East African Miocene Catarrhine Evolutionary Ecology

by

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Abstract

This dissertation assesses how East African Miocene catarrhines changed adaptively within their environments from the early to middle Miocene. This period records an important transition in catarrhine evolution that is relevant to the interpretation of later hominoid and hominin radiations. The adaptive and community restructuring of catarrhines from ~21-15 mya is posited to be associated with a shift from closed/forested habitats to more open/seasonal woodlands. However, the nature of catarrhine adaptive features and whether they reflect a response to environmental change is unclear. An analysis of the same dietary, locomotor, and environmental proxies across multiple fossil localities was conducted. This dissertation has three components.

First, herbivore enamel from the middle Miocene localities of Maboko and Kipsaramon was analyzed for $\delta^{13}C$ values. These fossil enamel $\delta^{13}C$ values are compared to enamel $\delta^{13}C$ values from modern African herbivores to reconstruct feeding ecology and infer habitats of a sample of middle Miocene mammals. Fossil enamel $\delta^{13}C$ values reflect a variable landscape of C_3 dominated open forests/woodlands at Maboko and possibly drier and open woodland with significant amounts of C_4 biomass at Kipsaramon.

Second, non-cercopithecoid catarrhine dietary change is assessed across eight early and middle Miocene localities using molar shear quotients (SQs). Patterns of SQ value changes is evaluated against an environmental backdrop of herbivore enamel $\delta^{13}C$ values from each fossil locality. The range of SQ values increases from the early to the middle Miocene, suggesting a possible increase in dietary diversity among middle Miocene catarrhines. This increase is driven

by a decrease in molar shear crest development in large bodied hominoids and an increase shear crest development among nyanzapithecines. The range of variation in fossil enamel $\delta^{13}C$ values also increased from the early to the middle Miocene. Thus, there appears to be an association between variation in herbivore feeding ecology and catarrhine diet through time. Early Miocene enamel $\delta^{13}C$ values indicate a mosaic of C_3 dominated open forest and woodland habitats, while middle Miocene sites include C_4 biomass. Overall, enamel $\delta^{13}C$ values do not support a shift from closed canopied forests to open forest and woodland habitats, contra previous environmental reconstructions.

Lastly, the postcranial functional diversity of early and middle Miocene catarrhines was examined by quantifying intermediate phalangeal morphology. The relative length and curvature of 20 fossil phalanges from five early and middle Miocene sites were compared to the relative length and curvature of 30 extant anthropoid taxa of known positional behavior. Phalange relative length and curvature indicate an increase in morphological diversity, and possibly positional behavioral diversity, through time. This pattern echoes the increase in dietary diversity among middle Miocene catarrhines documented in the previous chapter.

The molar and phalangeal morphological evidence suggests greater dietary and locomotor specialization in the middle Miocene of East Africa relative to the early Miocene. This study does not find evidence for a broad scale shift from closed to more open habitats as a driver of this adaptive expansion, however. Environmental reconstructions for primate rich localities using enamel $\delta^{13}C$ values as a proxy for vegetation instead finds evidence for open forest and woodland habitats throughout the early and middle Miocene, but with a broadening of habitat heterogeneity through time. Future studies should continue to characterize habitats and their primate communities at a regional scale to better understand the ecological underpinnings of catarrhine evolution.

Chapter 1

Introduction

Except for humans, modern hominoids (apes and humans) are restricted to mostly forested environments in Africa and Asia and their species diversity pales in comparison to the Old-World monkeys. During the early Miocene, fossil apes were much more diverse with upwards of approximately 20 species (Harrison, 2010). This high ape diversity likely extended well into the middle Miocene (Harrison, 1992).

Understanding how modern apes came to evolve their current dietary and locomotor adaptations requires an appreciation of their paleoecology (diet, locomotion, and environments) during the Miocene, paricularly in Africa after the initial radiation in the early Miocene. A putative transition from tropical, closed canopied forests to more open woodland habitats during the early-middle Miocene (~17-14 Ma) transition has been hypothesized to have had a profound influence on shaping modern catarrhine communities in Africa (e.g. Andrews & Van Couvering, 1975; Andrews, 1981, 2015; Pickford, 1983; Andrews et al., 1997; Benefit, 1999a,b; Andrews & Kelley, 2007). This change in vegetation is interpreted to reflect a response to changes in regional climatic conditions from the early to the middle Miocene (Andrews and Van Couvering, 1975; Pickford, 1983; Jacobs et al., 2010). Changing environmental conditions appears to be associated with the extinction of numerous primitive catarrhines and the diversification of the earliest cercopithecoids and more advanced hominoids. While there has been a wealth of research on the adaptations of early Miocene catarrhines, the environmental context going from the early to the middle Miocene is less well understood due to a paucity of comparable environmental data throughout the early and middle Miocene (Andrews and Kelley, 2007). The aim of this dissertation is to chronicle the dietary and locomotor specializations of East African early and middle Miocene catarrhines and their associated paleoenvironments to determine whether adaptive and environmental change occurred in tandem through time.

Knowledge of catarrhine habitats is critical for understanding their dietary and locomotor adaptations and distribution across time and space. The localities included in this dissertation span across three regions of East Africa (eastern Uganda, the Turkana Basin (northern Kenya) and western Kenya), and represent a temporal succession from early Miocene, late early Miocene, and the early Middle Miocene (Figure 1). These sites yielded multiple catarrhine taxa, including stem hominoids (proconsuloids), stem catarrhines (dendropithecoids), and early cercopithecoids (Harrison, 2010b). During the early Miocene (23-16 mya), proconsuloids and dendropithecoids were diverse and apparently restricted to tropical forests and woodlands (Andrews and Van Couvering, 1975; Andrews). A purported shift in East African primate communities is documented between 17 and 14 million years ago, characterized by 1) a decline in abundance and diversity of the primitive and thin-enameled proconsuloids and dendropithecoids; 2) the appearance of thick-enameled hominoids with novel dietary and locomotor adaptations (McCrossin, 1994,); 3) an increase in abundance of victoriapithecid cercopithecoids (McCrossin et al., 1998; Benefit, 1999a,b; Miller et al, 2009). It has been suggested that these changes in the catarrhine community occurred as the habitat became more open, drier, and seasonal (refs needed).

Previous studies investigating the dietary and locomotor adaptations of African early and middle Miocene catarrhines have several limitations (e.g. Kay, 1977; Kay & Ungar; 1997;

Rose, 1988, 1989; Ward, 1993, 1997; Sanders & Bodenbender, 1994; MacLatchy et al, 2000; Shearer et al., 2015). First, studies of postcranial anatomy have tended to be restricted to just a few specimens or individuals, and are most often based on partial skeletons associated with craniodental remains (e.g. Napier and Davis, 1959; Walker and Pickford, 1983; Ward, 1993, 1997, 1998; Ward et al., 1993, 1999; Rose et al., 1992). Few studies consider unassociated postcranial elements not assigned to a species (Harrison, 1982; Rose, 1988; Rose et al., 1992; Wuthrich, 2019). Second, dietary and locomotor adaptations from African middle Miocene catarrhines have not been directly and quantitatively compared to those of early Miocene taxa, which limits insights into adaptive changes between the early and middle Miocene. Likewise, speculation about environmental change is based on limited data using multiple methods (Andrews & Kelley, 2007), not on comparable ecological data from multiple localities. These limitations will be addressed in this dissertation by integrating systematically applied behavioral and environmental proxies at eight East African early and middle Miocene localities to address the following research questions:

1. How do catarrhine dietary and locomotor diversity change from the early to the middle Miocene?
2. How did local paleoenvironments vary between early and middle Miocene localities in East Africa?

Chapter 2 presents stable isotopic results from two Kenyan fossil localities dated to the middle Miocene. The paleoenvironments of Maboko (>14.7 to 13.8 Ma; Feibel and Brown, 1991) and Kipsaramon (15.8-15.4 Ma; Behrensmeyer et al., 2002) are inferred by comparing enamel $\delta^{13}C$ values from a sample of fossil mammalian fauna from both localities to published enamel $\delta^{13}C$ values of modern herbivorous mammalian lineages (Cerling et al., 2015). Maboko and Kipsaramon $\delta^{13}C$ values are also compared to published $\delta^{13}C$ values from the middle Miocene locality of Fort Ternan (Cerling et al., 1997), and the late Miocene localities of Nakali, Samburu Hills, and Lothogam (Uno et al., 2011). The vegetation (paleoenvironment) inferred from enamel isotopic data for Maboko and Kipsaramon are compared with previous paleoenvironmental reconstructions for the middle Miocene of East Africa (i.e. Andrews et al., 1979; Evans et al., 1981; Pickford, 1983).

Chapter 3 is a two-pronged attempt to address whether purported dietary changes in early and middle Miocene hominoids and other non-cercopithecoid catarrhines can be associated with environmental change. First, the diets of early and middle Miocene taxa are reconstructed based on shear quotients for early Miocene lower second molars and for middle Miocene taxa from Maboko, Kipsaramon, and Fort Ternan. Second, enamel stable carbon isotopic data from recent early Miocene studies is compiled and combined with middle Miocene enamel stable carbon values from chapter 2 to assess whether mammalian dietary ecologies reflect habitat changes. Results of these analyses are compared to determine if dietary change accompanies an environmental shift, as previously hypothesized.

In Chapter 4, quantitative analysis of 20 intermediate phalanges from five fossil localities (Songhor, Rusinga, West Turkana, Kipsaramon, and Maboko) is performed to expand on the knowledge of early and middle Miocene catarrhine locomotor diversity. Functionally informative metrics such as intrinsic relative length and phalangeal curvature of 30 extant anthropoid taxa of known positional behavior are evaluated and used to interpret positional behaviors of catarrhine taxa represented by intermediate phalanges.

Chapter 5 provides a summary of findings and a synthesis of the environmental and ecological evidence presented in the previous chapters. Some caveats of the present study and future research directions are also presented.

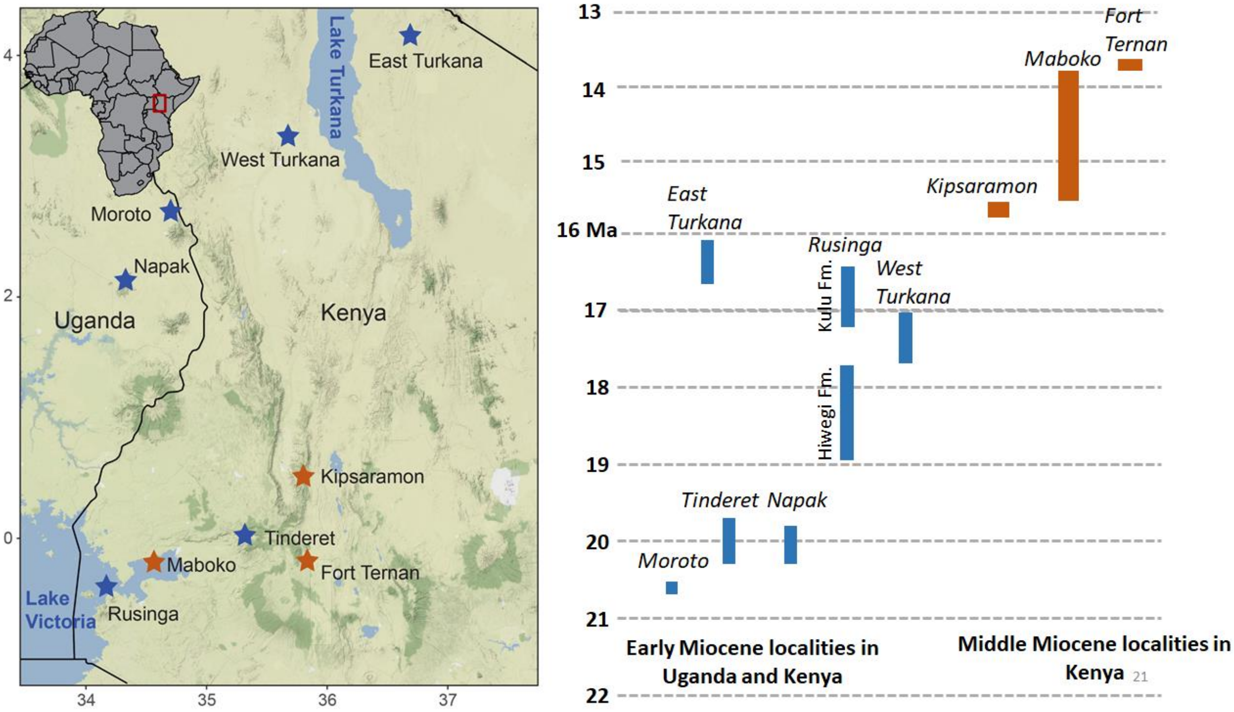

Figure 1. Map and timeline of fossil localities. The geographic location of East Africa localities included in this study is on the right and the chronological sequence of these localities is shown on the left. Early Miocene localities are indicated in blue and middle Miocene localities are indicated in orange.

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Chapter 2

East African Middle Miocene Environmental Reconstruction Using Herbivore Enamel Stable Isotopes

Introduction

Sedimentary sequences of the early and middle Miocene of East Africa preserves a rich assemblage of fossil catarrhine primates, including more than 30 species of apes (Harrison, 2010; 2013) and the earliest cercopithecoids (Pilbeam and Walker, 1968; Von Koenigswald, 1969; Leakey, 1985; Benefit, 1987, 1993; Pickford and Kunimatsu, 2005). Postcranial remains of early Miocene primate taxa suggest the earliest apes used an array of arboreal pronograde positional behaviors but they lacked the specializations for modern ape-like suspensory behaviors and African ape-like knuckle-walking (e.g. Napier and Davis, 1959; McHenry and Corruccini, 1983; Rose, 1988, 1992, 1993; Ward et al., 1993; Ward, 1997). Middle Miocene catarrhine taxa, however, are suggested to have expanded their locomotor repertoire to include semi-terrestriality (Von Koenisgwald, 1969; Delson, 1975; Harrison, 1989; McCrossin, 1994; McCrossin and Benefit, 1997; McCrossin et al., 1998; Patel et al., 2009). Several middle Miocene catarrhine taxa (see below) from three localities (Maboko, Kipsaramon, and Fort Ternan) are interpreted to display semi-terrestrial adaptations.

Species[1] documented to exhibit contain semi-terrestrial adaptations include the large bodied hominoid from Maboko (LBHM)[1] (McCrossin, 1994; McCrossin et al., 1998; Allen,

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[1] Before discussing the catarrhine taxa, some taxonomic clarifications are needed. For most of this paper, the taxonomic assignments summarized in Harrison (2010) for noncercopithecoid

2008), *Kenyapithecus wickeri* (McCrossin, 1994; McCrossin and Benefit, 1997; McCrossin et al., 1998), the large bodied hominoid from Kipsaramon (LBHK)[1](Sherwood et al., 2002; Patel et al., 2009), *Victoriapithecus macinnesi* (Harrison, 1989; McCrossin et al., 1998; Blue et al., 2006), and *cf. Noropithecus kipsaramanensis* (Gilbert et al., 2010). Terrestrial adaptations cited to be present in LBHM include a greater tubercle positioned superiorly above the humeral head, a deep olecranon fossa and dorsally extended olecranon process, transverse torus on the head of the 3rd metacarpal, short, robust, and straight middle phalange, a first metatarsal with a flatten medial surface of the mesocuneiform facet (McCrossin, 1994; McCrossin et al., 1998; Allen, 2008). For LBHK, the length of the proximal phalange relative to the fifth metacarpal length has been found to be similar to semi-terrestrial cercopithecoids such as *Macaca* (Patel et al., 2009), while *Kenyapithecus wickeri* has a short, retroflexed humeral medial epicondyle that is similar to those of terrestrial cercopithecoids (McCrossin, 1994; McCrossin and Benefit, 1997; McCrossin et al., 1998). For cercopithecoids, *Victoriapithecus* (Harrison, 1989) and *cf. Noropithecus* (Gilbert et al., 2010) also have retroflexed medial epicondyles. Additional terrestrial features proposed for *Victoriapithecus* include short, robust phalanges, a long ischial body, a short femoral neck set at a low-neck angle, short radial head, and a long and retroflexed olecranon process (Harrison, 1989; McCrossin et al., 1998). Terrestrial adaptations represent a fundamental adaptive shift in locomotion that is tied to the origin and diversification of multiple catarrhine

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catarrhines and Miller et al., (2009) for middle Miocene cercopithecoids are used. However, the taxonomic attributions of the large bodied hominoid(s) from Maboko and Kipsaramon are unresolved with *Kenyapithecus africanus* being used by some authors (Benefit and McCrossin, 2000) and *Equatorius africanus* being used by others (Ward *et al*., 1999). Given that unpublished additional large bodied hominoid dental material from Maboko has yet to be compared to Kipsaramon material, we prefer to wait to assign taxonomic designations. The designations "Large bodied hominoid from Maboko" (LBHM) and "Large bodied hominoid from Kipsaramon" (LBHK) will be used until these issues are resolved.

lineages, including cercopithecoids, African apes, and humans. McCrossin and Benefit 1994, 1997, McCrossin et al., 2000; Benefit 1999, 2000 contextualized the first appearance of terrestrial adaptations in the catarrhini in terms of faunal and environmental changes first documented at Maboko in the middle Miocene. Understanding the range of paleoenvironments during the middle Miocene in which terrestrial adaptations in some of these lineages first appear is essential to contextualize and differentiate ecological drivers for the origins of terrestriality among Miocene catarrhines and their subsequent radiations.

Of the three East African middle Miocene localities preserving catarrhines for which semi-terrestrial adaptations have been reconstructed, Fort Ternan (~13.9 Ma) (Shipman et al., 1981) is the only site where the paleoenvironment context has been studied through analysis of fossil herbivore enamel stable isotopes. Additional environmental proxies used to reconstruct habitats at Fort Ternan include faunal analysis (Shipman et al., 1981; Shipman, 1986; Pickford, 1983), vertebrate faunal ecological diversity (Evans et al., 1981), pollen remains (Bonnefile, 1984), bovid ecomorphology (Kappleman et al., 1991), paleosol descriptions (Retallack et al., 1990; Dugas and Retallack, 1993), and stable isotope analyses of both pedogenic carbonate and organic matter (Cerling, et al., 1991). Reconstructions from these proxies range from forests, closed woodland, open forest and woodland, wooded grassland, and open grassland. Andrews and Van Couvering (1975) were one of the first to describe a transition from forested habitats in early Miocene to more open woodlands by the middle Miocene. Later studies have also emphasized a predominance of forests in the early Miocene that are replaced by dry forests and woodlands in the middle Miocene (e.g. Andrews et al., 1979; Evans et al., 1981; Pickford, 1983). Preliminary results from recent paleoenvironmental reconstructions suggest a more complex scenario. Enamel stable carbon isotopic values from Ugandan early Miocene fossil catarrhine localities of Napak and Moroto (Kingston et al., 2011) and Kenyan early Miocene (Tinderet; Arney et al., 2017, and West Turkana, Butts et al., 2018) indicate more widespread open forest and woodland canopied environments than previously interpreted. Environmental data from Moboko and Kipsaramon have the potential to provide critical data to these interpretations. However, limited paleoenvironmental evidence from Maboko and Kipsaramon specifically (Andrews and Kelley, 2007), as well as preliminary enamel stable carbon isotopic data, do not support earlier habitat interpretations. Given these conflicting interpretations, it is imperative to apply paleoecological proxies across a greater range of sites and over a greater time interval to better characterize local paleoenvironments and to address environmental change.

Stable isotope ratios from fossil tooth enamel are commonly used to infer paleoenvironments from herbivore dietary ecology and provide a means to create comparative paleoecological datasets to directly reconstruct environments of fossil sites in East Africa. This approach has been implemented in East Africa to assess the paleodietary response of herbivores to the expansion of C_4 grasses in the late Miocene and to determine the proportion of C_3 and C_4 plants present at early hominin localities (e.g. Cerling et al., 1997; Kingston and Harrison, 2007; Levin et al., 2008; Uno et al., 2011; Cerling et al., 2015). In contrast, isotopic analyses are generally underutilized for ecological reconstruction in the early and middle Miocene because ecosystems are assumed to be C_3 dominant (Cerling et al., 1997; Uno et al., 2011; 2016). However, a recent increase in focus on the isotopic ecology of modern and ancient C_3 ecosystems demonstrates extensive isotopic variability in C_3 dominant environments linked to climatic and structural features of paleohabitats (e.g. Quade et al., 1995; Cerling et al., 2004; Feranec and MacFadden, 2006; Secord et al., 2008; Nelson, 2013; Eastham, 2016; Nelson et al., 2016).

This study utilizes mammalian enamel stable carbon and oxygen isotope analysis to reconstruct paleoenvironments at Maboko and Kipsaramon, whichpreserve some of the richest collections of middle Miocene vertebrate remains in equatorial Africa (McCrossin and Benefit, 1994; Retallack et al., 2002; Behrensmeyer et al., 2002). Enamel $\delta^{13}C$ values from this study add to our knowledge of East African Miocene herbivore dietary ecology and will be compared to published enamel $\delta^{13}C$ values known from Fort Ternan (Cerling et al., 1997), the late Miocene East African hominoid localities of Nakali and Samburu Hills (Uno et al., 2011), and modern herbivore enamel from relevant lineages.

Geological Context

Maboko

Maboko Island is in the northern portion of the Winam Gulf, which is situated in the northeastern portion of Lake Victoria in Western Kenya (Figure 1). The history of investigations on Maboko has been reviewed in Andrews (1981), McCrossin (1994) and McCrossin and Benefit (1994). Maboko has a long history of excavation spanning approximately six decades (MacInnes, 1943; Le Gros Clark, 1950, 1952; Andrews, 1981; Pickford, 1984, 1986; Benefit and McCrossin, 1989). It was first excavated from 1933-1934 by W.O. Owens and D.G. MacInnes (MacInnes, 1943). Subsequent excavations included teams lead by L.S.B. Leakey and D.M.S Watson in 1947 and 1949 (Le Gros Clark, 1950, 1952), D.R. Pilbeam and P. Andrews in 1973 (Andrews, 1981), M. Pickford from 1982-1984 (Pickford, 1984; 1986), and Benefit and McCrossin from 1987-1997 (Benefit and McCrossin, 1989).

The Maboko Formation sediments lie on top of granite and metavolcanics of Precambrian age and are capped by the Ombo Phonolite (Mboya, 1983; Pickford, 1984). The sediments extend 15 km northeast to the mainland at Majiwa Bluff, Kaloma, and Ombo and are geographically situated between the Tinderet volcano complex to the northeast and the Kisingiri volcano to the southwest. The Maboko Formation is present on Maboko Island, Majiwa Bluff and Kaloma (Pickford, 1982). On Maboko Island, the Maboko formation is approximately 50 m thick (Pickford, 1984; Feibel and Brown, 1991) and vertebrate fossiliferous material has been recovered from 15 of the 20 sedimentary beds recognized on the island (Figure 2; Pickford, 1984; 1986; McCrossin and Benefit, 1994). Most vertebrate fossils come from two lower lying bone beds, Beds 3 and 5, in the fine-grained sequence (Pickford, 1986; McCrossin and Benefit, 1994) (Figure 3). Feibel and Brown (1991) performed laser fusion $^{40}Ar/^{39}Ar$ analysis of alkali feldspars from the tuff of Bed 8, which produced a date of 14.7 Ma, and alkali feldspars and biotites from the Ombo Phonolite overlying the Maboko Formation that yielded an estimated date of 13.8 Ma. There are no additional radiometric dates for the lower fossiliferous Beds 3 and 5, but they are older than 14.7 Ma. Faunal comparisons across Miocene localities (Pickford, 1981; Pickford and Morales, 1994) have suggested that these beds are likely closer to 15 Ma but could be as old as 16 Ma.

Beds 3 and 5 are interpreted as flood plain deposits of clay and sand (Andrews et al., 1981), separated by a thick calcrete (Bed 4) (Feibel and Brown, 1991; McCrossin, 1994). Bed 3 consists of clay-like green sand (Andrews, 1981) with little foil formation and is interpreted as a stream side swale deposit (Retallack et al., 2002). Bed 5 consists of sediments of clay and carbonatite materials (McCrossin, 1994; Retallack et al., 2002). A lower lying layer of brown clay (Bed 5b) is overlain with a deposit of white clay (Bed 5w) (Benefit, 1999; Retallack et al., 2002). Fossil material from Beds 12-19, which lie between Bed 8 and the capping phonolite are constrained to between 14.7 and 13.8 Ma. These upper stratigraphic layers are comprised of coarse volcaniclastic sediments (Feibel and Brown, 1991).

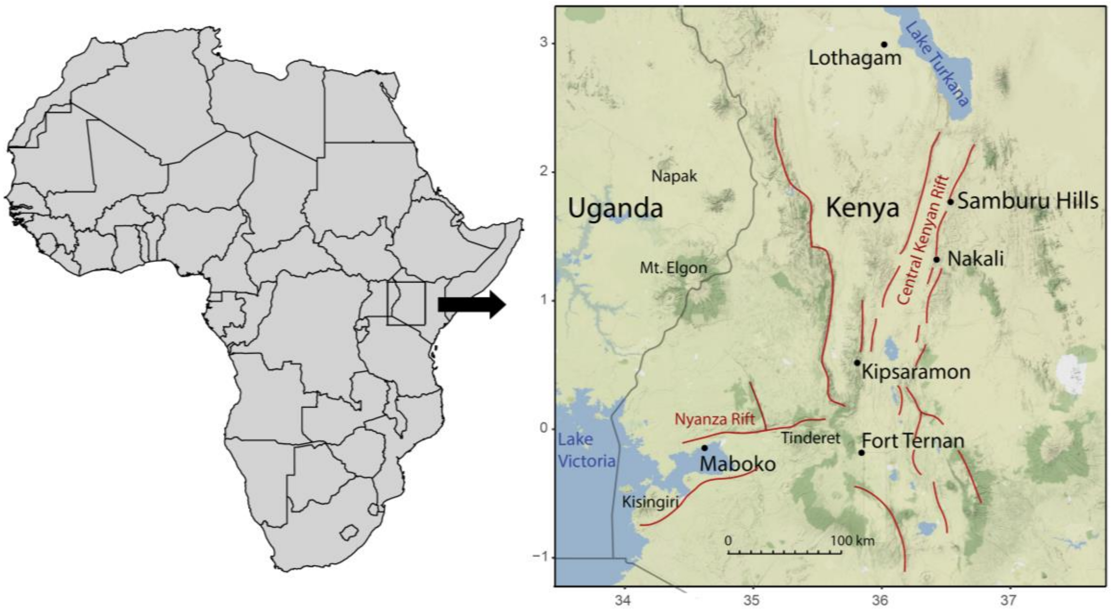

Figure 2. Map of Africa and study localities and comparative middle and late Miocene localities. Black rectangle depicts the location of Maboko and Kipsaramon, as well as other Miocene fossil vertebrate localities (black dots and bolded text) in which enamel isotopic values are compared and discussed in the text. Red lines show modern rift escarpment faults.

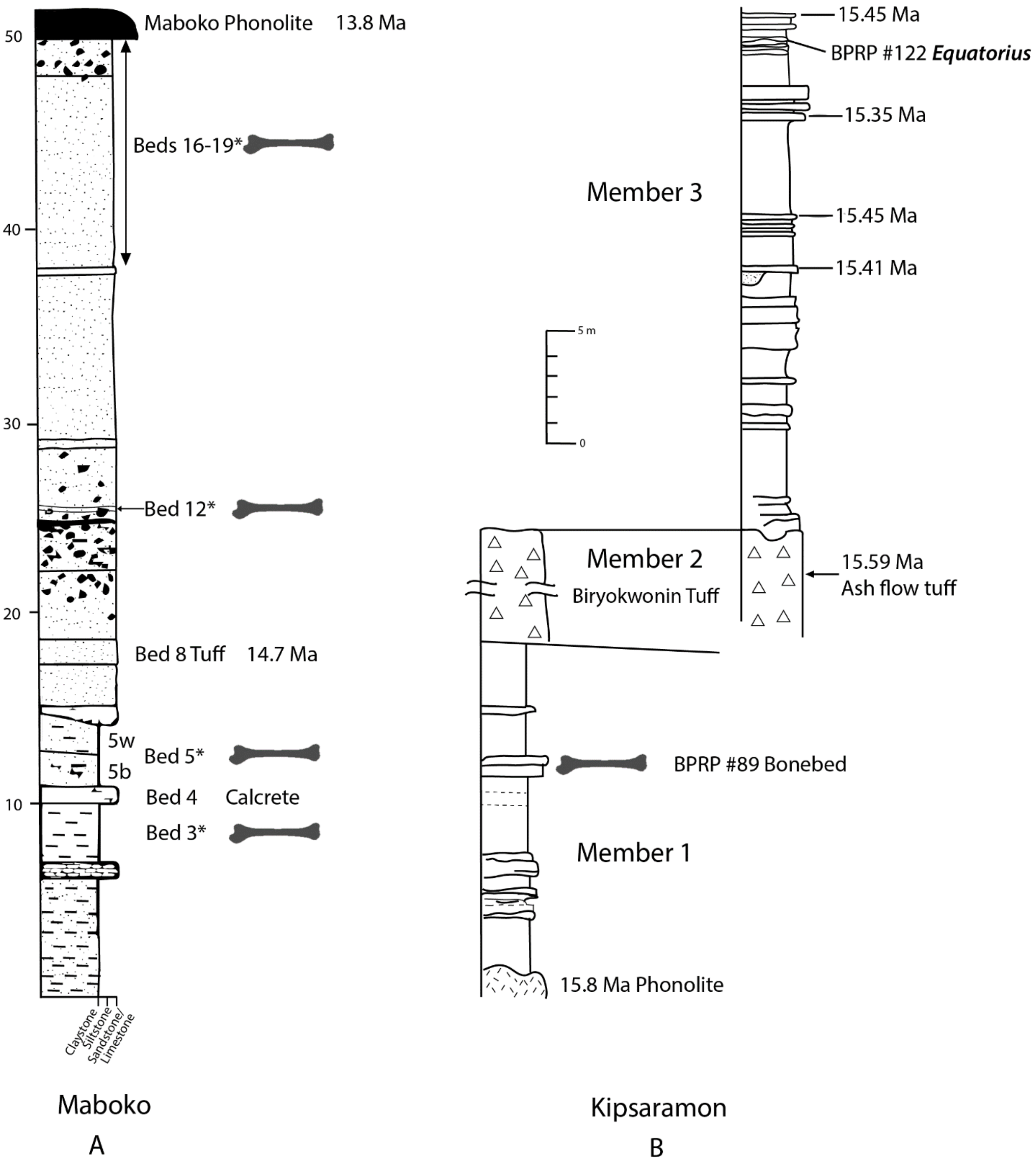

Figure 3. Composite geological sections from excavations on Maboko Island and Kipsaramon. Composite geological sections from excavations on Maboko Island and Kipsaramon. Stratigraphic sections for Maboko (A) and Kipsaramon (B) show positions of fossiliferous deposits and dated samples, and are modified from Feibel and Brown, (1991) and Behrensmeyer et al., (2002). Asteriks (*) indicate the fossiliferous stratigraphic beds fossils sampled for enamel powder were recovered.

Kipsaramon

The Kipsaramon sequence of volcanic deposits is associated with early rifting in the central Kenyan Rift Valley (Behrensmeyer et al., 2002), and is currently exposed along the crest of the Tugen Hills, Baringo District of Kenya, west of Lake Baringo (Figure 2). Fossiliferous deposits at Kipsaramon occur within the lower part of the Muruyur Beds, a lower sedimentary unit in the Tugen Hills Succession (Hill et al., 1986). The geology of the Muruyur Beds was first described in detail by Chapman (1971) with additional work and revision performed by Pickford (1975; 1988). Subsequent field research by the Baringo Paleontological Research Project (BPRP) by Hill and colleagues established a comprehensive stratigraphic and geochronological framework for the Muruyur Beds at the Kipsaramon site complex (Hill, et al., 1986; 1991; Behrensmeyer et al., 2002) (Figure 3). The Kipsaramon stratigraphic section is approximately 52 m thick and divided into three members (Figure 2) (Behrensmeyer et al., 2002). Sediments exposed at Kipsaramon overlie a 10 m thick sequence of phonolites that represent an irregular depositional surface for the Muruyur Beds (*ibid*.). Member 1 consists of fluvial and lacustrine sediments of clays and silts with some volcanic materials. ^{40}Ar/^{39}Ar dates indicate an age between 15.8 and 15.6 Ma for fossil sites within Member 1, which contains the highly fossiliferous BPRP#89 fossil vertebrate bone bed (Behrensmeyer et al., 2002) and includes some hominoid (Hill et al., 1991) and cercopithecoid remains (Pickford and Kunimatsu, 2005; Gilbert et al., 2010). At the same level of the bone bed is the less fossil rich locality of BPRP#91 that has produced other mammal and bird fossils. Members 1 and 3 are separated by the 1-10m thick non-fossiliferous Biryokwonin Tuff (Member 2). Member 3 consists of green clays and silts with some tuffaceous material and is dated to 15.6 and 15.4 Ma. (Behrensmeyer et al., 2002). This stratigraphic level contains locality BPRP#122, which has yielded a partial skeleton of *Equatorius africanus* (Ward et al., 1999).

