numbers of species and geographical distribution, the baboon lineage was more diverse and widespread than the colobus lineage. Baboons had a single dominant lineage (*Theropithecus* [geladas]) with one catholic species: *Theropithecus oswaldi*. Jablonski (1993b) gives a detailed account of the evolutionary dynamics of this baboon clade. The colobus lineage was also more diverse and widespread than today (Jablonski, 2002; Jablonski and Frost, 2010; Jablonski and Leakey, 2008a). Although today the colobus lineage is widely distributed in Central, West, and East Africa, it is not present in South Africa, and has been reduced to three genera: black and white, red, and olive colobus monkeys. Guenons and allies appeared in the mid-Pliocene but remained few in abundance and diversity until the mid-Pleistocene epoch, when they start diversifying (Leakey, 1988). Today, guenons and allies are more diverse than baboons and relatively widely distributed (Enstam and Isbell, 2007; Kingdon, 2001). The guenons' lineage, with a number of superspecies, is the dominant genus, and *Papio* is the dominant baboon.

The speciation dynamics reflected in cercopithecoids (branching patterns) during the Plio-Pleistocene are also evident among hominins (Jablonski and Frost, 2010; Jablonski and Leakey, 2008a; Jablonski and Leakey, 2008b; Leakey et al., 2008). Hominins appeared during the late Miocene (Brunet et al., 2002; Leakey and Walker, 2003; Senut et al., 2001; White et al., 2009), and diversified during the Plio-Pleistocene

(Ciochon and Fleagle, 2006; Dart, 1925; Leakey and Leakey, 1978; Leakey et al., 2001; Maclatchy et al., 2010; Walker and Leakey, 1993; Ward et al., 1999). Hominin lineages include sahelanthropines, orrorines, australopithecines, paranthropines, kenyanthropines, and early *Homo*, some with numerous successive species. During the Holocene to the present, only one hominin species (*Homo sapiens*) has persisted. Great apes are absent in East Africa during the Pliocene and early Pleistocene (McBrearty and Jablonski, 2005).

The Ecological Indicator Taxa Approach: Previous Work Testing the ‘‘Habitat Theory’’

Leading studies that utilize ecological indicator taxa approach to track postulates of the ‘‘Habitat Theory’’ using data from eastern African sites dating the last 5 Ma arrive at contradictory conclusions (Bobe, 2006; Bobe et al., 2007; Frost, 2007). Works by Bobe et al. (2002, 2007), Behrensmeyer et al. (1997), Bobe and Behrensmeyer (2004), Bobe and Eck (2001) and Frost (2007) are used below to demonstrate this point.

Recent work by Bobe et al. (2007) on bovids in eastern Africa supports postulates of the ‘‘Habitat Theory.’’ In earlier works, Bobe (2004; 2002; 2001), Behrensmeyer et al. (1997), Bobe and Eck (2001), and Bobe et al. (2007) did not capture speciation patterns postulated by the ‘‘Habitat Theory.’’ Bobe et al. (2007) look at taxonomic abundances and diversity in bovids from about 7 Ma to about 1 Ma. The following questions guide their thesis. How much variation in patterns of faunal change is there within different areas of a large sedimentary basin? How much variation is there between basins? How are these patterns related to broad signals of climatic change? What are the implications of the bovids for East African environments and for hominin

evolution in the late Cenozoic? Their results on species diversity show three peaks of richness in the Pliocene and Pleistocene: the first one occurred at about 3.8-3.4 Ma; the second 2.8-2.4 Ma; and the last about 2.0 to 1.4 Ma. These patterns fall within the periods that sub-tropical Africa is said to have experienced tremendous climatic changes as a result of complex orbital and orogenic events. These patterns support postulates of the ‘‘Habitat Theory.’’ Earlier works by these authors did not capture these patterns precisely (Behrensmeyer et al., 1997; Bobe, 2006; Bobe and Behrensmeyer, 2004; Bobe et al., 2002; Bobe and Eck, 2001).

Work by Frost (2007) used cercopithecid fossils from eastern Africa spanning from 2.8 to 2.5 Ma to examine postulates of the ‘‘Habitat Theory.’’ Examining the appearance and abundance data for the Afar depression and the Turkana Basin, and species range for all East African cercopithecid data, Frost’s (2007) work does not detect any turnover pulse between 2.8-2.5 Ma. Further, this work shows that the largest numbers of first and last appearances are clustered around 3.4 and 2.0 Ma, with a shift in abundance at 3.4 Ma. Frost (2007) concludes that these results are consistent with a relatively constant rate of turnover of cercopithecids between about 4 Ma and the Holocene.

Although the Bobe et al. (2007) work captures speciation patterns needed to test postulates of the ‘‘Habitat Theory’’, their use of ecological indicator taxa at the tribe level masks speciation patterns at the population and habitat levels. The Bobe et al. (2007) approach does not differentiate speciation patterns for warm and cold taxa within the bovid family. This approach also assumes that bovid taxa closely related at the tribe level share similar ecological habitats. On the basis of this assumption, Bobe et al.

(2007) have argued that the presence of Aepycerotini, Tragelaphini, and Bovini taxa indicate mostly closed and moist environments while Alcelaphini, Antilopini and Hippotragini reflect open and seasonally arid environments dominated by grasslands. Modern Reduncini and Bovini feed on fresh grasses in moist habitats, woodland clearings, or near waterlogged conditions, and are thus assumed to be poor indicators of seasonally arid grasslands. The approach used by Frost (2007) on eastern Africa fossil monkeys makes similar assumptions. These assumptions do not capture connections among speciation and habitat patterns precisely: warm and cold speciation patterns within a tribe are masked. Within a tribe there exist species/subspecies with diverse dietary and habitat patterns, and a lineage can easily switch from browsing to grazing and back without significant morphological changes (elephants).

The Ecological Indicator Taxa Approach: Challenges

Despite being the leading authority in hominin paleoecology, the ecological indicator taxa approach is marred by two major challenges (Evans and O'connor, 1999, p 177):

(1) This approach group's together species regarded as typical of a particular habitat or niche. The assumption is that a species modern ecology is a lead to the ecology of a closely related species. A number of studies have shown that the assumption does not always hold: a species may have previously occupied different habitats or niches. The ecological significance of a species may vary through time and space so that a species reflective of woodland at one point may be reflective of a more specialized grassy or forested habitat at another point.

(2) Some species mix habitat and niches. For example among beetles, difference between ‘phytophagus’ which describe their niche and ‘strongly plant-associated’ which describes their habitat. Phytophagus beetles will inevitably be strongly plant-associated, so that niche and habitat are linked, but a plant-associated species can also include predators of the phytophages (Evans and O'connor, 1999, p 177).

These challenges hamper a precise reconstruction of hominin paleoecology. Stable carbon isotope ecology offers an alternative approach that could be used to track different biomes utilized by members of the same species over time and space, and thus appropriate to reconstruct hominin paleoecology more precisely than the ecological indicator taxa approach (Cerling et al., 1999; Cerling et al., 2010a; Cerling et al., 2004; Cerling et al., 2011a).

In the next section, this thesis looks at stable carbon isotope ecology and its potential to shed more insights on the connections between speciation and habitat patterns among members of a lineage. First, a review of stable carbon isotope theory and applications in paleoanthropology is provided. Cases that demonstrate the ability of stable carbon isotopes to track a lineage’s genetic and behavioral flexibility in connection with climatic cycles are presented.

Stable Carbon Isotope Ecology: Theoretical Framework

Plants in Africa mainly use two photosynthetic pathways commonly referred to as the C_3 and C_4 photosynthetic pathways (Cerling et al., 2010a; Cerling et al., 2006; Dawson et al., 2002; Ehleringer et al., 1997; Ehleringer et al., 1991; Farquhar et al., 1989). In the C_3 photosynthetic pathway, the plant absorbs CO_2; the carbon in the CO_2 is processed and packaged into a 3-carbon acid chain. In the C_4 photosynthetic pathway,

the carbon is processed and packaged as a 4-carbon acid chain. Trees, in general, utilize the C_3 photosynthetic pathway, and grasses exploit the C_4 photosynthetic pathway.

Plants utilizing the C_3 photosynthetic pathway have different $\delta^{13}C$ values from those utilizing the C_4 pathway (Cerling et al., 2010a; Cerling et al., 2004). C_3 plants have an average of -27.5‰. C_3 plants in forested habitats have $\delta^{13}C$ values of between -27 and -37‰ and those in woodlands have $\delta^{13}C$ values of between -22‰ and -24‰ C_4 plants have values of between -9‰ and -17‰ (-12.5‰ average).

Temperature and humidity affect C_3 and C_4 photosynthetic pathways differently (Ehleringer, 1993; Ehleringer and Cooper, 1988; Hattersley, 1982; Hattersley, 1992). Available data shows that C_4 plants in mesic habitats are more enriched than those in arid habitats. The average $\delta^{13}C$ value of grasses in the Athi plains, Kenya, where average rainfall is 800 mm/yr and temperature is 18°C/yr is enriched by about 2‰ compared to grasses in the Turkana region, Kenya, where rainfall is 200 mm/yr and temperature is 29°C/yr (Cerling et al., 2010a). Among C_3 plants, those in more xeric habitats have more enriched $\delta^{13}C$ values than those in mesic habitats. In the Sonoran Desert, USA, wash microsite plants have more negative values (-26.6‰), plants in transitional microsite are intermediate (-24.9‰), and the values of slope plants are the most positive (-24.2‰) (Ehleringer and Cooper, 1988).

Browsing animals (C_3 feeders) feed on leaves and other tree parts while grazing animals (C_4 feeders) feed on grasses (Cerling et al., 1999; Cerling et al., 2003b; Cerling et al., 2010a; Cerling et al., 2003c; Cerling et al., 2004; Cerling et al., 2006). Mixed feeders utilize both browse and graze materials. The $\delta^{13}C$ values from plant material that

an animal consumes is carried, together with other nutrients, through the blood stream and deposited in body tissues.

To be able to carry out comparative stable carbon isotope ecology studies, $\delta^{13}C$ values from different tissues and time periods must be adjusted to a common datum via normalization and correction. Fractionation processes during photosynthesis in plants and processing food for body use in animals alters the $\delta^{13}C$ values acquired from the atmosphere and stored in an animal's tissue. Chemical processes in body tissues alter the $\delta^{13}C$ values from the atmosphere differently. Due to fossil fuel burning beginning the industrial age, the atmospheric $\delta^{13}C$ value has been depleted over time. Plant and animal tissues record these changes. Advances in stable carbon isotope ecology allow for precise normalization and correction of $\delta^{13}C$ values from modern samples (Cerling and Harris, 1999; Francey et al., 1999; Keeling et al., 2010).

By measuring the stable carbon isotope ratios of hair, collagen, or teeth, we can determine whether an animal was a C_3, C_4, or a mixed feeder (Codron et al., 2006; Lee-Thorp and Sponheimer, 2003; Sandberg et al., 2012 ; Sponheimer et al., 2009; Sponheimer and Lee-Thorp, 2003; Sponheimer et al., 2003; Sponheimer et al., 1999). C_3 feeders have adjusted diet $\delta^{13}C$ values of between -22‰ and -37‰ while C_4 feeders have $\delta^{13}C$ values of between -9‰ and -17‰. Mixed feeders have values that fall between -17 and -22‰. If an animal lived in mesic or xeric ecological conditions, the adjusted $\delta^{13}C$ values (diet value) will be between -27 to -37‰ (mesic) and between -22 to -24‰ (xeric) for a C_3 feeder. Animals that feed in the forest emergent canopy, main canopy, and the ones that feed in the understory will have adjusted $\delta^{13}C$ values of between -27 to -30‰, -30‰ to -33‰, and -33‰ to -37‰ respectively (Cerling et al.,

2004; Medina and Minchin, 1980; Medina et al., 1991; van der Merwe and Medina, 1989; 1991). A C_4 feeder living in mesic or xeric ecological conditions will have adjusted $\delta^{13}C$ value of between -9 to -14‰ (mesic) and -12 to -17‰ (xeric).

For tissues that do not recrystallize after formation, such as enamel, the $\delta^{13}C$ signal is preserved for millions of years (Bocherens et al., 1996; Cerling et al., 2010a; Lee-Thorp and Sponheimer, 2003; Sponheimer et al., 2009). The $\delta^{13}C$ values thus represent an archive of dietary behavior of a faunal group, which can be decoded for information on the connection between speciation and OFT climatic cycles.

Stable Carbon Isotope Ecology in Paleoanthropology

Numerous studies demonstrate the utility of stable carbon isotope ecology to provide insights on the connections between speciation and OFT climatic cycles (Cerling et al., 2010a; Lee-Thorp and Sponheimer, 2007; Sponheimer and Lee-Thorp, 2003; 2007; Sponheimer et al., 2006b; Sponheimer et al., 1999; Uno et al., 2011). Tracking the emergence and spread of C_4 vegetation during the late Cenozoic is feasible (Cerling et al., 1997a; Cerling et al., 2010a; Cerling et al., 1994; Ehleringer et al., 1997; Uno et al., 2011). Stable carbon isotope values from limestone nodules in paleosols are used to reconstruct vegetation cover in hominin sites dating the last 6 million years (Cerling et al., 2011b). Woody cover in tropical ecosystems have been quantified using $\delta^{13}C$ values in such soils. Paleosols from hominin sites in the Awash and Omo-Turkana basins in eastern Africa indicate that the fraction of woody cover was less than 40% at most sites from at least 6 Ma.

Stable carbon isotope values also track changing dietary and habitat patterns of faunal groups in response to climatic changes (Table 1) (Cerling et al., 1998; Cerling et

al., 1999; 2003a; 2005; Cerling et al., 1997b; Sponheimer et al., 2009; Uno et al., 2011). Work on fossil East African herbivore families at seven different time periods during the late Miocene to Pliocene (9.9-3.2 Ma) show that herbivores in this region underwent a change in dietary patterns in response to the expansion of grasslands (Uno et al., 2011). Significant amounts of C_4 grasses were present in equid diets beginning at 9.9 Ma and in rhinocerotid diets by 9.6 Ma. Bovids and hippopotamids have C_4-dominated signatures by 7.4 Ma. Suids adopt a C_4-dominated diet between 6.5 and 4.2 Ma. Gomphotherids and elephantids had mostly C_3-dominated diets through 9.3 Ma, but became dedicated C_4 grazers by 6.5 Ma. Deinotherids and giraffids maintained a predominantly C_3 diet throughout the record. A version of this Miocene to Pleistocene pattern is represented in Table 1. More evidence by Cerling et al. (1999) shows that from Pliocene times, *Elephas* and *Loxodonta* lineages had C_4-dominated diets (mean -1.0 and -1.5‰), but after the middle Pleistocene, both switched to C_3-dominated diets. Enamel $\delta^{13}C$ values from fossil fauna (Table 1) are more enriched than the ones from modern fauna (Table 2).

Table1. Median, minimum, and maximum enamel $\delta^{13}C$ values for some herbivore families from late Cenozoic sites in northern Kenya (Cerling et al., 1999)

Taxon	Time	Minimum $\delta^{13}C$	Maximum $\delta^{13}C$	Median $\delta^{13}C$
Bovidae	9.9	-11.8	-8.1	-10.4
Bovidae	7.4 Ma	-4.2	+2	-4.2
Gomphotheridae	9.9 Ma	-9.6	-6.9	-7.7
Gomphotheridae	7.4 Ma	-3.9	+0.7	-2.1
Gomphotheridae	4.2 Ma	-2.2	-0.7	-0.9
Elephantidae	7.4 Ma	-2.1	+0.3	-1.1
Elephantidae	6.5 Ma	-2.1	+0.3	-1.1
Elephantidae	4.2 Ma	-1.1	-0.2	-0.8
Deinotheriade	9.9 Ma	-11.7	-9.5	-10.4
Deinotheridae	9.6 Ma	-9.8	-8.9	-9.5
Deinotheridae	4.2 Ma	-12.5	-12.0	-12.3

Stable carbon isotope values from modern African elephants also track their dietary and habitat patterns (Cerling et al., 1999; Cerling et al., 2006) (Table 2). Elephants are mixed feeders (browser/grazers) and have $\delta^{13}C$ values that range from -18.3 to -5.7‰. Elephants in forested habitats in Kenya have different $\delta^{13}C$ values compared to elephants in primary rain forests in Congo. Kenyan elephants in Savanna/bushland habitat also have distinct $\delta^{13}C$ values.

Table 2. Enamel $\delta^{13}C$ values for Loxodonta africana from forested and savanna/bushland habitats in subtropical Africa (Cerling et al., 1999)

Element	Habitats	Minimum $\delta^{13}C$	Maximum $\delta^{13}C$	Median $\delta^{13}C$
Enamel	Forest, Kenya	-15.1	-11.7	-13.26
Enamel	Rain forest, Congo	-18.3	-14.9	-15.88
Enamel	Savanna/bushlands, Kenya	-15.80	-5.7	-11.4

Tracking habitat separation of sympatric forest fauna using $\delta^{13}C$ values is possible (Cerling et al., 2004; Medina and Minchin, 1980; van der Merwe and Medina, 1991) (Tables 3, 4, and 5). Evidence from Ituri forest in the Congo Basin shows that leaves of plants within gaps in the forest have a mean of -30.42‰, understory leaves and fruits have a mean of -34.0‰, canopy leaves, fruits, or seeds have a mean of -29.0‰ (Cerling et al., 2004). The pattern seen in the plants is also reflected in the $\delta^{13}C$ values of animals living in these habitats. The understory browsers have tooth enamel $\delta^{13}C$ values more negative than fruigivores that derive their food from the canopy top, and folivores and omnivores living in gap or clearing areas. Although limited, primates included in this study also indicate habitat separation within the forest (Table 3). Colobus monkeys mostly feed in the emergent canopy and sykes monkeys in the main canopy, these tendencies are captured in their $\delta^{13}C$ values. Stable carbon isotope values from baboons in Ituri demonstrate their use of both emergent and understory layers of the forested biome.

Table 3. Enamel $\delta^{13}C$ values for sympatric primates from Ituri forest (Congo Basin) (Cerling et al., 2004)

Taxon	Element	Habitat Type	$\delta^{13}C$ Values
Colobus angolensis (colobus monkey)	Enamel	Forest	-16.1
Colobus badius (colobus monkey)	Enamel	Forest	-16.5
Cercopithecus mitis (sykes monkey)	Enamel	Forest	-16.9
Papio anubis (baboons)	Enamel	Forest	-16.3 -17.1
Pan troglodytes (common chimpanzee)	Enamel	Forest	-16.0

Bonobo and limited monkey samples from Salonga also show habitat separation patterns (Table 4) (Oelze et al., 2011). *Pan paniscus* from Salonga have a mean $\delta^{13}C$ hair value of -25.8. Oelze et al. (2011) concluded that the $\delta^{13}C$ values from these *Pan paniscus* population reflect the middle canopy of the forest. Research conducted for this thesis instead argues that these *Pan paniscus* $\delta^{13}C$ values reflect the understory habitat.

Table 4. Hair $\delta^{13}C$ values for sympatric primates from Salonga (Oelze et al., 2011)

Taxon	Element	Habitat Type	$\delta^{13}C$ Values
Pan paniscus (Bonobo)	Hair	Forest	-25.8
Procolobus tholloni (Red colobus)	Hair	Forest	-24.25
Cercopithecus sp.	Hair	Forest	-23.6
Cercopithecus aterrimus	Hair	Forest	-26.3

Evidence from Kibale does not show habitat separation among sympatric primates (Table 5) (Carter, 2001). Except for Kibale, the $\delta^{13}C$ values for primates from other sites track the habitat patterns of primate taxa.

Table 5. Collagen and hair $\delta^{13}C$ values for sympatric primates from Kibale (Carter, 2001)

Taxon	Element	Habitats	$\delta^{13}C$ Values
Cercopithecus ascanius (Red tail guenon)	Collagen	Forest mosaic	-20.96
Lophocebus albigena (Grey-cheeked mangabey)	Collagen	Forest mosaic	-20.78
Papio anubis (Baboon)	Collagen	Forest mosaic	-21.20
Colobinae (red, and black and white colobus)	Collagen	Forest mosaic	-20.65
Pan troglodytes (common chimpanzee)	Hair	Forest mosaic	-21.45

Stable carbon isotope ecology studies have also been done on fossil primates (Cerling et al., 2011a; Lee-Thorp et al., 2003; Sponheimer et al., 2009; Sponheimer et al., 2005; Sponheimer and Lee-Thorp, 1999; Sponheimer and Lee-Thorp, 2003; 2007). Among the early Pliocene primates from Aramis and Gona, Ethiopia, *Ardipithecus ramidus* had a dietary pattern different from that of *Pliopapio alemui* and *Kuseracolobus aramisi* (Table 6) (Levin et al., 2008; White et al., 2009). Stable carbon isotope values for *Pliopapio alemui* and *Kuseracolobus aramisi* from Gona are significantly different from the $\delta^{13}C$ values for these species from Aramis.

Table 6. Enamel $\delta^{13}C$ values for the hominin Ardipithecus ramidus, and monkeys Kuseracolobus aramisi and Pliopapio alemui from Aramis (middle Awash), and Gona, Ethiopia (Levin et al., 2008; White et al., 2009)

Taxon	Site	Time	Minimum $\delta^{13}C$	Maximum $\delta^{13}C$	Mean $\delta^{13}C$
Ardipithecus ramidus	Aramis	4.4 Ma	-11.20	-8.50	-10.25
Kuseracolobus aramisi	Aramis	4.4 Ma	- 14.80	-7.5	-12.59
Pliopapio alemui	Aramis	4.4 Ma	-11.9	-9.5	-10.9
Kuseracolobus aramisi	Gona	5.2-3.9 Ma	- 11.3	-7.5	-9.44
Pliopapio alemui	Gona	5.2-3.9 Ma	-9.1	-5.5	-7.3

Evidence from the mid-Pliocene to Pleistocene shows that australopithecines, paranthropines, and early *Homo* had dietary patterns different from those of modern chimpanzees (Cerling et al., 2011a; Lee-Thorp et al., 2003; Sponheimer et al., 2009; Sponheimer and Lee-Thorp, 2003; 2007; van der Merwe et al., 2008). Paranthropines from Baringo Basin, Turkana Basin, Olduvai, and Peninj have a $\delta^{13}C$ mean of -1.3 ‰. Three samples from Olduvai *Homo habilis* have values of -8.8‰, -8.3‰, and -5.2‰.

Despite the success achieved in using stable carbon isotope ecology in paleoanthropology, a number of challenges hamper its use in testing postulates of the ‘‘Habitat Theory.’’

Stable Carbon Isotope Ecology: Challenges

Sandberg et al. (2012) discuss the challenges in stable carbon isotope ecology and its applicability to paleoanthropogical studies. Due to the changing patterns of the atmospheric $\delta^{13}C$ value, $\delta^{13}C$ values from animals that lived during different times did not share a common $\delta^{13}C$ atmosphere pool. Since the Plio-Pleistocene period, the $\delta^{13}C$ value of the atmosphere has fluctuated; modern animals' $\delta^{13}C$ values are more depleted than fossil animals. Tables 1 and 2 show the difference between fossil and modern elephant's $\delta^{13}C$ values. Extensive fossil fuel use that started with the industrial period is also captured in atmospheric $\delta^{13}C$ values, and reflected in the $\delta^{13}C$ values of modern fauna. This shifting trend of atmospheric $\delta^{13}C$ value makes it challenging to do a comparative analysis of $\delta^{13}C$ values from animals that lived at different times separated by centuries or millenia.

Controversy on the efficacy of $\delta^{13}C$ values to capture habitat separation among modern sympatric primates also exists. Reported $\delta^{13}C$ values from Kibale do not show habitat separation among sympatric primates for example (Carter, 2001).

Stable carbon isotope ecology is still establishing itself and so there is lack of $\delta^{13}C$ data from a number of sources that hamper comparative studies. Lack of $\delta^{13}C$ values for plant foods from some study sites as well as lack of enrichment factors for different animals and body tissues, limit both insightful reconstruction of the vegetation cover and comparative studies. Further, the cause of enrichment in tissue $\delta^{13}C$ values and variation of the enrichment factor among species is not well understood (probably methane) (Cerling and Harris, 1999). As organisms evolve, their enrichment factors also change. Approaches to track these changes in the fossil record are lacking.

The way C_4 diet and habitat type is reflected in the $\delta^{13}C$ values of some primates is not well understood. Despite feeding on C_4 foods, $\delta^{13}C$ values from chimpanzees continue to reflect a C_3 feeding strategy, and $\delta^{13}C$ values from some baboon species do not reflect habitat type precisely (Codron et al., 2006; Sponheimer et al., 2006a). Stable carbon isotope ecology is also not able to distinguish carnivores from herbivores within a lineage. These issues limit the amount of information that we can access from stable carbon isotopes.

The challenges in the application of stable carbon isotope ecology to paleoanthropological studies can be summed to one challenge: Understanding the partitioning of $\delta^{13}C$ values between the biosphere and atmosphere during the late Cenozoic (the cause of enrichment and depletion in signals from the fossil and modern $\delta^{13}C$ values). This challenge can be divided into two phases. Phase 1: Solving the biosphere-atmosphere stable carbon isotope partitioning conundrum during modern times. Phase 2: Solving the biosphere-atmosphere stable carbon isotope partitioning conundrum during mid-Miocene to Pleistocene times. This thesis uses data from modern African Great Apes to address the conundrum in biosphere-atmosphere stable carbon isotopes partitioning during modern times.

The significance of solving these challenges is captured in current debates within paleoanthropology (Cerling et al., 2010b; Levin et al., 2008; Levin et al., 2004; Sandberg et al., 2012 ; White et al., 2009; White et al., 2010). These challenges make inter-species and inter-habitats comparative analysis challenging. Due to these challenges contradictory interpretations of $\delta^{13}C$ values from modern and fossil primates

have been made (Cerling et al., 2010b; Levin et al., 2004; Oelze et al., 2011; Sandberg et al., 2012 ; White et al., 2009; White et al., 2010).

Apart from the advances made in stable carbon isotope studies, studies in oxygen and nitrogen stable isotopes promise to offer proxy approaches that will supplement and validate the utility of $\delta^{13}C$ values in hominin paleoecology. The following section gives an overview of the potential of these isotopes. The use of alternative stable carbon isotopes data closely related to the subtropical region of Africa to constrain the atmospheric $\delta^{13}C$ value fluctuations overtime during the modern and ancient times is also discussed in this section.

Stable Isotope Ecology: A Multi-Proxy Approach

Apart from stable carbon isotopes, other stable isotopes promise to offer data on the connections between paleoclimate and hominin evolution: oxygen and nitrogen. Stable oxygen isotopes ($\delta^{18}O$ values) from animal tissues promise to shed light on drinking patterns and stable nitrogen isotopes ($\delta^{15}N$ values) from modern animals promise to provide insights on carnivory (Ambrose, 1986; Cerling et al., 2010a; Levin et al., 2006; Sandberg et al., 2012 ; Schoeninger et al., 1999).

Different animals drinking strategies can be deduced from the stable oxygen isotopes extracted from body tissues (Cerling et al., 2010a; Levin et al., 2006). Animals that usually drink from water bodies have $\delta^{18}O$ values that are close to the meteoric water values while animals that mostly depend on the water in the food material that they subsist on will have $\delta^{18}O$ values higher than the meteoric water value. Certain extant African mammals show sensitivity to aridity (giraffids), while others do not show a significant $\delta^{18}O$ change with water deficit (hippopotamids, elephantids, rhinocerotids)

(Levin et al., 2006). Thus the difference between taxa that are ‘‘evaporation sensitive’’ and those that are not can be used as an indicator of aridity. Part of the forest-grassland transition is one of arid to wet conditions which can be evidenced in $\delta^{18}O$ values. This is promising for species living in East Africa, where meteoric water shows little seasonal variation at low latitudes (Cerling et al., 2010a).

Although not well understood, stable nitrogen isotopes promise to provide data on trophic level carnivory, and other dietary behaviors (Ambrose and DeNiro, 1986; Crowley et al., 2010; Oelze et al., 2011; Sandberg et al., 2012 ; Schoeninger et al., 1999; Smith and Epstein, 1971). Lack of preservation of organic matter in the fossil record limits the application of nitrogen in paleoecology, but establishing correlations between stable nitrogen and carbon or oxygen isotopes in modern animal tissues could help trace carnivory in the fossil record using stable carbon or oxygen isotopes. More studies in this area could provide an additional proxy that will help shed more light on the role of carnivory in the fossil record, especially of early hominins.

Paleoclimate work in different parts of Africa (terrestrial and ocean) offer proxies that will provide $\delta^{13}C$ values from different time periods and help constrain the available $\delta^{13}C$ atmosphere values (deMenocal and Bloemendal, 1995; Feakins and deMenocal, 2010). Detrital dust deposited in water bodies in Africa over long periods could offer more accurate data on $\delta^{13}C$ atmosphere changes than the ice core records used in this study (Francey et al., 1999; Keeling et al., 2010). Expanding stable carbon isotope studies to include as many sources of $\delta^{13}C$ atmosphere records will improve the accuracy of this approach.

Advancements in developing approaches that can help us use stable oxygen and nitrogen isotopes in paleoecological studies will provide proxies that will supplement and elaborate upon $\delta^{13}C$ values in hominin paleoecology. Proxy approaches to constrain the $\delta^{13}C$ atmosphere values will provide avenues to improve the $\delta^{13}C$ values approach. Together, these proxy approaches promise to give robust insights on the connections between paleoclimate and hominin evolution.

The next section provides a discussion that explains the use of modern African Great Apes in this study.

African Primates and the ‘‘Habitat Theory’’

African primates have been selected for use in the refined $\delta^{13}C$ values approach for a number of reasons. (1) African primate lineages (hominoids and cercopithecoids) share a close common ancestor (Ciochon and Fleagle, 2006; Fleagle, 1999). (2) African non-human primates have diverse speciation, dietary, and habitat patterns analogous to our early hominin ancestors (Boesch et al., 2002; Campbell et al., 2006; Hohmann et al., 2006; Kingdon, 2001). (3) African primates are vanguard indicators of ecological change and have lineages that represent forest (warm and wet cycles) and arid grassland habitats (cold and dry cycles) (Campbell et al., 2006; Jablonski and Frost, 2010; Jablonski and Leakey, 2008a). (4) They are well studied and prominent in the hominin fossil record (Jablonski and Leakey, 2008a; Sponheimer et al., 2009; Sponheimer and Lee-Thorp, 2007; Werdelin and Sanders, 2010). (5) A significant number of $\delta^{13}C$ values exist for African primates (Carter, 2001; Oelze et al., 2011; Schoeninger et al., 1999; Smith et al., 2010; Sponheimer et al., 2009; Sponheimer et al., 2006a). This thesis draws from these data to explore the viability of a refined $\delta^{13}C$ values approach.

African Great Apes: Taxonomy, Dietary and Habitat Patterns

The African Great Ape lineage consists of two chimpanzee species, one with four subspecies, and two gorilla species with two subspecies each (Table A1.1). All modern Great Apes inhabit equatorial forests, woodlands, and grasslands in Africa (Campbell et al., 2006; Fleagle, 1999; Kingdon, 2001) (Fig. A1.1 and A1.2).

For this study, a modified version of the primate habitat types described by Fleagle (1999) and Kingdon (1997) is used. Primate habitats are classified into three broad types: forests, woodlands, and savannah grasslands.

(1) Forests are further divided into four types:

(a) Primary rainforests are usually characterized by trees as tall as 80 m with a relatively continuous canopy cover. Three primate micro-habitats exist in forested biomes: the emergent canopy, main canopy, and understory. Fruits and leaves are concentrated in the main and emergent stories. The understory of a primary rainforest is usually spotted with herbaceous vegetation.

(b) Secondary rainforests develop where trees fall in the primary rainforest. Increased light leads to an abundance of leaves and fruits in these forests.

(c) Dry deciduous forests are characterized by trees that are between 30 to 45 m tall.

(d) Gallery forests along rivers are common in many dry areas within the tropics.

(2) Woodlands are divided into two types:

(a) Closed woodlands are characterized by trees approximately 15-25 m tall. Between the individual trees are continuous growths of grasses and low bushlands.

(b) Open woodlands are characterized by diminished tree cover, trees of uneven height (10-24 m tall), and more extensive grass cover.

(3) Savannah grasslands are characterized by dominant grass cover with little tree cover in varst areas.

***Pan troglodytes and Pan paniscus* (Common Chimpanzee and Bonobo)**

Common chimpanzees and bonobos are omnivores with highly variable diets (Boesch et al., 2002; Fleagle, 1999; Hohmann et al., 2006; Kingdon, 2001; Stumpf, 2007). Fruits comprise about half of their diet, but leaves, seeds, bark, stems and terrestrial herbaceous vegetation are also consumed. Animal foods include termites and other insects, adult birds, eggs, and nestlings. Small mammals are eaten occasionally.

Chimpanzees inhabit forests as well as closed and open woodlands (Boesch et al., 2002; Fleagle, 1999; Hohmann et al., 2006; Kano, 1992; Kingdon, 2001; Stumpf, 2007). Common chimpanzees are mainly found in dense, closed canopy, equatorial forests of West and Central Africa. A large population is also found in the closed to open woodlands of western Africa, central Africa, and eastern Africa. Bonobos live in lowland rain forests, swamp forests, dry forests, and grassland habitats south of the River Congo.

Chimpanzees have diverse dietary patterns that vary depending on their habitat. In forested biomes, such as the Tai forest in Cote d'Ivore, common chimpanzees consume plant material, as well as vertebrate and invertebrate fauna (Kingdon, 2001;

Smith et al., 2010; Stumpf, 2007). These chimpanzees also hunt red colobus monkeys, which comprise 80% of their vertebrate prey during the colobus birth season. Nuts are the single most important dietary resource during relatively dry months. The northernmost free-ranging common chimpanzees, found in the southeastern Senegal sites of Fongoli and Mt. Assirik, primarily consume fleshy fruits, but also eat hard-to-process foods such as seeds and pods (Kingdon, 2001; Sponheimer et al., 2006a). Eating grass is also reported for some chimpanzees (Carter, 2001; Sponheimer et al., 2006a).

Bonobos have a broad dietary repertoire (Boesch et al., 2002; Hohmann et al., 2006; Kano, 1992; Kingdon, 2001; Stumpf, 2007). They mainly feed on fruits and leaves, but also include some of the invertebrates and vertebrates found within their forested habitats (Kingdon, 2001; Stumpf, 2007). Some bonobo populations rely heavily on terrestrial herbaceous vegetation, some feed on foreign cultigens such as sugarcane and pineapples, and others include aquatic grasses in their diet (Boesch et al., 2002; Carter, 2001; Kano, 1992; Stumpf, 2007).

***Gorilla beringei* (Gorilla)**

Gorillas are found in the equatorial forests of sub-Saharan Africa (Fleagle, 1999; Hohmann et al., 2006; Kingdon, 2001; Robbins, 2007; Taylor and Goldsmith, 2003). Mountain gorillas show a preference for secondary and herbaceous forests. The lowland species are found in a wide range of forested biomes where they frequently climb trees to feed. In most areas gorillas prefer old clearings, valley bottoms, and landslides where there is a dense tangle of ground-level herbaceous growth.

Gorillas are largely vegetarians (folivore-fruigivores). The only non-vegetative foods in their diet are ants and termites (Hohmann et al., 2006; Taylor and Goldsmith,

2003). They feed on non-reproductive plant parts (leaves, stems, pith, and bark) as well as on fruit. The lowland subspecies (*G.b. graueri*, *G. g. gorilla*, and *G.g. diehli*) are largely fruigivorous. The highland subspecies (*Gorilla beringei beringei*), found in Rwanda, Uganda, and Democratic Republic of Congo, is mainly folivorous and has the most herbaceous diet of any living ape.