Fauna and Ecology of Maboko and Kipsaramon

The mammalian fauna from Maboko and Kipsaramon are listed in Table 1. Maboko is best known for a possibly semi-terrestrial large bodied hominoid (LBHM) and its high abundance of the victoriapithecid, *Victoriapithecus macinnesi* (Von Koenigswald, 1969; Delson 1975; Benefit, 1987; 1993; 1999; McCrossin and Benefit, 1992). Other catarrhine primates include the small bodied catarrhine *Simiolus leakeyorum* and the not yet comprehensively described, medium sized nyanzapithecines *Mabokopithecus clarki* and *Nyanzapithecus (Mabokopithecus) pickfordi* (Von Koenigswald, 1969; Harrison, 1986; Harrison, 1989b; McCrossin, 1992). Besides its catarrhine assemblage, Maboko also preserves a diverse mammalian fauna that is historically differentiated from western Kenya early Miocene fauna (Andrews, 1981; Pickford, 1981). Unlike earlier fauna, Maboko includes hippopotamids (Pickford, 1983, 1984, 2007), giraffoids with multi-tined ossicones (climacocertids) (MacInnes, 1936; Hamiliton, 1978), bovids (Thomas, 1979; Gentry, 2010), listriodont suids (Andrews, 1981; Pickford, 1981), and the derived cheorolophodont gomphothere *Afrochoerodon* (Pickford, 2001).

Kipsaramon is best known for the LBHK partial skeleton (KNM-TH 28860; attributed to "*Equatorius africanus"* (Hill et al., 1999; Ward et al., 1999; Kelley et al., 2000; Sherwood et al., 2002)), and an extensive underlying bonebed that has produced one of the richest deposits of *in situ* mammalian fossils in tropical Africa (Behrensmeyer et al., 2002). Kipsaramon has yielded approximately six species of catarrhine (Behrensmeyer et al., 2002; Pickford and Kunimatsu, 2005), including two species of small bodied catarrhine (*Simiolus cheptumoae* sp. nov. and *Limnopithecus sp.*), a nyanzapithecine (*Nyanzapithecus cf. pickfordi*), two large hominoids

(LBHK and *Ugandapithecus gitongai* sp. nov.) (Ward et al., 1999; Pickford and Kunimatsu, 2005), and a cercopithecoid (*Noropithecus kispsaramonensis*) (Miller et al., 2009). Specimens assigned to *Simiolus, Limnopithecus,* and *Ugandapithecus* by Pickford and Kunimatsu (2005) are not available for study at the Kenya National Museum or elsewhere. Many of the mammalian taxa found in the bonebed are potentially shared with Maboko, including *Prodeinotherium hobleyi, Protanacus macinnesi, Afrochoerodon kisumuensis, Kenyapotamus, Dorcatherium pigotti,* (Behrensmeyer et al., 2002; Retallack et al., 2002) and the suid species *Lopholistriodon pickfordi, Namachoerus moruoroti,* and *Megalochoerus khinzikebirus* (Pickford, 2007) (Table 1).

The taxonomic composition of the catarrhine communities from Maboko and Kipsaramon are broadly similar in at least two respects. First, as mentioned above, both localities are thought to contain evidence for terrestrial adaptations for both hominoid (McCrossin et al., 1998; Patel et al., 2009) and cercopithecoid remains (McCrossin et al., 1998; Blue et al., 2006; Gilbert et al., 2010). Second, both sites contain an abundance of at least three small to medium bodied non-cercopithecoid catarrhines (Benefit, 1999; Behrensmeyer et al., 2002; Pickford and Kunimatsu, 2005). These primate faunas maintain similar levels of catarrhine species diversity as early Miocene localities such as Rusinga and Songhor (although the latter do not preserve cercopithecoids). The comparative high catarrhine diversity contrasts with that at Nachola, Kenya (~14.9 -14.7 Ma; Nakatsukasa and Kunimatsu, 2009), which has documented only three catarrhine species so far.

Table 2 contains a summary of previous ecological interpretations for Maboko and Kipsaramon. In general, there is little published research on environment reconstructions for either locality. At Maboko, early studies of Miocene mammalian ecological diversity indicated a closed woodland with some forest elements (Evans et al., 1981). In addition, an analysis of the Maboko gastropod assemblage has been used to infer the presence of a dry woodland (Pickford, 1983). Paleosols associated with primate fossils have been interpreted to indicate wooded grassland that experienced seasonal waterlog (Bed 5w), riparian woodland (Bed 5b), and some bushland (Bed 12) (Retallack et al., 2002). No environmental characterization is provided for the Bed 3 green sand due to a lack of paleosol formation (Retallack et al., 2002). The abundance of aquatic birds reaffirms the interpretation of the presence of riparian woodland.

Mammalian species distributions and proportions at Maboko imply the existence of possible habitat differences between beds (Gitau et al., 1998; Retallack et al., 2002; Geraads et al., 2012). For example, the non-primate mammalian fauna of the purported wooded grassland in Beds 5w and bushland in Beds 12-16 are dominated by the giraffoid *Climacoceras,* which is thought to be a more open-adapted taxon (Retallack et al., 2002). The high abundance of the tragulid *Dorcatherium* and the suid *Lopholistriodon,* and lack of rhinocerotids, has been used to suggest that Bed 5b samples a more closed habitat than all other beds, perhaps representing a riparian woodland (Retallack et al., 2002) or an isolated forest (Gitau et al., 1998; Benefit, 1999).

Habitat interpretations based on fauna at Kipsaramon range from forests and some open habitat (Winkler 1992, 2002) and heavy woodland (Pickford and Kunimatsu, 2005), while biogeochemical analyses of pedogenic carbonate and organics and fossil enamel suggest the presence of C_4 plants and potentially more open environments (Kingston, 1992; Kingston et al., 1994; Morgan et al., 1994; Table 2). The presence of anomalurids (flying squirrels) from Site 89A has been interpreted to indicate extensive tropical forests, although the occurrence of pedetids (spring hares) also suggests the presence of open habitat (Winkler, 1992; 2002). Stable isotopic signatures from pedogenic carbonate collected from BPRP#91 within Member 1 range from -7.4‰ to -5.1‰, indicating the presence of C_4 biomass (Kingston, 1992; Kingston et al., 1994). Enamel stable carbon $\delta^{13}C$ values from a Rhinocerotidae (-7.4‰) from BPRP#91 indicates a minor component of C_4 vegetation in herbivore diets (Kingston, 1992; Morgan et al., 1994). In sum, the presence of forest adapted taxa and biogeochemical analyses of soil and mammalian enamel point to a mosaic habitat with forested and open components with possibly some C_4 plants.

Table 1. Faunal list for Maboko and Kipsaramon.

Taxon	**Maboko**	**Kipsaramon**
Primates		
Galagidae		
Komba winamensis	X	
Komba sp. nov.	X	
Dendropithecoidea		
Simiolus leakeyorum	X	
Simiolus cheptumoae		X
cf. Limnopithecus evansi	X	
Limnopithecus sp.		X
Nyanzapithecinae		
Mabokopithecus clarki	X	
Nyanzapithecucs. pickfordi	X	X
Proconsulinae		
Equatorius africanus		X
cf. *Proconsul major (gitongai)*		X

Kenyapithecinae		
Kenyapithecus africanus	X	
Cercopithecoidea		
Victoriapithecus macinnesi	X	
cf. Noropithecus kipsaramonensis		X
Insectivora		
Erinaceidae		
Amphechinus rusingensis	X	
Family indet.	X	
Rodentia		
Anomaluridae		
Anomalurus parvus		X
Thyronomyidae		
cf. Paraphiomys pigotti	X	
cf. P. stromeri	X	
Paraulacodus sp.n.	X	
genus indet.	X	
Diamantomyidae		
cf. Diamantomys luederitzi	X	X
Bathyergidae		
genus indet.	X	
Pedetidae		

Megapedetes pentadactylus	X	
Pedetes sp. indet.	X	
Gen. et. sp. indet		X
Cricetidae		
genus indet.	X	
Cricetodontinidae		
Notocricetodon sp. indet.		X
Myophiomyidae		
Elmerimys woodi		X
Family indet.		
genus indet.		
Lagomoropha		
Family indet.	X	
genus indet.	X	
Creodonta		
Hyaenodonta		
Anasinopa leakeyi	X	
Dissopsalis pyroclasticus	X	
cf. Pterodon nyanzae	X	
Hyaenailourus sp. indet.	X	
Family indet.		
genus indet.	X	
Carnivora		

Canidae		
cf. Cynelos eurydon	X	
Viverridae		
cf. Mioprionodon sp.	X	
genus indet.	X	
Family indet.		
genus indet.	X	
Tubulidentata		
Orycteropidae		
Orycteropus chemeldoi	X	
Proboscidea		
Gomphotheriidae		
Protanancus macinnesi	X	X
Afrochoerodon kisumuensis	X	X
genus indet.	X	
Deinotheriidae		
Prodeinotherium hobleyi	X	X
Hyracoidea		
Pliohyracidae		
Afrohyrax championi	X	
Family indet.	X	
Perissodactyla		
Rhinocerotidae		

Species A	X	
Species B	X	
Victoriaceros kenyensis	X	
Genus indet		X
Chalicotheriidae		
genus indet.	X	
Artiodactyla		
Sanitheriidae		
Diamantohyus nadirum	X	X
Tayassuidae		
genus indet.	X	
Hippopotamidae		
Kenyapotamus ternani	X	X
Suidae		
Nguruwe sp.		X
Kenyasus namaquensis	X	X
Libycochoerus jeanelli	X	
Megalochoerus khinzikebirus	X	X
Listriodon akatikubas	X	
Listriodon sp. indet.	X	
Lopholistriodon kidogasona	X	
L. pickfordi	X	X
Namachoerus moruoroti	X	X

Lopholistriodon sp. indet.	X	
Morotochoerus Ugandensis		X
Tragulidae		
Dorcatherium parvum	X	
Dorcatherium pigotti	X	X
Dorcatherium chappuisi	X	
Dorcatherium libiensis	X	
Dorcatherium sp. indet.	X	
Giraffoidea		
Climacoceras africanus	X	
Palaeotragus sp.	X	
Palaeotragus primaevus		X
Canthumeryx sp.	X	
Bovidae		
Eotragus sp.	X	
Hypsodontus pickfordi	X	
Gazella sp.	X	
Hypsodontinae sp. indet.	X	
genus indet.	X	

Lists are modified from Behrensmeyer et al. (2002) and Retallack et al. (2002). Data are from Pickford (1982; 1983; 1985; 2001; 2007), Thomas (1985), Cifelli et al, (1986), Benefit & McCrossin (1989), McCrossin (1992), Winkler (1990; 1992, 1994; 2002), McCrossin et al. (1998), Benefit (1999), Behrensmyer et al., (2002), Pickford and Kunimatsu (2005), Bishop (2010), Gentry (2010), Geraads (2010; 2012), Rasmussen and Gutierrez (2010).

Table 2. Published environmental reconstructions for Maboko and Kipsaramon from the literature.

Locality	Environmental Interpretation	Types of Analysis	Citation
Maboko	Heavy woodland to forest	Community reconstruction	Evans et al., 1981
	Dry woodland	Gastropods	Pickford, 1983
	Wooded grassland, riparian woodland, and some bushland	Fossil soils	Retallack et al., 2002
	Aquatic/semi-aquatic	Avifauna analysis	Mayr, 2014; McCrossin and Benefit., 2016
Kipsaramon	Tropical forest with some open habitat	Rodent fauna analysis	Winkler, 1992; 2002
	Forest to heavy woodland	Plant fossils	Pickford and Kunimatsu, 2005
	Open environments with some C_4 plants	$\delta^{13}C$ of pedogenic carbonate and organics	Kingston, 1992
	Open environments with some C_4 plants	$\delta^{13}C$ of fossil enamel	Morgan et al., 1994

Stable isotope analysis of herbivore enamel as a paleoenvironmental proxy

Stable carbon

Plants utilize different photosynthetic pathways (C_3, C_4 or CAM) to metabolize atmospheric CO_2, producing distinct $\delta^{13}C$ values in their tissues. In East Africa, C_3 plant tissue has $\delta^{13}C$ values that range from -36‰ to -23‰ (Tieszen et al., 1979; Young and Young, 1983; Cerling and Harris, 1999; Cerling et al., 2004), while $\delta^{13}C$ values for C_4 plants range from -14 ‰ to -10‰ (Tieszen et al., 1979; Young and Young, 1983; Cerling and Harris, 1999). A third, less common, photosynthetic pathway, Crassulacean Acid Metabolism (CAM) is used by some plants in arid ecosystems. CAM plants have $\delta^{13}C$ values intermediate to those of C_3 and C_4 plants but are rarely consumed by herbivores (Levin et al., 2008) and therefore, are not considered here. Since the stable carbon isotope composition of herbivore diets are recorded in the enamel during tooth formation, $\delta^{13}C_{enamel}$ values are useful for determining the proportion of C_3 and C_4 plants in a herbivore's diet, and by extension, inferring the structure of the vegetation (e.g. Bocherens et al., 1996; Cerling et al., 1997; 2003a, b; Schoeninger et al., 2003; Kingston and Harrison, 2007; Levin et al., 2008; Uno et al., 2011; Cerling et al., 2015). C_3 plants (shrubs, trees, and high-altitude grasses) discriminate against the heavier ^{13}C isotope during photosynthesis much more than C_4 plants. $\delta^{13}C$ values among C_3 plants vary naturally due to environmental factors, such as canopy, light, temperature, and precipitation (e.g. Heaton, 1999; Kohn et al., 2010). Studies have shown $\delta^{13}C$ values increase with lower levels of moisture and with higher irradiance (e.g. Ehleringer et al., 1986; Kohn et al., 2010). Closed, wet habitats such as closed-canopy forests have lower values than more open and arid habitats such as woodlands (e.g. Cerling et al., 1999; 2004). An important source of variation in $\delta^{13}C$ values among C_3 plants is the canopy effect, which influences the isotopic values of closed-canopy ecosystems. Among closed canopied forests, $\delta^{13}C$ values of plants present in the understory are lower than those from plants higher in the canopy (Medina, 1980; Ehleringer et al., 1987; Carlson and Kingston, 2014). Lower plant $\delta^{13}C$ values are caused by the photosynthesis of CO_2 with lower $\delta^{13}C$ values produced by soil respiration (van der Merwe and Medina, 1989; 1991). Low levels of light in the subcanopy also affect photosynthesis (Farquhar et al., 1982) as the $\delta^{13}C$ in leaves decreases with increased light intensity received by plants (Bonafini et al., 2013). This variation in plant $\delta^{13}C$ values is detectable among modern and fossil herbivore $\delta^{13}C_{enamel}$ values (e.g. Cerling et al., 2004; Secord et al., 2008; Nelson, 2013; Eastham et al., 2016).

Stable carbon isotope values of tooth enamel are also useful for detecting climatic and environmental changes within ancient C_3 dominated ecosystems (e.g. Nelson, 2007; Nelson and Rook, 2016). For example, Nelson (2005, 2007) used $\delta^{13}C_{enamel}$ of fossil herbivore to document a shift to more open habitats in the Swaliks during the late Miocene (Nelson, 200). Enamel $\delta^{13}C$ values have also been widely utilized to reconstruct the paleoenvironments of European middle to late Miocene hominoids, which lived in C_3 dominated habitats (e.g. Quade et al., 1995; Merceron et al., 2006; 2013; Nelson, 2013; Eastham et al., 2016). Therefore, $\delta^{13}C_{enamel}$ values of herbivore taxa should be useful for reconstructing the vegetation of middle Miocene paleohabitats of East Africa where C_3 vegetation was presumably dominant (Cerling et al., 1997).

Methods

Sample Collection and Analysis

103 fossil tooth enamel specimens were sampled and analyzed isotopically for this project: 84 specimens from 16 genera at Maboko and 18 specimens from 3 genera at Kipsaramon (Table 3). Taxonomic identification of mammalian fauna from Maboko and Kipsaramon is presented in Table 3. Enamel powder and fragments were collected from the National Museums of Kenya in June 2016. To broadly sample the Maboko fauna, samples from a few representative specimens of each taxon from Beds 3, 5, 12, and 13-16 were collected. Samples were also taken from historical excavations from the Maboko Main locality (i.e. Maboko Main), which did not record whether fossils originated from Bed 3 or 5. Enamel samples from Kipsaramon included only proboscidean and rhino specimens collected from the BPRP 89A bonebed (Table 3). While the bonebed preserved many more taxa (Behrensmeyer et al., 2002), proboscideans and rhinocerotids were the only abundant, prepared taxa (excavated from bonebed blocks) available for isotopic sampling. Permission to samples fossil for isotope analyses is restricted to fragmentary specimens, which impeded the identification of all teeth to genus or species level. For the entire sample, 66.7% were identified to species and genus, while 33.3% were identified

to family (e.g. gomphotheriidae, bovidae and rhinocerotidae). When it was possible, enamel was collected from second and third molars, which generally form after the onset of adult diet. Teeth formed prior to weaning, such as first molars and premolars, may be offset compared to second or third molars (DeNiro and Epstein, 1978).

Enamel samples for isotopic analyses were collected from archived material at the National Museums of Kenya in June 2016. Enamel fragments were cleaned using a high-speed dental drill with tungsten-carbide burs and then ground with an agate mortar and pestle into a fine powder. To explore the effects of pretreatment of fossil enamel, a subset of 14 enamel samples were treated using 3% sodium hypochlorite (NaOCl) solution for 12 hours and 0.1M solution of acetic acid (CH_3COOH) for 12 hours, rinsed after each treatment with deionized water to neutrality, and freeze dried before analysis. Results of treatment are reported in Table 4 and Figure 4. All the other fossil enamel samples were not pretreated, but values were corrected using the regression equation reported in Figure 4 and are also reported in a separate column in Table 3.

$^{13}C/^{12}C$ ratios of samples of tooth enamel powder were determined using facilities at the University of Florida, Department of Geosciences Light Stable Isotope Mass Spec Lab. Samples were analyzed with 8 NBS-19 standards. 30-50 mg of dried samples and standards were reacted with 99% phosphoric acid (H_3PO_4) at 70 °C in glass vials. The CO_2 produced from digestion with phosphoric acid was analyzed using mass spectrometry with a Kiel III carbonate preparation device coupled with a Finnigan-Mat 252 isotope ratio mass spectrometer. Results are reported in the standard per mil (‰) notation:

$$\delta^{13}C = (R_{sample}/R_{standard} - 1) * 1{,}000$$

$$R = {}^{13}C/{}^{12}C$$

The precision of the NBS-19 standard analyzed with these samples has a standard deviation of ±0.021‰ (N=8) for $\delta^{13}C$ ratios.

Interpreting Enamel Stable Isotope Ratios

Reconstructing herbivore foraging strategies is based primarily on variation in $^{13}C/^{12}C$ in enamel. Differentiating fossil feeding guilds and the specific isotopic dietary input requires correcting for two factors, 1) differences in the $\delta^{13}C$ value of atmospheric CO_2 at the time the animal was alive and 2) a physiological fractionation effect, where carbon isotopes undergo further discrimination as plant material is metabolized. Since plants fix atmospheric CO_2 into their tissues, changes in the atmospheric CO_2 $\delta^{13}C$ value ($\delta^{13}C_{CO2}$) must be considered when data is compared from different time periods when $\delta^{13}C$ values of atmospheric CO_2 varied. This is particularly important for fossil localities dated to the Miocene where $\delta^{13}C_{CO2}$ values range from approximately -6.3‰ in the early Miocene to -5.3‰ in the middle Miocene. $\delta^{13}C_{CO2}$ values estimated from North Atlantic benthic Foraminifera (Tipple et al., 2010) were used to correct fossil enamel $\delta^{13}C$ values to a common reference $\delta^{13}C_{atm}$ value before the Industrial Revolution, estimated to be at 1750 (Francey et al., 1999). A 1750 reference $\delta^{13}C_{atm}$ value of -6.3‰ was used to correct all enamel samples to $\delta^{13}C_{1750}$ values. Second, when dietary carbon is incorporated into enamel during tooth formation, physiological fractionation of carbon isotopes produces an different isotopic ratio relative to that of the vegetation consumed. This relatively consistent difference between diet and enamel carbon ratios is expressed as an enrichment factor. Enrichment factors between diet and enamel carbon ratios for extant mammalian herbivores average 14.1‰ for ruminant ungulates (Cerling and Harris, 1999) and 12-14‰ for non-ruminants such as domesticated pigs (Passey et al., 2005). However, 14.1‰ is consistently used for converting enamel carbon values of all fossil taxa to dietary carbon values (e.g. Kingston and

Harrison, 2007; Levin et al., 2008; Cerling et al., 2003a, b; 2015; Uno et al., 2011) because not enough is known about the digestive physiologies of fossil taxa to adjust the enrichment factor accordingly (Levin et al., 2008), so we use it here. Based on herbivore dietary categories defined in Uno et al., (2011) and Cerling et al. (2015), the terms "C_3-closed canopy understory browser" is used for enamel $\delta^{13}C$ values < -14‰, "C_3-browsers" for $\delta^{13}C$ values between -14‰ and -8‰, and "C_3/C_4 mixed feeders" for $\delta^{13}C$ values > -8‰. These demarcations are based on end member $\delta^{13}C_{1750}$ average values for C_3 and C_4 plants of -26.0‰ and 14.0‰ respectively and an enrichment factors between plant and enamel of 14.1‰.

Also, imperative to interpreting isotopic values from Maboko and Kipsaramon is a comparison to modern herbivore assemblages. Modern herbivore enamel $\delta^{13}C$ values were compiled from the literature with an emphasis on East and Central African assemblages and corrected to $\delta^{13}C_{1750}$ values (e.g. Bocherens et al., 1996; Cerling et al., 1999; 2004; 2015; Cerling and Harris, 1999; Kingston and Harrison, 2007). It is recognized that modern analogs do not provide a one-to-one correlation for fossil enamel $\delta^{13}C$ values because extant genera were not prevalent in the middle Miocene.

Statistics were performed in R (version 3.5.1, R Core Team, 2018). Non-parametric Mann-Whitney U tests were used for pairwise comparisons between specimens from different stratigraphic levels at Maboko and between additional middle and late Miocene comparative localities. Enamel $\delta^{13}C$ values from Fort Ternan (Cerling et al., 1997), Nakali, Samburu Hills, and Lothagam (Uno et al., 2011) were taken from the literature. All comparative modern and middle to late Miocene $\delta^{13}C$ values data were adjusted to common $\delta^{13}C_{1750}$ values to allow for comparisons between modern and fossil time periods.

Table 3. Carbon isotope data of fossil herbivore enamel from Maboko and Kipsaramon.

Family Organized Accession No.	Taxon	Element	$\delta^{13}C_{enamel}$ Untreated	$\delta^{13}C_{enamel}$ Treated	$\delta^{13}C_{1750}$	Stratigraphic Level
Bovidae						
MB 29591	*Gazella sp.*	M3	-11.78	-12.15	-12.79	Bed 3
MB 29577	*Gazella sp.*	Upper M2	-10.15	-10.48	-11.16	Bed 3
MB 20348	*Gazella sp.*	Lower M2	-10.6	-10.94	-11.61	Bed 12
MB 29587	Large Bovidae sp.	molar	-12.18	-12.55	-13.19	Bed 12
MB 20292	Large Bovidae sp.	Lower M3	-10.23	-10.56	-11.24	Maboko Main
MB 29578	Large Bovidae sp.	Upper M2	-10.59	-10.93	-11.6	Bed 3
MB 29575	Large Bovidae sp.	Upper M2	-8.23	-8.52	-9.24	Bed 3
MB 25063	Large Bovidae sp.	Upper M3	-10.44	-10.78	-11.45	Bed 12
MB 21537	Large Bovidae sp.	molar	-8.68	-8.98	-9.69	Bed 3
Climacocerotidae						
MB 35335	*Climacoceras africanus*	Upper M2	-9.61	-9.93	-10.62	Bed 3
MB 36680	*Climacoceras africanus*	Upper M2	-9.95	-10.28	-10.96	Bed 3
MB 35338	*Climacoceras africanus*	Lower M2	-12.83	-13.22	-13.84	Bed 3
MB 34455	*Climacoceras africanus*	Lower M3	-9.96	-10.29	-10.97	Bed 5w
MB 34494	*Climacoceras africanus*	Upper M2	-9.76	-10.08	-10.77	Bed 3
MB 25070	Large Giraffoidea sp.	Upper M2	-11.76	-12.13	-12.77	Bed 3
MB 35062	Large Giraffoidea sp.	Lower M1	-13.16	-13.55	-14.17	Bed 16-19
MB 22127	Large Giraffoidea sp.	Upper M1	-10.03	-10.36	-11.04	Bed 3
MB 25019	Large Giraffoidea sp.	Lower M3	-10.52	-10.86	-11.53	Bed 3
Deinotheriidae						
MB 7581*	*Prodeinotherium hobleyi*	molar	-8.58	-9.80	-9.59	Maboko Main
MB 12507*	*Prodeinotherium hobleyi*	molar	-11.32	-10.75	-12.33	Maboko Main
MB 19612	*Prodeinotherium hobleyi*	molar	-10.46	-10.80	-11.47	Maboko Main
MB 22078	*Prodeinotherium hobleyi*	molar	-11.14	-11.49	-12.15	Maboko Main
MB 21859*	*Prodeinotherium hobleyi*	molar	-10.61	-11.92	-11.62	Bed 12
MB 12499	*Prodeinotherium hobleyi*	molar	-12.57	-12.95	-13.58	Maboko Main

MB 25280	*Prodeinotherium hobleyi*	molar	-11.05	-11.40	-12.06	Maboko Main
MB 12514	*Prodeinotherium hobleyi*	molar	-11.83	-12.20	-12.84	Maboko Main
MB 12495	*Prodeinotherium hobleyi*	molar	-10.64	-10.98	-11.65	Maboko Main
Gomphotheriidae						
MB 403A	*Afrochoerodon kisumuensis*	Lower M3	-9.67	-9.99	-10.68	Maboko Main
MB 12491	*Afrochoerodon kisumuensis*	molar	-10.53	-10.87	-11.54	Maboko Main
MB 21505	*Afrochoerodon kisumuensis*	molar	-10.13	-10.46	-11.14	Bed 3
MB 25279	Gomphotheriidae	molar	-9.91	-10.24	-10.92	Bed 16-19
MB 12494	Gomphotheriidae	molar	-10.38	-10.72	-11.39	Maboko Main
MB 12481	Gomphotheriidae	molar	-10.87	-11.22	-11.88	Maboko Main
MB 12432	Gomphotheriidae	molar	-10.68	-11.02	-11.69	Maboko Main
MB 12431	Gomphotheriidae	molar	-10.97	-11.32	-11.98	Maboko Main
MB 12480	Gomphotheriidae	molar	-10.34	-10.68	-11.35	Maboko Main
MB 12479	Gomphotheriidae	molar	-10.99	-11.34	-12	Maboko Main
MB 12435	Gomphotheriidae	molar	-11.1	-11.45	-12.11	Maboko Main
MB 12482	Gomphotheriidae	molar	-9.11	-9.42	-10.12	Maboko Main
MB 12485	Gomphotheriidae	molar	-10.81	-11.15	-11.82	Maboko Main
MB 12489	Gomphotheriidae	molar	-11.16	-11.51	-12.17	Maboko Main
MB 12483	Gomphotheriidae	molar	-11.02	-11.37	-12.03	Maboko Main
MB 7582*	*Protanacus macinnesi*	molar	-11.26	-11.35	-12.27	Maboko Main
MB 7583	*Protanacus macinnesi*	molar	-9.2	-9.51	-10.21	Maboko Main
MB 21850	*Protanacus macinnesi*	molar	-11.26	-11.61	-12.27	Bed 12
MB 21858	*Protanacus macinnesi*	molar	-10.72	-11.06	-11.73	Maboko Main
MB 25284	*Protanacus macinnesi*	molar	-8.92	-9.22	-9.93	Bed 12
TH 19391	*Afrochoerodon kisumuensis*	molar	-5.91	-6.15	-6.92	89A
TH 28840	*Afrochoerodon kisumuensis*	Upper M2	-6.73	-6.99	-7.74	89A
TH 19389	*Afrochoerodon kisumuensis*	Upper M3	-6.1	-6.35	-7.11	89A
TH 28845	*Afrochoerodon kisumuensis*	Lower M2	-5.84	-6.08	-6.85	89A
TH 28849	*Afrochoerodon kisumuensis*	Lower M3	-5.28	-5.51	-6.29	89A
TH 19389	*Protanancus macinnesi*	Upper M3	-6.38	-6.63	-7.39	89A
TH 27696*	*Protanancus macinnesi*	molar	-7.02	-7.28	-8.03	89A

TH 19386	*Protanancus macinnesi*	Lower M2	-5.96	-6.20	-6.97	89A
TH 27691	*Protanancus macinnesi*	Lower M2	-5.92	-6.16	-6.93	89A
TH 19390	*Protanancus macinnesi*	Lower M2	-6.84	-7.10	-7.85	89A
TH 19383	*Protanancus macinnesi*	Lower M3	-6.47	-6.72	-7.48	89A
TH 19387	*Protanancus macinnesi*	Upper M2	-7.29	-7.56	-8.3	89A
TH 27695	*Protanancus macinnesi*	Upper M3	-5.96	-6.20	-6.97	89A
TH 27697*	*Protanancus macinnesi*	Upper M3	-6.83	-6.89	-7.84	89A
TH 27699	*Protanancus macinnesi*	Lower M2	-6.25	-6.50	-7.26	89A
Rhinocerotidae						
MB 29403*	Rhinocertidae gen. indet	molar	-11.2	-11.40	-12.21	Bed 3
MB 33350	Rhinocertidae gen. indet	premolar	-10.16	-10.49	-11.17	Bed 3
MB 54030	Rhinocertidae gen. indet	Upper Molar	-8.72	-9.02	-9.73	Maboko Main
MB 33351*	Rhinocertidae gen. indet	Premolar	-11.62	-11.96	-12.63	Bed 3
MB 28471*	Rhinocertidae gen. indet	Upper Molar	-9.57	-9.74	-10.58	Bed 5w
MB 28463	Rhinocertidae gen. indet	Lower M2	-10.41	-10.75	-11.42	Bed 3
MB 28462*	*Victoriaceros kenyensis*	Upper Molar	-10.46	-10.78	-11.47	Bed 3
MB 36189	*Victoriaceros kenyensis*	Upper P4	-9.78	-10.10	-10.79	Bed 12
MB 24459*	*Victoriaceros kenyensis*	Lower M2	-12.19	-12.34	-13.2	Bed 3
TH 31006	Rhinocerotidae gen. indet	Lower molar	-8.02	-8.31	-9.03	89A
TH 31007*	Rhinocerotidae gen. indet	Upper molar	-7.95	-8.12	-8.96	89A
TH 31004*	Rhinocerotidae gen. indet	molar	-8.01	-8.03	-9.02	89A
Sanitheriidae						
MB 12572	*Diamantohyus nadirum*	Upper M3	-11.1	-11.45	-12.11	Bed 5b
MB 21412	*Diamantohyus nadirum*	Upper M3	-8.98	-9.29	-9.99	Maboko Main
Suidae						
MB 27317	*Listriondon akatikubas*	Lower M3	-12.2	-12.57	-13.21	Bed 3
MB 27328	*Listriondon akatikubas*	Upper molar	-9.87	-10.20	-10.88	Bed 3
MB 27327	*Listriondon akatikubas*	Upper M3	-10.63	-10.97	-11.64	Bed 3
MB 34931	*Lopholistriodon sp.*	Lower M3	-12.27	-12.65	-13.28	Bed 5b
MB 34930	*Lopholistriodon sp.*	Upper M3	-13.21	-13.61	-14.22	Bed 5b
MB 36210	*Lopholistriodon sp.*	Upper M3	-12.7	-13.09	-13.71	Bed 5b

MB 10334	*Lopholistriodon sp.*	molar	-12.83	-13.22	-13.84	Maboko Main
MB 130	*Megalochoerus khinzibirus*	Lower M3	-10.97	-11.32	-11.98	Maboko Main
MB 131	*Megalochoerus khinzibirus*	Lower M3	-10.9	-11.25	-11.91	Maboko Main
Titanohyracidae						
MB 26180	*Afrohyrax championi*	P4	-11.09	-11.44	-12.1	Bed 3
MB 33358*	*Afrohyrax championi*	Lower M3	-12.43	-12.64	-13.44	Bed 5b
MB 14159	*Afrohyrax championi*	Lower molar	-11.78	-12.15	-12.79	Maboko Main
Tragulidae						
MB 14115	*Dorcatherium chappuisi*	Lower M3	-9.97	-10.30	-10.98	Maboko Main
MB 25702	*Dorcatherium chappuisi*	Lower M3	-9.19	-9.50	-10.2	Bed 3
MB 27244	*Dorcatherium chappuisi*	Lower M3	-9.87	-10.20	-10.88	Bed 3
MB 32179	*Dorcatherium pigotti*	Lower M2	-11.19	-11.54	-12.2	Bed 5b
MB 13940	*Dorcatherium pigotti*	Lower M3	-11.37	-11.73	-12.38	Maboko Main
MB 13905	*Dorcatherium pigotti*	Lower M3	-10.92	-11.27	-11.93	Maboko Main
MB 13890	*Dorcatherium pigotti*	Upper molar	-10.67	-11.01	-11.68	Maboko Main
MB 13913	*Dorcatherium pigotti*	Lower M3	-11.55	-11.91	-12.56	Maboko Main
MB 32239	*Dorcatherium pigotti*	Upper M3	-10.4	-10.74	-11.41	Bed 5b

The columns labeled “$\delta^{13}C_{enamel}$ Untreated” and “$\delta^{18}O_{enamel}$ Untreated” refer to the carbon and oxygen isotopic values of untreated enamel, respectively. The columns labeled “$\delta^{13}C_{enamel}$ Treated” and “$\delta^{18}O_{enamel}$ Treated” refer to isotopic values corrected for treatment using the regression equations in Figure3. The column labeled “$\delta^{13}C_{1750}$” refers to the untreated carbon isotopic values that have been corrected to the reference $\delta^{13}C$ value of atmospheric CO_2 of 6.3‰ at 1750 AD.
*Indicates samples that were treated.

Results

Sample Treatment

δ^{13}C values for treated and untreated powder from 14 teeth are reported in Table 4. The average difference between treated and untreated δ^{13}C values is 0.3‰. There is a close to1:1 ratio between enamel δ^{13}C values from treated and untreated powder (Figure 4).

Sample treatment is hypothesized to eliminate organic material and secondary carbonates that could alter the biogenic signal (Lee-Thorp and van der Merwe, 1991). Treatment, however, can also cause additional isotopic fractionation and produce new compounds (Koch et al., 1997; Lee-Thorp, 2000). In addition, a significant amount of sample powder can be lost during treatment. This impacts the ability to treat samples from specimens that yield smaller amounts of sample powder (such as tragulid, hyrax, and small suid teeth). Isotopic values from untreated samples were converted using the respective carbon and oxygen regression equations shown in Figure 3 and are listed in Table 3. However, since it is still not clear whether treated or untreated enamel δ^{13}C values best represent an animal's diet (Levin et al., 2008), results are presenting using untreated values.

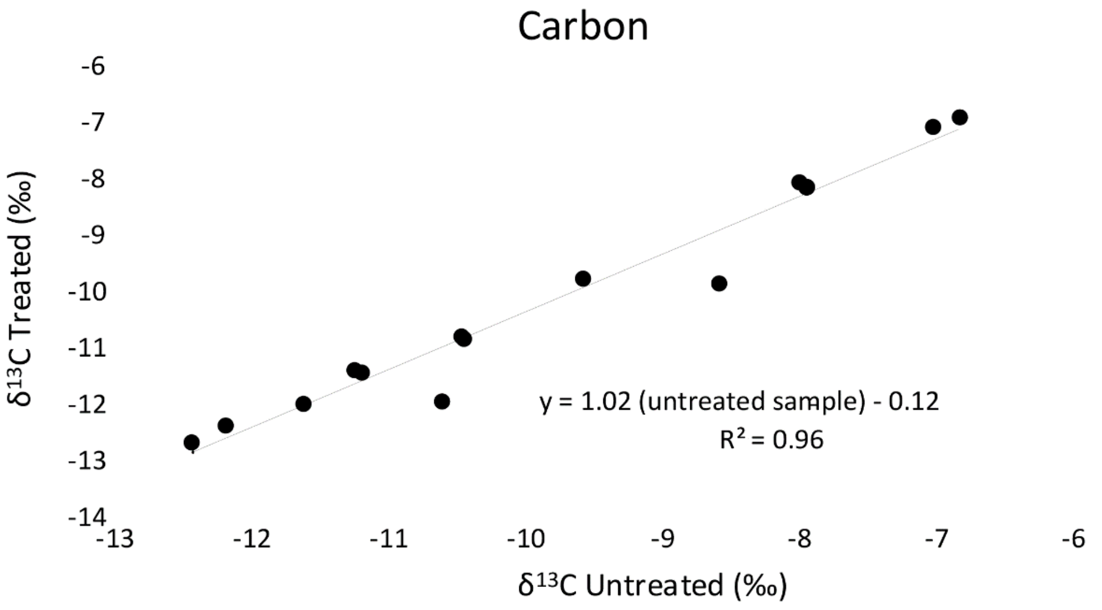

Figure 4. Bivariate plots of δ^{13}C values of treated and untreated enamel samples. δ^{13}C values are in parts per million (‰) units. The regression line and equation are reported on plots.

Table 4. Treated samples.

Accession	$\delta^{13}C_{enamel}$ Untreated	$\delta^{13}C_{enamel}$ Treated
MB 7581	-8.6	-9.8
MB 12507	-11.3	-10.7
MB 21859	-10.6	-11.9
MB 7582	-11.3	-11.3
TH 27696	-7.0	-7.3
TH 27697	-6.8	-6.9
MB 29403	-11.2	-11.4
MB 33351	-11.6	-12.0
MB 28471	-9.6	-9.7
MB 28462	-10.5	-10.8
MB 24459	-12.2	-12.3
TH 31007	-7.9	-8.1
TH 31004	-8.0	-8.0
MB 33358	-12.4	-12.6

General Patterns

At Maboko, 47 of 84 samples have associated provenience data indicating which bed the fossil originated from, while values lacking stratigraphic information (referred to here as Maboko Main), can be inferred to have originated from either Bed 3 or Bed 5 (Table 3). Figure 5 displays $\delta^{13}C$ values for herbivore enamel from Maboko relative to stratigraphic level. The $\delta^{13}C$ values from Bed 3 range from -12.8‰ to -8.2‰ (n=27). $\delta^{13}C$ values for Bed 5b (n=7) range from -13.21‰ to -11.1‰ and for Bed 12 (n=7) from -12.2‰ to -8.9‰. There were no statistical differences in $\delta^{13}C$ values from Beds 3, 5b, and 12. Only two teeth were sampled for Beds 5w and 16-19 and $\delta^{13}C$ values range from -9.6‰ to -9.96‰ and -13.1‰ to -9.9‰, respectively. The $\delta^{13}C$ values of all 84 herbivore fossil teeth from Maboko range from -13.2‰ to -8.2‰ and have a median value of -10.7‰ (Table 3).

At Kipsaramon, $\delta^{13}C$ values have a range from -8.0‰ to -5.3‰ (Figure 6). These values are statistically more positive than carbon ratios from Maboko (P-value < .001). 14 of the 18 samples have $\delta^{13}C$ values > -8‰, suggesting mixed C_3/C_4 diets. The more negative $\delta^{13}C$ values for rhinocerotids relative to gomphothere indicate a greater potential dependence on C_3 browse for some of the rhinocerotids.

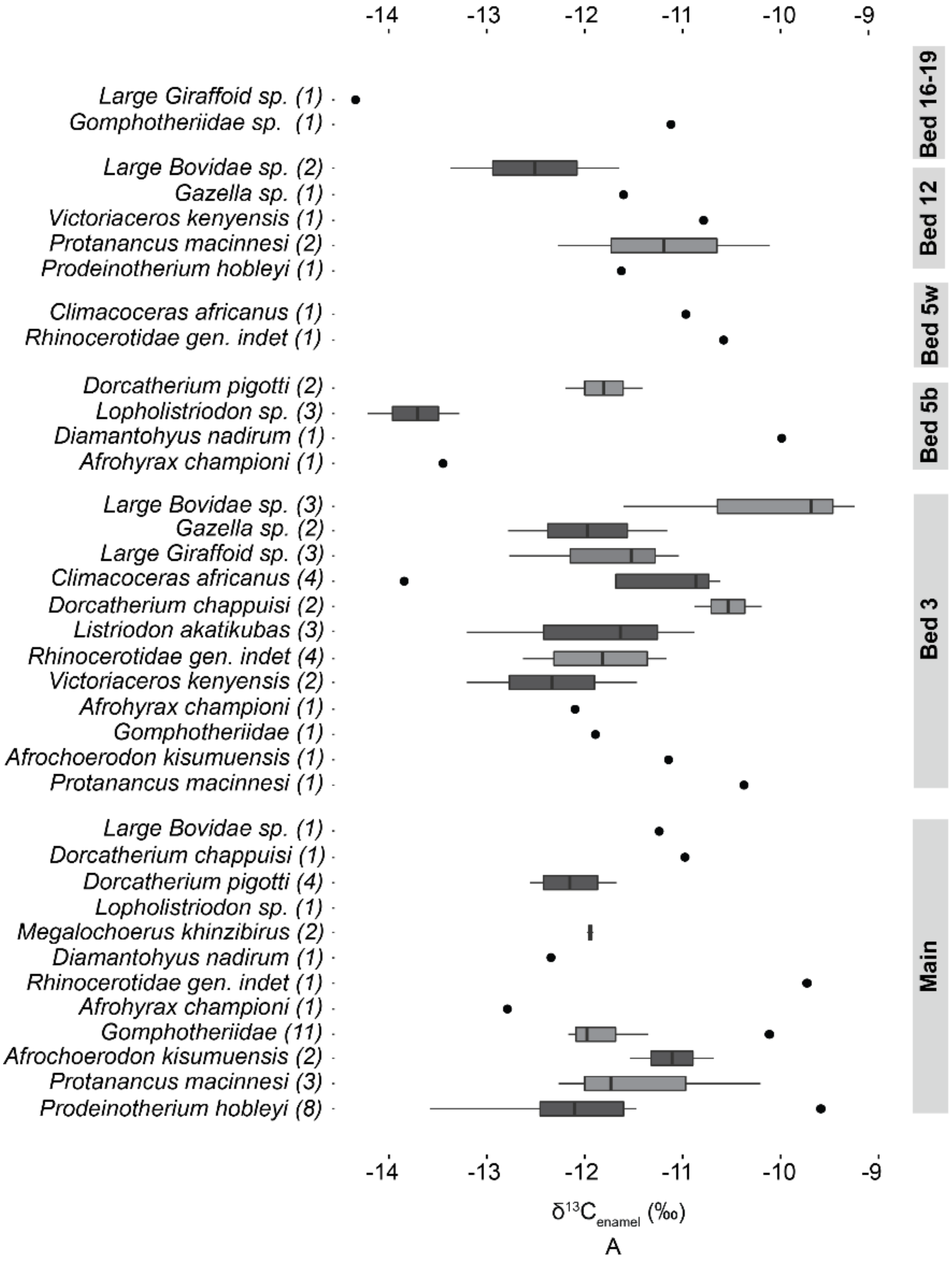

Figure 5. Stable carbon signatures from Maboko. Stable carbon values are arranged in stratigraphic order. Samples from older collections without stratigraphic information, indicated by "Main" at the base of the figure, are from the Maboko Main locality, which preserves Beds 3-5. All values are $\delta^{13}C_{1750}$ values. Plots are alternating dark and light grey for ease of visibility.

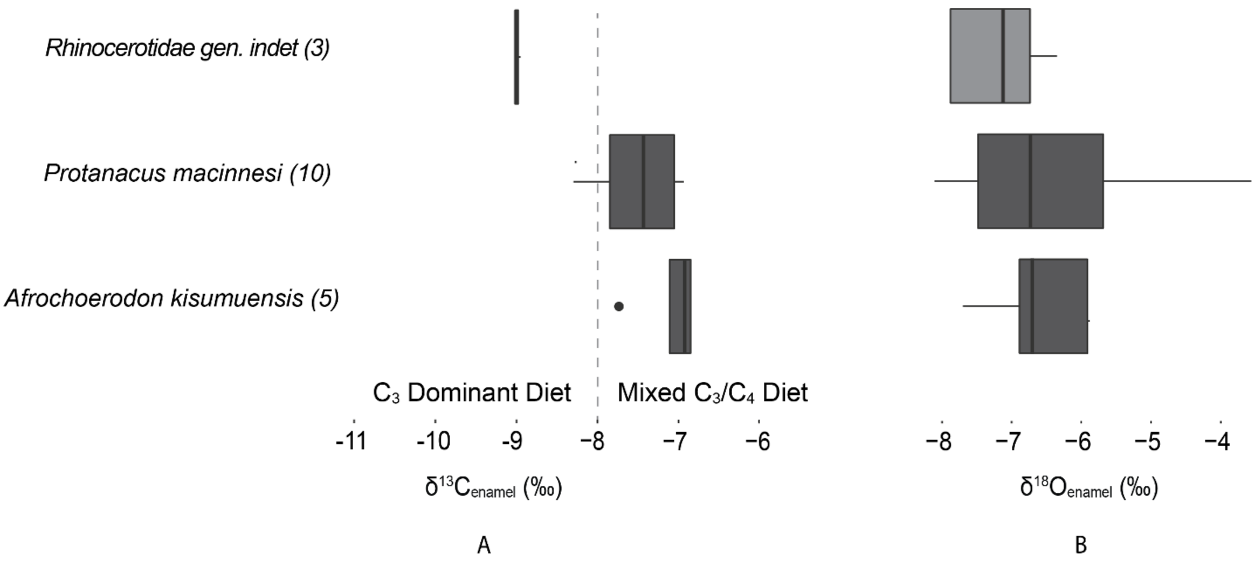

Figure 6. Box and whisker plots of carbon signatures from Kipsaramon. All δ^{13}Cvalues have been corrected to account for changes in $\delta^{13}C_{CO2}$ values.

Isotope Results by Taxa

Maboko

Proboscidea

Proboscidea material from Maboko has been attributed to three species, *Prodeinotherium hobleyi*, *Protanancus macinnesi*, and *Afrochoerodon kisumuensis* (Pickford, 2001; Retallack et al., 2002; Sanders, 2010). The choerolophodont material was previously referred to a *Choerolophodon kisumuensis* (Tassy, 1978), but has since been renamed *Afrochoerodon* by Pickford (2001). Most of the proboscidean material from Maboko was collected before 1988 and has no provenience data. The isotopic signatures from these taxa indicate similar foraging strategies. The ranges for dienothere and gomphothere samples overlap extensively and are consistent with an exclusive C_3 browsing signal (Figure 5; 7A). The low crowned, lophodont teeth of deinotheres indicate they were adept browsers with teeth that maintain cutting edges for processing browse and they are inferred to have likely maintained a C_3 browsing diet throughout their appearance in the African fossil record (Cerling et al., 1999; 2005; Sanders, 2010).

Prodeinotherium hobleyi $\delta^{13}C$ values range from -12.6‰ to -8.6‰ and are consistent with the pure C_3 browsing signal also found in carbon isotopic ratios of *P. hobleyi* from Nabwal Hills, Fort Ternan, Buluk, Nakali, and Lothogam (Cerling et al., 1999; Uno et al., 2011).

The low crowned, bunodont molars of early gomphotheres such as *Protanacus macinnesi* and *Afrochoerodon kisumuensis* are adapted for crushing and grinding (Tassy, 1986; Cerling et al., 1999). Gomphothere carbon isotopic values range from -11.3‰ to -8.9‰, with the range of $\delta^{13}C$ values for *P. macinnesi* encompassing all other gomphothere carbon values. *A. kisumuensis* $\delta^{13}C$ values range from -10.53‰ to -9.67‰. $\delta^{13}C$ values of modern elephants indicate mostly C_3 browsing diets with some mixed feeding.

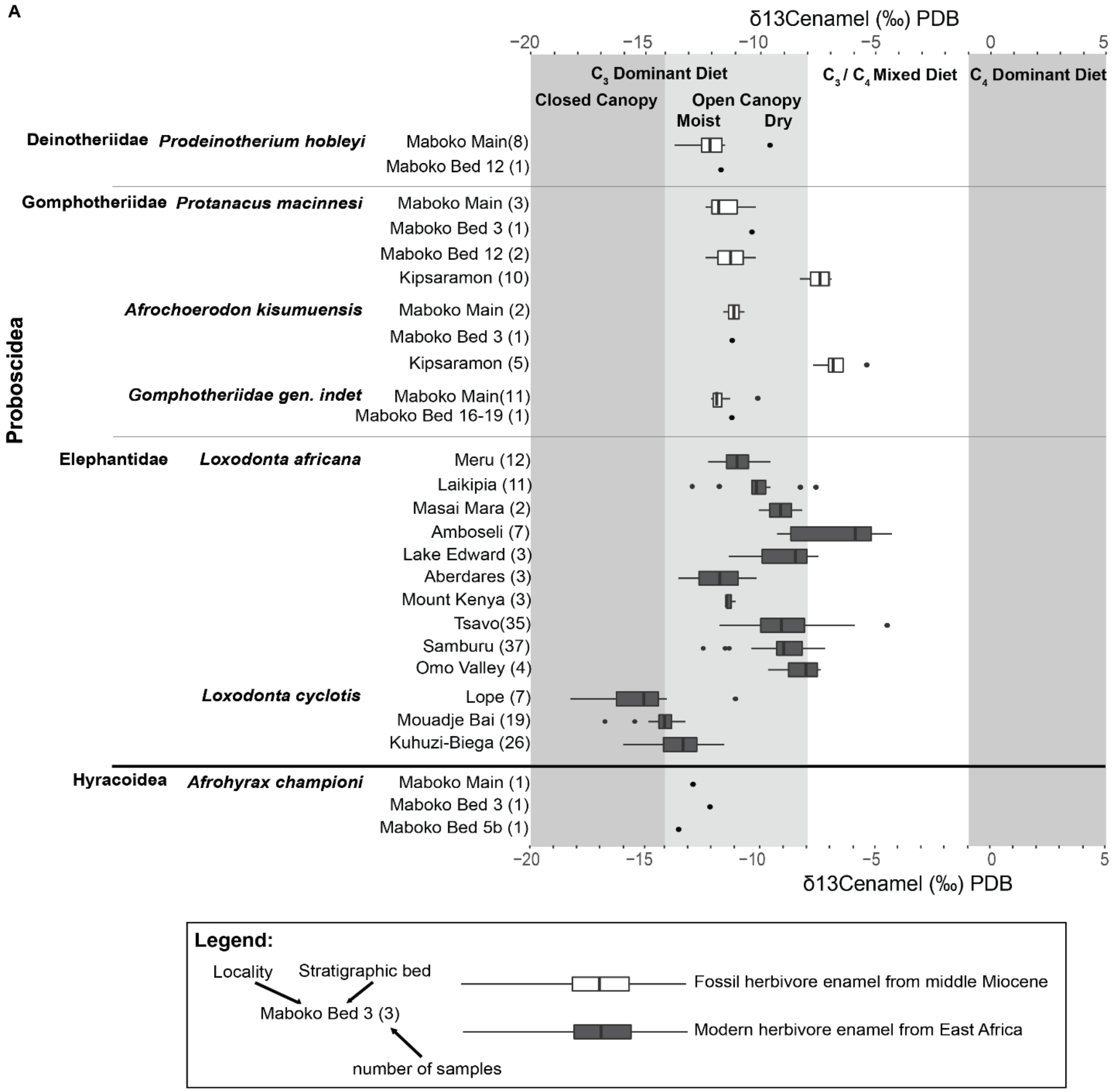

Figure 7 A-D. Box and whisker plots of δ13Cenamel of Maboko, Kipsaramon and relevant fossil and modern enamel samples. A) Proboscidea and Hyracoidea; B) Rhinocerotidae and Suoidea; C) Tragulidae and Giraffoidea; D) Bovidae. Modern, middle Miocene, and late Miocene samples are differentiated as indicated in the legend. Samples from Maboko are arranged temporally by stratigraphic bed with older samples above. Numbers in parentheses after locality indicate the number of samples analyzed. All modern and fossil samples have been corrected for differences in δ13C values atmospheric CO2.

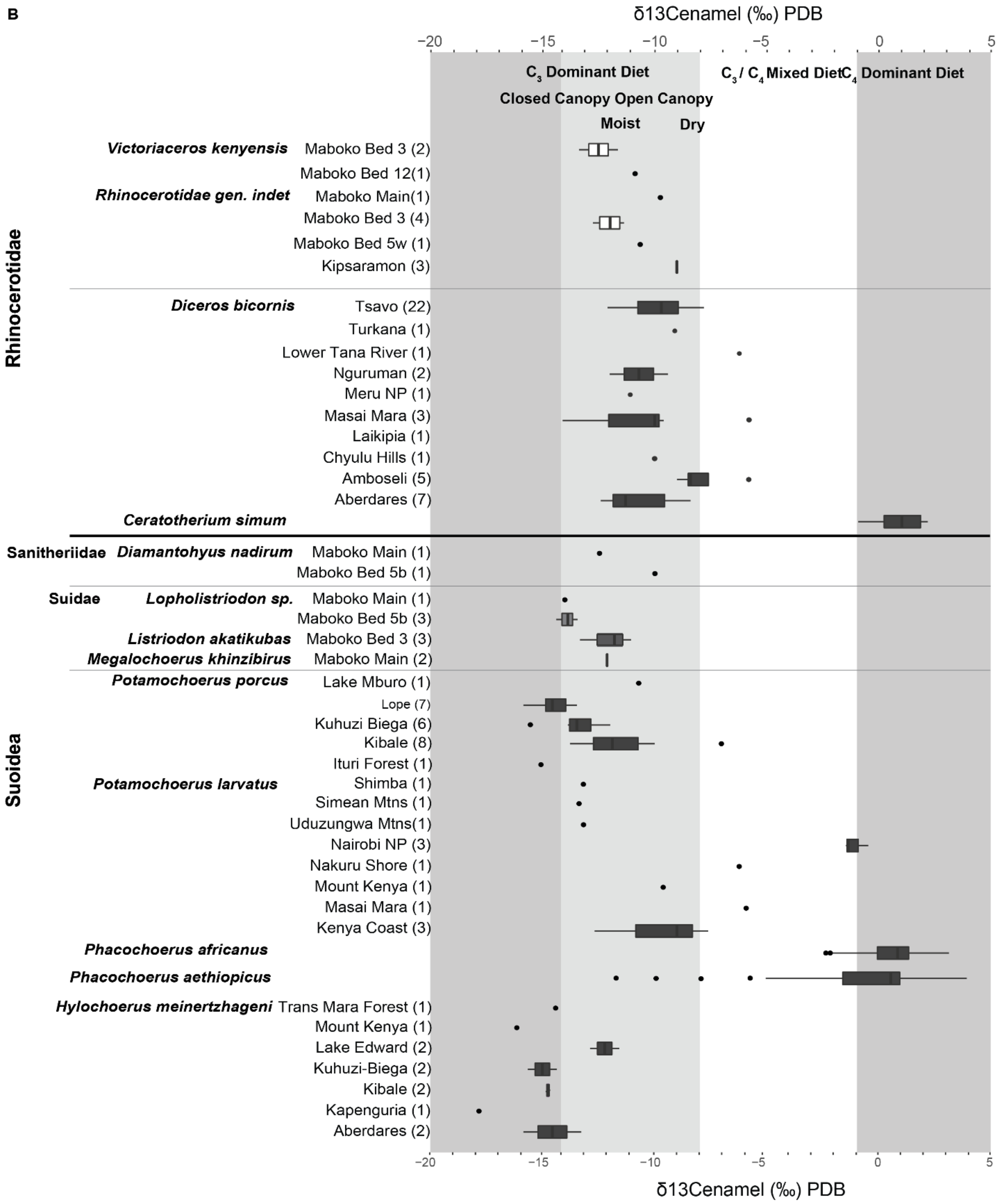

Figure 7 (Continued)

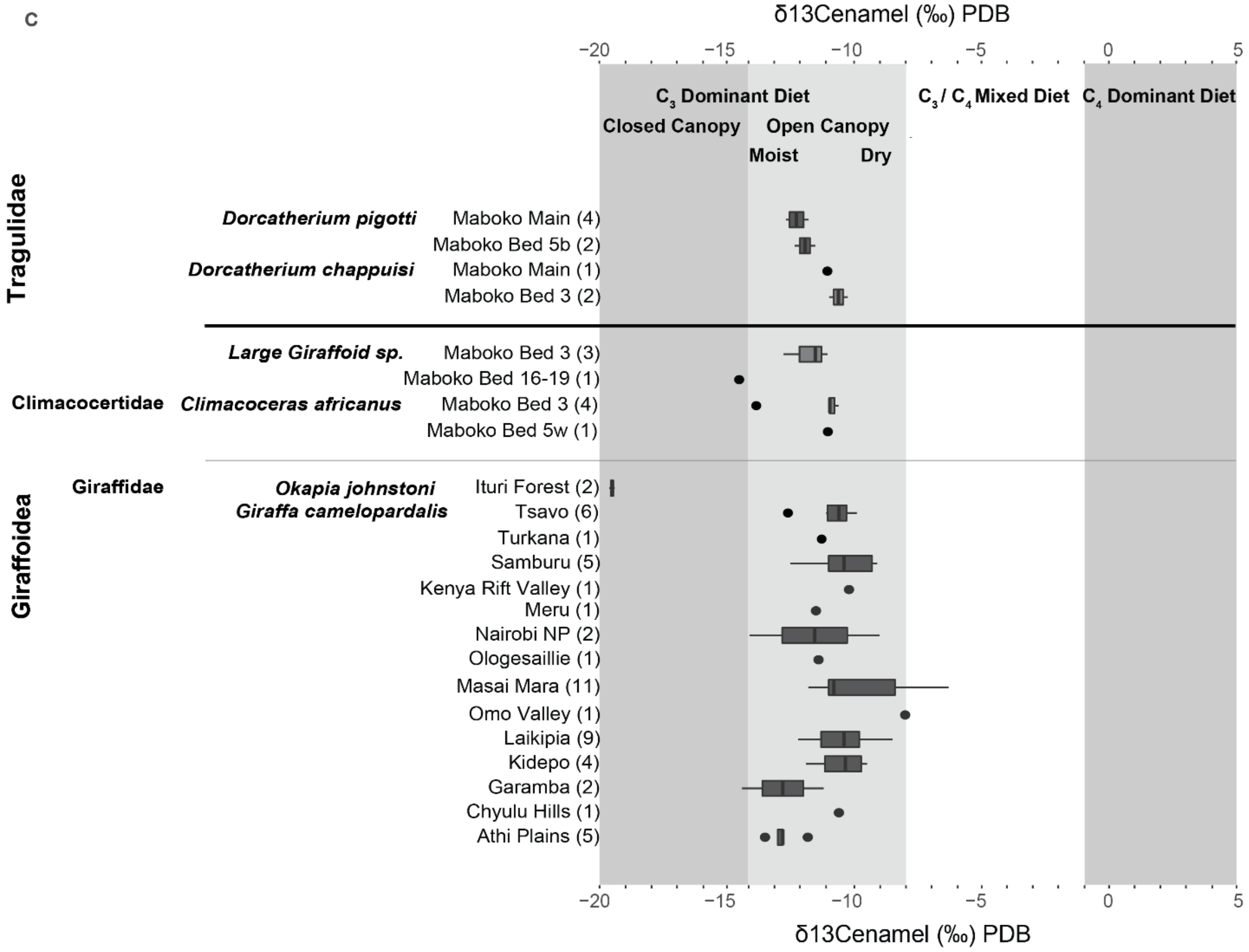

Figure 7 (Continued)

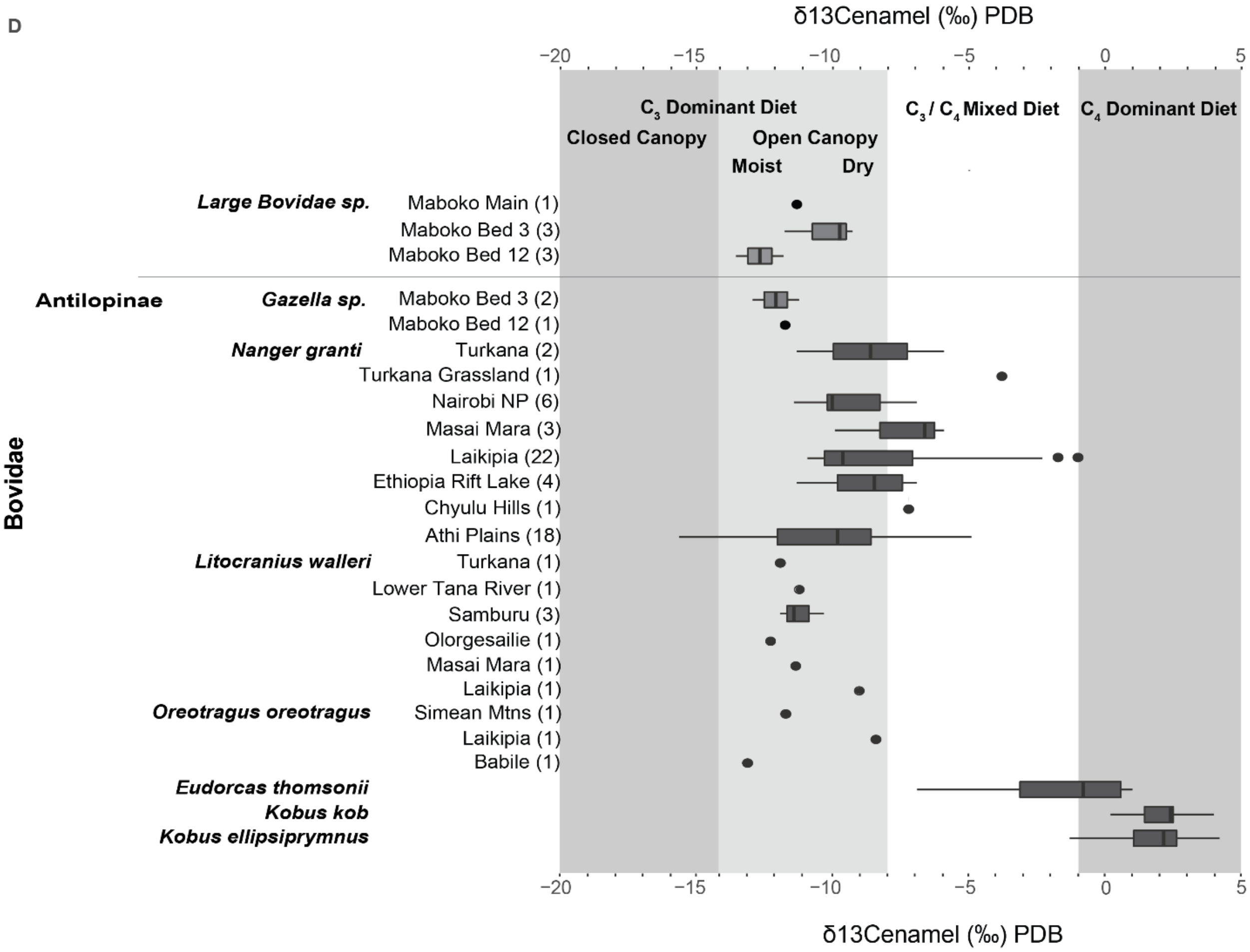

Figure 7 (Continued)

Gomphothere and deinothere δ^{13}C values from Maboko are similar to δ^{13}C values of *Loxodonta africana* (the African savanna elephant) sampled from evergreen mountain forest (Aberdares) and wooded grassland with riparian woodland (Meru) (Cerling et al., 1999; 2015). Some Maboko proboscidean δ^{13}C values also overlap with the lower δ^{13}C values of *L. africana* from a wooded grassland (Laikipia). The lowest *Prodeinotherium* δ^{13}C values overlap with the range of depleted values of *Loxodonta cyclotis* (the African forest elephant) from rainforest and evergreen mountain forest (Mouadje Bai and Kahuzi Biega; Figure 6).