Chapter Summary

In this chapter, a number of approaches used to unravel the connection between paleoclimate and hominin evolution were reviewed. A summary of the ‘‘Habitat Theory,’’ evidence on the connections between OFT climatic cycles, orogenic events and their effects on climatic patterns, and hominin evolution were provided. Challenges that hamper insightful understanding on the connections between OFT climatic cycles and hominin evolution were also reviewed. Stable carbon isotope ecology is identified as the most promising approach to improving our understanding of connections between paleoclimate, hominin evolution and habitat at the population level. Primates are proposed as the best faunal group to develop an approach to test postulates of the ‘‘Habitat Theory’’ using stable carbon isotope ecology. Reasons for the use of African Great Apes in this work is provided followed by a review on African Great Apes taxonomy, dietary and habitat patterns.

The next chapter of this thesis looks at the methods that were used to collect the data, refine, and analyze them.

CHAPTER 3

METHODS

The grand challenge will be to develop coordinated sets of observations to test proposed links between African climate and faunal change.

-deMenocal (2011, p 542)

This chapter looks at the methods used to gather, organize, refine, and analyze $\delta^{13}C$ values used in this thesis. The data set for this study was assembled from published and unpublished literature on the dietary and habitat patterns, and $\delta^{13}C$ values of modern African Great Apes. These data were collated and organized taxonomically. Apart from taxonomic categories, the database included details for location, country, region, habitat, substance, tooth type, year of sampling, and $\delta^{13}C$ values. Stable carbon isotope values were collated from eight locations for chimpanzee and gorilla subspecies. The $\delta^{13}C$ values were refined through a process that involved calculating fractionation and enrichment factors for enamel-collagen and enamel-hair. These were used to normalize the hair and collagen $\delta^{13}C$ values to enamel levels. After normalization, the 272 $\delta^{13}C$ values were corrected to offset the fossil fuel burning effect. The normalization and correction process produced refined $\delta^{13}C$ values.

To understand the connection between speciation, diet, and habitat patterns, the refined $\delta^{13}C$ values were analyzed using ANOVA. ANOVA uses means as a predictor

of the variables (taxa and habitat). Measures of central tendency and dispersion were also used in the analysis.

Normalization

As nutrients are transported throughout the body, the $\delta^{13}C$ signal is altered by fractionation (Carter, 2001; Cerling and Harris, 1999; Lee-Thorp and Sponheimer, 2003; Sponheimer et al., 2009). The $\delta^{13}C$ signal of different body tissues (hair, collagen and enamel) are altered at different rates (i.e. kinetics vary at each metabolic step). Ruminant mammals record a $\delta^{13}C$ signal that is enriched relative to diet by approximately 3.1‰, 5‰, 14‰, for horn (keratin), collagen, and enamel relative to diet, respectively. Large non-ruminant mammals have mean diet-enamel enrichment factors similar to ruminant mammals, but significant differences exist among families. For example, rhinos have a diet-enamel enrichment factor of -14.4‰, which is less enriched than horses, which have a diet-enamel enrichment factor of -13.8‰ (Cerling and Harris, 1999). After subtracting the diet-tissue enrichment factor, animal tissue $\delta^{13}C$ values reflect the values of the food and habitat (Cerling et al., 2010a; Cerling et al., 2004; Medina and Minchin, 1980; van der Merwe and Medina, 1989). Little has been reported on the fractionation and enrichment factors for African Great Apes and primates in general (Carter, 2001; Cerling et al., 2004).

The $\delta^{13}C$ values available for this study are from different body tissues (hair, collagen, and enamel) that formed during different years of life in each animal, some of which lived in different habitats. Due to lack of enamel, hair, and collagen $\delta^{13}C$ values from the same individuals for all African Great Ape subspecies, the enamel-hair and enamel-collagen fractionation and enrichment factors used in this study were calculated

from the gorilla database alone. This is the only African Great Ape species for which $\delta^{13}C$ values are available for all three tissue types. Data on diet-tissue fractionation and enrichment factors are unavailable; therefore the $\delta^{13}C$ values in this study are calibrated to the enamel level. The gorilla $\delta^{13}C$ values from Kahuzi Biega and Itombwe were used to calculate the enamel-collagen fractionation and enrichment factors while the $\delta^{13}C$ values from Kahuzi Beiga were used to calculate the enamel-hair fractionation and enrichment factors. These factors were used to transform the hair and collagen values to enamel levels. As a first step, however, values were corrected for the industrial fossil fuel burning effect.

Correcting the Industrial Period $\delta^{13}C$ Atmosphere Shifts

Before the industrial age (pre-1865), the $\delta^{13}C$ value of the atmosphere was relatively stable, averaging - 6.5‰. Due to an increase in fossil fuel burning after 1865 the $\delta^{13}C$ value of the atmosphere has changed and become more depleted over time. Data that track changes in atmospheric $\delta^{13}C$ values from 1837 to 2008 are available (Francey et al., 1999; Keeling et al., 2010). These data are used to correct the $\delta^{13}C$ values in this study to preindustrial levels (- 6.5‰).

Stable carbon isotopes are deposited in body tissues during growth. Body tissues grow at different rates, their $\delta^{13}C$ values track the $\delta^{13}C$ of the atmosphere while the tissue forms. Collagen is formed within several years of an animal's life, and enamel in permanent teeth is formed during early periods of life. Hair grows throughout life, but inherits its carbon from reservoirs with different residence times. The years of formation for the tissues sampled were back calculated from the year in which the sample was collected. The year of formation for hair was assumed to be the same as the year of

collection. Collagen's $\delta^{13}C$ value was back-dated by three years and enamel by ten years. These estimates represent the tissue maturation dates for most African Great Apes. The resulting date of formation was used in the correction process (Fig. 1). Tables A2.1 to A2.4 show the correction procedures for the tissues used in this study.

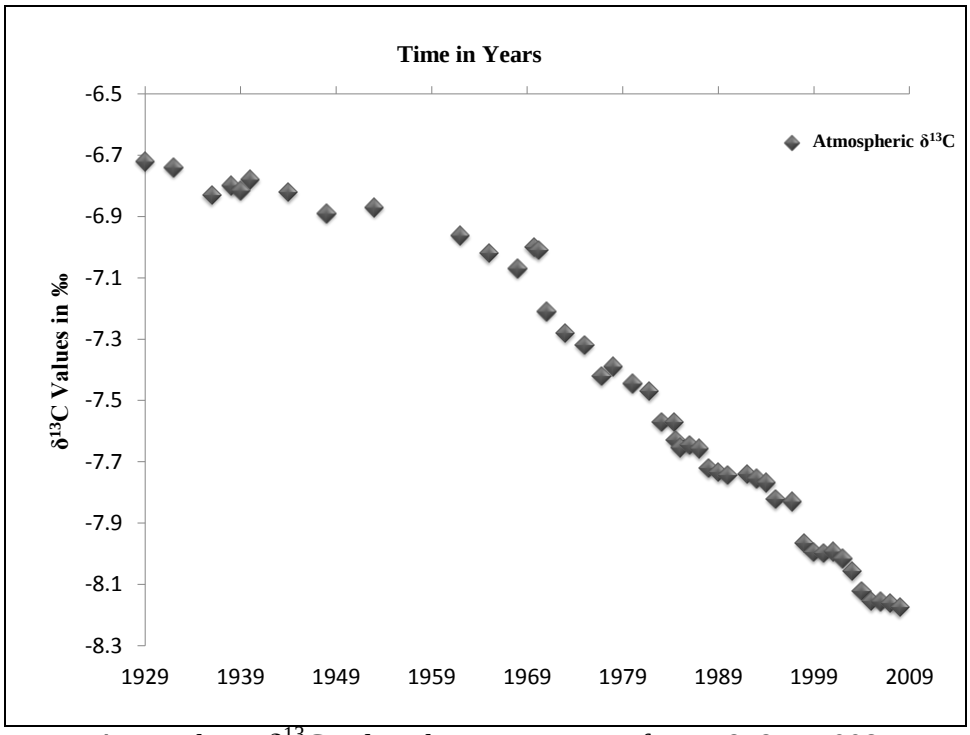

Fig. 1. Atmospheric $\delta^{13}C$ value change over time from 1929 to 2008. Data from Francey, et al. (1999) and Keeling et al. (2010).

Normalizing Hair and Collagen Values to Enamel Levels: Fractionation Factors

The formal definition of the fractionation factor involves isotope equilibrium of reversible reactions. The relationship between the source diet and the product (enamel, collagen or hair) in stable carbon isotope ecology is not reversible. The entire process is thus treated as an ‘‘apparent fractionation factor’’ (α*), where:

$\alpha^*_{\text{tissue - diet}} = (\delta^{13}C_{\text{(tissue)}} + 1000) / (\delta^{13}C_{\text{(diet)}} + 1000)$

The superscript ‘‘*’’ before α indicates that isotopic equilibrium is not assumed. To transform hair and collagen values to enamel values the formula becomes:

$\alpha^*_{\text{collagen or hair - enamel}} = (\delta^{13}C_{\text{(collagen or hair)}} + 1000) / (\delta^{13}C_{\text{(enamel)}} + 1000)$

The fractionation factors for enamel-collagen for each value were calculated and the median fractionation factor 1.008065 selected as the fractionation factor for enamel-collagen (Table A2.2). The fractionation factors in the Kahuzi-Biega and the Itombwe data overlap. Using the median as the enamel-collagen fractionation factor discards data from outliers that could skew the overall averaging method. The enamel-hair fractionation factor 1.008395 was calculated using the means for hair and enamel values (Table A2.3 and A2.4).

Normalizing Hair and Collagen Values to Enamel Levels: Enrichment Factors

Three alternative methods to convert hair/collagen values to enamel levels exist (see below). Methods 1 and 2 are less precise than Method 3. Method 1 gives the absolute difference between hair/collagen and enamel (fractionation factor not included), while in Method 2, the ε* (enrichment factor) is calculated separately before adding it to the tissue value. Method 3 converts, the values to enamel levels in a single, more precise, calculation (for examples, see Table A2.5). The enrichment factor calculated using α* and ε* (α* -1)*1000 is more precise than when calculated using the Δ (Table A2.6).

Enrichment Factor Formulae:

Method 1:

$\delta^{13}C_{(enamel)} = \delta^{13}C_{(hair\ or\ collagen)} + \Delta\ (\Delta = \delta^{13}C_{(enamel)} - \delta^{13}C_{(hair)})$ or $(\delta^{13}C_{(enamel)} - \delta^{13}C_{(collagen)})$

Method 2:

$\delta^{13}C_{(enamel)} = \delta^{13}C_{(hair\ or\ collagen)} + \varepsilon^*$

Method 3:

$\delta^{13}C_{(enamel)} = (\alpha^*)^* (\delta^{13}C_{(hair\ or\ collagen)} + 1000) - 1000$

The hair and collagen $\delta^{13}C$ values were normalized to enamel levels using Method 3. This work arrived at an enrichment factor of 8.1‰ for enamel-collagen and 8.4‰ for enamel-hair. To allow for comparison between values that were formed in different years, each $\delta^{13}C$ value was corrected to preindustrial $\delta^{13}C$ atmosphere level (normalized value – ($\delta^{13}C$ year of formation + 6.5‰). The normalization and correction procedure produced the 272 refined $\delta^{13}C$ values in Appendix 3.

To test whether the 272 refined $\delta^{13}C$ values reflect the habitats from which their samples were collected, ANOVA Pairwise comparisons by location were conducted (Fig. 2).

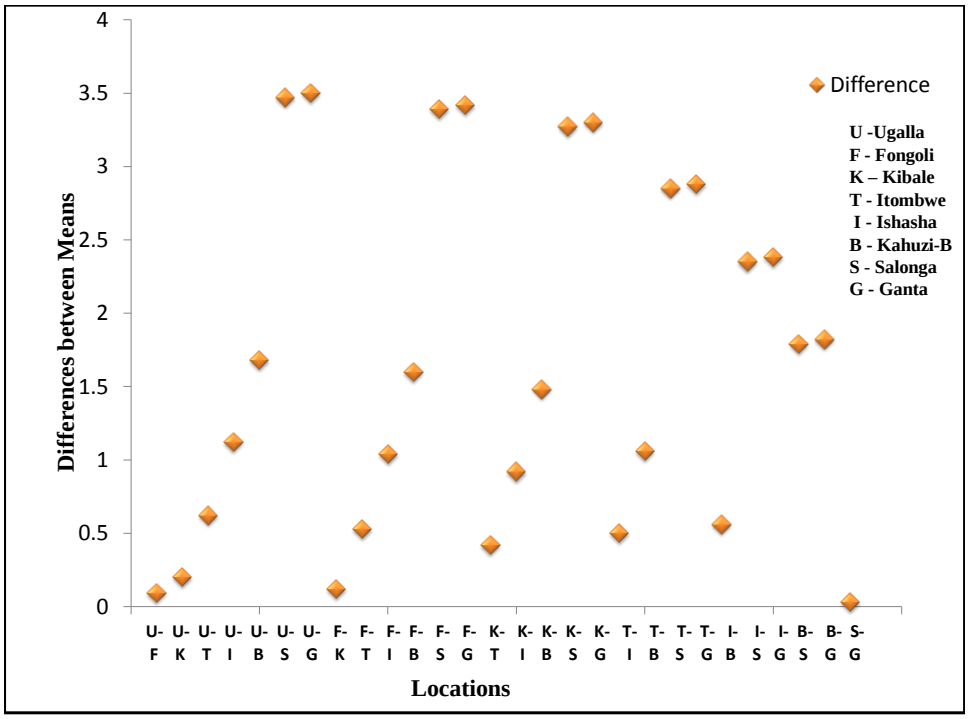

Fig. 2. Pairwise comparison of the 272 refined $\delta^{13}C$ values by location.

The refined $\delta^{13}C$ values from different locations separate in patterns that reflect the habitats occupied by different African Great Apes. Biomes with primate habitats that are similar (Ugalla, Fongoli, and Kibale; Salonga and Ganta) have lower mean differences while those that are substantially different have higher mean differences. The higher the mean difference, the further apart the habitats are while the lower the difference in mean the more similar these habitats are.

Analysis of Variance (ANOVA)

The 272 refined $\delta^{13}C$ values were analyzed using ANOVA based on taxa and location. Measures of central tendency and dispersion were also used to analyze the data.

CHAPTER 4

RESULTS

> Fisher's (1935) work on the design of experiments, his methods for analysis of variance (ANOVA), the notion of statistical significance, and the principle of randomizing experimental units to treatments have become the staples of careful research in the natural sciences, whether in the classroom, laboratory, or field.
>
> -Odum and Barrett(2005, p 490)

In this chapter, details for the results are presented. Details for the frequencies and summaries of the refined $\delta^{13}C$ values based on taxonomic levels and location are described and presented in Tables 7 - 12. Details for the ANOVA test results are provided in Appendices 4 and 5.

Refined $\delta^{13}C$ Values Summary: Frequencies and Percentages

The $\delta^{13}C$ data frequencies and percentages show the distribution of the data across taxa and region. The tables show that most of the taxa included in this study had a relatively good sample size for accurate statistical analysis. Only one gorilla subspecies, one pygmy chimpanzee, and two common chimpanzee subspecies are included in this study. In general, the sample taxa distributions are random with some taxa having samples twice the number of the least represented taxa. The samples' regional distribution also reflects the unequal distributions. Future studies should have a uniform sample size for all the taxa and regions. The tribe Gorilini represents 11% (29 samples

from one subspecies (*G. b. graueri*) from two locations in central Africa. The tribe Hominini represents 89% (243 samples from the genus *Pan* with two species, one with three subspecies). Eleven percent of the samples are from the genus *Gorilla* and 89% come from the genus *Pan.* *G. beringei* represents 11% of the samples (N = 29), *P. paniscus* 53% (N = 143), and *P. troglodytes* represents 37% (N = 100).

The species *G. beringei* represents 100% of the genus *Gorilla*. *P. paniscus* species represents 59% of the genus *Pan*, and *P. troglodytes* represents 41% (Table 7).

Table 7. Species frequencies and percentages per genus

Species per Genus				
Tribe	Genus	Species	Frequency	Percent
Gorillini	*Gorilla*	*beringei*	29	100
Hominini	*Pan*	*paniscus*	143	58.85
		troglodytes	100	41.15

All the *P. paniscus* samples are from central Africa; 14% of the *P. troglodytes* samples are from central Africa, 20% are from eastern Africa, and 66% of the samples are from western Africa (Table 8).

Table 8. Species per region for Pan only

Pan by Region				
Species	Region			
	Central Africa	Eastern Africa	Western Africa	Total
P. paniscus	143 100%			143
P. troglodytes	14 14%	20 20%	66 66%	100
Total	157	20	66	243

G. b. graueri represents 11%, *P. t. schweinfurthii* represents 13%, *P. t. verus* 24%, and *P. paniscus* (no subspecies) represents 53% of the samples summarized at the subspecies level (Table 9).

Table 9. Summary by subspecies

Subspecies		
Subspecies	Frequency	Percent
G. b. graueri	29	10.66%
*P. paniscus (*none*)*	143	52.57%
P. t. schweinfurthii	34	12.50%
P. t. verus	66	24.26%

The subspecies *P. t. verus* represents 66% of the species *P. troglodytes*, and *P. t. schweinfurthii* 34% (Table 10).

Table 10. Subspecies per species frequencies and percentages

Subspecies per Species					
Tribe	Genus	Species	Subspecies	Frequency	Percent
Gorillini	*Gorilla*	*beringei*	*graueri*	29	100%
Hominini	*Pan*	*paniscus*	none	143	100%
		troglodytes	*Schweinfurthii*	34	34%
		troglodytes	*verus*	66	66%

P. t. schweinfurthii from central Africa represents 41% of all *P. t. schweinfurthii* samples and 59% from eastern Africa. All the *P. t. verus* samples are from western Africa (Table 11).

Table 11. Subspecies per region for P. troglodytes only

P. troglodytes by Region				
Subspecies	Region			
	Central Africa	Eastern Africa	Western Africa	Total
P. t. schweinfurthii	14 41.18%	20 58.82%		34
P. t. verus			66 100%	66
Total	14	20	66	100

Stable carbon isotope values from central Africa represent 68% of the refined $\delta^{13}C$ values summarized by region, 7% from eastern Africa, and 24% from western Africa (Table 12).

Table 12. Regional frequencies and percentages

Region		
Region	Frequency	Percent
Central Africa	186	68.38%
Eastern Africa	20	7.35%
Western Africa	66	24.26%

ANOVA Results

Tables 13 to 18 in chapter 5 contain the summary statistics for the refined $\delta^{13}C$ values used in this study (measures of central tendency and dispersion). These measures provide insights on the connections between speciation and habitat patterns among members of the African Great Ape lineage.

Appendix 4 contains ANOVA results based on taxonomic levels. These includes results on pairwise comparisons (comparing species two at a time) to determine which species/subspecies have significantly different refined $\delta^{13}C$ values compared to other species/subspecies (Table A4.1 - A4.5).

Appendix 5 presents results for predicting primate habitats based on refined $\delta^{13}C$ values. This also includes results for pairwise comparisons (comparing locations two at a time) to determine which locations have significantly different refined $\delta^{13}C$ values compared to other locations (Table A5.1 - A5.2).

To unmask the effect of habitat on taxonomic groups, tests were done on the refined $\delta^{13}C$ values in subspecies from different locations. Tables A5.3 to A5.7 present results for *G. b. graueri* populations (Kahuzi-Biega and Itombwe), *P. t. verus* (Ganta and Fongoli), and *P. t. schweinfurthii* (Kahuzi-Biega, Kibale, Ugalla, and Ishasha). Results for pairwise comparisons to determine which locations are significantly different from which other locations are also presented in these tables.

To unmask the effect of taxonomic groups on refined $\delta^{13}C$ values, a final test comparing $\delta^{13}C$ values among individuals of different taxonomic identities living in the same location was done. The refined $\delta^{13}C$ values for this test are from a group of 23

gorillas and 4 Eastern chimpanzees living in Kahuzi-Biega. The results for these tests are presented in Table A5.7.

The utility of refined $\delta^{13}C$ values to unravel the connection between paleoclimate and hominin evolution through the connection between speciation, dietary patterns of a lineage, habitat changes, and OFT climatic cycles is discussed in the following chapter. The first hypothesis looks at the connection between dietary and speciation patterns as reflected in the refined $\delta^{13}C$ values. The second hypothesis looks at the habitats occupied by modern African Great Apes and how these are reflected in the refined $\delta^{13}C$ values.

CHAPTER 5

DISCUSSION

The future of stable isotopes for refining our understanding of the Cenozoic history of East African mammalian paleontology is bright.

-Thure Cerling (2010a, p 950)

The main objective of this thesis is to lay groundwork for the development of an approach using refined $\delta^{13}C$ values to reconstruct hominin paleoecology more precisely in the future. Two hundred and seventy two refined $\delta^{13}C$ values were subjected to ANOVA tests with the objective of testing the significance of the connections among lineage speciation, diets, and habitat patterns in African Great Apes. This approach demonstrates the potential of such work to reconstruct hominin paleoecology.

Connections between speciation and dietary patterns as reflected in the refined $\delta^{13}C$ values, and connections between refined $\delta^{13}C$ values and habitats occupied by modern African Great Apes are discussed in this chapter. Interpretations of refined $\delta^{13}C$ values match observational data for species dietary patterns in each location. The $\delta^{13}C$ values analyzed here had a mean $\delta^{13}C$ of -14.89‰. This is a value for a predominantly C_3 feeding lineage. There are marked overlaps in values analyzed at the genus level. ANOVA results show that refined $\delta^{13}C$ values define species with 51% confidence and subspecies with 54% confidence, but habitats occupied by modern African Great Apes are reflected with 88% confidence. This means that in a lineage with members having

overlapping dietary patterns, such as African Great Apes, stable carbon isotope ecology alone is not adequate to define a species and subspecies (cannot get taxonomy but can get diet and by analogy habitat). Once a species/subspecies has been defined using other approaches such as morphology, $\delta^{13}C$ values can provide insights into the dietary patterns within that species/subspecies/population. The high confidence in differentiating habitats means that precise insights on habitats can be reconstructed from $\delta^{13}C$ values. Pairwise comparisons show that populations of a subspecies occupying different habitats plot separately, and different subspecies of the same species with similar habitats plot together.

Hypothesis 1: Refined $\delta^{13}C$ Values, Dietary and Speciation Patterns

This approach considers the 272 refined $\delta^{13}C$ values to test hypothesis 1: the connection between dietary and speciation patterns among subspecies of the modern African Great Apes (common chimpanzees, bonobos, and gorillas) can be derived from their $\delta^{13}C$ values.

In the refined $\delta^{13}C$ values summary statistics Tables 13 - 16, ‘‘N’’ is the number of $\delta^{13}C$ values for each group: the ‘‘minimum’’ and the ‘‘maximum’’ are the smallest and largest $\delta^{13}C$ values recorded in each group, respectively; half of all $\delta^{13}C$ values in a group fall at or below the median, and half fall at or above; the mean is the average of the $\delta^{13}C$ values for the group; and the standard deviation (stdev), is a measurement of the variability in $\delta^{13}C$ values within a group.

The values ranged from a minimum $\delta^{13}C$ value of -17.97‰ to a maximum $\delta^{13}C$ value of -11.69‰ with a mean $\delta^{13}C$ value of -14.89‰, and stdev of 1.5196 (Table 13).

Table 13. Summary for all refined $\delta^{13}C$ values

Minimum	Median	Maximum	Mean	Stdev
-17.97	-15.65	-11.69	-14.89	1.5196

The $\delta^{13}C$ values for the genus *Gorilla* (one subspecies) ranged from a minimum $\delta^{13}C$ value of -16.7‰ to a maximum of -11.9‰ with a mean of -14‰, and stdev of 1.0408 while the genus *Pan* ranged from a minimum $\delta^{13}C$ value of -18.0‰ and a maximum of -11.7‰ with a mean of -15.0‰ and stdev of 1.5293 (Table 14).

Table 14. Summary of refined $\delta^{13}C$ values by genus

Genus	N	Minimum	Median	Maximum	Mean	Stdev
Gorilla	29	-16.65	-13.74	-11.84	-13.94	1.0408
Pan	243	-17.97	-15.75	-11.69	-15.00	1.5293

The values for the species *P. paniscus* (no subspecies) range from a minimum $\delta^{13}C$ value of -16.9‰ and a maximum of -15.4‰ with a mean of -16.0‰ and stdev of 0.3068 while the values for *P. troglodytes* range from a minimum $\delta^{13}C$ value of -18‰ and a maximum of -11.7‰ with a mean of -13.7‰ and stdev of 1.6396 (Table 15).

Table 15. Summary of refined $\delta^{13}C$ values by species

Species	N	Minimum	Median	Maximum	Mean	Stdev
G. beringei	29	-16.65	-13.74	-11.84	-13.94	1.0408
P. paniscus	143	-16.86	-15.85	-15.35	-15.91	0.3068
P. troglodytes	100	-17.97	-12.92	-11.69	-13.70	1.6396

The $\delta^{13}C$ values for the subspecies *P. t. schweinfurthii* range from a minimum $\delta^{13}C$ value of -15.9‰ to a maximum of -12.0‰ with a mean of -13‰ and stdev of 0.7735, while the values for *P. t. verus* range from a minimum $\delta^{13}C$ value of -18‰ to a maximum of -11.7‰ with a mean of -14.1‰ and stdev of 1.8378 (Table 16).

These $\delta^{13}C$ values reflect a lineage with taxa specialized in mainly C_3 feeding. This interpretation is consistent with the dietary patterns of apes included in this study.

Table 16. Summary of refined $\delta^{13}C$ values by subspecies

Subspecies	N	Minimum	Median	Maximum	Mean	Stdev
G. b. graueri	29	-16.65	-13.74	-11.84	-13.94	1.0408
P. paniscus						
(no subspecies)	143	-16.86	-15.85	-15.35	-15.91	0.3068
P. t. schweinfurthii	34	-15.87	-12.72	-12.04	-12.98	0.7735
P. t. verus	66	-17.97	-13.06	-11.69	-14.08	1.8378

There is a high percentage of overlap in dietary patterns among modern African Great Apes at the genus level (P-value <0.0003, R^2 0.0471, RMSE 1.4861, means: *Pan* -15.0‰ and *Gorilla* -13.9‰), only a small percentage of the differences in refined $\delta^{13}C$

values can be explained by genus alone (R-square 4.71%) (Table A4.1). Further, if predicting a genus from refined $\delta^{13}C$ values, the typical error expected would be high (1.4861), although the means show that *Pan* is different from G*orilla* (Table 14).

Refined $\delta^{13}C$ values are a more significant predictor of species (P-value <0.0001, R^2 0.5049, RMSE 1.0732) (Table A4.2). The R-square indicates that 51% of the variation in refined $\delta^{13}C$ values is associated with species, and the Root MSE indicates that the average error in predicting species with refined signatures would be 1.0732.

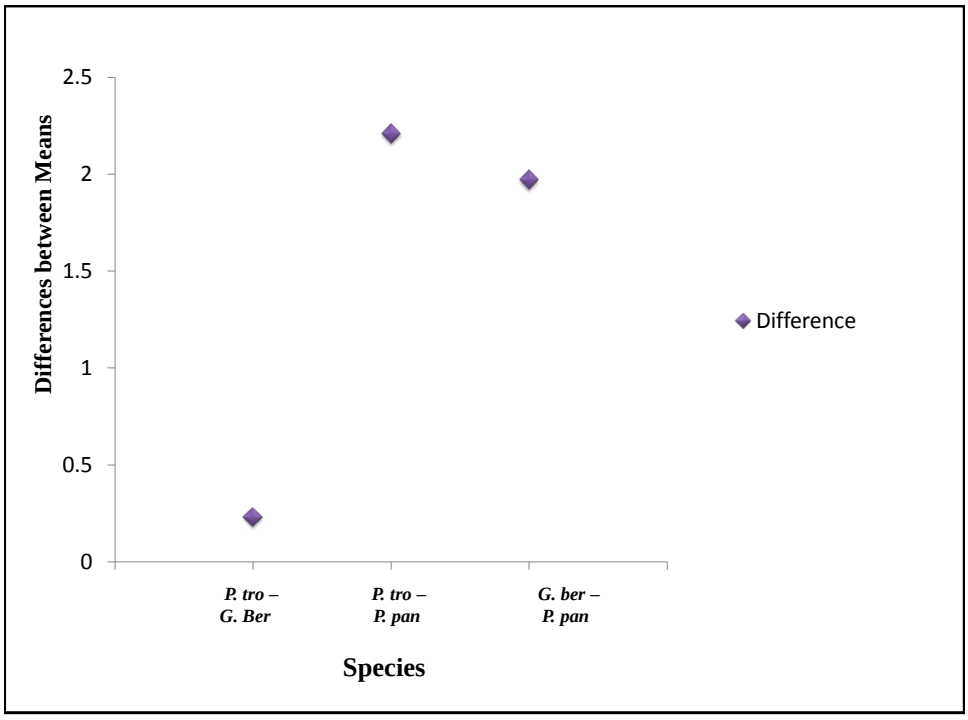

Fig. 3. Pairwise comparisons of refined $\delta^{13}C$ values by species.

Pairwise comparisons (comparing two species at a time) demonstrate that the differences between means (Fig. 3, Table A4.3) is the best single estimate of the difference in $\delta^{13}C$ values between each pair of species in the population (*P. troglodytes – G. beringei* 0.23 [difference in mean], *P. troglodytes – P. paniscus* 2.21, *G. beringei –*

P. paniscus 1.97). *P. paniscus* (mean -15.91‰) is significantly different from both *P. troglodytes* (mean -13.70‰) and *G. beringei* (mean -13.94‰), but *P. troglodytes* and *G. beringei* are not significantly different from one another. The 95% confidence limits mean we are 95% confident that the true difference between two species in population is between those two means.

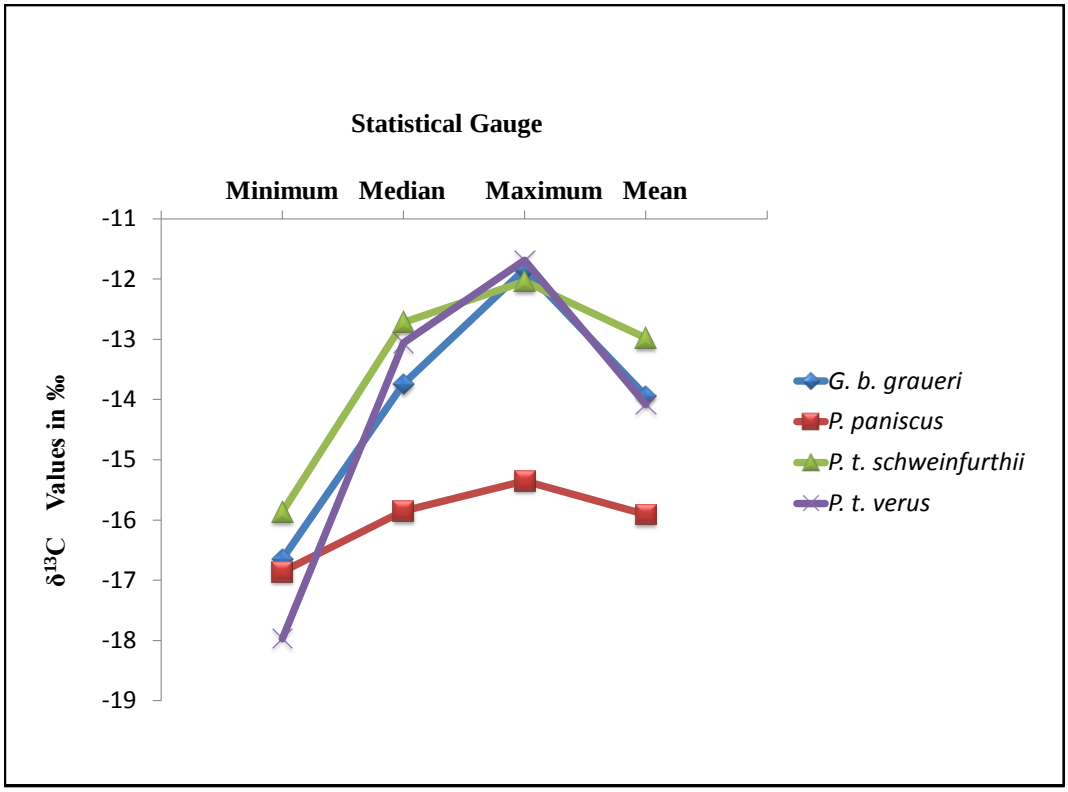

Fig. 4. Summary statistics for refined $\delta^{13}C$ values by subspecies.

P. paniscus has no subspecies.

Refined $\delta^{13}C$ values predict the subspecies taxonomic level at a higher resolution than the species taxonomic level (P-value <0.0001, R^2 0.5478, RMSE 1.0276) (Fig. 4, Table A4.4). The R-square indicates that 54.8% of the variation in $\delta^{13}C$ values is associated with subspecies, and the Root MSE indicates that the average error in

predicting subspecies with $\delta^{13}C$ values would be 1.0276. The $\delta^{13}C$ values prediction resolution in both species and subspecies does not allow precise prediction of a species or subspecies. This point is also reflected in the summary statistics for refined $\delta^{13}C$ values by subspecies. Although the means differentiate the subspecies clearly, the minimum, maximum, and median values show that there is overlap among subspecies.

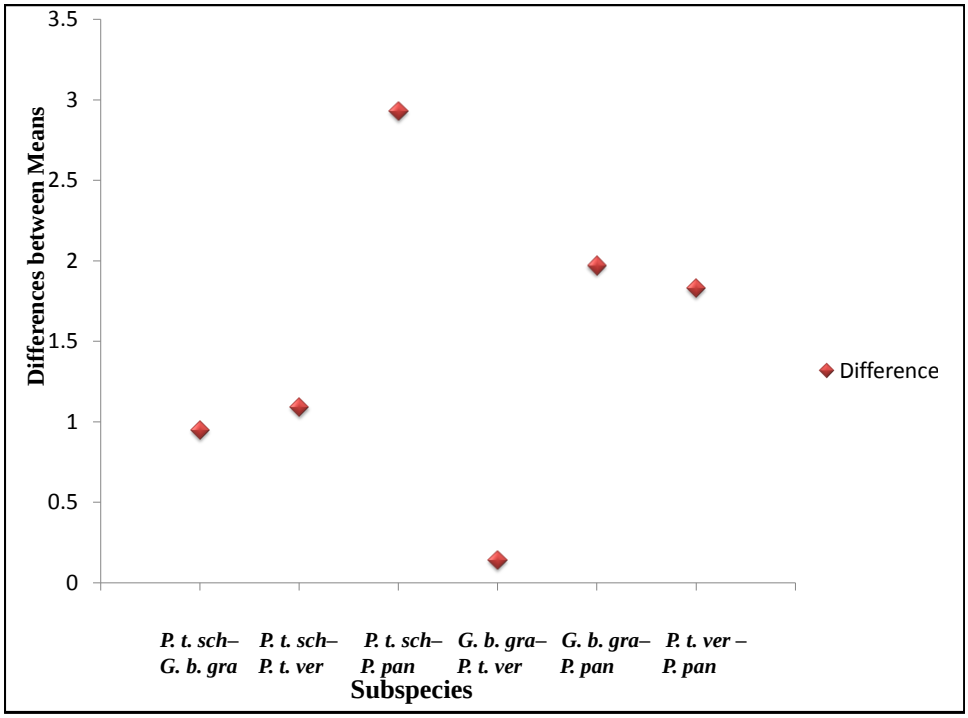

Fig. 5. Pairwise comparison of refined $\delta^{13}C$ values by subspecies.