Rhinocerotidae

At least three rhinocerotid species are present at Maboko. Material was previously attributed to *Brachypotherium heinzelini* and *Dicerorhinus leakeyi* (Andrews, 1981; Pickford, 1986; Retallack et al., 2002). However, a recent analysis of Maboko rhinocerotid material by Geraads et al., (2012) indicates the majority of rhinocerotid remains belong to the new species *Victoriaceros kenyensis*. Material not assigned to *V. kenyensis* has been assign to two groups of rhinocerotidae gen. indet, with the more robust material possibly assigned to aff. *Brachypotherium sp*. Material not confirmed to be *V. kenyensis* is referred to as rhinocerotidae gen. indet. Maboko is the type locality of *Victoriaceros kenyensis* (Geraads et al., 2012). *Victoriaceros*, and other rhinocerotid material from Maboko highlight a greater diversity for middle Miocene rhinocerotids than previously assumed (Geraads et al., 2012; 2016). *V. kenyensis* was put into the subfamily Elasmotheriinae, a sister group to the rhinocerotinae, which houses all living rhinos. Little is known about this genus and its dietary ecology. Rhinocerotid fossil represent approximately 2.3% of all mammalian fossils at Maboko (Table 5). Rhinocertids are absent from the purportedly more closed habitat of Bed 5b and their presence in Beds 3, 5w, and 12 are presumable consistent with interpretations of more open environments (Retallack et al., 2002; Geraads et al., 2012).

V. kenyensis $\delta^{13}C$ values and those of all other rhinocerotidae gen. indet teeth overlap extensively, indicating possible similarities in C_3 dominant browse feeding ecologies among Maboko rhinocerotids. The range of $\delta^{13}C$ values for *V. kenyensis* is -13.2‰ to -10.8‰ and all rhinocerotidae gen. indet range from -12.6‰ to -9.7‰. These wide ranges suggest variation in browsing strategies, but still fall within the range of variation of the extant browsing *Diceros bicornis* (black rhino) (Figure 7B). Maboko $\delta^{13}C$ values values are consistent with those of *D.*

bicornis from locations with wooded grassland (Masai Mara and Nguruman Escarpment) (Cerling et al., 2015) and open forest (Aberdares) (Cerling and Harris, 1999; Cerling et al., 2015).

Table 5. Number of mammal fossil from Maboko.

Taxon	Species	Bed 3	Bed 5b	Bed 5w	Bed 12	Bed 13-19
Primates						
Galagidae	*Komba winamensis*	1				
	Komba sp. nov.			1		
"Dendropithecoidea"	*Micropithecus (Simiolus) leakeyorum and cf. Limnopithecus evansi*	124	77	16	3	
Nyanpithecinae	*Mabokopithecus clarki and.Nyanzapithecus pickfordi*	5	177	4	1	
"Kenyapithecinae"	LBHM	120	132	19	12	
Cercopithecoidea						
Victoriapithecidae	*Victoriapithecus macinnesi*	840	1401	538		
Insectivora						
Erinaceidae	*Amphechinus rusingensis*	1	2	3		
Family indet.	sp. indet.	5		5		
Rodentia						
Thyronomyidae		2		1		
	cf. Paraphiomys pigotti, cf. P. stromeri, and Paraulacodus sp.n.					
	genus indet.	4	1	1		
Diamantomyidae	cf. *Diamantomys luederitzi*	2				
Bathyergidae	genus indet.	1				
Pedetidae	*Megapedetes pentadactylus*			1		
	Pedetes sp. indet.	16	5		1	
Cricetidae	genus indet.			1		
Family indet.	genus indet.	110	87	46	10	
Lagomorpha						
Family indet.	genus indet.	3		1		
Creodonta						

Hyaenodonta	*Anasinopa leakeyi*	7		4		
	Dissopsalis pyroclasticus			1		
	cf. *Pterodon nyanzae*	1	1			
	Hyaenailourus sp. indet.	13		10		
Family indet.	genus indet.	3		1		
Carnivora						
Canidae	cf. *Cynelos eurydon*	1				
Viverridae	cf. *Mioprionodon* sp.	1				
	genus indet.	5				
Family indet.	genus indet.	114	40	36	1	1
Tubulidentata						
Orycteropidae	*Orycteropus chemeldoi*	12	3	1		
Proboscidea						
Gomphotheriidae	*Protanancus macinnesi*	2				
	Afrochoerodon kisumuensis			1		
	genus indet.	29		4	4	1
Deinotheriidae	*Prodeinotherium hobleyi*	2				
Hyracoidea						
Pliohyracidae	*Afrohyrax championi*	14	54	6		
Family indet.	genus indet.	12	16	4		
Perissodactyla						
Rhinocerotidae	*Victoriaceros kenyensis*	137	1	4	3	
	Rhinocerotidae gen. indet.	41		3	4	5
Chalicotheriidae	genus indet.	1				
Artiodactyla						
Sanitheriidae	*Diamantohyus africanus*	7	13	2		
Tayassuidae	genus indet.	1				
Hippopotamidae	cf. *Kenyapotamus ternani*	8	3		1	2
	genus indet.	12				

Suidae	*Libycochoerus jeanelli* and *Megalochoerus khinzikebirus*	7			1	
	Listriodon akatikubas	14		5	1	2
	Listriodon sp. indet.	10		5		
	Lopholistriodon kidogasona		6			
	Namachoerus moruoroti	9	71	6		
	Lopholistriodon sp. indet.		4			
	genus indet.	73	102	19	1	
Tragulidae	*Dorcatherium parvum*	2				
	Dorcatherium pigotti	18	155	88		
	Dorcatherium chappuisi	72	14	23	4	
	Dorcatherium sp. indet.	191	771	128	9	2
Climacoceridae	*Climacoceras africanus*	572	85	165	19	4
	Palaeotragus sp. (Large Giraffoid sp.)	16			1	1
	Canthumeryx sp.			1		
Bovidae	*Eotragus* sp.	4	2			
	Hypsodontus pickfordi	1				
	Gazella sp.	1		1		
	Hypsodontinae sp. indet.		1			
	genus indet.	178	46	23	7	1
Family indet.	genus indet.	323	156	306	3	4
Order indet.	genus indet.	162	68	159	2	
Total specimens		3473	3494	1643	88	23

Numbers shown are numbers of specimens for that taxa. This table is modified from Retallack et al., (2002; Table 2). Bed numbers are from Pickford (1984; 1986a) and McCrossin et al., (1998). Specimen numbers are based on excavations by Benefit and McCrossin. Collections from Bed 3, 5b, and 5w are from the Maboko Main locality. Collections from Bed 12 are from S and SE localities and Beds 13-19 are from Maboko Cliffs. Taxonomic identifications are from Hamilton (1978), Pickford (1982; 1983; 1985; 2001), Thomas (1984, 1985), Cifelli et al, (1986), Benefit & McCrossin (1989), McCrossin (1992), Winkler (1992, 1994), McCrossin et al. (1998), Benefit (1999), Bishop (2010), Gentry (1994, 2010), Geraads (2010; 2012), Rasmussen and Gutierrez (2010).

Suoidea

Suoids include the sanitheriidae and suidae. While Plio-Pleistocene suids, are useful for relative dating and reconstructing hominin paleoecologies because of their rapid evolution and eclcectic feeding behaviors (Bishop, 1999; Harris and Cerling, 2002; Kingston and Harrison, 2007), those from the early and middle Miocene of East Africa are poorly known (Bishop, 2010). Past evaluations of Maboko suoid material indicates a highly diverse assemblage of suoids, including the sanithere *Diamantohyus africanus* and possibly up to six suid species, including *Namachoerus (Lopholistriodon) moruoroti*, *Lopholistriodon kidogosana*, *Listriodon akatidogus*, *Kubanochoerus mancharensis*, and *Listriodon* (*Bunolistriodon) akatikubas* (Van der Made, 1996). However, more recent surveys of Maboko's fauna indicate *Diamantohyus nadirum, Libycochoerus janelli*, *Listriodon akatikubas, Lopholistriodon kidogasona, Namachoerus moruoroti*, and *Megalochoerus khinzibirus* are present (Retallack et al., 2002; Bishop, 2010). Despite their high diversity, suoids make up a small proportion of the herbivore fauna (~ 4.1% of total mammalian specimens) (Table 5).

Four species of suoid were sampled for isotope analysis in this study: *Diamantohyus nadirum, Megalochoerus kinzikebirus, Listriodon akatikubas*, and *Lopholistriodon sp*. δ^{13}C values for *Lopholistriodon sp.* are lower than all other suoid species, indicating *Lopholistriodon sp.* likely had a different foraging strategy than other suoids at Maboko (Figure 5, 7B). The overlapping values of D. nadirum, *M. khinzibirus*, and *L. akatikubas* indicate more similar foraging strategies. *D.* nadirum and *L. akatikubas* values are more like those of *Potamochoerus porcus* from open to closed canopy forest (Kibale National Park) and values from *Hylochoerus meinertzhageni* (giant forest hog) from a wooded grassland (Lake Edward, N=2) (Nelson, 2013; Cerling et al., 2015). Carbon signatures of *P. porcus* from Kibale are higher than those from closed canopy forests (Ituri,N=2), Kuhuzi Biega N=2, and Lope N=2), which is consistent with Kibale's classification as an open to closed canopy forest (Nelson, 2013). In addition, $\delta^{13}C$ values of *H. menertzhageni* from a wooded grassland (Lake Edward; White, 1983), are higher than values from open to closed or "closed" canopy forests (Kibale, Kuhuzi Biega, and Aberdares; White, 1983). $\delta^{13}C$ values of *Lopholistriodon sp*. from Bed 5b overlap with the lower $\delta^{13}C$ values of *P. porcus* from closed canopy forests (Kuhuzi Biega and Lope; Cerling et al., 2015; Martin et al., 2015), suggesting *Lophoistriodon sp*. possibly foraged in more covered habitats than *Diamantohyus, M. khinzibirus* and *L. akatikubas*.

Giraffoidea

Giraffoids from have been assigned to three genera *Climacoceras africanus*, *Paleotragus sp.,* and *Canthumeryx sp.* (McInnes, 1936; Thomas, 1984; Pickford, 1986). However, *Canthumeryx* is extremely rare, represented by a single specimen (Retallack et al., 2002). Maboko was long cited to preserve the earliest appearance of climacoceratid giraffoids (McInnes, 1936; Hamilton, 1976; McCrossin et al., 1998), however, a cranial appendage from Kalodirr has been recently assigned to *Climacoceras* (Grossman and Solounias, 2014). Giraffoid specimens too large to be *Climacoceras africanus* have been assigned to *Paleotragus* by McCrossin and Benefit (Retallack et al., 2002). However, a review of giraffoid systematics by Harris et al., (2010) does not recognize the presence of *Palaeotragus* during the Miocene of Kenya. Until this giraffoid material is studied further, these large giraffoid specimens will be referred to as Large Giraffoid sp.

Climacoceras africanus is the most abundant giraffoid on Maboko (comprising approximately 97.8% of giraffoid specimens) (Table 5). *Climacoceras* varies in abundance between the Maboko Beds and is the least abundant in Bed 5b (2.4% of all mammalian fossils in

Bed 6b). Further, large giraffoid material represents only 2.0% of all giraffoid specimens. It co-occurs with *Climacoceras* in Bed 3 (.46% of all mammalian fossils in Bed 3) but is absent from Bed 5 and extremely rare in the upper Beds 12-16. Several thousand fossils are known from both layers of Bed 5 and only 111 have been recovered from Beds 12-16 (Table 5). Sampling the large giraffoid in such a small sample from Beds 12-16 relative to density of fossils in Bed 5 suggest Bed 5 represents an ecosystem not favorable to this animal. Little is known about *Climacoceras* anatomy (Pickford et al., 2001) and that of the large giraffoid species at Maboko.

δ^{13}C values for all giraffoids at Maboko range from -13.1‰ to -9.6‰ (Table 3). The range of *Climacoceras* δ^{13}C values appears to be larger and encompasses the range of δ^{13}C values of the large giraffoid sp. (Figure 7C). However, one *Climacoceras* δ^{13}C value of a second molar from an adult mandible from Bed 3 is extremely low relative to all other values for this species. All other *Climcacoceras* δ^{13}C values are higher and do not overlap with values from *Large Giraffoid sp*., indicating possible slight differences in feeding ecology. A single carbon value of a *Large Giraffoid sp*. lower first molar from Beds 16-19 is lower than all other giraffoid carbon values and is < -14‰ after correction for changes in atmospheric CO_2, which suggests possible forested elements present later in time. However, it is possible that this low value is the product of sampling preweaning diet.

While Maboko giraffoid δ^{13}C values fall within the range of C_3 dominant diets, they do not fall within the range of δ^{13}C values for the Okapi (*Okapia johnstoni*, N=2) from the Ituri Forest, a closed forest subcanopy browser (Cerling et al., 2004). Modern giraffes (*Giraffa camelopardalis*) are C_3 browsers in open canopied forests and woodland with approximately 10% of δ^{13}C values falling within the range of mixed C_3/C_4 diets (Cerling et al., 2015). Maboko giraffoid δ^{13}C values are more similar to carbon ratios of modern *Giraffa* from riparian with wooded grassland (Tsavo), mixed woodland to grassland (Nairobi National Park), and wooded grassland (Masai Mara) habitats (Cerling et al., 2015).

Bovidae

Bovid material preserved at Maboko represents the earliest appearance of bovids in East Africa (Thomas, 1984). Retallack et al. (2002) list the following bovid taxa at Maboko: *Eotragus sp., Nyanzameryx (Hypsodontus) pickfordi*, *Gazella sp.*, and Hypsodontinae sp. indet. A recent review of African Bovidae by Gentry (2010) indicates Maboko preserves only two bovid species, *Hypsodontus pickfordi*. and *Homoiodorcas sp.* However, Gentry's (2010) identifications do not include material recovered by Benefit and McCrossin and cited in Retallack et al. (2002). The bovid material is currently under study by McCrossin and Geraards. Until this material is published, it is still unclear as to how many species of bovid are present Maboko. The occurrence of *Eotragus* in Africa is still uncertain (Suraprasit et al., 2015) and two horn cores from Maboko previously referred to the genus have been placed in Hypsodontinae (Morales et al., 2003), and have been considered to be morphologically comparable to *Homoiodorcas* (Thomas, 1981). For this study, at least two species of bovid were sampled. Smaller bovid dental specimens are assigned to *Gazella* sp. (Thomas, 1979) and a second, larger species whose identity remains to be clarified (it could be *Hypsodontus* based on the larger molar size (Gentry, 2010)) is referred to as Large Bovidae sp. (Figure 5; 7D). Based on specimen counts in Table 4, bovids are more abundant in Bed 3, making up 5.2% of all mammalian fossils from that Bed. Bovids are rarer and less well preserved in Bed 5 and no dental specimens were available for sampling.

The Maboko bovid material represents some of the earliest crown bovid material, but their relationships to modern bovids are unclear, making direct comparisons to modern tribes difficult. Fossil bovid carbon values were compared to carbon values of modern members of the subfamily Antilopinae (Harris and Cerling, 2002; Cerling et al., 2003; Levin et al., 2008; Van der Merwe, 2013; Cerling et al., 2015) since one of the Maboko species sampled, *Gazella sp*., is also member of this subfamily (Gentry, 2010). Maboko bovid $\delta^{13}C$ values range from -12.2‰ to -8.2‰ (Table 3) and are consistent with modern browsing antilopines (Figure 7D). Carbon values from Maboko fall within the total range of carbon values for the Grant's gazelle (*Nanger granti*) from the wooded grassland habitat at Athi Plains in Kenya (Levin et al., 2008; van der Merwe, 2013; Cerling et al., 2015). Interspecific and intraspecific variation of carbon values within and between beds suggest possibly niche partitioning between bovid species and dietary changes through time (Figure 5; 7D). First, $\delta^{13}C$ values for *Gazella sp.* (n=2) from Bed 3 are lower relative to values from *Large Bovidae sp*. (n=3) from Bed 3. The average $\delta^{13}C$ value of *Gazella sp*. is 1.8‰ lower than the average $\delta^{13}C$ value *Large Bovidae sp*. This difference is equivalent to the 1.9‰ difference between the mean $\delta^{13}C$ value of canopy foragers and gap clearing foragers in the Ituri Forest (Cerling et al., 2004). Second, the $\delta^{13}C$ values of the *Large Bovidae sp*. (n=3) from Bed 3 are higher than values from Bed 12 (n=3) for this taxon and differ on average by approximately by 2‰, indicating a dietary shift from Bed 3 to Bed 12 (Figure 5; 7C). This suggests that large bovids from Bed 3 may have fed on more water stressed vegetation than large bovids from Bed 12, which likely fed on more moist vegetation.

Tragulidae

Two species of tragulids were sampled in this study, *Dorcatherium pigotti* and *Dorcatherium chappuisi*. Some have proposed at least two additional species are likely present at Maboko, *D. parvum* and *D. libiensis,* (Pickford, 2001; Retallack et al., 2002). However, *D. libiensis* has recently been absorbed into *D. pigotti* (Geraads, 2010), making only three species of tragulid recognized at Maboko. Species percentages reported in Retallack et al., (2002) indicate

D. parvum is rare (only 0.06% of all mammalian fossils in Bed 3); however, hundreds of *Dorcatherium* sp. indet specimens have yet to be studied in detail. *Dorcatherium* material is highly abundant throughout the Maboko Beds (18.8% of all mammalian material) and show considerable variation between stratigraphic layers. *Dorcatherium* fossils are most abundant in Bed 5b (26.9%), possibly indicating more forested conditions (Benefit, 1999; Gitau et al., 1998). However, as shown below, the carbon isotope values (-11.6 to -9.2) for *Dorcatherium* in Bed 5b do not fall within values associated with foraging in closed canopied forests (Figure 5; 7D). Tragulids are less common in Beds 3 and 5w (12.8% and 14.5% of mammalian fossils, respectively). Until tragulid material collected between 1988-1997 is studied in detail, the number of tragulid species within each Bed remains unknown.

The molars of fossil tragulids are more selenodont than the only living African tragulid species, *Hyemoschus aquaticus* (the water chevrotain). *H. aquaticus* has bunodont molars (Geraards, 2010) and is a frugivore/browser that inhabits the closed canopied forests near fresh water sources in west and central Africa (Webb, 1998). Little research has been conducted on the stable isotope dietary ecology of the water chevrotain. However, an upper third molar of *H. aquaticus* from the closed canopied Ituri Forest in the Democratic Republic of Congo has a $\delta^{13}C$ value of -13.9‰ (Cerling et al., 2004) which is at the more positive limit of closed canopied forest foraging.

For the *D. pigotti* and *D. chappuisi* teeth sampled, all $\delta^{13}C$ values fall within the range of C_3 dominant diets but are above the range for closed canopy subcanopy browsers. Further, the range of $\delta^{13}C$ values for each species do not overlap. *D. pigotti* has a range of values from -11.6 ‰ to -10.4‰ and *D. chappuisi* has a range from -10.0‰ to -9.2‰ (Figure 5; 7C), indicating a possible difference in foraging strategies. While the $\delta^{13}C$ differences between species could be due to differences in the amount of C_3 grasses versus browse in the species' diets, the contrasting values could also be attributed to habitat differences between Beds 3 and 5b, since *D. chappuisi* was sampled from Bed 3 and *D. pigotti* was sampled from 5b. All other *Dorcatherium* $\delta^{13}C$ values have no provenience data. Additional sampling of *D. pigotti* from Bed 3 and *D. chappuisi* from Bed 5 will determine if *Dorcatherium* species changed their diet through time and/or partitioned their diets within the same ecosystem.

The overall higher (by ≥ 1.3‰) $\delta^{13}C$ values for the tragulids are unlike those of their aquatic, subcanopy forest dwelling living descendent. However, when considered in a broader evolutionary context, these results are consistent with fossil tragulid $\delta^{13}C$ values from Eurasia, which imply ancient tragulid diets likely had a wider range of dietary variation including browsing and general feeding in closed canopied forest, open forests, and open woodlands than their modern relatives (Nelson et al., 2003; 2007; Merceron et al., 2009; 2012; Aiglstorfer et al., 2014; Eastham et al., 2016).

Hyracoidea

Hyracoid material from Maboko has been attributed to one species, *Afrohyrax championi* (Retallack et al., 2002; Rasmussen and Gutiérrez, 2010). *A. championi* is considered a cursorial mammal with some folivory that occupied more open environments (Whitworth, 1954; Tsujikawa and Pickford, 2006). Hyracoid material makes up a small percentage of the total mammalian fauna at Maboko (1.2% of all mammal specimens) with *A. championi* comprising only 0.8% of all mammal specimens (Table 5). Three *A. championi* teeth were sampled in this study. $\delta^{13}C$ values range from -12.3‰ to -11.1‰ (Table 3). When corrected for change in $\delta^{13}C$ values of paleoatmospheric CO_2, *A. championi* $\delta^{13}C$ (-13.4 to -12.1‰) values are consistent with C_3 hyperbrowsers but not with occupying the moist open areas (Figure 7C). Extant African hyraxes inhabit a variety of environments such as moist, tropical forests, moist and dry savanna, and rocky areas, and feed on both browse and graze (Kingdon, 1971; DeNiro and Epstein, 1978; Milner and Harris, 1999; Barry et al., 2008). Though carbon isotopes of bone carbonate demonstrate differences in feeding ecology between sympatric hyrax species (DeNiro and Epstein, 1978), enamel stable isotope ecology of extant hyraxes has yet to be investigated.

Kipsaramon

Proboscidea

Proboscidea material from Kipsaramon has also been attributed to three species (Behrensmeyer et al., 2002; Sanders, 2010), *Prodeinotherium hobleyi*, *Protanancus macinnesi*, and *Afrochoerodon kisumuensis*. *Protanancus* and *Afrochoerodon* molar $\delta^{13}C$ values indicate mixed C_3/C_4 diet with values ranging from -7.3‰ to -5.3‰ (Figure 6, 7A, Table 3). Isotopic signatures for gomphothere taxa, *Protanancus macinnesi* and *Afrochoerodon kisumuensis* at Kipsaramon show some overlap, which indicates a possible similarity in foraging strategies. However, two *A. kisumuensis* $\delta^{13}C$ values are more enriched than all *P. macinnesi* samples. The range of fossil gomphothere $\delta^{13}C$ values are consistent with carbon isotope ratios of *L. africana* from a grassland to wooded grassland ecosystem (Amboseli), where $\delta^{13}C$ values fall within the range of mixed feeding (Figure 6a). The Kipsaramon proboscidean $\delta^{13}C$ values overlap with gomphothere $\delta^{13}C$ values from the late Miocene locality of Samburu Hills (9.6-9.3 Ma), supporting our conclusion that they participated in some mixed C_3/C_4 feeding (Figure 8, 9).

Rhinocerotidae

Rhinocerotid material from Kipsaramon was first attributed to *Aceratherium acutirostratum* by Pickford (1988) but has since been reassigned to Rhinocerotidae indet (Behrensmeyer et al., 2002; Geraads, 2010). Material recovered from the Baringo Paleontological Research Project (Hill et al., 1986) housed at the Kenya National Museum has yet to be studied in detail. While it is recognized that rhinocerotid fossils from Kipsaramon have been attributed to *Dicerorhinus leakeyi* and *Aceratherium acutirostratum* by Guérin (2011), such attributions are based on material not found by the Baringo Paleontological Research Project and are not housed at the National Museums of Kenya. The three rhinocerotid teeth sampled in this study will be referred to Rhinocerotidae indet.

The three $\delta^{13}C$ values for rhinocerotid specimens are all equal to -9.0‰. These values fall within the range of C_3 dominant diets and outside the range of all rhinocerotid material from Maboko (-12.6‰ to -9.7‰) (Figure 7B). Values are consistent with the higher values of the browsing black rhino from a riparian forest with wooded grassland habitat (Tsavo) (Cerling et al., 2015). This suggests Kipsaramon rhinocerotids could have foraged on more xeric C_3 plant material or incorporated a small amount of C_4 material into their diet.

Summary and comparison

Collectively, carbon isotopic samples of Maboko herbivores indicate a tendency towards pure C_3 browsing with no taxa engaging in exclusive closed canopied subcanopy browsing. Important findings from Maboko include: (1) the negative $\delta^{13}C$ values of *Lopholistriodon sp.* from Bed 5b, which indicate the possible presence of more extensive wooded/forested habitats relative to Beds 3 and 12 and (2) a possible dietary shift from foraging in more open and water stressed vegetation to foraging in more closed and/or moister areas among the large bovidae sp.

between Bed 3 and Bed 12. As more herbivore taxa from Maboko are studied and additional specimens are sampled, further comparisons of intraspecific feeding ecologies between Beds can be made.

Carbon isotopic values from Kipsaramon indicate a tendency towards mixed C_3/C_4 foraging strategies among proboscidean taxa while rhinocerotids likely incorporated more C_3 browse. Proboscideans from Kipsaramon show major differences in foraging strategies compared to those from Maboko, with Kipsaramon proboscideans foraging on more water stressed plants and incorporating some C_4 biomass into their diet. While the number of taxa available for sampling at Kipsaramon was limited to two proboscidean species and rhinocerotidae, the range of $\delta^{13}C$ values do not overlap between the two sites. This indicates a range of foraging habitats were available during the middle Miocene.

Discussion

Maboko and Kipsaramon Paleoecology

The Maboko fauna sampled in this study have enamel $\delta^{13}C$ values consistent with a diet of pure C_3 vegetation. This finding is in accordance with previous isotopic studies of Miocene ecosystems in East Africa, which suggest herbivores had predominantly C_3 diets prior to 10 Ma (Kingston, 1992; Cerling et al., 1997; 1999; 2003a; Morgan et al., 1994; Uno et al., 2011) and is compatible with previous interpretations that indicate the presence of woodland with more closed and forested elements (Evans et al., 1981; Pickford, 1983; Retallack et al., 2002). The range of Maboko enamel $\delta^{13}C$ values is equivalent to a dietary $\delta^{13}C$ value range of -28.3‰ to -23.3‰, utilizing a -14‰ fractionation. These dietary values resemble $\delta^{13}C$ values of C_3 plants from open forests, bushlands, and mesic savannas from Kenya, which have $\delta^{13}C$ values of -27.8‰ ± 0.3‰,

-27.0‰ ± 0.2‰, and -24.6‰ ± 0.3‰, respectively (Cerling and Harris, 1999; Cerling et al., 2003a).

Most carbon values from Maboko indicate the presence of open canopied forest and woodland. In Retallack and colleague's (2002) paleosol analysis, the green clay of Bed 3 was interpreted as a swale deposit with no paleosol formation and therefore its paleoenvironment was not interpreted. Most δ^{13}C values from Bed 3, except for one *Climococeras* value, are ≥ -13‰ and consistent with woodland to bushland type habitats. Large Bovidae sp. (-11.6‰ to -9.2‰) and *D. chappuisi* (-10.8‰ to -10.2‰) teeth from Bed 3 have the highest carbon values and translate to a dietary δ^{13}C value range of -25.7‰ to -23.3‰, which falls within the range of δ^{13}C values of C_3 plants from modern Kenya bushland and grasslands (Samburu and Turkana; Cerling and Harris, 1999). Carbon values from Bed 12 are similar to Bed 3, in line with predominantly open woodland with broken canopy (Figure 5).

δ^{13}C values from *Lopholistriodon sp.* (-14.2‰ to -13.3‰), *A. championi* from Bed 5B (-13.4‰) are < -13‰ and indicate the possible presence of more dense covering. The enamel δ^{13}C values for these taxa are consistent with dietary δ^{13}C values that range from -28.2‰ to -27.3‰, which fall within the range of the carbon isotopic composition of C_3 plants from Afromontane forests such as Aberdare National Park, Kenya (−27.8 ± 0.3‰; Cerling et al., 2003) and the upper range of Bwindi Impenetrable National Park, Uganda (-28.1‰ ±2.2‰; Blumenthal et al., 2012). The presence of tree cover in Bed 5b is also supported by cited presence of tree root traces and stump casts (Retallack et al., 2002). The multiple low δ^{13}C values from Bed 5b could be suggestive of more closed habitats, but this inference is tenuous with the current sample size.

In contrast to Maboko, δ^{13}C values from Kipsaramon proboscideans show that they consumed a diet of mixed C_3/C_4 vegetation. The δ^{13}C values from BPRP #89 presented here are similar to $\delta^{13}C$ values of rhinocerotid (-7.4‰) and proboscidean (-8.5‰) teeth from the adjacent site BPRP#91 (Kingston, 1992; Morgan et al., 1994). Of the 19 teeth sampled from Kipsaramon, 14 have $\delta^{13}C$ values greater than the -8‰ cut off for C_3 diets. The rhinocerotidae and proboscidean carbon values give an estimated vegetation $\delta^{13}C$ value range of -23.1‰ to -19.5‰, which is more positive than the range of $\delta^{13}C$ values for modern African C_3 plant and more negative than the range of modern C_4 values. This lends support to the inference of mixed feeding, particularly in gomphothere diets at Kipsaramon. Using the two end-member mixed model from Uno and colleagues (2018), Kipsaramon proboscidean mixed feeders have a diet that ranges between 19.5% and 38.2% C_4 biomass. Given the large size of proboscideans, the available C_4 biomass in the environment must be significant to contribute up to 38.2% of their diet. Though gomphothere and possibly rhino diets incorporated some C_4 biomass at Kipsaramon, it is not known at this time how many other mammalian guilds also had mixed C_3/C_4 diets.

An estimate of up to 38.2% dietary C_4 biomass implies C_4 vegetation must have been an important component in the ecosystem, more so than previously captured by past enamel (Kingston, 1992: Morgan et al., 1994) and pedogenic carbonate and organics (Kingston et al, 1994), and suggests a mixed habitat of woody cover and some grassland. C_4 plants are adapted to higher temperatures, drier conditions, and low atmospheric CO_2 levels and are associated with open grasslands (Cerling et al., 1997b, 2015; Sankaran et al., 2005). Therefore, environmental conditions at Kipsaramon are interpreted to be drier and/or hotter and more open than Maboko in order to sustain a moderate level of C_4 biomass. This is in line with previous interpretations of open areas as suggested by the presence of pedetid rodents (Winkler, 1992; 2002).

Maboko and Kipsaramon catarrhine environments

The enamel δ ^{13}C values presented here are consistent with Maboko catarrhines living in a mosaic of open forested/woodland and possible bushland habitats. There is some evidence from Bed 5b that it was likely more closed than other Beds. Four of the seven samples from Bed 5b are depleted and are lower than -13‰, suggesting *Lopholistriodon sp*. and *Afrohyrax* could have been feeding in more closed woodland conditions relative to carbon values from Bed 3, which are higher than -13‰. However, more data is needed to see if diets of other mammalian species are also depleted relative to other Beds. At Maboko, the primate taxa have distinct distributions (Benefit, 1999; Retallack et al., 2002). LBHM and small catarrhine (*Simiolus leakeyorum*) material are found throughout Maboko's fossiliferous section (Bed 3, 5, and 12, Table 4 above). However, *Victoriapithecus* is only present in Beds 3 and 5. Nyanzapithecines (*Mabokopithecus*) are restricted to a single stratigraphic level, Bed 5b (Retallack et al., 2002). While differences in the proportions of primate and other mammal species between Maboko beds are suggested to support possible habitat differences between Maboko's Beds (Retallack et al., 2002), it is recognized that the current sample of bulk δ^{13}C values are not sufficient to support such claims. Additional sampling is necessary to examine mammalian interspecific dietary strategies across stratigraphic beds to address whether habitats differed through time. Also, isotopic sampling of Maboko catarrhine enamel would provide additional clues to their preferred habitats within Maboko's environments.