Pairwise comparison (Fig. 5, Table A4.5) demonstrates that all subspecies are significantly different from all other subspecies (*P. t. schweinfurthii – G. b. graueri* 0.95, *P. t. schweinfurthii – P. t. verus* 1.09, *P. t. schweinfurthii – P. paniscus* 2.93, *G. b. graueri – P. t. verus* 0.14, *G. b. graueri – P. paniscus* 1.97, *P. t. verus – P. paniscus* 1.83) with the exception of *G. b. graueri* and *P. t. verus*, which do not have significantly different values from one another. *P. t. schweinfurthii* has the largest values, *P. t. verus*

and *G. g. graueri* have the second highest values, and *P. paniscus* has the lowest values (Table 14).

Refined $\delta^{13}C$ values are a true reflector of a species dietary patterns. The $\delta^{13}C$ values summary by taxa demonstrates the dietary heterogeneity within the African Great Ape lineages (Tables 13 -16). The measures of central tendency and dispersion track the dietary heterogeneity within a species. The data summary for the genus *Gorilla* and *Pan* shows that there is more dietary heterogeneity within the genus *Pan* than within *Gorilla*.

The species summary shows that there is a higher dietary heterogeneity within *P. troglodytes* than between *G. beringei* and *P. paniscus*. The low standard deviation in the species *P. paniscus* indicates dietary homogeneity within this species.

The subspecies summary refines the picture of dietary heterogeneity farther. There is a broader dietary range within *P. t. verus* than between *G. b. graueri* and *P. t. schweinfurthii*. The low standard deviation for *P. t. schweinfurthii* indicates dietary uniformity within this subspecies.

Field observation data on dietary patterns among modern African Great Apes explains the differences in $\delta^{13}C$ values observed among the species studied. *P. t. verus* are folivore/fruigivores with the forest-adapted populations (Ganta location) feeding more frequently on fruits than do open-woodland-adapted populations (Fongoli location). The open-woodland-grassland populations also consume some proportion of C_4 foodstuff. The gorilla subspecies *G. b. graueri* are folivore/fruigivores with lowland populations (Kahuzi-Biega location) feeding on a higher percentage of fruits than do highland populations (Itombwe location). *P. t. schweinfurthii* have dietary patterns similar to *P. t. verus*. Members of the *P. t. schweinfurthii* subspecies population in

Kibale location are predominantly C_3 folivore/fruigivores and also feed on C_4 foods (sugarcane, maize, and elephant grass). Members of this subspecies from Ishasha location are predominantly fruigivores. The inclusion of some C_4 vegetation in their diets could explain why these chimpanzees have high $\delta^{13}C$ values. *P. paniscus* are folivore/fruigivores in densely forested biomes. Dietary patterns of populations of this chimpanzee species vary from folivory to fruigivory. The population in Salonga feed more commonly on terrestrial herbaceous vegetation. The shifting values of measures of central tendency and the results from pairwise comparisons (Fig. 5) capture the dietary heterogeneity within these subspecies and species.

Approach 1 has one main weakness and two strengths. The approach tracks speciation patterns, but not reliably at the genus level and with limited confidence at higher levels. It is possible to separate $\delta^{13}C$ values based on genus but with low confidence (5%). The confidence increases for species (51%) and subspecies (55%). Dietary overlap among subspecies means that they cannot be distinguished precisely using $\delta^{13}C$ values. Despite its weakness in identifying a species at the genus and subspecies levels, this approach does track the dietary patterns of the African Great Ape subspecies populations (geographical variants) included in this study.

The next hypothesis looks at the connection between species and habitat patterns as reflected in refined $\delta^{13}C$ values from modern African Great Apes. This part exposes the effect of habitats on speciation patterns within African Great Apes.

Hypothesis 2: Refined $\delta^{13}C$ Values and Habitat Patterns

Stable carbon isotope values from animal tissues record the habitats in which an animal lives in (Cerling et al., 1999; Cerling et al., 2010a; Cerling et al., 2003c; Cerling et al., 2004; Lee-Thorp and Sponheimer, 2007; Lee-Thorp et al., 2003; Sponheimer et al., 2009). Biomes with grasslands (C_4 vegetation), woodlands (open and closed), and forests (C_3 vegetation) correlate with $\delta^{13}C$ values from animal tissues with a high degree of confidence. Different habitats within a forest structure (understory, middle canopy, and emergent canopy) can also be detected. The refined $\delta^{13}C$ values approach 2 addresses hypothesis 2: The connection between speciation patterns and habitats occupied by different modern African Great Apes can be verified from the $\delta^{13}C$ values of these primates.

The 272 refined $\delta^{13}C$ values used in this study are from apes living in different biomes. This thesis demonstrates that refined $\delta^{13}C$ values reflect habitat separation within modern African Great Apes. Speciation patterns related to habitat differences are reflected in the refined $\delta^{13}C$ values more precisely than the way they are reflected in other approaches (Fig. 6, Table 17). Differences in refined $\delta^{13}C$ values that reflect differences in vegetation cover in different regions are also evident (Table 18).

Refined $\delta^{13}C$ values are a significant predictor for habitat and its effect on potential speciation patterns within African Great Apes subspecies (P-value <0.0001, R^2 0.8796, RMSE 0.5343) (Table A5.1). Apart from reflecting habitat types, the results here also reflect potential speciation patterns within a subspecies at the population level. The R-square indicates that close to 90% of the variation in $\delta^{13}C$ values is associated

with habitat (better than approach 1 presented above). The Root MSE indicates that the average error in predicting carbon isotope values with habitat would be 0.5343.

The measures of central tendency and dispersion reflect the vegetation diversity within African Great Ape habitats and its effect on potential speciation patterns. Fongoli (Fig. 6, Table 17) is a mosaic biome with woodlands dominating the vegetation cover, grasslands and wooded grasslands are also common. Ganta until recently was an upper Guinean Forest, but the forest has been cleared. Ishasha is a riparian corridor composed of closed-canopy, semi-deciduous (mixed evergreen and deciduous) forest surrounded by dry forest and open wooded grasslands. Itombwe is a dense lowland forest. Kahuzi Biega has two biomes: the highland region is mainly montane forest while the lowland region is tropical forest (primary and secondary forest, abandoned fields, and ancient secondary forests). The measures of central tendency and dispersion for Ishasha are different from the ones for Itombwe, Kahuzi-Beiga, Ganta and Salonga. Ishasha also has the lowest standard deviation value among forested habitats, which is also the second lowest among all habitats included in this study. Kibale is a mosaic biome – lowland and montane rainforest, mixed deciduous forest, woodlands, and grasslands. Salonga is a closed canopy forest biome interrupted occasionally by small, circular savanna patches. Ugalla is a mosaic biome with patches of forests, open woodlands and grasslands. All the refined $\delta^{13}C$ values reflect the biomes inhabited by the specific species population in question.

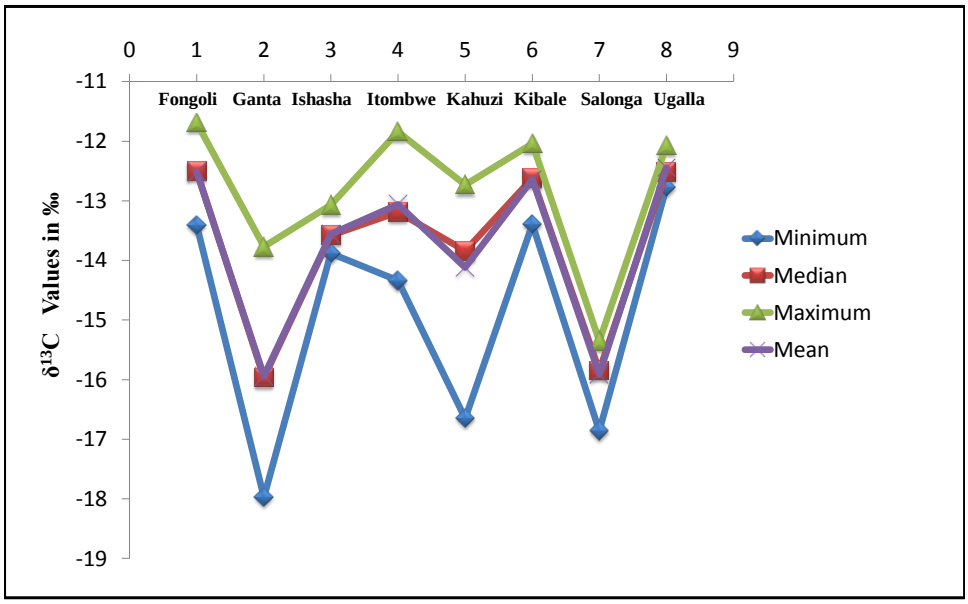

Fig. 6. Summary statistics for refined $\delta^{13}C$ values by location.

Table 17. Summary of refined $\delta^{13}C$ values by location

Location	N	Minimum	Median	Maximum	Mean	Stdev
Fongoli	36	-13.41	-12.50	-11.69	-12.52	0.4105
Ganta	30	-17.97	-15.97	-13.77	-15.94	0.8801
Ishasha	10	-13.88	-13.58	-13.07	-13.56	0.2884
Itombwe	6	-14.34	-13.19	-11.84	-13.06	0.9326
Kahuzi-Beiga	27	-16.65	-13.84	-12.73	-14.12	1.0107
Kibale	8	-13.39	-12.62	-12.04	-12.64	0.4098
Salonga	143	-16.86	-15.85	-15.35	-15.91	0.3068
Ugalla	12	-12.77	-12.52	-12.07	-12.44	0.2697

The average vegetation cover in the sampled regions is also reflected in the refined $\delta^{13}C$ values (Table 18). Central Africa is predominantly a forested biome, eastern Africa is predominantly woodlands to grasslands biome, and western Africa, is a mosaic biome with dense forests, woodlands and grasslands.

Table 18. Summary of refined $\delta^{13}C$ values by region

Region	N	Minimum	Median	Maximum	Mean	Stdev
Central Africa	186	-16.86	-15.75	-11.84	-15.43	1.0218
Eastern Africa	20	-13.39	-12.59	-12.04	-12.52	0.3383
Western Africa	66	-17.97	-13.06	-11.69	-14.08	1.8378

Pairwise comparisons of refined $\delta^{13}C$ values (Fig. 2, Table A5.2) show that although most biomes are significantly different from most other biomes, similar trends exist. Apart from being significantly similar, Ugalla, Fongoli, and Kibale have significantly higher values than most other biomes. Kibale and Itombwe and Itombwe and Ishasha, have low values, and Kahuzi-Beiga, Salonga, and Ganta locations have the lowest $\delta^{13}C$ values. Ugalla, Fongoli, and Kibale are all mosaic biomes, but most of the chimpanzees within them feed in open woodlands and grasslands in those biomes. The $\delta^{13}C$ values from forested biomes also reflect use of different habitats within each forest.

The measures of central tendency and dispersion, and pairwise comparisons of refined $\delta^{13}C$ values based on location captures the connection between speciation patterns and habitat partitioning at the population level among African Great Apes precisely.

The interpretations presented here are in line with data from field observations. Gorillas occupy the lower middle story of the forest and old clearings, valley bottoms, and landslides where there is a dense tangle of terrestrial herbaceous vegetation (Kingdon, 2001; Robbins, 2007). The Kahuzi Biega signals reflect this pattern. Chimpanzees in this area overlap with gorillas in the forest but they concentrate on the upper middle canopy (reflected in the Kahuzi Biega stdev). The dense tangled terrestrial herbaceous vegetation exploited by gorillas probably explains their lower mean compared to chimpanzees. Chimpanzees in Itombwe and Ishasha mainly exploit the main forest canopy. The $\delta^{13}C$ values from Salonga and Ganta show that the chimpanzees here occupy the understory, but the high stdev in Ganta reflects variation in habitat patterns among members of this population (some occupy the understory and others middle canopy). Some bonobo populations in Salonga depend more on terrestrial herbaceous vegetation (Boesch et al., 2002; Stumpf, 2007). The signals from Salonga indicate this type of dietary pattern. The results presented here closely track habitat partitioning as reported by other scholars (Cerling et al., 2004; Medina and Minchin, 1980).

To further verify whether the refined $\delta^{13}C$ values reflect the habitat's effect on population dynamics, pairwise comparisons of the means of $\delta^{13}C$ values from members of the same subspecies from different biomes was carried out (not including *P. paniscus*, for which all samples are from a single location).

Refined $\delta^{13}C$ values for gorillas are from two locations: Itombwe and Kahuzi-Biega (P-value <0.0172, R-square 0.1927, Root MSE 0.9523) (Table A5.3). The Itombwe population has a mean of -13.06‰, which is significantly higher than that

found in the gorilla population from Kahuzi-Biega, -14.17‰. The differences in the feeding patterns in gorillas from Kahuzi Biega and Itombwe (discussed above) explain the differences in their mean $\delta^{13}C$ values.

P. t. verus samples are from two locations: Fongoli and Ganta (P-value <0.0001, R-Square 0.8708, Root MSE 0.6657) (Table A5.4). The average $\delta^{13}C$ value for chimpanzees from Fongoli is -12.5‰ and from Ganta is -15.9‰. The different feeding and habitat patterns of chimpanzees in these two locations are the probable source of these differences.

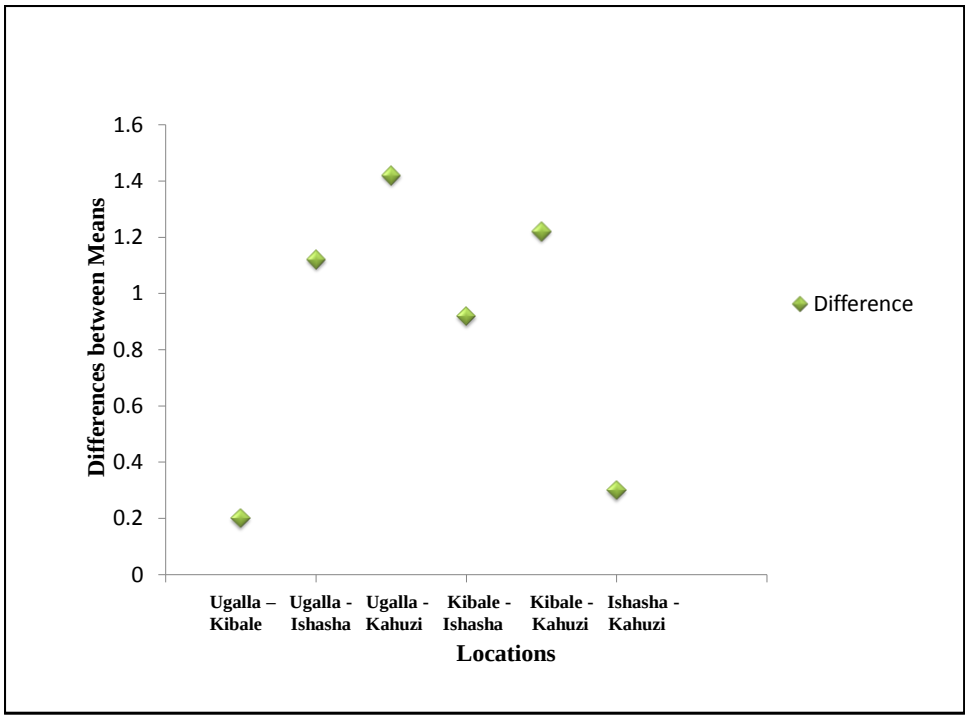

Fig. 7. Pairwise comparisons for refined $\delta^{13}C$ values by location for *P. schweinfurthii.*

Pairwise comparisons of refined $\delta^{13}C$ values by location for *P. schweinfurthii* revealed more information about the effect of habitat on lineages (Figure 7 and Table A5.5). The samples for *P. t. schweinfurthii* (P-value <0.0001, R-Square 0.5530, Root

MSE 0.5424) are from four locations (Ugalla, Kibale, Ishasha, and Kahuzi-Biega). Pairwise comparisons show that *P. t. schweinfurthii* living in Ugalla (-12.4‰) and Kibale (-12.6‰) have similar average $\delta^{13}C$ values, as do those living in Ishasha (-13.6‰) and Kahuzi-Biega (-14.1‰) (Table A5.6). However, values for apes from Ugalla and Kibale are significantly higher than those of apes from Ishasha and Kahuzi-Biega. Ugalla and Kibale are mosaic biomes while Ishasha and Kahuzi-Biega are forested biomes.

To test the effect of habitat on different species, comparison of $\delta^{13}C$ values according to different taxa living in the same biome was done. The only two groups for which this is possible in this study is a group of 23 *G. b. graueri* and four *P. t. schweinfurthii* living in Kahuzi-Beiga (Table A5.7). The results reveal no statistically significant difference between refined $\delta^{13}C$ values of *G. b. graueri* and *P. t. schweinfurthii* living in Kahuzi-Biega (P-value <0.5869, R-square 0.0120, RMSE 1.0245). However, in order to produce reliable results, a larger sample of *P. t. schweinfurthii* living in Kahuzi-Biega should be considered.

Refined $\delta^{13}C$ values track habitat patterns more precisely than do taxonomic groups. The differences in $\delta^{13}C$ patterns within subspecies indicate potential speciation responding to habitat differences similar to what has been reported from the Galapagos Island (Grant and Grant, 2008). The potential of habitat changes such as those associated with climate change to lead to speciation is imprinted in $\delta^{13}C$ values. These are the patterns postulated by the ‘‘Habitat Theory.’’

Stable Carbon Isotope Ecology in the 21st-century African Paleoanthropology

The results presented here and those reported by other researchers demonstrate the utility of stable carbon isotope ecology in paleoanthropology. This approach promises to enable paleoanthropologists to unearth insights on the connections between speciation, diet, habitat, and climatic patterns driven by OFT patterns in fossil primates and other faunal lineages from the Miocene to the present.

It will be intriguing to have a comparative look at the $\delta^{13}C$ values from different primate taxa during the Miocene with the Plio-Pleistocene and modern times. Will patterns in primates $\delta^{13}C$ value look similar to those observed in proboscids from the Miocene to modern period? Do bovids taxa have consistent C_4 signatures throughout the Plio-Pleistocene into the Holocene? Do $\delta^{13}C$ value patterns of warm-adapted species differentiate them from cold-adapted species? Are there patterns that place a population, subspecies, species, and genus in different and similar biomes in the fossil record? Are there similarities in the $\delta^{13}C$ values of species that become extinct during episodes of climate switching? Perspectives tailored towards probing these questions promise to provide insights into the connections between paleoclimate and hominin evolution. Insights on the connections among dietary flexibility, morphology, and behavior could be obtained.

The approach presented here demonstrates the potential of $\delta^{13}C$ values to provide insights that are not accessible when using ecological indicator taxa approach. An elaborate stable carbon isotope ecology of both modern and fossil primates promises to provide a roadmap to testing postulates of the ‘‘Habitat Theory’’ and mapping the

connections between speciation, diet, and habitat patterns of primates and other faunal lineages, and OFT climatic cycles at finer details.

CHAPTER 6

SYNTHESIS, FUTURE WORK, AND CONCLUSION

Thus we are faced with a very intriguing problem. Both the *Elephas* and *Loxodonta* lineages go back about 5 million years to the late Miocene of Africa. Their initial appearance coincides with the worldwide expansion of the C_4 biomass from which they and contemporary gomphotheres fed almost exclusively. However, after the middle Pleistocene, both *Elephas* and *Loxodonta* abandoned the diet that had served them well for their previous history and for which their teeth had become increasingly specialized.

-Cerling et al. (1999, p 373)

Synthesis

This thesis had three main objectives nested in one goal: resolve the normalization and correction conundrum in stable carbon isotope ecology for modern times by refining $\delta^{13}C$ values; evaluate the efficacy of refined $\delta^{13}C$ values to reflect the connections between dietary and speciation patterns among modern African Great Apes; and evaluate the precision with which refined $\delta^{13}C$ values reflect the habitats occupied by modern African Great Apes. The goal for this work is to develop an approach based on refined $\delta^{13}C$ values that can be used to reconstruct hominin paleoecology more precisely.

The normalization and correction conundrum was resolved in several steps. Fractionation and enrichment factors used to transform hair and collagen $\delta^{13}C$ values

were calculated from the gorilla data set. The $\delta^{13}C$ values were then corrected to the preindustrial $\delta^{13}C$ atmosphere levels. This processes produced refined $\delta^{13}C$ values that reflect their sources more precisely.

Approach 1 highlights both the power and weaknesses of $\delta^{13}C$ values to explain the connection between dietary and speciation patterns within modern African Great Apes. The refined $\delta^{13}C$ values indicate that all modern African Great Apes are predominantly C_3 feeders (folivores and fruigivores). The effect of C_4 foods on refined $\delta^{13}C$ values from modern African Great Apes is captured as enrichment of $\delta^{13}C$ values to the boundary point of C_3/mixed C_3/C_4 signatures. Analyzing $\delta^{13}C$ values based on taxonomic categories using ANOVA provides evidence that connects dietary to speciation patterns. The measures of central tendency and dispersion provide insights on the dietary diversity among species. Due to dietary overlaps among the African Great Ape lineages, however, it is not possible to differentiate lineages at the genus, species and subspecies levels.

Approach 2 unravels the connection between speciation and habitat patterns for modern African Great Apes as reflected in refined $\delta^{13}C$ values. The measures of central tendency and dispersion capture the vegetation heterogeneity within African Great Apes habitats and its effect on potential speciation. This approach also captures speciation patterns at the population levels. Significant differences in $\delta^{13}C$ values between most pairs of biomes are found. This approach explains close to 90% of the variability in $\delta^{13}C$ values. Pairwise comparisons of $\delta^{13}C$ values from the same subspecies from different biomes and from different subspecies in the same biome, revealed the significance of habitats dictating speciation patterns.

Refined $\delta^{13}C$ values have the potential to map speciation, diet, and habitat patterns in the fossil record as postulated by the ‘‘Habitat Theory.’’ This approach offers perspective that could provide high resolution insights into connections between paleoclimate and hominin evolution by capturing speciation and habitat transformations during OFT climatic cycles in the fossil record. Finer details within the 2.8 – 2.6 Ma, 1.8 – 1.6 Ma, and 0.9 Kyr packets may be unraveled. Insights on speciation and habitat transformations within these packets will expose patterns that mark warm and cold-adapted lineages and track their speciation patterns during glacial and interglacial cycles.

These approach and evidence from other stable carbon isotope ecology investigations point to a paradigm shift in our understanding of hominin paleoecology in the near future. This approach promises to unearth insights on the connections between hominin evolution, habitat changes, and OFT climatic patterns in combination with other proxy data.

Future Work

The partitioning of stable carbon isotopes between the biosphere and atmosphere during the late Cenozoic is a major conundrum in the application of stable carbon isotope ecology to paleoanthropological investigations. Understanding this conundrum has been divided into two phases in this study: Phase 1: solving the conundrum in the modern global system, and Phase 2: solving the conundrum for the mid-Miocene to Pleistocene times. This thesis offers a template to solve the modern conundrum. Solving the existing conundrum over the partitioning of carbon between atmosphere and biosphere during the mid-Miocene to Pleistocene remains open. The success in refining

$\delta^{13}C$ values presented here paves the way for solving the second conundrum. This will pave the way for high resolution testing of postulates of the ‘‘Habitat Theory’’ in the fossil record using stable carbon isotope ecology.

Further development of the refined $\delta^{13}C$ values approach requires a number of things to be done:

1) More investigations on primate fractionation and enrichment factors need to be done. The enamel-hair enrichment factor for gorillas (used here, 8.4‰) is different from the ones reported for large mammals such as buffalo, hartebeest, and wildebeest (11.1‰). There is a high probability that other primate lineages (modern and fossil) have different diet and tissue enrichment factors. More work needs to be done to address these issues.

2) More investigations of both hominoids and cercopithecoids from different habitats including work on sympatric lineages in different regions of Africa needs to be done. African Great Apes represent a lineage of predominantly C_3 feeders (moist/warm adapted). Monkey lineages are largely C_4 feeders (grassland/cold adapted). Including data from modern African monkeys will provide patterns closely similar to what might be found in a cold cycle, thus making the refined $\delta^{13}C$ values approach insightful.

3) Understanding the way sympatric African primate habitats are reflected in refined $\delta^{13}C$ values is paramount. More data to support mapping the number of primate habitats and their characteristics as reflected in the refined $\delta^{13}C$ value measures of central tendency and dispersion are needed. Mapping primate habitats in a rain forest, riparian forest, closed woodlands and open woodlands, and grasslands is also paramount.

4) A multi-proxy approach that will incorporate $\delta^{18}O$ and $\delta^{15}N$ data with $\delta^{13}C$ data is also needed. More work that will define the applicability of this multi-proxy approach is needed.

Conclusion

This thesis demonstrates the potential of refined $\delta^{13}C$ values. Refined $\delta^{13}C$ values from modern African primates will provide insights on the connections between paleoclimate and hominin evolution. Using these values, detailed reconstructions of speciation, dietary, and habitat patterns of African fossil primates and other faunal lineages that will shed more light on hominin paleoecology should be possible. These approach promises to take a leading role in the 21st century paleoanthropological investigations.

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APPENDICES

A1. AFRICAN GREAT APES STUDY LOCATIONS AND TAXONOMY

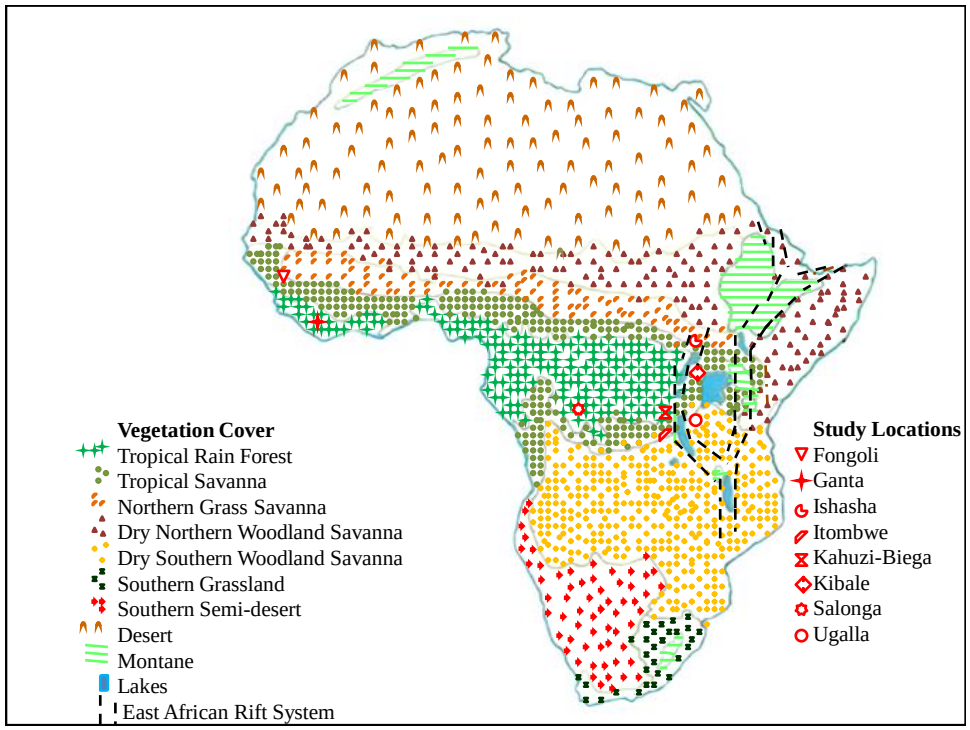

Fig. A1.1. Map of Africa showing different biomes and study locations.

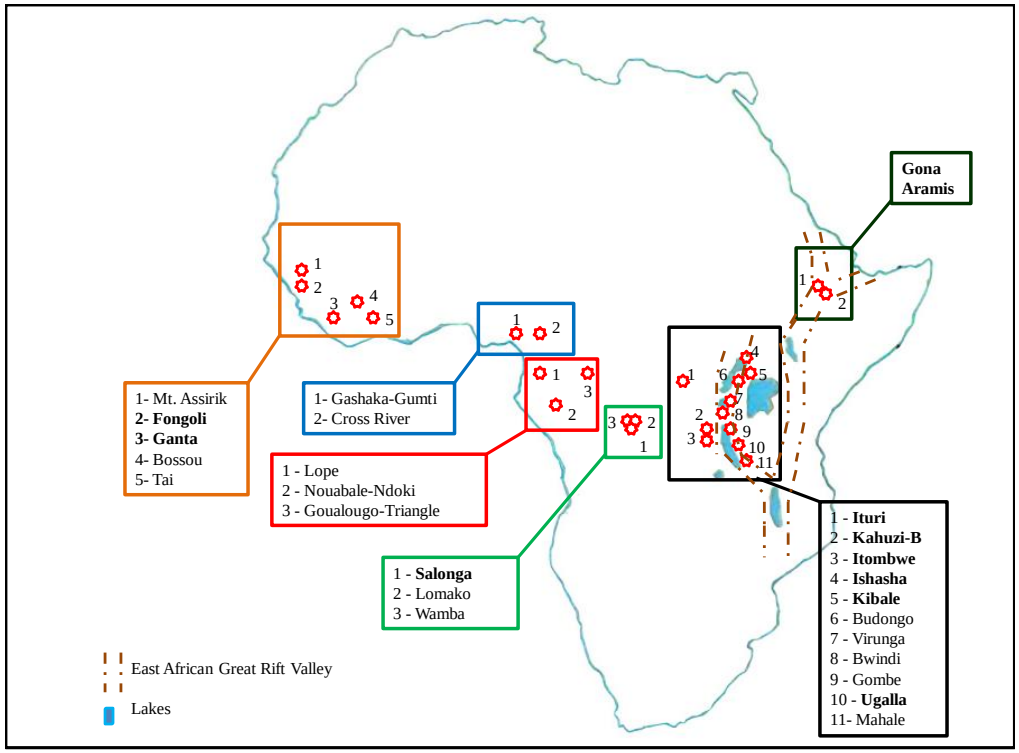

Fig. A1.2. Map of Africa showing the main African Great Apes study locations. Locations with $\delta^{13}C$ values data included in this study are highlighted as are fossil primate sites – Gona and Aramis also are included.

Table A1.1. African Great Apes taxonomy and major study locations

(Family – Hominidae, Subfamily – Homininae)

Tribe	**Subtribe**	**Genus**	**Species**	**Subspecies**	**Major Study Sites**
Hominini	Panina	*Pan*	*troglodytes*	*troglodytes* (Central Chimpanzee)	Lope Nouabale-Ndoki Goualougo- Triangle (Central Africa)
Hominini	**Panina**	***Pan***	***troglodytes***	***verus* (Western Chimpanzee)**	**Fongoli** **Ganta** Tai Bossou Mt. Assirik
Hominini	**Panina**	***Pan***	***troglodytes***	***schweinfurthii* (Eastern**	**Kibale** Gombe

				Chimpanzee)	Mahale Budongo Bwindi
		Pan	*troglodytes*	*vellerosus* (Nigerian-Cameroon Chimpanzee)	Gashaka-Gumti
Hominini	**Panina**	***Pan***	***paniscus*** ***(*Bonobo*)***	*None*	**Salonga** Lomako Wamba
Gorillini		***Gorilla***	***beringei***	***graueri*** **(Graueri's gorilla)**	**Kahuzi-Biega** **Itombwe**
		Gorilla	*beringei*	*beringei* (Mountain gorilla)	Virunga volcanoes (Rwanda)

		Gorilla	*gorilla*	*gorilla* (Western lowland gorilla)	Losi Lope
		Gorilla	*gorilla*	*dielhi* (Cross River gorilla)	Cross River (Cameroon)

Taxa and study locations included in this study are highlighted.

A2. PROCEDURE FOR CALCULATING THE ENAMEL-COLLAGEN AND ENAMEL-HAIR FRACTIONATION AND ENRICHMENT FACTORS FOR AFRICAN GREAT APES USING DATA FROM KAHUZI-BIEGA AND ITOMBWE GORILLAS

In the following tables (Table A2.1 to A2.4), corrected $\delta^{13}C$ values are calculated by: (1) finding the difference between the tissues' year of formation (collagen, hair, or enamel) $\delta^{13}C$ atmosphere value and the preindustrial $\delta^{13}C$ atmosphere value (-6.5‰) (YFC and YFE $\delta^{13}C$ Atmosphere), (2) adding the difference in 1 above to the raw tissue value (RCS or RES $\delta^{13}C$ Atmosphere value + YFC or YFE $\delta^{13}C$ Atmosphere value). The result of this process is the corrected collagen or enamel $\delta^{13}C$ value (Cor CS or Cor ES $\delta^{13}C$). For the columns on tissue type in Tables A2.1 and A2.4, m^1 refers to upper molar, m_1 to lower molar, and B refers to bone collagen.

Table A2.1. Procedure for correcting the industrial effect on collagen and enamel $\delta^{13}C$ values used in calculating the fractionation and enrichment factors

T	**YC**	**YFC**	**YFE**	**RCV $\delta^{13}C$**	**REV $\delta^{13}C$**	**YFC $\delta^{13}C$ Atmos**	**YFE $\delta^{13}C$ Atmos**	**Cor CV $\delta^{13}C$**	**Cor EV $\delta^{13}C$**
m^1	2004	01	94	-21.3	-16.8	1.493	1.268	-19.807	-15.532
m^1	1996	93	86	-25.4	-17.8	1.255	1.146	-24.145	-16.654
m^3	1997	94	87	-22.1	-14	1.268	1.158	-20.832	-12.842
m^3	2003	00	93	-23.2	-15.1	1.499	1.255	-21.701	-13.845
B	1997	94	87	-24.8		1.268	1.158	-23.532	
m^2	1997	94	87	-22.3	-15.9	1.268	1.158	-21.032	-14.742
m_1	1997	94	87	-21.5	-14.1	1.268	1.158	-20.232	-12.942
m_2	1997	94	87	-22.4		1.268	1.158	-21.132	
					-14.2				-13.042
m_3	1997	94	87	-22.3		1.268	1.158	-21.032	
					-14.9				-13.742
m_2	1997	94	87			1.268	1.158		**-14.167**

m_3	1997	94	87	-22.9		1.268	1.158 **Mean**	-21.632 **-21.507**	

Note: T – Tissue type, YC – Year of Collection, YFC – Year of Formation Collagen,

YFE – Year of Formation Enamel, RCV – Raw Collagen Values, REV - Raw Enamel Values,

YFC – Year of Formation Collagen, YFE – Year of Formation Enamel,

Cor CV - Corrected Collagen Values, Cor EV – Corrected Enamel Values, Atmos - Atmosphere.