Isotopic evidence does supports previous statements that terrestrial adaptations among LBHM and the small bodied *Victoriapithecus* occurred in more wooded habitats such as open forest/closed woodlands habitats (Retallack et al., 2002; Blue et al., 2006). Published body mass estimates for *Victoriapithecus* (Gingerich et al. 1982; Conroy 1987; Harrison, 1989; Delson, 2000; Blue et al., 2006) are similar to *Chlorocebus aethiops*, a small bodied, terrestrial cercopithecine that strictly uses gallery forests and woodland habitats within the savanna and grassland localities they inhabit likely for predator protection, access to water sources, and food sources which are closer spaced together than more open habitats (Kavanagh, 1981; Nakagawa, 1999). The more wooded habitats at Maboko would have also supported the small bodied ape, *Simiolus*, and the purported acrobatically arboreal nyanzapithecines (McCrossin, 1992). Future research on the carbon and oxygen isotopic signatures of Maboko's catarrhines would provide additional information on their dietary foraging habits and possible habitat preferences.

At Kipsaramon, enamel isotopic results suggest catarrhines were living in a more open environment than previously expected. It is currently not clear as to how much woody cover was present at Kipsaramon. The presence of flying squirrels has been used to suggest the presence of forested habitat (Winkler, 1992; 2002). The catarrhine primates from Kipsaramon would have likely experienced similar challenges faced by extant catarrhines living in open, non-forested environments. Modern catarrhines living in open environments such as woodland and savannas (i.e. *Pan troglodytes versus, Erythrocebus patas, Papio,* and *Chlorocebus aethiops*) experience differences in water availability, food availability and distribution (Pruetz and Isbell 2000), increased solar radiation and high temperatures (McGrew et al., 1981; Hill et al., 2004; Hill, 2006), and increased predation risk (Hill and Dunbar, 1998) relative to catarrhines living in forested environments. These factors influence microhabitat preference within a mosaic environment (e.g. Pruetz and Isbell, 2000; Enstam and Isbell, 2004) and activity levels (Hill, 2006). Kipsaramon primates would have also preferred different habitats within their environment based on their size and adaptations. For example, small bodied, terrestrial monkeys such as *Chlorocebus aethoiops tantalus* primarily inhabit gallery forests and woodlands

(Nakagawa, 1999) where food patches are larger and more closely spaced (Pruetz and Isbell, 2000). Also, water is more consistently available, and woody cover supplies protection from predators (Nakagawa, 1999). However, the larger bodied, sympatric *Erythrocebus patas* can utilize grasslands more efficiently likely because of cursorial terrestrial adaptations allow it to access even sparsely distributed food items more quickly (Nakagawa, 1999).

Middle to late Miocene mammalian diets and catarrhine habitats

The isotope data presented here illustrates regional patterns of dietary variation and allows for a deeper temporal evaluation of herbivore diets and catarrhine environments than previously published for the Miocene of East Africa (Cerling et al., 1997; Uno et al., 2011). Isotope data from East African Middle Miocene to early Pliocene fossil sites associated with hominoids were compiled (Figure 8). In general, during the middle Miocene, $\delta^{13}C$ values show a diversity of mammal diets, and therefore possibly habitats, including mainly C_3 browsing and some mixed feeding. Mammal diets, during the late Miocene, became more diverse to include more mixed feeding taxa and grazing.

$\delta^{13}C$ values from Kipsaramon are statistically different from those from Maboko and Fort Ternan (P-value < .01) and statistically similar to values from Samburu Hills (9.6-9.3 Ma; Sawada et al., 1998; Uno et al., 2011). On the other hand, Maboko and Fort Ternan's carbon values are not statistically different from each other and indicate open forest/woodland environment. This result is consistent with the large number of paleoecological studies on Fort Ternan that favor a C_3 dominated mosaic habitat with open to closed woodland/brushland and some grasslands (Evans et al., 1981; Shipman et al., 1981; Pickford, 1983; Bonnefile, 1984; Retallack et al., 1990; Kappleman et al., 1991; Retallack, 1992; Dugas and Retallack, 1993) with little to no C_4 isotopic input (Cerling et al., 1991, 1997) (although some plant fossils have been identified to the C_4 Chlorideae subfamily (Retallack et al., 1990; Dugas and Retallack, 1993). The similarity between Maboko and Fort Ternan enamel $\delta^{13}C$ values support the previous suggestion from Harrison (1992) that differences in fauna between the sites likely have more to do with time than ecology.

A major faunal difference between Fort Ternan and Maboko is the extreme rarity of primate remains at Fort Ternan, comprising only 0.9% of all mammal specimens, although three taxa (the semi-terrestrial *Kenyapithecus wickeri,* the small catarrhine *Simiolus andrewsi* (a large nyanzapithecine), and a small, indeterminate species of catarrhine (Shipman et al, 1981; Harrison, 1992)) have been identified. This raises the question of whether Maboko may have represented a more suitable/preferred habitat for primates? While the range of Fort Ternan enamel carbon values fall within that of Maboko, however, Maboko's $\delta^{13}C$ value range is marginally larger, and includes lower values compatible with more closed canopied forested components. While this could also be a product of sample sizes and taxa included in the studies, ecological differences, such as riverine setting, as indicated by the numerous aquatic birds (McCrossin and Benefit, 2016) and the seasonally waterlogged soils (Retallack et al., 2002), could have contributed to Maboko's capacity to maintain a higher density of primates.

$\delta^{13}C$ values from Nakali and Samburu Hills (9.6-9.3 Ma; Sawada et al., 1998; Uno et al., 2011) suggest these localities were more wooded areas than Kipsaramon, but more open and/or arid than Maboko and Fort Ternan (Figure 7). Comparisons with Kipsaramon and the late Miocene should be viewed as preliminary because of the limited sample size and low diversity of taxa sampled.

Among later localities, the number of hominoid species seems to decline with an increase in enamel $\delta^{13}C$ values, which reflects an increase in the amount of C_4 plants across the landscape

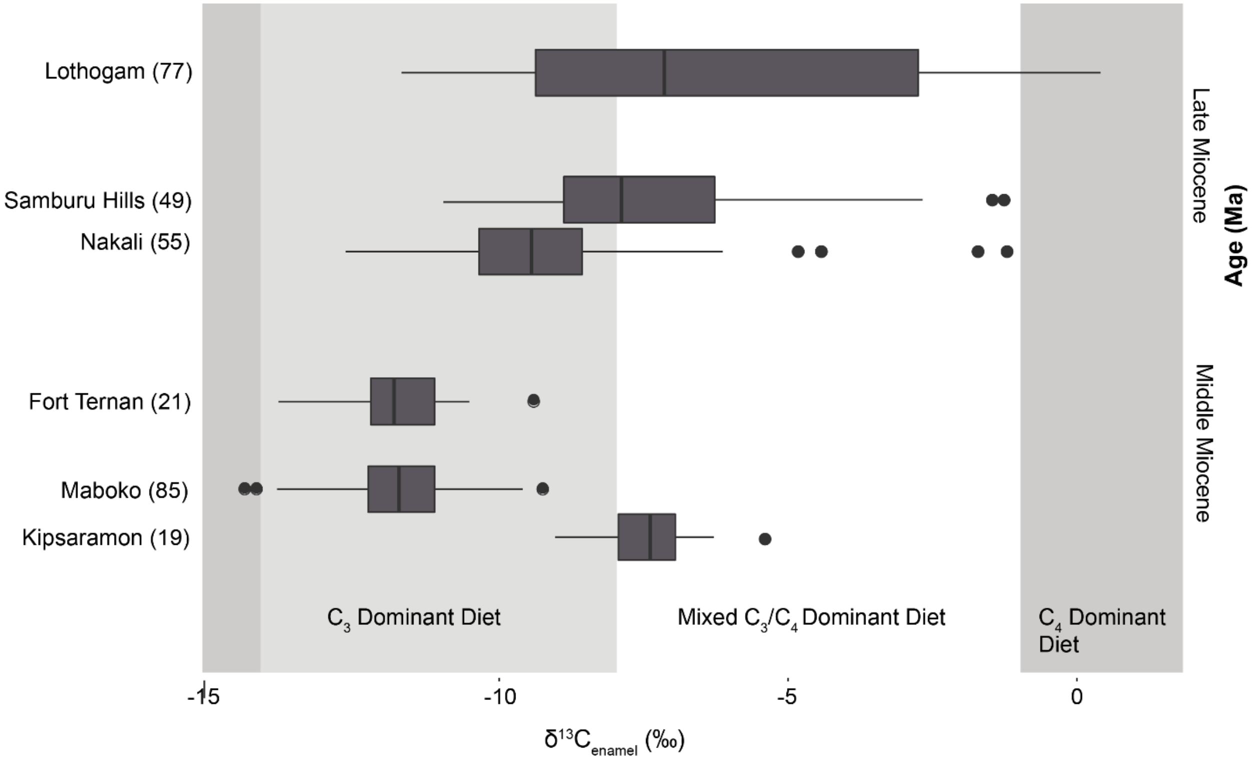

Figure 8. Middle Miocene to Pliocene enamel carbon isotope values from Kenya. Localities are arranged by time period. The dark grey shaded area on the left side indicates carbon values consistent with closed canopy browsers, while the lighter grey shaded area indicates open canopy habitats such as open forests and woodland. Data from Fort Ternan (13.7 Ma) are from Cerling et al., (1997) and Nakali (9.9 Ma), Samburu Hills (9.6-9.3 Ma), and the Upper and Lower Nawata formation at Lothagam (7.4-6.5 Ma) are from Cerling et al., (2003b) and Uno et al., (2011).

and their consumption by mammals (Uno et al., 2011). Nakali, which preserves four catarrhine taxa (two large hominoids (Kunimatsu et al., 2007, 2016), a nyanzapithecine (Kunimatsu et al., 2017), and the small colobine *Microcolobus* (Nakatsukasa et al., 2010)), has the lowest δ^{13}C values of the late Miocene with a range of -12.7‰ to -1.3‰. The slightly younger Samburu Hills locality has higher enamel δ^{13}C values (-11‰ to 0.41‰) than Nakali (Uno et al., 2011) with more mammalian species with mixed feeding. Samburu Hills preserves only one species of catarrhine, *Samburupithecus* (Ishida et al., 1984; Ishida and Pickford, 1997; Tsujikawa, 2005). By 7.4 Ma at Lothpgam (McDougall and Feibel, 1999), the catarrhine community has completely changed; non-cercopithecoid, non-hominoid catarrhines, including nyanzapithecines, are absent and the three catarrhine fossils recovered are attributed to an early hominin (Leakey et al., 2003, 2011).

C_4 plant evolution in East Africa

The signal of substantial mixed feeding from the herbivores at Kipsaramon is relevant to other lines of evidence documenting C_4 biomass expansion. Stable isotopic evidence from biomarkers in deep sea cores and pedogenic carbonates has indicated that the onset of C_4 vegetation expansion in East Africa occurred at 10 Ma (Cerling, 1992; Levin et al., 2011; Uno et al., 2011; 2016; Feakins et al., 2013). Though pedogenic carbonate evidence has previously been used to suggest C_4 vegetation emerged prior to 10 Ma, at Kipsaramon (Kingston, 1992; Kingston et al., 1994; Morgan et al., 1994), its presence has been interpreted to have been a minor component of vegetation (Kingston, 1992; Kingston et al., 1994; Bestland and Krull, 1999; Levin et al., 2011; Uno et al., 2016). Uno and colleagues (2016) have noted that pedogenic carbonate $\delta^{13}C$ values from Kipsaramon range from -7.4‰ and -5.2 ‰ but claimed only one value (7.4‰) is reliable because its enrichment value falls within a theoretical offset of +14-17‰. Kingston and colleagues (1994) recognized this discrepancy between pedogenic carbonate $\delta^{13}C$ values and corresponding organic carbon $\delta^{13}C$ values, and remained conservative in their assessment of these values and corresponding evidence from enamel (Morgan et al., 1994), representing the data as possibly the earliest evidence of C_4 plants documented in East Africa and not an expansion event per se. The enamel isotopic values presented here give more support to these prior indications of C_4 vegetation at Kipsaramon, with multiple proboscidean enamel carbon values that are higher than the -8‰.

The $\delta^{13}C$ values from Kipsaramon also suggest that proboscideans may have been among the first mammalian groups to incorporate C_4 plants into their diets. Previously, equids have been cited to be the first mammals in East Africa to mix feed starting at 9.9 Ma at Nakali (Uno et al., 2011) with a rapid transition to mixed feeding and grazing amongst other mammalian groups, including proboscideans, starting between 9.6 and 9.3 Ma (Cerling et al., 1997; Uno et al., 2016). This study shows that proboscideans incorporated C_4 graze into their diets by 15.8-15.6 Ma, pushing back the date for mixed feeding among proboscideans by six million years, and possibly the date for an increase in C_4 grass abundance in East Africa by a similar amount (Figure 9).

These results add complexity to the inference, based on multiple lines of evidence, that grassland expansion in Africa began after 10 Ma (Cerling et al., 1999; Uno et al., 2011; 2016). Plant wax biomarkers for the Miocene of East Africa taken from core samples in the Red Sea and the Somali Basin, though informative, lack the spatial and chronological resolution to reflect regional and local patterns of plant evolution (Uno et al., 2016). Obviously, additional sampling of mammalian teeth from Kipsaramon and other middle Miocene localities is necessary to capture a more complete picture of mammalian diets and by inference foraging habitats during the middle Miocene. Ultimately these data can be used to assess the role of environmental change as a driver of the faunal turnover.

Faunal Turnover from the early to the middle Miocene

It has long been recognized that the early- middle Miocene transition represents a period of faunal turnover, contrasting assemblages from the early Miocene sites of Tinderet and Rusinga with those from Maboko faunas (Hopwood, 1933; MacInnes, 1943; LeGros Clark & Leakey,1950, 1951; Andrews & Van Couvering,1975; Andrews, 1981; see summary in Harrison, 2002). Specific comparisons between Rusinga and Maboko assemblages highlight the arrival of multiple new mammalian lineages at Maboko (Pickford, 1981, 1984, 1986) such as

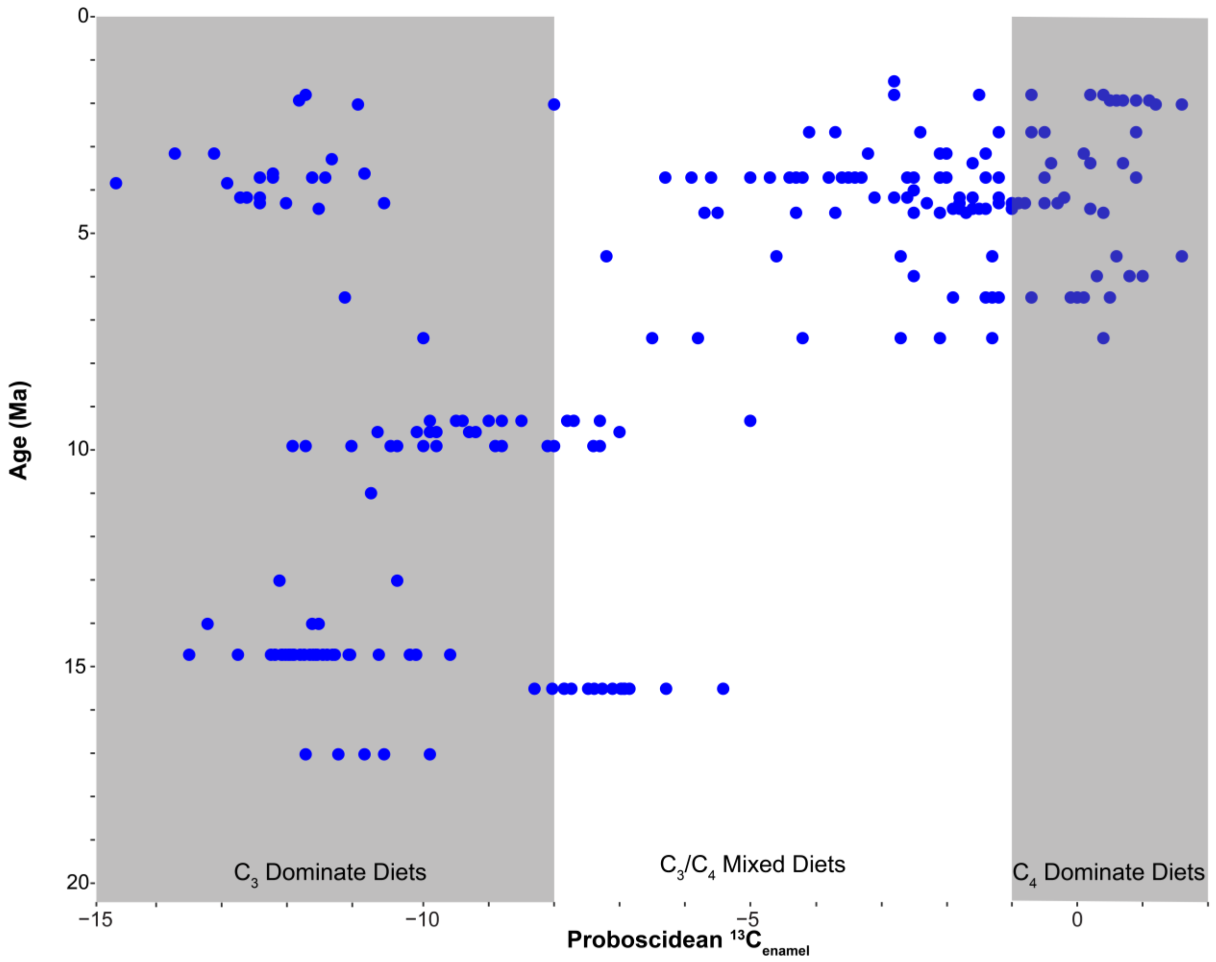

Figure 9. Tooth enamel δ13C data from fossil east and central African proboscideans from 17 Ma to 2 Ma. Data are compiled from Cerling et al., (1999), Zazzo et al., (2000), Harris et al., (2003), Schoeninger et al., (2003), Semaw et al., (2005), Kingston and Harrison (2007), Levin et al., (2008), Kingston (2011), Plummer et al., (2009), Uno et al., (2011), Lister et al., (2013).

hippopotamids, the choerolophodont proboscidean *Afrochoerodon*, antlered Climacocerotid giraffoids, and bovids.

The picture of mammal turnover based on a limited number of sites, is slowly becoming more intricate, due to research at early Miocene sites in the Turkana Basin and at early Ugandan Miocene (Orliac et al., 2010; Leakey et al., 2011; Grossman and Solounias, 2014). For example, although the first appearance of hippopotamidae was recorded to occur in the middle Miocene at Maboko by Pickford (1983), and later at Kipsaramon (Behrensmeyer et al., 2002; Pickford, 2007; Weston and Boisserie, 2010; Boisserie et al., 2005, 2010); a taxon from the early Miocene site of Moroto, Uganda (<20.6 Ma; Gebo et al., 1997), *Morotochoerus ugandensis* (Orliac et al., 2010), purportedly pushes back the earliest appearance of hippopotamids to the early Miocene (Orliac et al., 2010; Lihoreau et al., 2015; but see Pickford, 2011). The earliest member of choerolophodont Proboscideans, *Afrochoerodon kisumuensis*, likely makes its appearance in East Africa at Kipsaramon after its first appearance at in North Africa at Wadi Moghara (18-17 Ma; Miller, 1996, 1999; Sanders and Miller, 2001). A choerolophodont species is claimed to be present at Buluk (Leakey et al., 2011), which is radiometrically dated to between 16-17.2 Ma (McDougall and Watkins, 1985) and possibly pushes the appearance of *Afrochoerodon* in East Africa to the late early Miocene. Listriodontine suids are generally considered to have appeared in Africa during the middle Miocene (Pickford, 1981, 1995; 2006, 2007; Harris and Liu, 2008, but see Van der Made, 1995). The earliest listriodont in East Africa is possibly *Lopholistriodon pickfordi* (Van der Made, 1996) named from material at Buluk. This listriodont has also been recognized at Kipsaramon (Pickford, 2007) and at Maboko (Van der Made, 1996; 2007). Pickford (1981) first recognized the presence of listriodonts at Buluk and Maboko and suggests that Buluk’s age is closer to Maboko, but this hypothesis has yet to be tested with more precise dating at Buluk.

Among ruminant taxa, the purported earliest occurrence of climacocerotid giraffoids on Maboko (MacInnes, 1936; Hamilton, 1978) could be called into question. While *Climacoceras* is absent from Kipsaramon (Behrensmeyer et al., 2002), a giraffoid cranial appendage from Kalodirr (Harris et al., 2010; Grossman and Solounias, 2014) has been identified as *cf. Climacoceras* (Grossman and Solounias, 2014). If the Kalodirr giraffoid material is truly a climacocerotid, then the first appearance of climacocerotids could be much earlier. So far, the appearance of the earliest true bovids in East Africa at Maboko (Whitmore, 1958; Thomas, 1979) are what distinguish it from early Miocene localities and Kipsaramon. Nonetheless, the faunal turnover event previously suggested to have occurred between early Miocene and Maboko assemblages could have been a more transitional change rather than an abrupt turnover when new finds from the early Miocene of the Turkana Basin and Uganda are examined.

Many differences between the early and middle Miocene faunal assemblages have also been suggested to mark a transition from forests to more open environments with greater seasonality (Van Couvering and Van Couvering, 1976; Shipman et al., 1981; Pickford, 1983). Conversely, preliminary carbon isotopic results of mammalian enamel from early Miocene Ugandan localities, Napak and Moroto, and the Kenyan locality of Tinderet resemble the results from Maboko and Fort Ternan and fall within the range of C_3 dominate, open forest and woodland habitats (Kingston et al., 2011; Arney et al., 2017). These early and Middle Miocene isotopic comparisons suggest that closed canopied forested environments were probably not as pervasive in the early Miocene as previously interpreted (Andrews et al., 1979; Evans et al., 1981; Andrews and Kelley, 2007).

Conclusion

Reconstruction of dietary patterns by isotopic analyses of mammalian herbivore taxa from the middle Miocene sites of Maboko and Kipsaramon and, by inference the habitat types present, indicate the presence of different dietary patterns and potentially different ecosystems for the two localities. $\delta^{13}C$ values from Maboko indicate pure C_3 diets and therefore predominantly C_3 ecosystems. There appear to be possibly dietary differences between herbivores recovered from different stratigraphic beds, with Bed 5b with the lowest values, indicating wetter and/or more wooded conditions than Bed 3. However, the current sample cannot confirm differences between Bed 5b and Bed 5w due to limited sampling for 5w. There is evidence of dietary niche differentiation among the suids, tragulids, bovids, and giraffoids. Some of these differences could be attributed to differences in stratigraphic sampling. Additional sampling of individual species from multiple beds will better address whether diets are stable through time and/or track habitat changes between beds.

Dietary patterns from Kipsaramon gomphothere and rhinocerotid teeth reveal variable foraging patterns with rhinos consuming water stressed browse and/or C_3 graze. Gomphothere carbon values are consistent with mixed C_3/C_4 diets, indicating the presence of drier and more open habitats were present at Kipsaramon compared to Maboko. The presence of multiple enamel $\delta^{13}C$ values from proboscideans at 15.8-15.6 Ma that fall within the range of modern mixed C_3/C_4 diets conflicts with interpretationsof a minor C_4 vegetation component in East Africa prior to 10 Ma. Comparisons with the later middle Miocene localities such as Fort Ternan and Maboko, where no mixed feeding is present, indicates an ecosystem with a significant C_4 component may have been localized to the Tugen Hills and expanded regionally later. This reconstruction situates middle Miocene catarrhines and new mammalian fauna in an ecologically variable landscape with mixed feeders and browsers and has important implications for the divergence and evolution of the cercopithecoid and hominoid clades, specifically for changes in the diversity of non-cercopithecoid and cercopithecoid taxa.

Kipsaramon represents a hominoid locality with a mixed C_3/C_4 landscape. By contrast, Nakali had more closed habitats and C_3 plants as evident by lower herbivore enamel $\delta^{13}C$ values than those from other localities such as Samburu Hills and Lothogam where hominoid material is scarce and C_4 plants are more abundant. In contrast, cercopithecoids were more abundant where the later Miocene environments were reconstructed as more C_4 plant dominanted and hominoids were sparse. These data suggest an apparent association of hominoid decline with an increase of C_4 biomass.

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Chapter 3

Dental Evidence for Dietary Change from the Early to the Middle Miocene of East Africa

Introduction

Foraging strategies have long been regarded as significant for understanding Miocene non-cercopithecoid catarrhine dispersals (Andrews and Kelley, 2007), diversification (Kay, 1977; Kay and Ungar, 1995; Kay and Ungar, 1997; Ungar et al., 2004), and adaptive response to environmental changes (Harrison, 1992; McCrossin et al., 1998; Benefit, 1999; 2000; Harrison, 2010). Reconstructions of catarrhine diets in the Miocene indicate a dietary diversity that may have approached the level of variation documented in extant hominoids (Kay, 1977; Kay and Ungar, 1997; Deane, 2009), yet appears to be accompanied by less accentuated morphological specializations (Kay and Ungar, 1997; Deane, 2009; Shearer et al., 2015). For example, it has been noted that molar shearing was less developed among early Miocene catarrhines than among middle to late Miocene Eurasian hominoids (and extant hominoids) (Kay, 1977; Kay and Ungar, 1997). The higher overall molar shearing and expanded range of shear quotient variation (Kay and Ungar, 1995, 1997) in the Middle Miocene of Eurasia was accompanied by increased variation in dental microwear patterns (Teaford and Walker, 1984; Ungar, 1996; King et al., 1999; Ungar et al., 2004; Merceron et al., 2005; Alba et al., 2010; DeMiguel et al, 2014), leading to an inferred increase in dietary breadth, that included hard object feeding, frugivory, and folivory.

Morphological differences between early Miocene catarrhines and later catarrhine lineages (Kay and Ungar, 1997; Deane, 2008), have been cited to be an example of the Red Queen Effect (Van Valen, 1973), which states that organisms must constantly adapt to ecological pressures to survive. Kay and Ungar (1997) proposed that Miocene catarrhines increased their shear crest heights over time in response to pressure from changes in plant tissue structures and/or competition with sympatric cercopithecoids. Higher shear crests would have increased a hominoid's or small bodied catarrhine's efficiency in extracting nutrients from plants that evolved characteristics (e.g. becoming more fibrous) to better resist consumption (*ibid*.). With respect to competition with cercopithecoids, the authors cited Temerin and Cant (1983), who interpreted the earliest cercopithecoids to have had a competitive advantage due to their bilophodont dental structure. However, Benefit (1999) has suggested that strong, direct competition between small and large bodied non-cercopithecoid catarrhines and cercopithecoids was unlikely in the early Miocene, due to the paucity of cercopithecoid fossils at early Miocene sites.

The early Miocene specimens measured for shearing crest lengths by Kay (1977) and used later in Kay and Unger (1997) were measured in the 1970s and did not include lower second molar fossils from Uganda, or from Middle Miocene specimens in Kenya, due to their meager representation in the fossil record at that time. However, since these studies, new research has been conducted, and new specimens have come to light. First, Benefit (1988, 1993, 1999; 2000) compared the relative M_2 shearing of early and middle Miocene ape taxa using a slightly different shear index (total of shearing crest lengths divided by molar length (SUMS/L)). This analysis indicated small primitive catarrhines such as *Dendropithecus, Simiolus enjiessi* and *Micropithecus "Simiolus" leakeyorum* were likely the most folivorous, but the nyanzapithecines from Maboko were not included. Since the 1970s, additional catarrhine fossils have been recovered from the early Miocene of Uganda and the early and middle Miocene of Kenya and have either been attributed to new species (Fleagle and Simons, 1978; Leakey and Walker, 1985; Leakey et al.,, 1986a, b; Leakey and Leakey, 1987; Harrison, 1989: Ward et al., 1999) or have expanded the hypodigms of previously recognized taxa (e.g. McCrossin and Benefit, 1993; Rossie and MacLatchy, 2013; Cote et al., 2014; MacLatchy et al., 2019).

Kay (1977) and Kay and Ungar's (1997) work on African Miocene catarrhine dietary trends using molar shearing crests has been augmented by additional lines of evidence. For example, the increased enamel thickness in *Ekembo* and *Afropithecus* has been used to infer a shift from a diet of soft fruit to a more variable diet (Andrews and Martin, 1991; Leakey and Walker, 1997; McCrossin and Benefit, 1993, 1997; Kay, 1981; Leakey and Leakey, 1986; Andrews and Martin, 1991; Smith et al., 2003) that was likely a result of increased seasonality (Andrews and Martin, 1991; Benefit, 1999). In the case of *Afropithecus* (but not *Ekembo*), the thicker enamel is coupled with lower molar occlusion, robust mandibles, enlarged premolars, and procumbent anterior dentition, which in combination have been used to infer a sclerocarp feeding niche (Leakey et al., 1998; Leakey and Walker, 1997; McCrossin and Benefit, 1993, 1997; Deane, 2012). *Ekembo* molar shear crest lengths are not as low as in *Afropithecus* relative to tooth length (Benefit, 1993, 1999) and are more similar to shearing crest lengths of *P. major* (Benefit, 1993, 1999; Kay, 1977; Kay and Ungar, 1997). A shift to more specialized folivory has also been proposed to have occurred among nyanzapithecine taxa in the middle Miocene, based on increased molar shearing crests and a high percentage of microwear scratches (Benefit, 1999; 2000; Benefit et al., 2005).

These shifts in dietary regime in the late early Miocene and middle Miocene have been suggested to be in response to climatic and habitat changes from closed to open habitats and an increase in seasonality (Harrison, 1992; McCrossin et al., 1998; Benefit, 1999; 2000). Efforts to reconstruct and compare the paleoenvironments across multiple East African Miocene localities have been previously conducted (Andrews and Van Couvering, 1975; Andrews et al., 1979; Evans et al., 1981; Pickford, 1983; 1995). Andrews and Van Couvering (1975) summarized floral, faunal, and climatic evidence from the Miocene and concluded that the early Miocene was dominated by forested environments. Andrews and colleagues (1979) and Evans and colleagues (1981) use ecological diversity measures to reconstruct paleoenvironments and conclude that early Miocene fauna are more similar to fauna from modern forests. The above research, along with locality-specific environmental data from heavily studied localities, such as Rusinga (e.g. Chester, 1957; Bestland and Krull, 1999) and Fort Ternan (e.g. Kappleman, 1991; Retallack et al., 1990; Dugas and Retallack, 1993; Cerling et al., 1991, 1997), have been interpreted to indicate that moist, evergreen forests graded into drier woodlands with forest patches from the earliest to later early Miocene, and ultimately to seasonal woodlands in the middle Miocene (Andrews & Kelley, 2007; Andrews, 2016). However, this interpretation requires testing with data from more sites (Andrews and Kelley, 2007; Andrews, 2016) such as Kalodirr, Buluk, Moroto, and Kipsaramon. Further, in a recent summary of Miocene paleoenvironments by Andrews (2016), the author suggest paleoenvironments in the early Miocene could have sampled various forms of woodland habitats rather than forests. Establishing the link between evolutionary change and paleoenvironmental conditions is hampered by a scarcity of comparable environmental data applied across multiple localities in East Africa.

The first goal of this study is to use Kay and Ungar's (1997) shearing crest technique to further explore the range of dietary diversity that was present among East African catarrhines during the early to middle Miocene. This will be carried out by calculating molar shearing quotients for additional Early Miocene catarrhine specimens (including three additional species), made available through field work carried out since Kay and Ungar's seminal work. Critically, the molar shearing quotients for Middle Miocene African catarrhines will be calculated for the first time, spanning 22 specimens across five taxa.

A second goal is to compare the environments of the eight African fossil localities where Early and Middle Miocene catarrhine diets are being assessed, using stable carbon isotope ratios extracted from fossil herbivore enamel samples. The use of this paleoecological proxy will allow for the identification of any broad-scale shifts in vegetation, and for the investigation of whether any environmental shifts and dietary shifts in hominoids, reflected in herbivore enamel and shearing crest data respectively, were linked in time and space.

Paleodietary Inference

While microwear can provide evidence of what an animal ate just prior to death, occlusal morphology provides information on the type of foods an animal was adapted to consume. The shear quotient (SQ), one of the most widely accepted methods for inferring dietary adaptations in fossil taxa (Kay and Simons, 1980; Kay et al., 2002; Kay and Cozzuol, 2006; Kirk and Simon, 2001; Boyer et al., 2015; Allen et al., 2015), was developed through extensive research on the functional significance of morphological variation of tooth form and wear patterns (Hiiemae and Kay, 1973; Kay and Hiiemae, 1974; Kay, 1975, 1978; Sheine and Kay 1977, 1982; Kay et al., 1978; Anthony and Kay, 1993). SQs values quantify the extent of total molar shear in proportion to molar mesiodistal length. Generally, primates that consume larger proportions of structural carbohydrates (i.e. plant fibers or chitin in insects) have higher SQs and longer shear crests relative to molar length than do frugivores and hard object feeders (Kay, 1975). Studies indicate SQs are the better predictor of diet for extant taxa when dietary classification rates are compared to those of 3-dimensional crown surface topology indices such as Relief Index (RFI) and Occlusal Relief (OR) (Bunn et al., 2011; Allen et al., 2015; Boyer et al., 2015).

Dental features such as occlusal morphology and enamel thickness are thought to be highly influenced by phylogenetic constraints. For example, cercopithecoids have more developed shear crests than hominoids when diet is controlled for (Kay and Covert, 1984). Moreover, it has been suggested that occlusal morphology in particular likely reflects what an animal was able to eat rather than actually ate (Kay and Ungar, 1997). However, it is possible to partially control for phylogenetic influences on tooth form by comparing closely related taxa.

While this study focuses on morphological changes with respect to diet over time, diet can also be augmented by non-morphological means. Non-morphological methods such as microwear and stable isotopes theoretically provide direct evidence of the types of plants ingested by a fossil primate. Stable isotope analysis of modern and fossil primate enamel provides direct insight into the chemical composition of ingested food based on carbon isotopic distinctions between C_3 and C_4 plants (e.g. Sponheimer and Lee-Thorp, 1999; Lee-Thorp et al., 2010; Levin et al., 2015) as well as oxygen isotopic distinctions are related to canopy height (Krigbaum et al., 2013). However isotopic sampling of East African Miocene catarrhines is destructive to rare specimens and is therefore limited, preventing widespread application of this method. Unlike isotopic analyses, dental microwear non-invasively looks at the textured surface of enamel that food particles likely left behind. Microwear analysis suffers from the ‘last supper effect’, where it reflects only short-term alterations in diet (Grine, 1986), and there is some doubt as to whether microwear is a reflection of the physical properties of objects consumed (e.g. hardness) (e.g. Merceron et al., 2016) or the consumption of exogenous grit from soil or dust adhering to food (Sanson et al., 2007; Lucas et al., 2013; Hoffman et al., 2015).

Miocene Catarrhine Diets

Kay (1977) was the first to carry out dietary reconstructions for African Early Miocene catarrhines using shear crest development. Kay found fossil taxa had relatively lower shear crest lengths than do modern hominoids, with *Limnopithecus*, *Proconsul*, and *Dendropithecus* having lower crest development than *Rangwapithecus* (Kay, 1977). It was later inferred that these first three taxa were relatively more frugivorous and *Rangwapithecus* was relatively more folivorous (Kay and Ungar, 1997). Dental microwear analysis (Ungar et al., 2004) supported Kay and Ungar's (1997) interpretation that *Rangwapithecus* was folivorous. Ungar and colleagues (2004) also found that *Rangwapithecus* and *Micropithecus* had microwear profiles similar to those of modern folivores, while *Proconsul* and *Dendropithecus* had pit percentage ranges similar to modern soft fruit-eaters. Further, *Afropithecus* was found to have a relatively high pit percentage, although lower than the value for inferred hard object-feeder *Ouranopithecus* (Ungar et al., 2004). More recent microwear techniques such as dental microwear texture analysis (Scott et al., 2005; 2012) has been applied to other early Miocene taxa from Kenya (Shearer et al., 2015). Shearer and colleagues (2015) reported that microwear did not reveal discernable dietary variation between taxa and concluded that fossil taxa likely consumed foods of similar abrasive properties. Currently the validity and utility of microwear texture analysis is a topic of active research.

East African middle Miocene diets have received considerably less attention. SQs have been estimated for middle Miocene Eurasian catarrhines, but not for their African contemporaries. However, craniodental morphology and microwear analysis using scanning electron micrographs of large bodied hominoid and *Victoriapithecus* lower second molars from Maboko indicate these taxa were hard object-feeders [refs needed]. In addition, the microwear of "*Simiolus*", and *Mabokopithecus* resemble modern folivores with high molar cusps and an abundance of long parallel scratches on the enamel surface (Benefit, 1993; 1999; 2000; Palmer et al, 1998).

Phylogenetic background

Kay and Ungar's (1997) broad phylogenetic examination of crest development in Miocene catarrhines lumped all early Miocene catarrhines into one phylogenetic group to be compared to middle and to late Miocene Eurasian catarrhines. Based on comparison with this undifferentiated grouping, Kay and Ungar suggested that increased molar shearing occurred across all noncercopithecoid catarrhine groups. This supposition warrants a more detailed examination of shearing quotients within phylogenetic groups (i.e. large bodied hominoids, small bodied primitive catarrhines, and nyanzapithecines). The discovery of additional material from the early to middle Miocene as well as new phylogenetic assessments of African Miocene catarrhines makes a more detailed taxonomic examination of shear crests among Miocene African taxa necessary.

Large Bodied Hominoids:

All large bodied catarrhines (*Morotopithecus, Proconsul, Afropithecus, Ekembo,* and *Equatorius*) are grouped together as hominoids for the following reasons: 1) multiple cladistic analyses using cranial and postcranial characters suggest these taxa are basal hominoids (e.g.

Andrews and Martin, 1987; Begun et al., 1997; Singleton, 2000; Young and MacLatchy, 2004) they share derived hominoid traits including greater limb mobility and enhanced grasping abilities relative to other catarrhines (Ward et al., 1993, 1997); and 3) inferred longer life histories in several taxa (Kelley, 1997). (Although see Harrison (2010) for a counter view concerning the hominoid status of these taxa).

Note that large bodied hominoid material from Kisingiri have been moved from the genus *Proconsul* to the genus *Ekembo* (McNulty et al., 2015). There is some agreement on this usage (Nakatsukasa et al., 2016; MacLatchy et al. in press)

The large-bodied hominoid from Maboko, previously *Kenyapithecus africanus* (Leakey, 1967), was moved to the genus *Equatorius* by Ward and colleagues (1999) two decades ago, along with material from Kipsaramon (TH 28860). However, the taxonomic status of the Maboko hominoid material has yet to be settled. Some still consider Maboko and Fort Ternan hominoid material to be congeneric because the variation displayed by maxillary central incisors and maxillary root heights fall within the range of modern hominoids species (McCrossin and Benefit, 1997; Benefit and McCrossin, 2000), and Benefit and McCrossin (2000) state that female premolars from Maboko match those from Fort Ternan. It has also been suggested that similarities between a lower canine from Maboko and canines from Fort Ternan indicates the presence of both *Equatorius* and *Kenyapithecus* on Maboko (Kelley et al., 2000, 2002). Until new material from Maboko is properly sorted and made available to study for comparison with material from Kipsaramon, the validity of *Equatorius* cannot be further tested (Kelley et al., 2000). This quandary is further complicated by erection of the penecontemporaneous genus *Nacholapithecus* (Ishida et al., 1999). In this study, the Maboko hominoid will be referred to as

LBHM (Large Body Hominoid from Maboko) while the Kipsaramon hominoid will be referred to as LBHK (Large Body Hominoid from Kipsaramon).

Small-Bodied Stem Catarrhines

The small bodied, stem catarrhines are a diverse, yet poorly understood radiation of catarrhines (Harrison, 2010; 2013) represented in this study by *Dendropithecus, Simiolus*, *Limnopithecus,* and *Kalepithecus.* While these genera have similar body sizes, their phylogenetic relationships are less clear. Unlike the large bodied hominoids, life history has not yet been inferred for these small catarrhines. In addition, the postcranial elements of small bodied catarrhines lack the features, such as those associated with greater limb joint mobility, that fossil hominoids have in common with modern apes (Rose, 1988, Rose et al., 1992). Thus, although their phylogenetic affinities remain unknown, all primitive small bodied forms are considered together here.

Nyanzapithecines

The Nyanzapithecines are a group of small to intermediate-sized catarrhines, overlapping in size with some small bodied primitive catarrhines, but with some overlap in size with the smaller species of *Ekembo* and *Proconsul* (Andrews, 1978; Harrison, 1986, 2010; Kunimatsu, 1997). The nyanzapithecines included in this study (*Rangwapithecus, Nyanzapithecus,* and *Mabokopithecus)* are all thought to be closely related by dental specializations including mesiodistally elongated lower molars and elevated, conoidal cusps (Koenigswald, 1969; Harrison, 1986; 2002; 2010; Kunimatsu, 1992, 1997) and will be treated as a separate phylogenetic group from large bodied hominoids and small-bodied stem catarrhines.

Paleoenvironmental Background

As mentioned above, a general synopsis of the environmental setting of East Africa Miocene environments posits that the early Miocene represented mostly forested habitats that gradually transitioned to more open habitats with forest patches by the late early Miocene, and then to woodland habitats in the middle Miocene (Andrews and Van Couvering, 1975; Andrews and Kelley, 2007). Andrews (2016) has recently added the caveat that the early Miocene was represented by mostly woodland habitats but does not provides new data. In order to test either environment scenario, a consistent environmental reconstruction proxy must be applied across space and time to all the sites so that systematic comparisons of environmental datasets can be made. This has yet to be undertaken.

Table 6 lists early and middle Miocene fossil catarrhine localities from East Africa with their published paleoenvironmental interpretations. The penecontemporaneous localities of Napak, Songhor, Koru, Legetet, and Chamtwara are generally characterized as forested environments. Napak has also been inferred to include patches of dry, open environments (Pickford, 1995, 2004), which has been corroborated by enamel stable isotope analysis of the herbivorous mammalian fauna (Kingston et al., 2009, 2011; Kingston and MacLatchy, 2012). For later early Miocene localities dated to after 19 Ma, Rusinga's environmental setting has been extensively studied using a number of proxies (Chester, 1957; Andrews and Van Couvering, 1975; Evans et al., 1981; Pickford, 1995; Bestland and Krull, 1999; Forbes et al., 2004; Collinson et al., 2009; Maxbauer et al., 2011; Ungar et al., 2012; Michel et al., 2014; Garrett et al., 2015), while paleoenvironments in the Turkana region are understudied (Grossman, 2008; Butts et al., 2019). Rusinga's habitat characterizations have sometimes produced conflicting results, and range from dense, closed canopy forests to open woodland, and to savanna bushland, which is a result of using time-averaged assemblages (Michel et al., 2015). Stable carbon isotopic analysis of mammalian enamel from Rusinga span the range of pure C_3 habitats including closed canopied forest to open woodland (Garrett et al., 2019, submitted). West Turkana localities such as Kalodirr and Moruorot are interpreted as open woodland (Grossman, 2008; Butt et al., 2019), but there are no published habitat inferences for the East Turkana locality of Buluk. For the middle Miocene, past research has indicated woodland habitats to be a primary characteristic of Maboko (Evans et al., 1981; Pickford, 1983; Retallack et al., 2002), Kipsaramon (Pickford and Kunimatsu, 2005), and Fort Ternan (Andrews et al., 1979; Evans et al., 1981; Pickford, 1983; Kappleman, 1991; Retallack et al., 1990; Dugas and Retallack, 1993; Cerling et al., 1991, 1997) paleoenvironments. However, forested elements are also indicated for each locality.

More recent paleoecological research using stable carbon isotope analysis from herbivore enamel (Kingston et al., 2009, 2011; Arney, 2017; Butts et al., 2019) have inferred more open habitats in the early Miocene than previous research has indicated. This preliminary work supports Andrews' (2016) supposition that the early Miocene could have included woodland habitats, but notably does so with a single, consistently applied paleoenvironmental method.

Stable isotope analysis of modern and fossil tooth enamel has been a useful tool to infer paleoenvironments via mammalian dietary resource partitioning and habitat use in response to vegetation change (Quade et al., 1995; Kingston et al., 2007; 2011; Nelson, 2007; Secord et al., 2008; Cerling et al., 2011; 2015; Eastham et al., 2016; Nelson and Rook, 2016), even among ancient C_3 ecosystems (Quade et al., 1995; Nelson, 2007; Secord et al., 2008; Merceron et al., 2013; Eastham et al., 2016; Nelson and Rook, 2016). During tooth formation, the isotopic composition of an animal's diet is recorded within its tooth enamel. Studies on the variation in enrichment factors of metabolic processes among mammalian taxa allow for the direct comparison of enamel signatures to those of modern vegetation. Of value to reconstructing past vegetation, is the proportion of C_3 (shrubs and sedges) and C_4 (grasses) plants (Sponheimer et al., 1999; Kingston and Harrison, 2007; Levin et al., 2008; Cerling et al., 2015; but also see Feakins et al., 2013). The sites included here predate the expansion of C_4 plants across East Africa (Cerling et al., 1997; Edwards et al., 2010; Uno et al., 2016). However, there is extensive variation in the isotopic ecology of modern C_3 ecosystems (Cerling et al., 2004; 2015; Codron et al., 2005; Nelson, 2013), and $\delta^{13}C_{enamel}$ values can be used to examine mammalian resource partitioning and habitat differences (McFadden & Higgins, 2004; Merceron et al., 2006; Nelson, 2007; Secord et al., 2008; Aiglstorfer et al., 2014; Eastham et al., 2016; Nelson et al., 2013; 2016). C_3 plants yield $\delta^{13}C$ values that range between -22% and -36% ; within this range, closed canopied habitats have lower values and open canopied and drier C_3 habitats have higher values (Van der Merwe & Medina, 1991; Cerling et al., 1999; 2004; Nelson, 2013). In this study we use stable carbon isotope ratios of tooth enamel from herbivorous mammals to evaluate patterns of habitat differences at eight early and middle Miocene localities that span ~21.6 – 13.6 Ma.

Table 6. Previously published environmental reconstructions for early and middle Miocene localities included in this study for isotopic analysis.

Locality	Age (Ma)	Paleoenvironmental Reconstruction	Reference
Moroto	>20.6[1]	Mosaic open and arid forest and woodland	Kingston et al., 2009; 2011; Kingston and MacLatchy, 2012
Napak	20[2]	rain forest or wetland; thick brush to closed evergreen forest	Bishop, 1968
		dry forest	Gommery et al., 1998
		lowland forest	Andrews and Van Couvering, 1975
		forested habitats with some patches of dry open environments	Pickford, 1995; Pickford 2004
		open forest to woodland	Kingston et al., 2009; Kingston et al., 2011; Kingston and MacLatchy, 2012
Songhor	19	evergreen forest with montane conditions	Andrews and Van Couvering, 1975
		dry forest	Pickford, 1983;1995
		forest with some grasses	Ungar et al., 2012
Koru	19	lowland montane forest	Andrews and Van Couvering, 1975
		wet, rain forest	Pickford, 1983

Legetet	19	wet, rain forest	Pickford, 1983
Chamtwara	19	forest	Evans et al., 1981
Rusinga	~20-17	seasonal woodland	Evans et al., 1981
		semi-arid seasonal climate	Bestland and Krull, 1999
		open country, savanna and bush with interspersed gallery forests	Pickford, 1995
		woodland with trees and shrubs	Collinson et al., 2009
		Gallery forest-drier woodland	Chester, 1957
		lowland forest	Andrews and van Couvering, 1975
		mosaic of humid to semi-arid conditions	Forbes et al., 2004
		tropical season forest and tropical woodland	Maxbauer et al., 2013
		dense forest	Michel et al., 2014
		forest with some grasses	Ungar et al., 2012
Karungu	17.5	woodlands with seasonal climate	Lakhanpal and Prakash, 1970
		open woodland	Bonnefile, 1984; 1985
		forests and woodland-bushland	Evans et al., 1981
		swamp	Pickford, 1983
		mosaic of humid to semi-arid conditions	Forbes et al., 2004
		Open, arid environment with C_4 plants	Lukens et al., 2017

West Turkana	17.5-16.8	closed to open woodland	Grossman, 2008
		Woodland with some C_4 biomass	Butts et al., 2019
Buluk	17.2-16	-	-
Kipsaramon	15.8-15.4	forest with some grassland	Winkler, 1992, 2002
		Forest to heavy woodland	Pickford and Kunimatsu, 2005
		Open environments with some C_4 plants	Kingston, 1992; Kingston et al., 1994; Morgan et al., 1994
Maboko	>14.7-13.8	Dry woodland	Pickford, 1983
		closed woodland with some forest elements	Evans et al., 1981
		seasonally flooded, wooded grassland, riparian woodland and bushland	Retallack et al., 2002
Fort Ternan	13.7	Woodland to mixed woodland/forest habitats	Kappelman, 1991
		open deciduous woodland	Andrews and Nesbit-Evans, 1979; Evans et al., 1981
		open woodland with nearby forests	Bonnefile, 1984
		woodland to dry forest	Pickford, 1983

	wooded grassland	Retallack et al., 1990; Dugas and Retallack, 1993
	wooded or forested conditions, no grassland	Cerling et al., 1991; 1997
	open habitat or savannah	Shipman et al., 1981; Shipman, 1986

Material and Methods

Shear Crests

The lower second molars of 78 fossil catarrhines from seven localities were measured in this study. Miocene fossil specimens used in this study, broken down by phylogenetic group, are listed in Table 7. The mesial-distal length and shear crests (1-8) of early and middle Miocene catarrhine lower second molars were taken using a microscope fitted with a reticle eyepiece of 10x magnification. Measurements were taken in reticle units and converted to millimeters. Raw shear crest measurements of extant hominoids used in Kay and Ungar (1997) were kindly provided by Richard Kay. Early Miocene catarrhine specimens included in Kay (1977) and Kay and Ungar (1997) were remeasured for consistency. Shear crests on fossil specimens were taken by I.A. and checked with measurements provided by Kay for precision. The percent difference between Kay and Ungar's (1997) measures and those by I.A. was 3%. SQ values reported in the results for fossil material were taken by I.A. The "Total shear" was calculated as the sum of shearing crests 1-8. Following Kay and Ungar (1997), an ordinary least squares regression line was fitted to the Log10 sum of shearing crests versus lower molar mesiodistal length of extant frugivorous hominoids (*Pan, Pongo,* and *Hylobates*):

$$\log_{10} \text{total shear} = (\log_{10} M_2 \text{ length x slope}) + \text{intercept}$$

Regression coefficients from (Kay and Ungar, 1997) were used to calculate an expected total shear value from M2 length of each extant individual from the equation above. Expected total shear values were then converted from log10:

$$\text{total shear} = 10^{\text{intercept}} * (M_2 \text{ length})^{\text{slope}}$$

The shear quotient is a percentage representing the difference between observed total shear and expected total shear, divided by the expected total shear:

$$SQ = 100 \times (\text{observed total shear} - \text{expected total shear})/\text{expected total shear}$$

The effects of using means of modern species versus individual data points on SQ calculation and *posthoc* dietary categorization has been investigated for extant platyrrhines and strepsirrhines (Boyer et al., 2015). Boyer and colleagues (2015) found no significant effects on the dietary signal when individual data points were used versus species means to calculate SQ values. This comparison has yet to be undertaken for catarrhines. A similar analysis using extant hominoids was performed here by IA using the same dietary categories as Kay (1975) for hominoid species. To determine if using species means or individual data point affects the power of calculated SQ values to discriminate between diet groups, regression lines were fitted to individual data points and to species means of extant frugivores.

Benefit (1988; 1993; 1999; 2000) explored the relationship between diet and lingual versus total shear crest lengths in an effort to include worn lower molars. Lingual shear crests were shown to be more correlated with diet than the total of all shearing crests among cercopithecoid teeth (Benefit, 1987,1993). Here we explore whether shear quotients calculated using lingual shear crests produces similar statistical effects on *posthoc* comparisons. SQ values were calculated using regression coefficients estimated using the sum of lingual shear crests for species means and individuals with the standard method described above. Regression equations calculated from lingual crests are reported in Table 2. *Posthoc* T-testsof SQ values between pairs of dietary groups was performed to determine the number of statistical differences between group pairs The number of significantly different SQ values between diet group pairs was compared for SQ calculation methods using all shearing crests and lingual shear crests. It should be noted that sample sizes for SQ values for each fossil taxa are too low for substantial statistical testing.

Table 7. List of fossils measured for SQs.

	Specimen	Reference
Early early Miocene	*Morotopithecus bishopi*	
	UMP MORII 03'551	MacLatchy et al., (2019?)
	Proconsul major	
	KNM SO 396	Kay, 1977; Kay and Ungar, 1997
	KNM SO 415	Kay, 1977; Kay and Ungar, 1997
	KNM SO 914	Kay, 1977; Kay and Ungar, 1997
	KNM CA 395	This study
	KNM CA 1298	This study
	KNM CA 2229	This study
	KNM LG 452	This study
	UMP 62-15	This study
	UMP 62-14	This study
	Limopithecus evansi	
	KNM SO 424	Kay, 1977; Kay and Ungar, 1997
	KNM SO 444	Kay, 1977; Kay and Ungar, 1997
	KNM SO 911	Kay, 1977; Kay and Ungar, 1997
	Limnopithecus legetet	

	KNM LG 1708	Kay, 1977; Kay and Ungar, 1997
	KNM KO 8	Kay, 1977; Kay and Ungar, 1997
	Kalepithecus songhorensis	
	KNM SO 388	This study
	Rangwapithecus gordoni	
	KNM SO 906	Kay, 1977; Kay and Ungar, 1997
	KNM SO 908	Kay, 1977; Kay and Ungar, 1997
	KNM SO 909	Kay, 1977; Kay and Ungar, 1997
	KNM SO 374	Kay, 1977; Kay and Ungar, 1997
	KNM SO 486	Kay, 1977; Kay and Ungar, 1997
	KNM SO 420	Kay, 1977; Kay and Ungar, 1997
	KNM SO 1958	This study
Late early Miocene	*Ekembo heseloni*	
	KNM RU 2036A	Kay, 1977; Kay and Ungar, 1997
	KNM RU 1706	Kay, 1977; Kay and Ungar, 1997
	KNM RU 1823	Kay, 1977; Kay and Ungar, 1997
	KNM RU 1959	Kay, 1977; Kay and Ungar, 1997
	KNM RU 1945	Kay, 1977; Kay and Ungar, 1997
	KNM RU 7290	Kay, 1977; Kay and Ungar, 1997

Ekembo nyanzae	
KNM RU 2087	Kay, 1977; Kay and Ungar, 1997
KNM RU 1710	Kay, 1977; Kay and Ungar, 1997
KNM RU 1678	Kay, 1977; Kay and Ungar, 1997
KNM RU 1695	Kay, 1977; Kay and Ungar, 1997
KNM RU 1676	Kay, 1977; Kay and Ungar, 1997
KNM RU 1734	Kay, 1977; Kay and Ungar, 1997
KNM RU 17377	This study
Afropithecus turkanensis	
KNM WT 24300	MacLatchy et al., (2019?)
KNM-WT 17024	This study
Dendropithecus macinnesi	
KNM RU 2015a	Kay, 1977; Kay and Ungar, 1997
KNM RU 1849	Kay, 1977; Kay and Ungar, 1997
KNM RU 1850b	Kay, 1977; Kay and Ungar, 1997
KNM RU 1893	Kay, 1977; Kay and Ungar, 1997
KNM RU 2003	Kay, 1977; Kay and Ungar, 1997
KNM RU 1992	Kay, 1977; Kay and Ungar, 1997
KNM MW 53	Kay, 1977; Kay and Ungar, 1997
Simiolus enjiessi	

	KNM WK 16956	This study
	Limnopithecus legetet	
	KNM RU 1708	Kay, 1977; Kay and Ungar, 1997
Middle Miocene	MLBH	
	KNM MB 20573	This study
	KNM MB 29154	This study
	KNM MB 32307	This study
	KNM MB 24755	This study
	KLBH	
	KNM TH 28860	This study
	Micropithecus “Simiolus” leakeyorum	
	KNM MB 11660	This study
	KNM MB 35946	This study
	KNM MB 31395	This study
	KNM MB 24777	This study
	KNM MB 31338	This study
	KNM MB 11652	This study

Simiolus andrewsi	
KNM FT 21	This study
KNM FT 20	This study
Mabokopithecus clarki	
KNM MB 32099	This study
KNM MB 35886	This study
KNM MB 32105	This study
KNM MB 35520	This study
KNM MB 32076	This study
KNM MB 35889	This study
Mabokopithecus pickfordi	
KNM MB 31328	This study
KNM MB 35530	This study

The Reference column indicates if a fossil specimen's SQ has been calculated prior to this study. LBHM refers to Large Bodied Maboko Hominoid, and LBHK refers to Large Bodied Kipsaramon Hominoid.

Stable Isotope analysis

Enamel stable carbon isotope values were compiled from eight East African early and middle Miocene catarrhine localities. Carbon isotopic values for Maboko and Kipsaramon, Kenya were collected and analyzed by Arney et al. (2019), as were those from Buluk, Kenya (Arney et al., in prep.), and Tinderet, Kenya (Arney et al., 2017 and in prep). Carbon isotopic values for Moroto and Napak, Uganda were provided by Kingston et al. (2011 and in prep), for

Kalodirr, Kenya by Butts et al., (2018 and in prep) and for Rusinga by Garrett *et al*., (2015 submitted). All $\delta^{13}C$ values were corrected to a common reference time before the Industrial Revolution (1750) to account for fluctuations in the $\delta^{13}C$ value of atmospheric CO_2. Past $\delta^{13}C$ values for atmospheric CO_2 are based on North Atlantic benthic Foraminifera (Tipple et al., 2010) and were used to correct fossil carbon values to an atmospheric, pre-industrial $\delta^{13}C$ value of -6.3‰. All corrected carbon values are reported as $\delta^{13}C_{1750}$ values. The following enamel $\delta^{13}C$ ranges were used for distinguishing between herbivore foraging strategies, following Cerling et al. (2015): C_3-closed canopy understory browser, enamel $\delta^{13}C$ values < -14‰; open canopy C_3 browsers, enamel $\delta^{13}C$ values between -14‰ and -8‰; and C_3/C_4 mixed feeders, enamel $\delta^{13}C$ values > -8‰.

The sample sizes of bulk $\delta^{13}C$ values vary between localities and are not sufficient for statistical testing. Since environmental change through time is being assessed, $\delta^{13}C$ values for localities are binned into three time periods for comparative purposes. The time bins are as follows: early early Miocene = 21–18 Ma; late early Miocene = 18-16 Ma, and middle Miocene = 16-13.7 Ma. Pairwise comparisons of $\delta^{13}C$ values grouped by time period were performed using the non-parametric Wilcoxon rank sum test.

Results

Regression equations, shear crests, and SQ calculation

Regressions 2-4 as depicted and described in Table 8 represent alternatives depending on whether species means, or individuals were used, and on whether just lingual shear crests or total shearing crests were included in the analysis. There is a slight discrepancy between the regression coefficients using the standard method in equation 1 as calculated here and as reported in Kay and Ungar (1997). This is likely due to the inclusion of four *Hylobates agilis* individuals in the dataset provided by Kay rather than the five reportedly used in the original regression. However, this discrepancy did not drastically change calculated SQ values for extant taxa.

SQ values calculated using the sum of all shearing crests supplied the best distinction between diet groups, while SQ values calculated using the sum of lingual shearing crests resulted in poor distinction between extant frugivores and folivores (Table 9). ANOVA *posthoc* comparisons show significant differences between folivores and frugivores when all shearing crests are used for SQ calculation. There is no statistical differentiation between diet categories using lingual shearing crests. Surprisingly, there was some improvement of diet group distinction using individual shear crest data points instead of species means for regression estimation. However, it has been advised that species mean data should be used when some taxa are more sampled than others (Boyer et al., 2015). Since species of *Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla* were sampled in higher numbers relative to *Hylobates*, the regression coefficients published in Kay and Ungar (1997) and calculated from species means (Regression equation # 1, Table 8) were used (see also Figure 10; Table 9).

Table 8. Regression parameters for shear quotient calculations.

Reg #	Description	n	Slope	Error	Intercept	error

1	Total shear, mean	9	.963	.033	.384	.030
2	Total shear, individuals	70	.935	.025	.406	.023
3	Lingual shear, mean	9	1.021	.036	.036	.033
4	Lingual shear, individuals	70	.986	.033	.063	.031

The regression coefficients of this table describe the relationship between the log10 of lower second molar length and shear crest lengths of sampled hominoid molars measured by Richard Kay (Kay, 1977; Kay and Ungar, 1997). Ordinary Least Squares (OLS) was used for all regression equations. The column titled “Description” indicates whether the sum of all shearing crests versus the sum of lingual shearing crests and whether species means or individual data points were used. The column titled “n” indicates the number of data points in the regression. The column titled “Error” is the standard error of the coefficient to the left. All regressions were generated by the same protocol as in Kay and Ungar (1997). See text for more details.

Table 9. Posthoc comparisons of ANOVA on versions of SQ.

Method	LvF	LvF/L	LvL/F	FvF/L	FvL/F	L/FvF/L
All crests, means	.00028	3.2x10^-5	ns	ns	ns	.00148
All crests, individuals	6.6x10^-7	2.3x10^-6	ns	ns	.0048	.0018
Lingual crests, means	ns	ns	ns	ns	ns	ns
Lingual crests, individuals	ns	ns	ns	ns	ns	ns

The *post hoc* comparisons represent the relationship between shearing quotients generated from alternate regressions and dietary groups. Comparisons were carried out with Pairwise *t*-tests, and bonferroni corrected *P* values. The bonferroni correction to α = .05 is α = .0083 for 6 comparisons among extant hominoid diet groups. ANOVAs for shearing quotients generated using all shear crests produced statistically significant among group variance, justifying the *post hoc* follow up. ANOVAs for shearing quotients generated using lingual shearing crests did not indicate significant among group variance. “L” = leaves; “F” = fruit’ “F/L” = fruit/leaves; “L/F” = leaves/fruit.

Shear Crests

Large-bodied *stem hominoids*

The earliest early Miocene large bodied stem hominoids (20.8-19 Ma) are represented by *Proconsul major* (N=9) and *Morotopithecus* (N=1) (Table 9). *P. major* has an average SQ value of -8.0% and the SQ values for the single Morotopithecus molar is -1.7%. SQs in the later early Miocene (18-17 Ma) are represented by *Ekembo nyanzae* (N=6), *Ekembo heseloni* (N=6), and *Afropithecus turkanensis* (N=2). The average SQ value for *E. nyanzae* is -9.3%, for *E. heseloni* average SQ is -12.5, and Afropithecus is -17.2%. Middle Miocene putative hominoids, represented by the large bodied hominoid from Kipsaramon ("*Equatorius" africanus*; N=1) and large bodied hominoid from Maboko (*Kenyapithecus africanus*: N=4), have average SQ values of -15.2% and -11.9%, respectively. This is also shown in Figure 10A.

Small-bodied stem catarrhines

The earliest small-bodied, stem catarrhines are represented by *Limnopithecus legetet* (N=2), *L. evansi* (N=3), and *Kalepithecus songhorensis* (N=1). *L. legetet* and *L. evansi* have similar average SQ values of -3.4% and -3.1%, respectively. *K. songhorensis* has a SQ value of -7.8%. For later early Miocene taxa, *Dendropithecus macinnesi* (N=7) has an average SQ value of -7.7% and *Simiolus enjiessi* (N=1) has a value of -2.8%. For the Middle Miocene, *Micropithecus "Simiolus" leakeyorum* (N=6) has an average SQ value of -0.7% and *Simiolus andrewsi* (N=2) has an average value of =11.1%.

Nyanzapithecines

*Rangwapithecus gordon*i (N=7) is the only known species of Nyanzapithecine in the early Miocene (20-19 Ma). Its average SQ value is -0.5%. Nyanzapithecine specimens from the late early Miocene are rare and poorly preserved and could not be sampled at this time. For the middle Miocene, Nyanzapithecines are represented by *Mabokopithecus pickfordi* (N=2) and *Mabokopithecus clarki* (N=6). Nyazapithecines are present at Kipsaramon (Kelley et al., 2002; Pickford and Kunimatsu, 2005) and Fort Ternan (Harrison, 1986, 1992, 2010) but material is sparse and fragmentary. *M. pickfordi* has a mean SQ value of 5.9% and *M. clarki* has a mean value of 8.5%.