Table A2.2. Enamel - Collagen fractionation factor calculation procedure

(data from Kahuzi-Biega and Itombwe)

YC	YF	L	RCV $\delta^{13}C$	REV $\delta^{13}C$	YFC $\delta^{13}C$ Atmos Shift	YFE $\delta^{13}C$ Atmos Shift	Cor CV $\delta^{13}C$	Cor EV $\delta^{13}C$	Fractionation Factors
2001	94	K	-21.3	-16.8	1.493	1.268	-19.807	-15.532	1.004361
1993	86	K	-25.4	-17.8	1.255	1.146	-24.145	-16.654	1.007676
1994	87	K	-22.1	-14	1.268	1.158	-20.832	-12.842	1.00816
2000	93	K	-23.2	-15.1	1.499	1.255	-21.701	-13.845	1.00803
1994	87	K	-21.5	-15.9	1.268	1.158	-20.232	-14.742	1.005603
1994	87	K	-22.4	-14.1	1.268	1.158	-21.132	-12.942	1.008367
1994	87	K	-22.9	-14.9	1.268	1.158	-21.632	-13.742	1.008064
1993	86	I	-22.8	-14.8	1.255	1.146	-21.545	-13.654	1.008065
1993	86	I	-21.5	-13.3	1.255	1.146	-20.245	-12.154	1.008258

1993	86	I	-22.1	-13	1.255	1.146	-20.845	-11.854	1.009182
1993	86	I	-23.8	-14.3	1.255	1.146	-22.545	-13.154	1.009608
1993	86	I	-23.1	-14.4	1.255	1.146	-21.845	-13.254	1.008783
1993	86	I	-21.4	-15.5	1.255	1.146	-20.145	-14.354	1.00591
								Median	**1.008065**

YC - Year of Collection, YF - Year of Formation, L - Location, K - Kahuzi Beiga, I - Itombwe, RCV - Raw Collagen Values, REV - Raw Enamel Values, YFC - Year of Formation Collagen, YFE - Year of Formation Enamel, Atmos - Atmosphere, Cor CV - Corrected Collagen Values, and Cor EV - Corrected Enamel Values. The median 1.008065 was selected as the ideal enamel-collagen fractionation factor for African Great Apes.

Table A2.3. Procedure for correcting enamel $\delta^{13}C$ values

Tooth	**YC**	**YF**	**REV**	**$\delta^{13}C$ Atmos Shift**	**CEV**
m^1	2004	1994	-16.8	1.26	-15.532
m^1	1996	1986	-17.8	1.146	-16.654
m^3	1997	1987	-14	1.1	-12.842
m^3	2003	1993	-15.1	1.255	-13.845
m_1	1997	1987	-15.9	1.158	-14.742
m_2	1997	1987	-4.1	1.158	-12.942
m_2	1997	1987	-14.2	1.158	-13.042
m_3	1997	1987	-14.9	1.158	-13.742
				Mean	**-14.168**

YC - Year of Collection, YF - Year of Formation, REV - Raw Enamel Values,

Atmos - Atmosphere, CEV – Corrected Enamel Values. Data from Kahuzi-Biega gorillas.

Table A2.4. Procedure for correcting hair $\delta^{13}C$ values used in calculating the enamel-hair fractionation factor

Hair Formation Year	**Raw Hair Values $\delta^{13}C$**	**Hair Value Shift from preindustrial atmosphere value (- 6.5‰)**	**Corrected Hair Value (Raw Value + Hair Value shift from - 6.5‰**
2005	-23.7	1.655	-22.045
2005	-24.4	1.655	-22.745
2005	-23.5	1.655	-21.845
2005	-23.3	1.655	-21.645
2005	-23.6	1.655	-21.945
2005	-24.2	1.655	-22.545
2005	-23.8	1.655	-22.145
2005	-24.6	1.655	-22.945
2005	-24.7	1.655	-23.045

2005	-24.7	1.655	-23.045
2005	-24.6	1.655	-22.945
2000	-23.1	1.499	-21.601
		Mean	**-22.375**

Data from Kahuzi Biega gorillas.

Table A2.5. Precision of method 3 in refining $\delta^{13}C$ values

Raw Values $\delta^{13}C$	**Method 1**	**Method 2**	**Method 3**
-15.00	-6.80	-6.61	-6.74
-16.00	-7.80	-7.61	-7.75
-17.00	-8.80	-8.61	-8.75
-18.00	-9.80	-9.61	-9.76
-19.00	-10.80	-10.61	-10.77
-20.00	-11.80	-11.61	-11.78
-21.00	-12.80	-12.61	-12.79
-22.00	-13.80	-13.61	-13.80
-23.00	-14.80	-14.61	-14.81
-24.00	-15.80	-15.61	-15.81
-25.00	-16.80	-16.61	-16.82
-26.00	-17.80	-17.61	-17.83

-27.00	-18.80	-18.61	-18.84
-28.00	-19.80	-19.61	-19.85

Method 1:

$\delta^{13}C_{(enamel)} = \delta^{13}C_{(hair\ or\ collagen)} + \Delta\ (\Delta = \delta^{13}C_{(enamel)} - \delta^{13}C_{(hair)})$ or $(\delta^{13}C_{(enamel)} - \delta^{13}C_{(collagen)})$

Method 2:

$\delta^{13}C_{(enamel)} = \delta^{13}C_{(hair\ or\ collagen)} + \varepsilon^*$

Method 3:

$\delta^{13}C_{(enamel)} = (\alpha^*)^* (\delta^{13}C_{(hair\ or\ collagen)} + 1000) - 1000$

Table A2.6. Example demonstrating the significance of using α and ε* to calculate enrichment factor instead of Δ*

$\delta^{13}C$ hair	**$\delta^{13}C$ enamel**	**$\alpha^*_{\text{enamel-hair}} = (\delta^{13}C_{\text{enamel}} + 1000) / (\delta^{13}C_{\text{hair}} + 1000)$**	**$\varepsilon^*_{\text{enamel-hair}}$ ε*=(alpha*-1)*1000**	**$\Delta = \delta^{13}C_{\text{(enamel)}} - \delta^{13}C_{\text{(hair)}}$**
-22.37	-14.17	1.0084	8.39	8.20

Δ refers to absolute difference between $\delta^{13}C$ enamel and $\delta^{13}C$ hair.

Data from Kahuzi-Biega gorillas.

A3. AFRICAN GREAT APES DATABASE (COMPRESSED VERSION)

KEY

Column Labels	**Location**	**Sample Type**
Sam Number – Sample Number **Loc** – Location **Sam** – Sample Type **R Val** – Raw Values **N Val** – Normalized Values **F Yr** – Fomation Year **δ^{13}C Atmos – 6.5** - δ^{13}C Atmosphere minus 6.5‰ (- 6.5‰ is the preindustrial δ^{13}C atmosphere average value) **Cor Val** – Corrected Values	**Gant** – Ganta **Fong** – Fongoli **Ugal** – Ugalla **Isha** – Ishasha **Kib** – Kibale **Salo** – Salonga **Kah-B** – Kahuzi Biega **Itom** – Itombwe	**E** – Enamel **D** – Dentine **B** – Bone **H** – Hair **M** – Molar **C** – Canine **P** – Premolar

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
48-36-50/N6941.0	Gant	E M3	-15.6	-15.6	-0.23	-15.37	Smith et al., 2010
48-36-50/N6956.0	Gant	E M3	-16.5	-16.5	-0.23	-16.27	Smith et al., 2010
48-36-50/N6966.0	Gant	E M3	-15.1	-15.1	-0.23	-14.87	Smith et al., 2010
48-36-50/N7002.0	Gant	E M3	-16.9	-16.9	-0.23	-16.67	Smith et al., 2010
48-36-50/N7003.0	Gant	E M3	-16.2	-16.2	-0.23	-15.97	Smith et al., 2010
48-36-50/N7007.0	Gant	E M3	-17	-17	-0.23	-16.77	Smith et al., 2010
48-36-50/N7012.0	Gant	E M3	-16.4	-16.4	-0.23	-16.17	Smith et al., 2010
48-36-50/N7018.0	Gant	E M3	-16.8	-16.8	-0.23	-16.57	Smith et al., 2010
48-36-50/N7028.0	Gant	E M3	-16.2	-16.2	-0.23	-15.97	Smith et al., 2010
48-36-50/N7037.0	Gant	E M3	-15.5	-15.5	-0.23	-15.27	Smith et al., 2010
48-36-50/N7104.0	Gant	E M3	-15.9	-15.9	-0.23	-15.67	Smith et al., 2010
48-36-50/N7107.0	Gant	E M3	-16.1	-16.1	-0.23	-15.87	Smith et al., 2010

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
50-41-50/N7258.0	Gant	E M3	-15.6	-15.6	-0.23	-15.37	Smith et al., 2010
00-0-50/N7563.0	Gant	E M3	-14	-14	-0.23	-13.77	Smith et al., 2010
48-36-50/N6906.0	Gant	E M3	-18.2	-18.2	-0.23	-17.97	Smith et al., 2010
48-36-50/N6907.0	Gant	E M3	-17.1	-17.1	-0.23	-16.87	Smith et al., 2010
48-36-50/N6937.0	Gant	E M3	-16.4	-16.4	-0.23	-16.17	Smith et al., 2010
48-36-50/N6969.0	Gant	E M3	-16.8	-16.8	-0.23	-16.57	Smith et al., 2010
48-36-50/N6981.0	Gant	E M3	-16.6	-16.6	-0.23	-16.37	Smith et al., 2010
48-36-50/N7006.0	Gant	E M3	-16.3	-16.3	-0.23	-16.07	Smith et al., 2010
48-36-50/N7040.0	Gant	E M3	-16.9	-16.9	-0.23	-16.67	Smith et al., 2010
48-36-50/N7056.0	Gant	E M3	-16.4	-16.4	-0.23	-16.17	Smith et al., 2010
48-36-50/N7069.0	Gant	E M3	-17.7	-17.7	-0.23	-17.47	Smith et al., 2010
48-36-50/N7079.0	Gant	E M3	-16.1	-16.1	-0.23	-15.87	Smith et al., 2010

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
48-36-50/N7085.0	Gant	E M3	-15.7	-15.7	-0.23	-15.47	Smith et al., 2010
48-36-50/N7089.0	Gant	E M3	-14.4	-14.4	-0.23	-14.17	Smith et al., 2010
48-36-50/N7103.0	Gant	E M3	-15	-15	-0.23	-14.77	Smith et al., 2010
50-41-50/N7257.0	Gant	E M3	-16	-16	-0.23	-15.77	Smith et al., 2010
50-41-50/N7260.0	Gant	E M3	-16.1	-16.1	-0.23	-15.87	Smith et al., 2010
50-41-50/N7291.0	Gant	E M3	-15.6	-15.6	-0.23	-15.37	Smith et al., 2010
4540	Ugal	H	-22.2	-13.99	-1.32	-12.67	Schoeninger et al., 1999
4357	Ugal	H	-22.2	-13.99	-1.32	-12.67	Schoeninger et al., 1999
4535	Ugal	H	-22.1	-13.89	-1.32	-12.57	Schoeninger et al., 1999
4534	Ugal	H	-22.2	-13.99	-1.32	-12.67	Schoeninger et al., 1999
4537	Ugal	H	-21.8	-13.59	-1.32	-12.27	Schoeninger et al., 1999
4536	Ugal	H	-22.2	-13.99	-1.32	-12.67	Schoeninger et al., 1999

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
4533	Ugal	H	-21.7	-13.49	-1.32	-12.17	Schoeninger et al., 1999
4539	Ugal	H	-21.7	-13.49	-1.32	-12.17	Schoeninger et al., 1999
4356	Ugal	H	-22.3	-14.09	-1.32	-12.77	Schoeninger et al., 1999
4532	Ugal	H	-21.6	-13.39	-1.32	-12.07	Schoeninger et al., 1999
4538	Ugal	H	-21.6	-13.39	-1.32	-12.07	Schoeninger et al., 1999
4542	Ugal	H	-22	-13.79	-1.32	-12.47	Schoeninger et al., 1999
4062	Isha	H	-22.6	-14.39	-1.32	-13.07	Schoeninger et al., 1999
4055	Isha	H	-23.4	-15.2	-1.32	-13.88	Schoeninger et al., 1999
4060	Isha	H	-23	-14.8	-1.32	-13.48	Schoeninger et al., 1999
4347	Isha	H	-23.1	-14.9	-1.32	-13.58	Schoeninger et al., 1999
4061	Isha	H	-22.7	-14.5	-1.32	-13.18	Schoeninger et al., 1999
4346	Isha	H	-23.4	-15.2	-1.32	-13.88	Schoeninger et al., 1999

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
4350	Isha	H	-23.2	-15	-1.32	-13.68	Schoeninger et al., 1999
4348	Isha	H	-23.1	-14.9	-1.32	-13.58	Schoeninger et al., 1999
4345	Isha	H	-23.4	-15.2	-1.32	-13.88	Schoeninger et al., 1999
4349	Isha	H	-22.9	-14.7	-1.32	-13.38	Schoeninger et al., 1999
FOC 1	Fong	H	-22.6	-14.39	-1.49	-12.9	Sponheimer et al., 2006a
FOC 2	Fong	H	-22.2	-13.99	-1.49	-12.5	Sponheimer et al., 2006a
FOC 3	Fong	H	-21.9	-13.69	-1.49	-12.2	Sponheimer et al., 2006a
FOC 4	Fong	H	-22.1	-13.89	-1.49	-12.4	Sponheimer et al., 2006a
FOC 5	Fong	H	-21.8	-13.59	-1.49	-12.1	Sponheimer et al., 2006a
FOC 6	Fong	H	-21.9	-13.69	-1.49	-12.2	Sponheimer et al., 2006a
FOC 7	Fong	H	-22	-13.79	-1.49	-12.3	Sponheimer et al., 2006a
FOC 8	Fong	H	-21.7	-13.49	-1.49	-12	Sponheimer et al., 2006a

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
FOC 9	Fong	H	-22.3	-14.09	-1.49	-12.6	Sponheimer et al., 2006a
FOC 10	Fong	H	-22	-13.79	-1.49	-12.3	Sponheimer et al., 2006a
FOC 11	Fong	H	-22	-13.79	-1.49	-12.3	Sponheimer et al., 2006a
FOC 12	Fong	H	-21.7	-13.49	-1.49	-12	Sponheimer et al., 2006a
FOC 13	Fong	H	-23	-14.8	-1.49	-13.31	Sponheimer et al., 2006a
FOC 14	Fong	H	-22.5	-14.29	-1.49	-12.8	Sponheimer et al., 2006a
FOC 15	Fong	H	-22.5	-14.29	-1.49	-12.8	Sponheimer et al., 2006a
FOC 17	Fong	H	-22.2	-13.99	-1.49	-12.5	Sponheimer et al., 2006a
FOC 18	Fong	H	-22.4	-14.19	-1.49	-12.7	Sponheimer et al., 2006a
FOC 19	Fong	H	-22.2	-13.99	-1.49	-12.5	Sponheimer et al., 2006a
FOC 20	Fong	H	-22.5	-14.29	-1.49	-12.8	Sponheimer et al., 2006a
FOC 21	Fong	H	-22.5	-14.29	-1.49	-12.8	Sponheimer et al., 2006a

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
FOC 22	Fong	H	-22.6	-14.39	-1.49	-12.9	Sponheimer et al., 2006a
FOC 23	Fong	H	-22.8	-14.6	-1.49	-13.11	Sponheimer et al., 2006a
FOC 24	Fong	H	-22.3	-14.09	-1.49	-12.6	Sponheimer et al., 2006a
FOC 25	Fong	H	-22.7	-14.5	-1.49	-13.01	Sponheimer et al., 2006a
FOC 26	Fong	H	-22.6	-14.39	-1.49	-12.9	Sponheimer et al., 2006a
FOC 27	Fong	H	-22.5	-14.29	-1.49	-12.8	Sponheimer et al., 2006a
FOC 28	Fong	H	-22.1	-13.89	-1.49	-12.4	Sponheimer et al., 2006a
FOC 29	Fong	H	-21.4	-13.18	-1.49	-11.69	Sponheimer et al., 2006a
FOC 30	Fong	H	-21.8	-13.59	-1.49	-12.1	Sponheimer et al., 2006a
FOC 31	Fong	H	-22	-13.79	-1.49	-12.3	Sponheimer et al., 2006a
FOC 33	Fong	H	-23.1	-14.9	-1.49	-13.41	Sponheimer et al., 2006a
FOC 34	Fong	H	-21.7	-13.49	-1.49	-12	Sponheimer et al., 2006a

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
FOC 35	Fong	H	-22.1	-13.89	-1.49	-12.4	Sponheimer et al., 2006a
FOC 36	Fong	H	-21.5	-13.29	-1.49	-11.8	Sponheimer et al., 2006a
FOC 37	Fong	H	-22.1	-13.89	-1.49	-12.4	Sponheimer et al., 2006a
FOC 39	Fong	H	-22.7	-14.5	-1.56	-12.94	Sponheimer et al., 2006a
KFB 17/ K2B	Kib	B	-21.99	-14.1	-1.16	-12.94	Carter, 2001
KFB 105/ K4B	Kib	B	-21.83	-13.94	-1.24	-12.71	Carter, 2001
KFB/106/ K5B	Kib	B	-22.51	-14.63	-1.24	-13.39	Carter, 2001
KFB 18/ K6B	Kib	B	-21.31	-13.42	-1.16	-12.26	Carter, 2001
KFB 20/ K7B	Kib	B	-21.65	-13.76	-1.16	-12.6	Carter, 2001
KFB 1/ K55B	Kib	B	-21.09	-13.2	-1.16	-12.04	Carter, 2001
KFB 4/ K59B	Kib	B	-21.69	-13.8	-1.16	-12.64	Carter, 2001
KFB 107/ K1B	Kib	B	-21.68	-13.79	-1.24	-12.55	Carter, 2001