General

Data points of SQ values for each species and box-and-whisker plots of each taxonomic group are divided into the time bins described above and are shown in Figure 10. *P. major* has the lowest SQ values from ~21-18 Ma and *R. gordoni* has the highest. The *Morotopithecus* SQ value is higher than those of the average SQs for the earliest small bodied, stem catarrhines species but lower than those *R. gordoni*. *Morotopithecus* also has the highest SQ value of all other hominoids sampled.

Afropithecus has the lowest average SQ among all taxa sampled. All later early Miocene hominoid taxa have average SQ values that are lower than those found in earlier hominoids. Among late early Miocene taxa, the average SQ values for small bodied catarrhine taxa, *D. macinnesi* and *S. enjiessi*, are higher than the values found in large bodied hominoids, *Ekembo* and *Afropithecus*. *D. macinnesi's* average SQ value is lower than those of earlier small stem catarrhines except for *K. songhorensis*; the SQ value for *S. enjiessi* is slightly higher than the all early stem catarrhines.

In the middle Miocene, taxonomic groups have less overlap in SQ values, specifically among taxa from Maboko. The hominoids have the lowest SQ values among middle Miocene taxa, the nyanzapithecines *M. clarki* and *M. pickfordi* have the highest SQ values among middle

Miocene and all other taxa sampled, and the small stem catarrhines have intermediate values between middle Miocene hominoids and nyanzapithecines. Middle Miocene hominoid average SQ values are lower than those of the earliest hominoids but overlap extensively with late early Miocene hominoids. *Micropithecus "Simiolus" leakeyorum* has the highest average SQ value of all small stem catarrhines and *S. andrewsi* has the lowest SQ value. *M. clarki* and *M. pickfordi* SQ values are clearly much higher than those of earlier nyanzapithecines and are higher than extant folivorous hominoid SQ values reported in Kay and Ungar (1997).

Two major patterns are present in this shear quotient data. First, the hominoid SQ values appear to decrease from early to late early Miocene and middle Miocene. Second, SQ plots for nyanzapithecines increase from the early Miocene to the middle Miocene. Together, these two patterns translate to an increase in the range of SQ values among East African non-cercopithecoid catarrhines over time. The range of SQs is consistently ~18% during the early and late early Miocene. However, the range of SQ values among middle Miocene non-cercopithecoid catarrhines is 33%. It should be noted that the current sample size for SQ values is not sufficient to perform extensive statistical analyses.

Carbon isotopes

δ^{13}C values from the earliest localities (~21-19 Ma) fall within the range of open-canopied C_3 dominated environments (Figure 11; Table 11). Although there are differences between fossil sites within localities, the majority of values cluster between -14‰ to -8‰. The range of variation in carbon values for this time interval is 8.6‰. For the late early Miocene (~18-16 Ma), the range of variation in δ^{13}C values has expanded to 9.5‰. The δ^{13}C values for this time period range from -16.8‰ to -7.3‰. During the middle Miocene starting at 16 Ma -13 Ma, enamel δ^{13}C values have a slightly lower range of variation of 7.9‰ with δ^{13}C values ranging from -14.2‰ to -6.3‰. The distributions of $\delta^{13}C$ values between each combination of time bins differ statistically (p-values < .05). The distribution of $\delta^{13}C$ values from the early early Miocene are statistically different from the distribution of $\delta^{13}C$ values from the late early (p-value < .001) and middle Miocene time bins (p-value<.001). It should be noted that the statistical difference between the distributions of late early Miocene and middle Miocene $\delta^{13}C$ values is not as strong (p-value = .02).

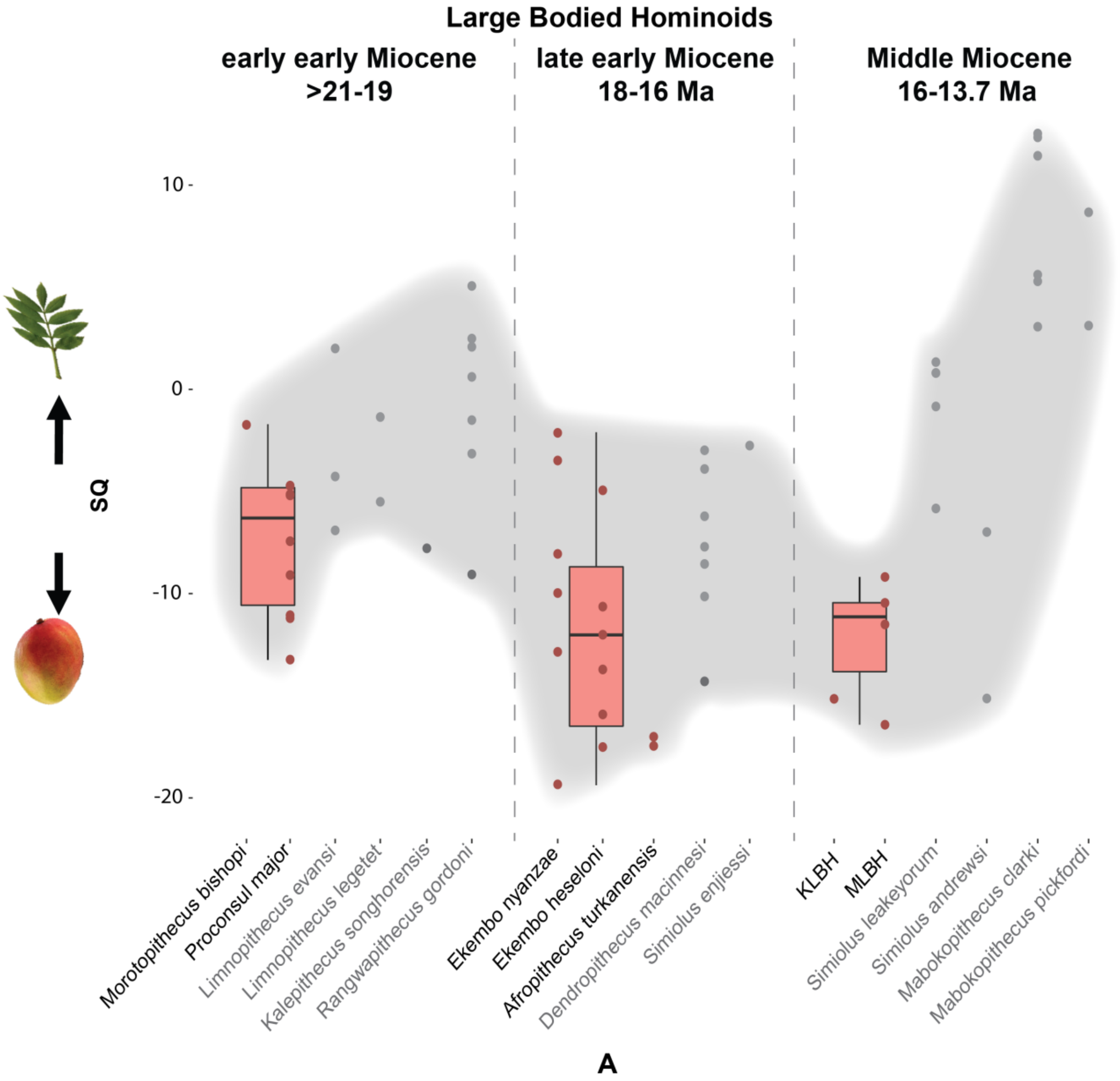

Figure 10A-C. SQ values for fossil taxa organized by taxonomic group and time. From top to bottom are large bodied hominoids, small bodied noncercopithecoid primitive catarrhines, and nyanzapithecines. Time periods are separated by grey lines and include early early Miocene (20-18 Ma), late early Miocene (18-16 Ma), and middle Miocene (16-14 Ma). Large bodied hominoids (A) appear to decrease molar shearing development from the early to the late early Miocene. Small bodied primitive catarrhines do not show any clear pattern of change (B). Nyanzapithecines display a shift toward increasing molar shearing (C).

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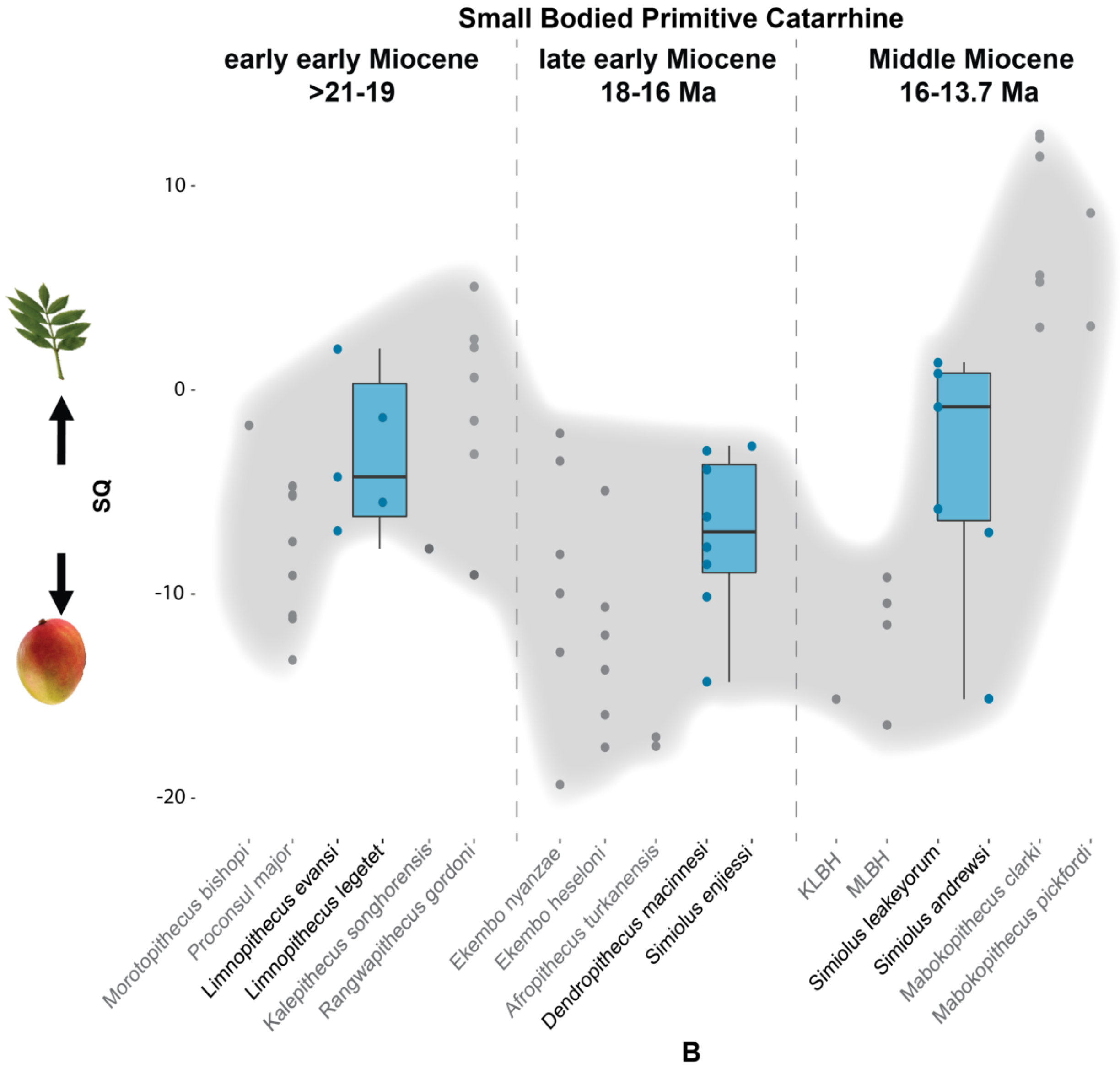


Figure 10 (Continued).

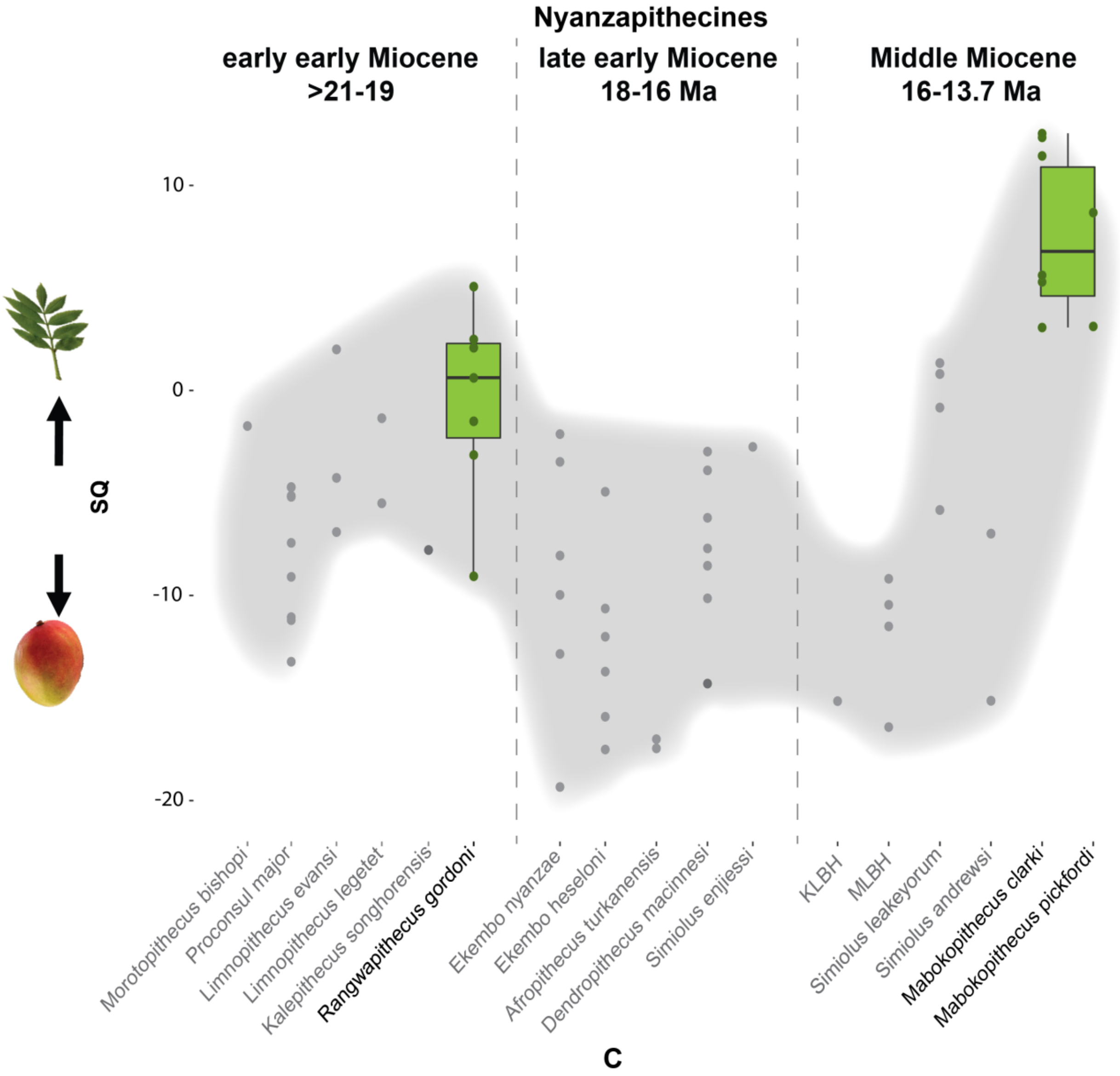


Figure 10 (Continued)

Table 10. Summary table of second molar mesiodistal length, Total shear crests, and shear quotient (SQ) of fossil taxa.

Species	**N**	**M2 Length (mm)**		**Total Shear (mm)**		**SQ**	
		Mean	**Range**	**Mean**	**Range**	**Mean**	
Large bodied stem hominoids							
Morotopithecus bishopi	1	17.2	-	36.6	-	-1.7	
Proconsul major	9	12.3	10.8 - 14.1	24.8	22.0 - 27.4	-8.0	
Ekembo heseloni	6	9.1	8.5 - 9.9	17.7	16.5 - 18.9	-12.5	
Ekembo nyanzae	6	11.2	10.1 - 12.5	22	18.5 - 24.0	-9.3	
Afropithecus turkanensis	2	12.3	12.0 - 12.5	22.3	21.9 - 22.6	-17.2	-
LBMK	1	10.8	10.8	20.1	20.1	-15.2	
LBHM	4	11.9	11.3 - 21.4	23	22.3 - 24.4	-11.9	
Small bodied stem catarrhines							
Limnopithecus evansi	3	5.8	5.6 - 6.1	12.7	11.9 - 13.3	-3.1	
Limnopithecus legetet	2	6.2	6.0 - 6.4	13.1	12.8 - 13.4	-3.4	
Kalepithecus songhorensis.	1	6.6	-	13.8	-	-7.8	
Dendropithecus macinnesi	7	7.1	6.9 - 7.5	14.6	13.3 - 15.5	-7.7	-14
Simiolus enjiessi	1	6.6	-	14.5	-	-2.8	
Micropithecus "Simiolus" leakeyorum	6	5.6	5.1 - 6.4	12.3	11.5 - 14.3	-0.7	
Simiolus andrewsi	2	7	6.8 - 7.2	14	13.8 - 14.2	-11.1	
Nyazapithecines							
Rangwapithecus gordoni	7	8.8	8.1 - 9.5	19.5	16.5 - 20.8	-0.5	
Mabokopithecus pickfordi	2	7.3	7.1 – 7.5	17.4	16.5 – 18.3	5.9	
Mabokopithecus clarki	6	8.4	8.1 - 8.7	20.3	18.7 - 21.7	8.5	

Table 11. Summary statistics of enamel carbon $\delta^{13}C_{1750}$ values from herbivorous mammals.

Locality	**$\delta^{13}C_{1750}$ (‰)**		**Date (Ma)**	**Data Reference**
	Median	**range**		
Tinderet	-10.4	-12.5 - -7.1	~20[1]	Arney et al., 2017
Moroto	-9.9	-11.8 - -8.8	>20.6[2]	Kingston et al., 2011
Napak	-10.1	-14.3 - -6.6	20[3]	Kingston et al., 2011
Rusinga	-13.0	-16.8 - -10.0	~18-16[4,5]	Garrett et al., 2015
Kalodirr	-10.1	-11.7 - -7.3	16.8-17.5[6]	Buttes et al., 2018
Buluk	-10.4	-12.3 - -8.9	<17[7]	This study
Kipsaramon	-6.8	-9.0 - -6.3	15.8-15.6[8]	Arney et al., 2019
Maboko	-11.1	-14.2 - -9.2	>14.7-13.8[9]	Arney et al., 2019
Fort Ternan	-11.8	-13.8 - -9.4	13.7[10, 11]	Cerling et al., 1997

References for locality dates are as follows: [1] Bishop et al., 1969; [2]Gebo et al., 1997; [3]MacLatchy et al., 2006; [4]Peppe et al., 2009; [5]McCollum et al., 2012; [6]Boschetto et al., 1992; [7]McDougall and Watkins, 1985; [8]Behrensmeyer et al., 2002; [9]Feibel and Brown, 1991; [10]Pickford et al., 2006; [11]Shipman et al., 1981.

Discussion

Diet Changes Through Time

Since sample sizes are too small for statistical analyses, we follow Kay and Ungar (1997) and evaluate dietary variation as the range of SQ values. Results indicate a substantial increase in the range of shearing quotient values among East African non-cercopithecoid catarrhines over time. The SQ values in the middle Miocene also exceed the range of SQ values found in extant folivorous hominoids. The range of SQs for early Miocene taxa are consistent with previous SQ studies (Kay, 1977; Kay and Ungar, 1997). However, while the range of SQs of all early Miocene taxa is equivalent to that of modern SQs, a more detailed look at shearing quotients with respect to time and phylogenetic group reveals some interesting patterns. The earliest taxa, which date between 20-19 Ma, show a range of SQ of 18%. *Rangwapithecus* and *Morotopithecus* have the highest SQs, implying they are the most folivorous (Kay Ungar, 1997; Ungar et al., 2004). *Proconsul* has the lowest SQs indicating more frugivory (Kay, 1977; Kay and Ungar, 1997). Their thin enamel indicates they likely were not hard object feeders (Beynon et al., 1998; Smith et al., 2003). Divergent enamel microwear features between *Proconsul* and *Rangwapithecus* (Ungar et al., 2004; Schearer et al., 2015) supports the interpretation that *Proconsul* was a soft-fruit eater and *Rangwapithecus* was likely more folivorous (Kay, 1981). The intermediate SQs of the small bodied stem catarrhines likely indicate a mixed diet of both fruits and leaves (Kay and Ungar, 1997), which is broadly supported by mixed microwear features (Ungar et al., 2004; Shearer et al., 2015).

The range of SQs in the late early Miocene is similar to that found in the early early Miocene (17%), but overall shearing is lower, which is driven by the lower shearing crests of large-bodied stem hominoids. It is important to note that nyanzapithecines were not sampled for this period because of their poor preservation and rare occurrence. For example, though there is craniodental material that preserves lower second molars for *Nyanzapithecus vancouveringorum* from Rusinga (RU 1855; Andrews, 1974), this material is highly weathered and cracked and could not be included in this study. Molar morphology of *N. vancouveringorum* is similar to that of *Nyanzapithecus* from Maboko with moderately inflated cusps and elongate crowns (Harrison, 1986; 2002). With the future inclusion of better-preserved material of nyanzapithecines from the late early Miocene, the range of SQs and dietary adaptations could exceed the SQ range for earlier Miocene taxa.

Late early Miocene hominoids have lower relative shearing (Table 4) and an increased enamel thickness relative to earlier forms such as *Proconsul* (Beynon et al., 1998; Smith et al., 2003) and *Morotopithecus* (MacLatchy et al., 2019). *Afropithecus* (-17.2%), *Ekembo heseloni* (-12.5%), *and Ekembo nyanzae* (-9.3%) display lower shearing and thickened enamel relative to Proconsul (-8%). *Afropithecus* has the lowest average SQ values and is considered to be durophagous (Leakey et al., 1988; Leakey and Walker, 1997; Deane, 2012). Craniodental features associated with modern sclerocarp foraging primates such as a proclined mandibular symphysis, robust mandibular corpus, and procumbent lower incisors are also recognized to be present in *Afropithecus* (Leakey and Walker, 1997; Walker, 1997; Ward, 1998; Rossie and MacLatchy 2013). However, the lack of these additional craniodental features in material for the *E. heseloni* and *E. nyanzae* (Smith et al., 2003), suggests they were not hard object feeders, but could possibly have been consuming a more abrasive diet than earlier thinner-enameled, soft fruit eaters such as *Proconsul* (Andrews et al., 1991; Smith et al., 2003).

There are two hypotheses for the adaptive function of thick molar enamel in primates: 1) thick enamel protects the tooth from fracture in species that consume hard objects (e.g. Kay, 1981; Dumont, 1995; Lampert et al., 2004; Vogel et al., 2008; Lucas et al., 2008; Constantino et al., 2011); and 2) thick enamel may serve as wear resistance to abrasive diets during a longer life span (Molnar and Gantt, 1977; King et al., 2005; Pampush et al., 2013). Pampush et al., (2013) found that primates with abrasive diets and longer maximum recorded lifespans have thicker enamel crowns and predict that a fossil species with abrasive diets and an ape-like lifespan would have thick enamel. These are not necessarily mutually exclusive and enamel thickness could be a response to either factor (Pampush et al., 2013). A purported hominoid-like longer life span (Kelley, 1997; Kelley and Smith, 2003) and/or an abrasive diet in *Ekembo* could have contributed to its thick enamel with an absence of sclerocarp feeding adaptations.

For small bodied stem hominoids, *Dendropithecus* has the lowest SQs of early Miocene small bodied catarrhines and was likely more frugivorous than earlier taxa such as *Limnopithecus* (Kay and Ungar, 1997). The smaller catarrhine, *Simiolus enjiessi*, has a higher SQ than *Dendropithecus*, but the sample size is too small to confirm whether *S. enjiessi* has on average higher shear development. A folivorous diet has previously been hypothesized for *Simiolus enjiessi* based on its mesiodistally elongated molars and high cusp relief (Benefit, 1999; 2000).

The amount of dietary variation in the middle Miocene (33%) exceeds that of the early Miocene and of extant hominoids (26%) (Table 4; Figure 2). MLBH and KLBH have the lowest development of shear crests. Microwear of phase II grinding facets on MLBH lower second molars display frequent, large pits, and this finding, along with the morphological feature of a proclined mandibular symphysis, are consistent with hard object feeding (Palmer et al., 1998; Benefit, 1999). At this time, it is not known if second molars of KLBH also contain a high percentage of large pits on the enamel surface. In addition, the mandible of KNM TH 28860 is too fragmentary to determine if the symphyseal axis is proclined like those of *Afropithecus* (Leakey et al., 1988; Deane, 2012) and MLBH (McCrossin and Benefit, 1993; McCrossin, 1994; McCrossin and Benefit., 1997).

SQs for *Micropithecus “Simiolus” leakeyorum* are on average higher than are those of all other small bodied apes (Table 2). These results are consistent with an increase in dedicated folivory among “*Simiolus”* from Maboko relative to early Miocene small bodied catarrhines, which has long, parallel scratches that comprise of 88% of microwear features (Palmer et al., 1998; Benefit, 2000; Benefit et al., 2005).

The only clear shift among molar shearing heights within a group of catarrhines occurs among the nyanzapithecines. The shearing quotients for middle Miocene nyanzapithecines, *M. clarki* and *M. pickfordi*, are the highest among all fossil taxa sampled (Table 4). The higher shear quotients and long, frequent scratches on the enamel surface of Maboko nyanzapithecines (Palmer et al., 1998) support specialized folivory among these primates (Benefit, 1999, 2000).

Environmental Change

Carbon isotopic values of enamel from four mammalian guilds (Proboscidea, Perissodactyla, Artiodactyla, and Hyracoidea) support the presence of an environmental shift from the early to the middle Miocene, but not in accord with previous interpretations. Early Miocene carbon isotopic values do not coincide with former interpretations of wide spread closed canopy forests in the early Miocene as suggested by faunal ecological diversity indices from Napak or Tinderet (Andrews et al., 1979; Evans et al., 1981) or from terrestrial gastropod assemblages (Pickford, 1983; 1995; 2004). In contrast, $\delta^{13}C$ values between 21-19 Ma from Ugandan and Kenyan localities indicate a mosaic of open forest and woodland habitats that vary between more humid and dry conditions (Kingston et al., 2009, 2011; Arney et al., 2017; Figure 2). The range of $\delta^{13}C$ values of -14.3‰ to -6.6‰ for this time period shows some overlap with mixed C_3 and C_4 feeding. Five of the 93 isotopic samples from 21-19 Ma are > -8‰, suggesting a minor presence of C_4 biomass and consumption.

Based on the enamel stable isotopic data presented here, early Miocene environments span the range of C_3 dominated ecosystems and were likely primarily open forest and woodland habitats. The only evidence of mammalian foraging in closed canopy forests comes from the late early Miocene at Rusinga (Michel et al., 2014; Garrett et al., 2015). The isotopic values from Rusinga are lower than those of all other localities sampled and increase the range of $\delta^{13}C$ values in the late early Miocene. In total, there appears to be a broad variety of habitats available to catarrhine primates at the regional scale during the early Miocene. More forested and possibly wetter environments were present at Rusinga compared to habitats in Uganda and at the Tinderet and West Turkana localities. Additional evidence from other, less catarrhine abundant localities such as Karungu, also suggest open and drier habitats with a soil C_4 biomass signal (Lukens et al., 2017). Enamel isotopic values have yet to be published to indicate how much C_4 biomass was consumed by mammalian fauna at Karungu, however, Lukens and colleague's (2017) study does suggest that habitats during the late early Miocene of East Africa could have been even more diverse than what is shown in this study.

Possible habitats present during the middle Miocene include open forests, woodlands, and mixed C_3/C_4 open habitat, which confirm past interpretations of open woodland habitats present in the middle Miocene (Andrews and Van Couvering, 1975; Andrews et al., 1979; Evans et al., 1981; Retallack et al., 2002). For Kipsaramon, the occurrence of values > -8‰ (Figure 2), strongly support the presence of C_4 biomass (See chapter 2). Most samples from Kipsaramon (13 out of 18) displayed higher than the estimated end member for C_3 biomass. This is consistent with the presence of a considerably higher C_4 biomass component than present in earlier localities and supports mixed C_3/C_4 foraging (Arney et al., 2018) (Figure 2; Table 5). Since modern C_4 plants grow and thrive in open, drier and hotter environments (Taiz and Zeigler, 2006), drier and hotter conditions would seem to have occurred at Kipsaramon compared to the other sites sampled. It should also be noted samples from Kipsaramon are from a more limited number of taxa than those sampled at other middle Miocene localities. Thus, the range of $\delta^{13}C$

values for the middle Miocene could potentially be higher as additional mammalian taxa are sampled.

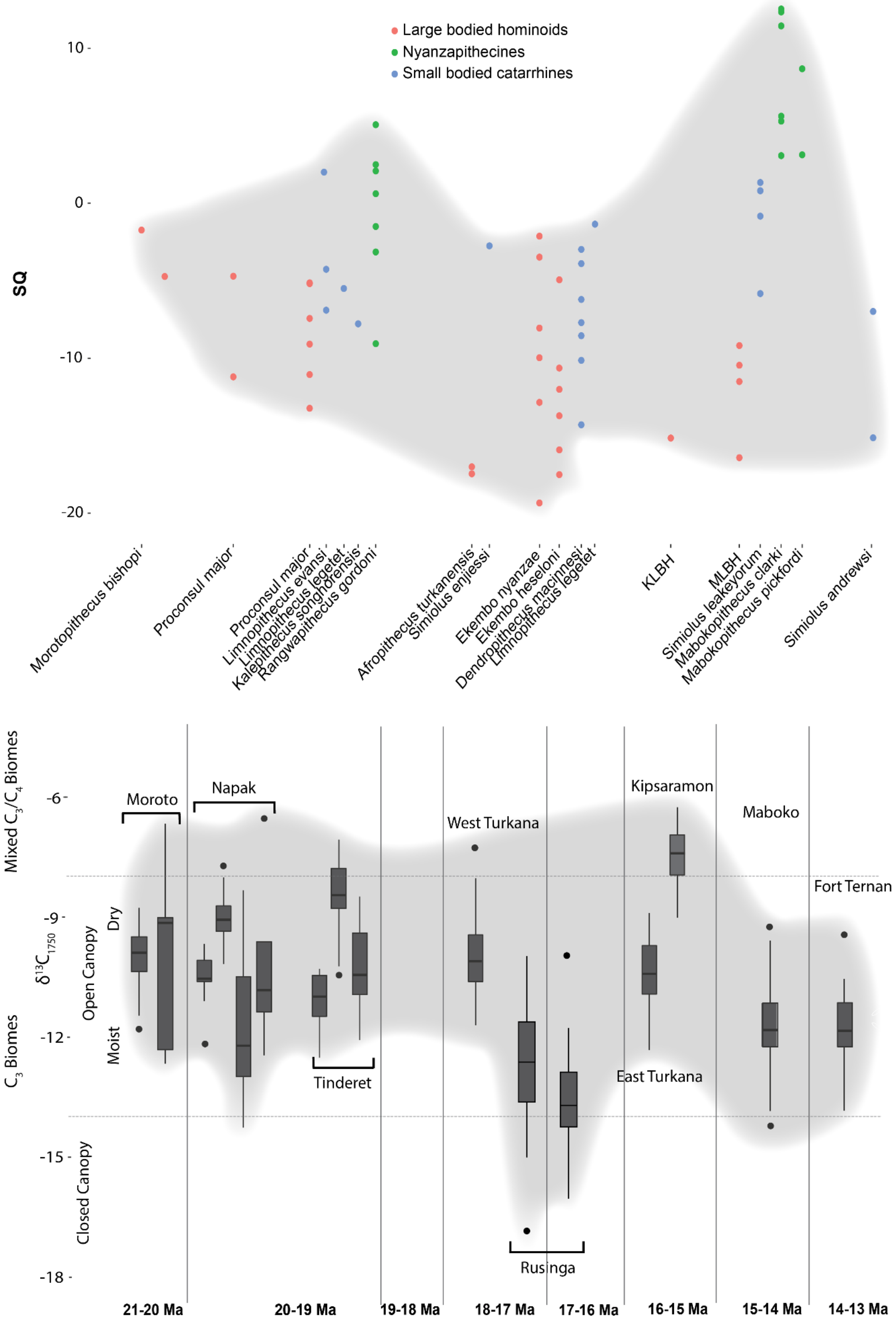
In sum, enamel $\delta^{13}C$ values from the eight East African early and middle Miocene localities presented in this study do not support a gradual change from closed to open environments. Instead, the data here indicate more widespread open canopy conditions in *both* the early and middle Miocene within an overall diverse environmental landscape that includes one site in the late early Miocene (Kipsaramon) that is significantly more open than previously supposed.