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
LP2370	Kah-B	H	-21.37	-13.15	-0.42	-12.73	Cerling et al., unpublished
Chi Be 001D	Kah-B	D	-22.3	-14.42	-1.45	-12.97	Cerling et al., unpublished
VN 015B	Kah-B	B	-25.22	-17.36	-1.49	-15.87	Cerling et al., unpublished
Number not assigned	Kah-B	E	-15.32	-15.32	-1.45	-13.87	Cerling et al., unpublished
13504A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13504B	Salo	H	-26.7	-18.53	-1.67	-16.86	Oelze et al., 2011
13405A	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13405B	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
14098A	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
14098B	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13506A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13506B	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
13507A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13507B	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
14100A	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
14100B	Salo	H	-26.1	-17.92	-1.67	-16.25	Oelze et al., 2011
13508A	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
13508B	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13509A	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13509B	Salo	H	-26.4	-18.23	-1.67	-16.56	Oelze et al., 2011
14097A	Salo	H	-25.4	-17.22	-1.67	-15.55	Oelze et al., 2011
13510A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13510B	Salo	H	-26.3	-18.13	-1.67	-16.46	Oelze et al., 2011
12577A	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
12577B	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13511A	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13512A	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13512B	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13513A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13513B	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13514A	Salo	H	-26.2	-18.03	-1.67	-16.36	Oelze et al., 2011
13515A	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13516A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13516B	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13517/18A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13517/18B	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
13517/18C	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13518A	Salo	H	-25.2	-17.02	-1.67	-15.35	Oelze et al., 2011
13518B	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13518C	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13518D	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
14099A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
14099B	Salo	H	-26.1	-17.92	-1.67	-16.25	Oelze et al., 2011
14099C	Salo	H	-26.1	-17.92	-1.67	-16.25	Oelze et al., 2011
14099D	Salo	H	-26.4	-18.23	-1.67	-16.56	Oelze et al., 2011
12580A	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
12580B	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13520A	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
13520B	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13521A	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
13521B	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13521C	Salo	H	-26.3	-18.13	-1.67	-16.46	Oelze et al., 2011
13519A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
12579A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
12579B	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13522A	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
13522B	Salo	H	-25.2	-17.02	-1.67	-15.35	Oelze et al., 2011
12578A	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
12578B	Salo	H	-26.4	-18.23	-1.67	-16.56	Oelze et al., 2011
13523A	Salo	H	-25.2	-17.02	-1.67	-15.35	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
13523B	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13525A	Salo	H	-25.4	-17.22	-1.67	-15.55	Oelze et al., 2011
13525B	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13526A	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
13527A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13527B	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
14096B	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
14096C	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
12573A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
12573B	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
12573C	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
12574	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
13529A	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13529B	Salo	H	-26.3	-18.13	-1.67	-16.46	Oelze et al., 2011
13530A	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13530B	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13531A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13531B	Salo	H	-25.4	-17.22	-1.67	-15.55	Oelze et al., 2011
13532A	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13532B	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13532C	Salo	H	-26.2	-18.03	-1.67	-16.36	Oelze et al., 2011
13532D	Salo	H	-26.2	-18.03	-1.67	-16.36	Oelze et al., 2011
14101A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
14101B	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
14101C	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13533A	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
13533B	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13533C	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13534A	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13534B	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
13535A	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13525B	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13535C	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
13535D	Salo	H	-26.2	-18.03	-1.67	-16.36	Oelze et al., 2011
13535E	Salo	H	-26.2	-18.03	-1.67	-16.36	Oelze et al., 2011
13536A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011

					$\delta^{13}C$		
			R	N	Atmos	Cor	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
13536B	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
12575	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13537A	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
13537B	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
13538A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13538B	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13538C	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
13538D	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13538E	Salo	H	-26.3	-18.13	-1.67	-16.46	Oelze et al., 2011
13539A	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
13539B	Salo	H	-25.4	-17.22	-1.67	-15.55	Oelze et al., 2011
13540A	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
13540B	Salo	H	-25.6	-17.42	-1.67	-15.75	Oelze et al., 2011
13541A	Salo	H	-25.4	-17.22	-1.67	-15.55	Oelze et al., 2011
13541B	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13541C	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13541D	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
13542/43A	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
13542/43B	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13542/43C	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13542/43D	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13542/43E	Salo	H	-26.1	-17.92	-1.67	-16.25	Oelze et al., 2011
12581A	Salo	H	-26	-17.82	-1.67	-16.15	Oelze et al., 2011
12581B	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
12581C	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
12581E	Salo	H	-26.1	-17.92	-1.67	-16.25	Oelze et al., 2011
12582A	Salo	H	-26.3	-18.13	-1.67	-16.46	Oelze et al., 2011
12582B	Salo	H	-26.2	-18.03	-1.67	-16.36	Oelze et al., 2011
13544A	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
13544B	Salo	H	-26.1	-17.92	-1.67	-16.25	Oelze et al., 2011
13545A	Salo	H	-26.1	-17.92	-1.67	-16.25	Oelze et al., 2011
13545B	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13546A	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13546B	Salo	H	-25.8	-17.62	-1.67	-15.95	Oelze et al., 2011
13547A	Salo	H	-25.2	-17.02	-1.67	-15.35	Oelze et al., 2011
13547B	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
13548A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13549A	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
13549B	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
13549C	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
13549D	Salo	H	-25.9	-17.72	-1.67	-16.05	Oelze et al., 2011
13550A	Salo	H	-26.3	-18.13	-1.67	-16.46	Oelze et al., 2011
13550B	Salo	H	-26.1	-17.92	-1.67	-16.25	Oelze et al., 2011
13551A	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
13551B	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
14102A	Salo	H	-25.4	-17.22	-1.67	-15.55	Oelze et al., 2011
14102B	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
14103A	Salo	H	-25.2	-17.02	-1.67	-15.35	Oelze et al., 2011

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
14103B	Salo	H	-25.3	-17.12	-1.67	-15.45	Oelze et al., 2011
14103C	Salo	H	-25.5	-17.32	-1.67	-15.65	Oelze et al., 2011
14104A	Salo	H	-25.7	-17.52	-1.67	-15.85	Oelze et al., 2011
Gor_KB_002 H	Kah-B	H	-23.7	-15.5	-1.66	-13.84	Cerling et al., unpublished
Gor_KB_003 H	Kah-B	H	-24.4	-16.21	-1.66	-14.55	Cerling et al., unpublished
Gor_KB_004 H	Kah-B	H	-23.5	-15.3	-1.66	-13.64	Cerling et al., unpublished
Gor_KB_005 H	Kah-B	H	-23.3	-15.1	-1.66	-13.44	Cerling et al., unpublished
Gor_KB_006 H	Kah-B	H	-23.6	-15.4	-1.66	-13.74	Cerling et al., unpublished
Gor_KB_007 H	Kah-B	H	-24.2	-16.01	-1.66	-14.35	Cerling et al., unpublished
Gor_KB_008 H	Kah-B	H	-23.8	-15.6	-1.66	-13.94	Cerling et al., unpublished
Gor_KB_009 H	Kah-B	H	-24.6	-16.41	-1.66	-14.75	Cerling et al., unpublished
Gor_KB_010 H	Kah-B	H	-24.7	-16.51	-1.66	-14.85	Cerling et al., unpublished

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
Gor_KB_011 H	Kah-B	H	-24.7	-16.51	-1.66	-14.85	Cerling et al., unpublished
Gor_KB_012 H	Kah-B	H	-24.6	-16.41	-1.66	-14.75	Cerling et al., unpublished
Gor_KB_070 H	Kah-B	H	-23.1	-14.9	-1.5	-13.4	Cerling et al., unpublished
ICCN KB 064	Kah-B	E M1	-16.8	-16.8	-1.27	-15.53	Cerling et al., unpublished
ICCN KB 065	Kah-B	E M1	-17.8	-17.8	-1.15	-16.65	Cerling et al., unpublished
ICCN KB 066	Kah-B	E M3	-14	-14	-0.76	-13.24	Cerling et al., unpublished
ICCN KB 070	Kah-B	E M3	-15.1	-15.1	-1.26	-13.84	Cerling et al., unpublished
ICCN KB 071 B	Kah-B	B	-24.8	-16.94	-1.27	-15.67	Cerling et al., unpublished
ICCN KB 076	Kah-B	D M2	-22.3	-14.42	-1.27	-13.15	Cerling et al., unpublished
ICCN KB 078 m1	Kah-B	E m1	-15.9	-15.9	-1.16	-14.74	Cerling et al., unpublished
ICCN KB 078 m2	Kah-B	Em2	-14.1	-14.1	-1.16	-12.94	Cerling et al., unpublished
ICCN KB 087	Kah-B	Dm3	-22.3	-14.42	-1.27	-13.15	Cerling et al., unpublished

					$\delta^{13}C$		
			R	**N**	**Atmos**	**Cor**	
Sam Number	**Loc**	**Sam**	**Val**	**Val**	**- 6.5‰**	**Val**	**Reference**
ICCN KB 088	Kah-B	Em2	-14.2	-14.2	-1.16	-13.04	Cerling et al., unpublished
ICCN KB 089	Kah-B	E m3	-14.9	-14.9	-1.16	-13.74	Cerling et al., unpublished
ICZN 022	Itom	E P4	-14.8	-14.8	-1.16	-13.64	Cerling et al., unpublished
IZCN 040	Itom	E M3	-13.3	-13.3	-1.16	-12.14	Cerling et al., unpublished
ICZN 074	Itom	E m3	-13	-13	-1.16	-11.84	Cerling et al., unpublished
ICZN 075	Itom	E C	-14.3	-14.3	-1.16	-13.14	Cerling et al., unpublished
IZCN 075	Itom	E M2	-14.4	-14.4	-1.16	-13.24	Cerling et al., unpublished
ICZN 076	Itom	E M2	-15.5	-15.5	-1.16	-14.34	Cerling et al., unpublished

A4. ANOVA RESULTS BY TAXA

The ANOVA compares the means of the refined $\delta^{13}C$ signature values across the levels of the categorical predictor variable (for example, genus or species) (Dean and Voss, 2000; Moore and McCabe, 2007). If the differences are large enough compared to the variability of the responses within each level of the categorical predictor variable, then the difference is considered statistically significant. The results of an ANOVA are often presented as ANOVA tables. The determination of statistical significance for ANOVA is based on a calculated F-statistic, which results in a P-value. The P-value for the analysis can be defined as the probability that a population with no differences among the taxonomic categories would produce differences as large as or larger than the differences found in the chosen random sample. If that probability is very small, typically less than 0.05 (5%), then we determine that it is not likely that the sample came from a population with no differences between the taxonomic categories, and it is therefore likely that there are differences between the taxonomic categories in the population. Additional statistics calculated by ANOVA include the R-square statistics, which ranges from 0 to 1 and indicates the proportion of variation in the response that can be ‘‘explained’’ by the predictor variable, and the RMSE, which can be considered the ‘‘typical error’’ one might encounter when trying to predict the response with the predictor variable. The following paragraph uses table A4.1 to explain the ANOVA terminologies.

Among the 272 refined $\delta^{13}C$ values, differences exist. Some of these differences are due to the genera of the individuals, and some differences will be due to other reasons (Table A4.1). Because this thesis is not accounting for the other reasons in this particular model, the combination of all of those other reasons are called "error" (every model has some error, as we can never account for all of the reasons individuals might vary from one another). The total sum of squares measures the total variability among the individuals. In table A4.2, the Genus Sum of Squares and the Error Sum of Squares add up to the total Sum of Squares (29.46 + 596.32 = 625.78). The Sum of Squares for Genus is the part of that total variability that is due to the differences between the two genera, and the Sum of Squares for Error is a measure of how much the individuals vary from the average for their genera (and therefore is variability for reasons other than genera). The R-square, which is the proportion of variability explained by Genus, is simply 29.46/625.78. The mean squares for Genus is the sum of squares divided by the Genus degrees of freedom (DF = 1) and the mean square for error is the sum of squares divided by the error degrees of freedom (DF = 270). After dividing, if Genus doesn't explain any significant variability in the individuals, then the mean square for Genus and the mean square for error should be approximately equal. The F-statistic is the mean square for Genus, divided by the mean square for error, if the two mean squares are equal, this will be about 1.

Table A4.1. ANOVA results for predicting genus with refined $\delta^{13}C$ values

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value	R-Square	Root MSE
Genus	1	29.46	29.46	13.34	0.0003	0.0471	1.4861
Error	270	596.32	2.21				
Corrected Total	271	625.78					

Table A4.2. ANOVA results for predicting species with refined $\delta^{13}C$ values

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value	R-Square	Root MSE
Species	2	315.95	157.97	137.15	<.0001	0.5049	1.0732
Error	269	309.84	1.15				
Corrected Total	271	625.78					

Table A4.3. Pairwise comparison of refined $\delta^{13}C$ values by species

Comparisons significant at the 0.05 level are indicated by ***

Species Comparison	Difference Between Means	95% Confidence Limits Lower	Upper	
P. troglodytes – G. beringei	0.23	-0.2136	0.6777	
P. troglodytes – P. paniscus	2.21	1.931	2.4819	***
G. beringei – P. paniscus	1.97	1.5441	2.4047	***

Table A4.4. ANOVA results for predicting subspecies with refined $\delta^{13}C$ values

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value	R-Square	Root MSE
Subspecies	3	342.80	114.27	108.22	<.0001	0.5478	1.0276
Error	268	282.99	1.06				
Corrected Total	271	625.78					

Table A4.5. Pairwise comparison of refined $\delta^{13}C$ values

Comparisons significant at the 0.05 level are indicated by ***

Subspecies Comparisons	Difference Between Means	95% Confidence Limits Lower	Upper	
P. t. schweinfurthii – G. b. graueri	0.95	0.4426	1.4654	***
P. t. schweinfurthii – P. t. verus	1.09	0.6668	1.5209	***
P. t. schweinfurthii – P. paniscus	2.93	2.5423	3.3144	***
G. b. graueri – P. t. verus	0.14	-0.3108	0.5906	
G. b. graueri – P. paniscus (no subspecies)	1.97	1.5624	2.3864	***
P. t. verus – P. paniscus (no subspecies)	1.83	1.5334	2.1356	***

A5. ANOVA RESULTS FOR PREDICTING LOCATION WITH REFINED $\delta^{13}C$ VALUES

Table A5.1. ANOVA results for predicting location

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value	R-Square	Root MSE
Location	7	550.42	78.63	275.46	<.0001	0.8796	0.5343
Error	264	75.36	0.29				
Corrected Total	271	625.78					

Table A5.2. Pairwise comparison of refined $\delta^{13}C$ values by location

Comparisons significant at the 0.05 level are indicated by ***

Location Comparison	Difference Between Means	95% Confidence Limits Lower	Upper	
Ugalla - Fongoli	0.09	-0.2649	0.4364	
Ugalla - Kibale	0.20	-0.2766	0.6837	
Ugalla - Itombwe	0.62	0.0945	1.1465	***
Ugalla - Ishasha	1.12	0.6722	1.5731	***
Ugalla - Kahuzi-Beiga	1.68	1.3186	2.0486	***
Ugalla - Salonga	3.47	3.1577	3.7901	***
Ugalla - Ganta	3.50	3.1445	3.8631	***
Fongoli - Kibale	0.12	-0.2934	0.5290	
Fongoli - Itombwe	0.53	0.0708	0.9986	***
Fongoli - Ishasha	1.04	0.6609	1.4130	***

Fongoli - Kahuzi-Beiga	1.60	1.3300	1.8656	***
Fongoli - Salonga	3.39	3.1920	3.5843	***
Fongoli - Ganta	3.42	3.1580	3.6781	***
Kibale - Itombwe	0.42	-0.1513	0.9850	
Kibale - Ishasha	0.92	0.4201	1.4181	***
Kibale - Kahuzi-Beiga	1.48	1.0565	1.9035	***
Kibale - Salonga	3.27	2.8881	3.6525	***
Kibale - Ganta	3.30	2.8816	3.7188	***
Itombwe - Ishasha	0.50	-0.0410	1.0455	
Itombwe - Kahuzi-Beiga	1.06	0.5883	1.5379	***
Itombwe - Salonga	2.85	2.4151	3.2918	***
Itombwe - Ganta	2.88	2.4129	3.3538	***
Ishasha - Kahuzi-Beiga	0.56	0.1715	0.9503	***
Ishasha - Salonga	2.35	2.0071	2.6953	***
Ishasha - Ganta	2.38	1.9970	2.7653	***

Kahuzi-Beiga - Salonga	1.79	1.5696	2.0111	***
Kahuzi-Beiga - Ganta	1.82	1.5412	2.0993	***
Salonga - Ganta	0.03	-0.1814	0.2412	

Table A5.3. ANOVA results for predicting location with refined $\delta^{13}C$ values for G. b. graueri only

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value	R-Square	Root MSE
Location	1	5.85	5.85	6.45	0.0172	0.1927	0.9523
Error	27	24.49	0.91				
Corrected Total	28	30.33					

Table A5.4. ANOVA results for predicting location with refined $\delta^{13}C$ values for P. t. verus only

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value	R-Square	Root MSE
Location	1	191.18	191.18	431.41	<.0001	0.8708	0.6657
Error	64	28.36	0.44				
Corrected Total	65	219.54					

Table A5.5. Results for predicting location with refined $\delta^{13}C$ values for P. t. schweinfurthii only

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value	R-Square	Root MSE
Location	3	10.92	3.64	12.37	<.0001	0.5530	0.5424
Error	30	8.83	0.29				
Corrected Total	33	19.75					

Table A5.6. Pairwise comparison of refined $\delta^{13}C$ values by location for P. t. schweinfurthii

Comparisons significant at the 0.05 level are indicated by ***.

Location Comparisons	Difference Between Means	95% Confidence Limits Lower	Upper	
Ugalla – Kibale	0.20	-0.3020	0.7092	
Ugalla - Ishasha	1.12	0.6484	1.5970	***
Ugalla - Kahuzi-Beiga	1.42	0.7838	2.0629	***
Kibale - Ishasha	0.92	0.3937	1.4446	***
Kibale - Kahuzi-Beiga	1.22	0.5414	1.8981	***
Ishasha - Kahuzi-Beiga	0.30	-0.3547	0.9560	

Table A5.7. ANOVA results for predicting location with refined $\delta^{13}C$ values for G. b. graueri and P. t. schweinfurthii from Kahuzi-Biega only

Source	DF	Sum of Squares	Mean Square	F-Value	P-Value	R-Square	Root MSE
Genus	1	0.32	0.32	0.30	0.5869	0.0120	1.0245
Error	25	26.24	1.05				
Corrected Total	26	26.56					