Adaptation and habitat change

With respect to the Red Queen hypothesis invoked by Kay and Ungar (1997), it is still unclear to as to what could have pushed the increase in molar shearing seen in modern hominoids. The possibility that the range of SQ variation among non-cercopithecoid taxa could be higher in the late early Miocene, perhaps pushes back the occurrence of noticeably higher molar shear development among nyanzapithecines. This coupled with the absence of fossil cercopithecoids among late early Miocene localities, suggests competition with cercopithecoids could not have driven the initial increased molar shearing among nyanzapithecines. Further, there was no drastic increase in molar shearing among the other Maboko taxa sampled, where victoriapithecids were highly abundant.

Based on results here, diets among catarrhine groups changed in different ways. The hominoids lowered their shearing crests, while nyanzapithecines increased their shearing. Dietary changes among hominoids appeared to occur in tandem with changes in habitat variation (Figure 2). These results align with previous observations of a shift to lower shearing (Kay, 1977) and increased enamel thickness among the large-bodied hominoids starting in the late early Miocene (Andrews and Martin, 1991; Beynon et al., 1998; Smith et al., 2003), which coincided with changes in the heterogeneity of local environments. The shift to less developed shearing and greater enamel thickness among large-bodied hominoids (Andrews, 1992; Beynon et al., 1998; Smith et al., 2003) occurred when the range of carbon isotopic values in the East African fauna expanded to include the entire range of C_3 dominated open canopied habitats including closed canopied forests. However, the taxon with the lowest shearing (*Afropithecus*) did not occupy an environment discernably different from those currently reconstructed for earlier Miocene localities, at least with the proxy used in this study. Nyanzapithecines increased their shearing in the middle Miocene, at a time when habitats expanded regionally to include discernable amounts of C_4 biomass in the landscape, although C_4 is not detected locally at Maboko where nyanzapithecines were sampled. Whether nyanzapithecine shearing crests from Kipsaramon, where C_4 was detected, are as high as those from Maboko, remains to be determined.

As mentioned above, changes in climate to increased seasonality purportedly starting in the later early Miocene are also suggested to have influenced catarrhine dietary changes such as increased hard object feeding among hominoids (Andrews and Martin, 1991; Benefit, 1999). Fossil pollen and grass cuticle proportions point to a possible increase in rainfall seasonality from the early to the middle Miocene (Morley and Richards, 1993). Potentially driving changes in seasonality are changes in moisture availability that have been linked to increasing regional topography associated with the formation of the East African Rift System during the Miocene (e.g. Andrews and Van Couvering, 1975; Pickford, 1983; Malone, 1988; Sepulchre et al., 2006). However, seasonality at the regional and local scale has yet to be defined and still is largely qualitative for the Miocene of East Africa (Jacobs, 1999). More research is needed to further explore climate change and seasonality during the early and middle Miocene and their influence on catarrhine communities.



Large bodied hominoids
Nyanzapithecines
Small bodied catarrhines
SQ
10
0
-10
-20
Morotopithecus bishopi
Proconsul major
Proconsul major
Limnopithecus evansi
Limnopithecus legetet
Kalepithecus songhorensis
Rangwapithecus gordoni
Afropithecus turkanensis
Simiolus enjiessi
Ekembo nyanzae
Ekembo heseloni
Dendropithecus macinnesi
Limnopithecus legetet
KLBH
MLBH
Simiolus leakeyorum
Mabokopithecus clarki
Mabokopithecus pickfordi
Simiolus andrewsi
Mixed C_3/C_4 Biomes
C_3 Biomes
$\delta^{13}C_{1750}$
Dry
Open Canopy
Moist
Closed Canopy
-6
-9
-12
-15
-18
Moroto
Napak
Tinderet
West Turkana
Rusinga
Kipsaramon
East Turkana
Maboko
Fort Ternan
21-20 Ma
20-19 Ma
19-18 Ma
18-17 Ma
17-16 Ma
16-15 Ma
15-14 Ma
14-13 Ma

Figure 11. Composite figure of SQs and enamel $\delta^{13}C$ values for early and middle Miocene taxa.SQs (top) and carbon isotopic values (bottom). Enamel $\delta^{13}C$ values from early and middle Miocene localities arranged chronologically into 1 million-year bins (vertical lines). $\delta^{13}C$ values for sites at the Moroto, Napak, and Tinderet localities have been separated out. For Rusinga, enamel $\delta^{13}C$ values from the Hiwegi (18-17 Ma) and Kulu (17-16 Ma) formations are distinguished. The gray background outlines the range of variation within each chronological bin. Enamel $\delta^{13}C$ value limits for closed canopy and open canopy C_3 ecosystems and mixed C_3/C_4 ecosystems are indicated by the horizontal lines. The gray shadow highlights the range of variation for SQ values and $\delta^{13}C_{1750}$ values. SQ values of fossil species are lined up with the locality of origin.

Conclusion

Diet reconstructions based on lower second molar SQs among Miocene catarrhines show a substantial increase in dietary variability from the early to the middle Miocene. A substantial increase among Nyanzapithecine shearing development in the middle Miocene and a decrease in shearing development among large bodied middle Miocene hominoids have the combined effect of increasing the range of SQs for East African non-cercopithecoid catarrhines, such that the range of SQ values for the middle Miocene exceeds those for both early Miocene hominoids and extant hominoids. It should be noted, however, that the middle Miocene encompasses a wider range of phylogenetic sampling than for extant hominoids.

In addition, environmental reconstructions for primate rich localities using stable carbon isotopes as a proxy for vegetation, are not consistent with prior interpretations of environmental change from closed to open habitats from the early to the middle Miocene. Instead, this study finds evidence for a broadening of habitat heterogeneity through time.

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Chapter 4

Catarrhine manual intermediate phalange morphology, positional behavioral diversity and the early and middle Miocene of East Africa

Introduction

The early to the middle Miocene is known for a diverse radiation of catarrhine taxa. Postcranial functional morphology of the fossil non-cercopithecoid catarrhine taxa has a long history of documentation and research (e.g. MacInnes, 1943; Le Gros Clark and Leakey, 1951; Napier and Davis, 1949; Preuschoft, 1973; Andrews and Simon, 1977; Harrison, 1982; Walker and Pickford, 1983; Rose, 1988; 1996; Rose et al., 1992; Ward, 1993, 1994; McCrossin 1994; McCrossin et al., 1998; Gebo et al., 1997; Ward et al., 1999; MacLatchy et al., 2000; Ishida et al., 2004; Nakatsukasa et al., 2003; 2007; 2012; Davers and Nakatsukasa, 2015; Wuthrich et al., 2019). The posctcranial skeleton is best known for the early Miocene Genus, *Ekembo*. The positional repertoire of Ekembo has been interpreted to include primarily above-branch, pronograde arboreal quadrupedalism (McHenry and Corruccini, 1983; Ward, 1993, 1997; Rose, 1983; 1993; Rose et al., 1992), including the capacity for powerful grasping with the hands and feet during bouts of climbing and possibly bridging (Corruccini et al., 1975; Morbeck, 1975; Walker and Pickford, 1983, 1993; Ward, 1998; Dunsworth, 2006; Rein et al., 2011; Davers and Nakatsukasa, 2015). Few early Miocene taxa are considered to have deviated from the generalized *Ekembo* functional repertoire.

However, some studies have alluded to the presence of more variable positional behaviors in the early Miocene. For example, the skeleton of large bodied hominoid

Morotopithecus demonstrates adaptations associated with orthograde postures (Sanders and Bodenheimer, 1994; Gebo et al., 1997; MacLatchy et al., 2000; MacLatchy, 2004). Among small bodied non-cercopithecoid catarrhines, *Dendropithecus macinnesi* from Rusinga and *Simiolus enjiessi* from West Turkana are cited to have adaptations consistent with suspension (Napier and Davis, 1959; Simons and Fleagle, 1973; Rose, 1983, 1993; Rose, et al., 1992). More recently, a sample of unassociated capitates from Tinderet, indicates the presence of more habitual suspension among small bodied catarrhines (Wuthrich et al., 2019).

Fewer postcranial remains are known from the Middle Miocene of East Africa. However, hominoids are thought to have increased their positional and locomotor diversity to include possible semi-terrestriality (McCrossin, 1994; McCrossin, 1997; McCrossin et al., 1998; Patel et al., 2009) and forelimb dominated climbing (Ishida et al., 2004). In addition, *Mabokopithecus* has been reconstructed as an active acrobatic climber (McCrossin, 1992). A hinderance to quantifying and comparing levels of adaptive diversity from the early to the middle Miocene is the preservation and study of common postcranial elements across fossil localities. Though considerable work has been done to describe and characterize the functional morphology of partial skeletons where the taxonomic identify of the postcranial fossils are known (see above), fewer studies focus on the functional morphology of fossils that are not attributed to a taxon (Harrison, 1982; Rose, 1988; Rose, et al., 1992; Wuthrich et al., 2019).

A survey of early and middle Miocene catarrhine postcranial material at the Kenya National Museum established that one of the most well-preserved elements across Miocene taxa is the intermediate manual phalange. At least 21 non-cercopithecoid catarrhine taxa and two cercopithecoids are known from the fossil localities where complete intermediate manual phalangeal specimens have been recovered in Kenya (Table 1). As such, the intermediate phalange represents a unique opportunity to examine positional behavior diversity through time. However, this element has been subjected to very little study (Patel and Maiolino, 2016). The first goal of this chapter is to quantify relative curvature and relative length in the intermediate manual phalanges of extant taxa in order to determine if these parameters are broadly correlated with positional behavior in the wild. Metapodials (Susman, 1979; Preuschoft et al., 1993; Patel 2008; Kirk et al., 2008; Patel and Wunderlich, 2010; Patel and Maiolino, 2016) and proximal phalanges (Jolly, 1967; Rose, 1986; Harrison, 1989; Hamrick et al., 1995; Stern, 1995; Deane and Begun, 2008; Patel et al., 2009: Almécija et al., 2007, 2009; Rein et al., 2011) have been quantified in this way in numerous studies of anthropoid hands and it has been demonstrated that arboreal, especially suspensory taxa, tend to have longer and more curved rays than nonsuspensors. A handful of studies have quantified the relative length of isolated intermediate phalanges among mostly hominoids, *Ateles*, and a limited number of cercopithecids (Susman, 1979; Begun et al., 1994; McCrossin, 1994; McCrossin et al., 1998; Madar et al., 2002; Nakatsukasa et al., 2003; Almécija et al., 2009) and even fewer studies have examined curvature (Matarazzo, 2008).

If a correlation between the intermediate manual phalangeal morphology and positional behavior is established, relative curvature and relative length will be used to reconstruct the extent of positional behavioral diversity among early and middle Miocene catarrhines. In doing so this study will contribute to the overarching goal of this dissertation, which is to test whether behavioral changes track with environmental change.

Table 12. Fossil catarrhine species known from Songhor, Rusinga, West Turkana, Kipsaramon, and Maboko with published body mass estimates.

Taxon	Localities	Body mass	References
Proconsul major	Songhor	63.4 - 86.7kg	Rafferty et al., 1995
Proconsul africanus	Songhor	Similar to *E. heseloni*	Harrison, 2010
Rangwapithecus gordoni	Songhor	Similar to *E. heseloni*	Andrews, 1978; Langdon, 1984
Dendropithecus macinnesi	Songhor, Rusinga	6 – 8 kg[a]	Bilsborough and Rae, 2015; Harrison, 2013
Kalepithecus songhorensis	Songhor	5 – 6 kg[a]	Harrison, 2013
Limnopithecus evansi	Songhor	5 kg[a]	Harrison, 2010
Limnopithecus legetet	Songhor, Rusinga	5 kg[a]	Harrison, 2010
Ekembo heseloni	Rusinga	8-19 kg	Rafferty et al., 1995; Ruff, 2003
Ekembo nyanzae	Rusinga	25.6–46.3 kg	Rafferty et al., 1995; Ruff, 2003
Nyanzapithecus vancouveringorum	Rusinga	8-11 kg	Harrison, 2010
Afropithecus turkanensis	West Turkana	35 kg[b]	Leakey and Walker, 1997
Simiolus enjiessi	West Turkana	4-6 kg[a]	Rose, 1992
"Equatorius" africanus	Kipsaramon	27 kg[c]	Ward et al., 1999
Nyanzapithecus sp.	Kipsaramon	?	Kelley et al., 1999; Pickford and Kunimatsu, 2005
Simiolus cheptumoae	Kipsaramon	Smaller than *S. enjiessi*	Pickfrod and Kunimatsu, 2005
Limnopithecus sp.	Kipsaramon	Similar to L. legetet and L. evansi	Pickfrod and Kunimatsu, 2005
Cf. Noropithecus kipsaramonensis	Kipsaramon	Similar to V. macinnesi	Pickford and Kunimatsu, 2005
Kenyapithecus africanus	Maboko	17.3-36.2 kg	McCrossin, 1994
Mabokopithecus clarki	Maboko	7.5-8.6 kg[a]	McCrossin, 1992
Mabokopithecus pickfordi	Maboko	7.5-8.6 kg[a]	McCrossin, 1992
Micropithecus ("Simiolus") leakeyorum	Maboko	2.3-3.2 kg[a]	Harrison, 1989
Victoriapithecus macinnesi	Maboko	2.4-6 kg[d]	Zambon et al., 1999; Blue and McCrossin, 2001; Blue, 2002; Arney et al., 2015

Body weight estimates are based on qualitative and quantitative comparisons.

[a] Body mass estimates based on qualitative comparisons.

[b] Body mass estimate based on the regression equations published in Rafferty et al., (1995).

[c] Body mass estimate based on regression equations published in Ruff et al., (1988).

[d] Based on quantitative comparisons with extant cercopithecoid postcranials.

Phalange Relative Length

Relative length and curvature of the metapodials and phalanges of the hands have been shown to correlate with positional behavior in anthropoids. Relative length of proximal (Jolly, 1967; Susman, 1979; Harrison, 1989; Hamrick et al., 1995; Nakatsukasa et al., 2003; Rein, 2011) and intermediate phalanges of anthropoid taxa (Harrison, 1989; McCrossin, 1994; McCrossin et al., 1998; Madar et al., 2002; Almécija et al., 2007, 2009) have been shown to discriminate between arboreal and terrestrial species as well as between suspensory and nonsuspensory anthropoid taxa. Among cercopithecoids, arboreal species have longer phalanges, which contribute to longer digits (Jolly, 1967; Harrison, 1989; Patel et al., 2009). The same pattern holds for hominoids where the more arboreal and suspensory hylobatids and orangutans have longer phalanges than the knuckle walking African apes, and the more terrestrial gorilla has shorter phalanges than do chimpanzees (Susman, 1979; Almécija et al., 2007, 2009). Longer digits are related to facilitating enhanced grasping of branches during arboreal modes of locomotion (Washburn, 1951; Jolly, 1967; Rose, 1988). Conversely, shorter phalanges are interpreted to protect against ground reaction forces from weight bearing loads associated with terrestrial locomotion (Schmitt, 1999; Schmitt and Hanna, 2004; Franz et al., 2005; Young, 2009) by reducing the torque due to the ground reaction force acting on the phalangeal shaft (Nieschalk and Demes,1993). The proximal phalangeal length of extant anthropoid taxa has been shown to increase with higher proportions of suspension and arboreal locomotion (Rein, 2011). Intermediate phalanges, though less studied (Patel and Maiolino, 2016), have been shown to display a similar pattern of distinction between suspensory, arboreal, and terrestrial taxa (Harrison, 1989; Begun et al., 1994; Madar et al., 2002; McCrossin, 1994; McCrossin et al., 1998; Almécija et al., 2009). Therefore, the relative length of intermediate phalanges could provide a useful metric for examining functional variation among fossil taxa through time.

Phalangeal Curvature

Like relative phalangeal length, phalangeal curvature correlates with positional behavior in anthropoids. It is inferred to provide an adaptive advantage to arboreal locomotion, specifically suspensory behaviors (Stern et al., 1995; Deane et al., 2005; Almecija et al., 2007; Congdon, 2012) and is associated with higher proportions of climbing behaviors in modern anthropoids (Rein et al., 2015). Curvature is theorized to facilitate the grasping of arboreal supports by increasing the amount of surface area of the phalange that contacts the support (Hunt, 1991), and/or by dissipating the bending stresses along the phalangeal shaft that are associated with substrate reaction forces while grasping (Preuschoft, 1973; Richmond, 1998, 2007; Jungers et al., 2002). Curvature of anthropoid intermediate phalanges has been examined in a limited number of species by Matarazzo (2008).

Matarazzo's (2008) study quantified intermediate phalangeal curvature in eight anthropoid taxa (*Pongo pygmaeus, Pan troglodytes, Gorilla gorilla, Gorilla beringei, Hylobates lar, Ateles sp. , Cebus apella, Macaca fascicularis,* and *Macaca nemestrina*) using the included angle method (Jungers et al., 1997). Results indicated a weaker yet significant relationship between intermediate phalange curvature and suspensory propensity than that displayed by curvature in corresponding proximal phalanges. Despite the weaker correlation, intermediate phalange curvature was consistent with expectations based on locomotor repertoire. Thus, intermediate phalange curvature could also be valuable for inferring positional behaviors among fossil catarrhines.

Materials and Methods

Extant Comparative Sample

Manual intermediate phalanges from rays II-IV of 157 adult, extant individuals (30 taxa) were measured. Extant species were sampled from the Museum of Comparative Zoology, Cambridge (MCZ), the National Museum of Natural History, Washington D.C. (NMNH), and the Field Museum of Natural History, Chicago (FM). Species with individual samples sizes are presented in Table 12. The extant anthropoid comparative sample includes nine ceboid taxa (*Cebus albifrons, Cebus imitator, Alouatta seniculus, Alouatta palliata, Alouatta caraya, Ateles paniscus, Ateles geoffroyi, Ateles belzebuth, Ateles fusciceps*), nine hominoid taxa (*Gorilla gorilla, Gorilla beringei, Pan troglodytes troglodytes, Pan paniscus, Pongo abelli, Pongo pygmaeus morio, Pongo pygmaeus wurmbii, Hylobates lar lar,* and *Syphalangus syndactylus),* and 11 cercopithecoid taxa (*Nasalis larvatus, Presbytis rubicunda, Trachypithecus cristatus, Procolobu badius, Colobus guereza, Cercopithecus mitis, Macaca fascicularis, Papio ursinus, Papio cynocephalus, Papio anubis,* and *Mandrillus spinx*). Age was determined by tooth eruption and fusion of epiphyses.

Manual and pedal bones are not always properly curated in museum collections. Table 13 lists features used to distinguish between hand and foot phalanges for extant taxa and fossil specimens. While these features work well for hominoids and many other, especially large, anthropoids, hand and foot phalanges are not easily distinguishable in *Cebus, Alouatta* and small to medium bodied cercopithecoids, as their hand and foot phalangeal dimensions overlap extensively (Allen, 2008). Since manual and pedal phalanges are indistinguishable for these taxa, in cases where hand and foot bones were comingled, intermediate phalangeal measurements for the indeterminate (i.e pedal vs. manual) elements were still included to increase sample sizes.

Locomotor and Positional Behavior Data

Extant taxa were assigned to positional behavioral categories based on published observations and descriptions. The extant taxa were assigned to one of the following five most frequently utilized positional behaviors during locomotion (after Wuthrich, 2017; Wuthrich et al., 2019): 1) KW= Knuckle-walking; 2) DG=terrestrial digitigrade quadrupedalism; 3) PG=arboreal palmigrade quadrupedalism; 4) L= arboreal palmigrade quadrupedalism with leaping, and 5) S=suspension, brachiation, orthograde climbing.

The L category deserves some explanation. The category includes those colobines that have been reported to utilize frequent amounts of leaping in their locomotor repertoire such as *Procolobus badius, Colobus guereza*, and *Trachypithecus cristata* (Bernstein, 1968; Gebo and Chapman, 1995; McGraw, 1998). While it is to be expected these leapers have modified hindlimbs, study of skeletal features of leaping colobines has shown these taxa also differ from other colobines and cercopithecines in the wrist and scapula (Dunham et al., 2015; 2016; Wuthrich, 2017). Leaping in colobines is generally associated with a drop where the torso is oriented vertically and the arms are raised in order to grasp branches above the head for stability (Fleagle, 1980; Gebo and Chapman, 1995). Frequent leaping with below branch grasping for stability could lead to enhanced manual grasping. Thus, leapers are distinguished here from other non-leaping palmigrade taxa. Leaping and suspension has been mentioned to be a part of the locomotor repertoire of *Nasalis* (Napier and Napier, 1967). However, the proportions of positional behavioral activities in *Nasalis* are still unknown and *Nasalis* is therefore categorized as PG here. *Presbytis rubicunda* is also categorized as PG due to a lack of detailed knowledge about its locomotor and positional behavior.

Table 13. Extant comparative sample, individual sample sizes, and locomotor group, and body mass.

Taxa	N*	Sex	Museum	Locomotor Type	Locomotor Reference	Body Mass (kg)[1]
Alouatta caraya	1	F(1)	NMNH	PG	Youlatos and Guillot, 2015	5.4 (F)
Alouatta fusca	1	F(1)	NMNH	PG	Youlatos and Guillot, 2015	4.4 (F)
Alouatta palliata	8	M(1); F(2); ?(5)	NMNH	PG	Youlatos and Guillot, 2015	7.2 (M); 5.3(F)
Ateles belzebuth	1	F(1)	FM	S	Cant et al., 2001	7.9 (F)
Ateles fusciceps	6	M(2); F(4)	NMNH	S		8.9(M); 9.2(F)
Ateles geoffroyi	5	M(1); F(3); ?(1)	FM	S	Mittermeier, 1978; Cant, 1986; Fontaine (1990)	7.8(M); 7.3(F)
Ateles paniscus	2	F(2)	NMNH	S	Mittermeier, 1978; Youlatos, 2002	8.4(F)
Cebus albifrons	6	F(4); ?(1)	FM	PG	Youlatos, 1999	3.2(M); 2.3(F)
Cebus capucinus	2	?(2)	MCZ	PG	Garber and Rehg, 1999; Bezanson, 2006; 2009	
Cercopithecus mitis	6	M(3); F(3)	NMNH	PG	Gebo and Chapman, 1995	5.9(M); 3.9(F)
Procolobus badius	2	F(2)	MCZ	L	Gebo and Chapman, 1995; McGraw, 1998	5.7(F)
Colobus guereza	3	M(1); (2)	NMNH	L	Gebo and Chapman, 1995	8.2(M); 7.5(F)
Gorilla beringei	5	M(3); F(2)	NMNH	KW	Doran, 1996; 1997	162.5(M); 97.5(F)
Gorilla gorilla	13	M(7); F(6)	MCZ, NMNH	KW	Remis, 1994	170.4(M); 71.5(F)
Hylobates lar	15	M(7); F(8)	MCZ	S	Nowak and Reichard, 2016	5.9(M); 5.3(F)
Macaca fascicularis	9	M(5); F(4)	MCZ	PG	Cant, 1988	5.4(M); 3.4(F)
Mandrillus spinx	1	M(1)	MCZ	DG		31.6(M)
Nasalis larvatus	10	M(5); F(5)	MCZ	PG		20.4(M); 9.8(F)
Pan pansicus	1	M(1)	MCZ	KW	Doran and Hunt, 1994	45(M)
Pan troglodytes troglodytes	13	M(6); F(6); ?(1)	MCZ, NMNH	KW		59.7(M); 45.8(F)
Papio anubis	3	M(2); ?(1)	FM, NMNH	DG	Hunt, 1991	21.2 (M)
Papio cynocephalus	2	M(1); F(1)	NMNH	DG		21.8(M); 15(F)
Papio ursinus	1	F(1)	NMNH	DG		14.8(F)

Pongo abelli	5	M(1); F(4)	NMNH	S	Thorpe and Crompton, 2006	77.9(M); 35.6(F)
Pongo pygmaeus morio	5	M(2); F(3)	MCZ, NMNH	S	Thorpe and Crompton, 2009	78.5(M); 35.8(F)
Pongo pygmaeus wurmbii	2	M(2)	MCZ, NMNH	S	Manduell et al., 2011	78.5(M)
Presbytis rubicunda	8	M(4); F(4)	MCZ	PG		6.3(M); 6.2(F)
Symphalangus syndactylus	4	M(1); F(3)	NMNH	S	Hunt, 2004	12.8(M); 10.5(F)
Trachypithecus cristata	12	M(6); F(6)	MCZ	L	Napier and Napier, 1985	6.6(M); 5.8(F)

*N represents the number of individuals measured.

[1] Mean body masses for each taxa are from Smith and Jungers, 1997.

Table 14. Features distinguishing the manual and pedal intermediate phalanges of most anthropoids. Augmented from features mentioned in Madar et al., 2002.

Foot phalanges	Hand phalanges
Shaft has an hourglass shape in ventral view	Shaft profile tapers distally
Proximal end is triangular in shape	Proximal end is rectangular or oval in shape
Weakly developed flexor sheath ridges	Better defined flexor sheath ridges
Diminished or absent median ridge	More prominent median ridge
Less dorsoventral shaft curvature	More pronounced collateral pits
Shorter relative length	Deeper trochlea

Fossil material

The fossil material included in this study is listed in Table 4 and shown in Figure 1. Measurements were taken on the original fossils at the Kenya National Museum for all specimens. Definitive assignment to ray was not possible for most specimens. Several phalangeal specimens from Songhor and Maboko are unassociated with partial skeletons or craniodental remains and their taxonomic identifications are preliminary. Plausible taxonomic identities were based on size comparisons with extant anthropoids in terms of proximal phalangeal width measurements. Fossil Intermediate phalanges were recovered from five localities from the early and middle Miocene that span from ~20-14.7 Ma.

Table 15. List of undescribed and comparative fossil phalanges included in this study

Accession	Locality	Taxonomic identification	Ray	Reference
SO 974	Songhor	***Proconsul africanusl/Rangwapithecus gordoni***	Ray 3 or 4	
SO 986	Songhor	***Limnopithecus evansi, Kalepithecus songhorensis***	Ray 2?	
SO 1966	Songhor	***cf*. Dendropithecus *macinessi***	Ray 3 or 4	
SO 35514	Songhor	***Limnopithecus evansi, Kalepithecus songhorensis***	Ray 3 or 4	
RU 15100J	Rusinga	*Ekembo nyanzae*	Ray 5?	Begun et al., 1994
RU 15100I	Rusinga	*Ekembo nyanzae*	Ray 3	Begun et al., 1994
PH 64	Rusinga	*Ekembo heseloni*	Ray 3 or 4	Begun et al., 1994
PH 222	Rusinga	*Ekembo heseloni*	Ray 3	Begun et al., 1994
WK 18356B	Kalodirr	*Afropithecus turkanensis*	Ray 4?	Leakey et al., 1988
TH 28860	Kipsaramon	*"Equatorius" africanus*	?	Sherwood et al., 2002
MB 28393	Maboko	*Kenyapithecus africanus*	Ray 3	McCrossin, 1994; McCrossin et al., 1998; Allen, 2008

MB 28433	Maboko	***Micropithecus (“Simiolus”)***	Ray 3	
MB 32417	Maboko	**_Mabokopithecus_?**	Ray 4?	
MB 35585	Maboko	***Micropithecus (“Simiolus”)***	Ray 2 or 5	
MB 32420	Maboko	***Mabokopithecus***	Ray 2 or 5	
MB 28430	Maboko	***Micropithecus (“Simiolus”)***	Ray 2 or 5	
MB 340	Maboko	*Victoriapithecus macinnesi*	?	Harrison, 1989
MB 11982	Maboko	*Victoriapithecus macinnesi*	?	Harrison, 1989
MB 9433	Maboko	*Victoriapithecus macinnesi*	?	Harrison, 1989
MB12020	Maboko	*Victoriapithecus macinnesi*	?	Harrison, 1989
MB 12017	Maboko	*Victoriapithecus macinnesi*	?	Harrison, 1989

Bolded taxonomic identifications indicate plausibly identities based on qualitative size comparisons to extant anthropoid intermediate phalanges.

Figure 12. Unassociated early and middle Miocene non-cercopithecoid catarrhine phalanges. Specimens are shown in lateral and palmar views and are of the same scale.

Measurements

Seven standard linear measurements were taken with digital calipers on intermediate manual phalanges following Almécija et al. (2007, 2009; Figure 1). Measurements were taken to the nearest 0.01 mm on the right side unless the right elements were damaged or missing, in which case the left side was measured. The intrinsic relative length of intermediate phalanges has been quantified in multiple ways, usually as an index of total length to either base width (Begun et al., 1994; McCrossin, 1994; McCrossin et al., 1998; Madar et al., 2002) or midshaft width (Harrison, 1989). Relative length has also been assessed by examining allometric residuals of total length versus the geometric mean (GM) of all seven linear measurements shown in Figure 1 (Almécija et al., 2009). This latter approach was followed in this study. Chimpanzee individuals were used as the reference baseline for calculating residuals among all other taxa. The regression eqation for chimpanzee intermediate phalanges was found to be Log(Total Length) = 1.3 + 1.0 * Log(GM). Coefficients from this regression were used to estimate the expected length, and residuals were calculated by subtracting the expected length from the measured total length. Almécija and colleagues (2009) argue that using allometric residuals as a assessment of relative phalangeal length removes scaling effects, and is suitable for examining features of shape that reflect differences in locomotor behavior (see also the discussion in Alba et al., 2003). Use of allometric residuals have been criticized, however, as the approach may result in a failure to identify informative shape attributes that may be related to size (Jungers et al., 1995; see also Alba et al., 2003). However, use of allometric residuals is in line with the aim of this study, which is to examine variation in length with respect to positional behaviors in a broader sample of anthropoid taxa.

Phalangeal curvature was quantified by estimating the included angle (Susman et al., 1984; Stern et al., 1995; Junger et al., 1997). Measurements for calculating included angle (Figure 2B) were taken from digital images using the NIH image software ImageJ (Schneider et al., 2012) and include: articular length (L); midshaft depth (D); projected height (H). H is taken from the dorsum of the midshaft to a line draw between the proximal and distal articular surfaces. The included angle is calculated by the equations shown in Figure 2B.

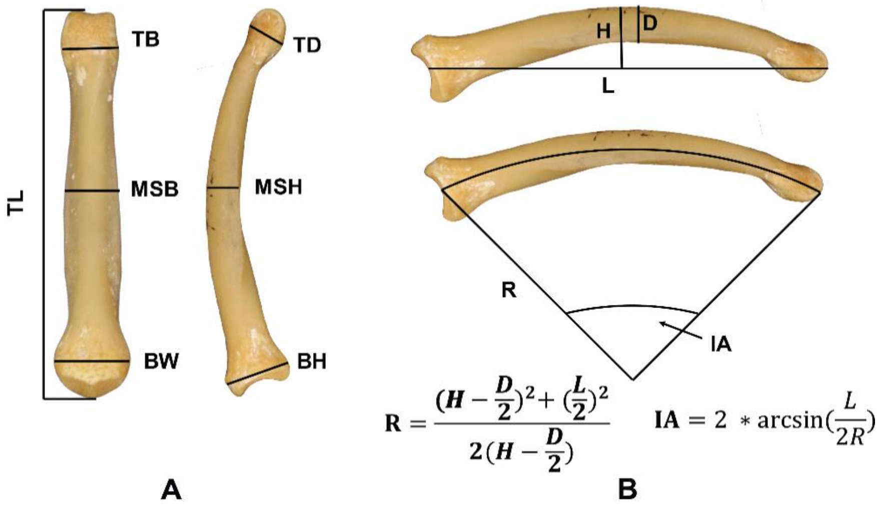

Figure 13. Measurements taken on extant and fossil intermediate phalanges. Linear measurements taken with calipers on extant and fossil phalanges (A). TL total length, BW base width, BH base height, MSB midshaft breadth, MSH midshaft height, TB trochlea breadth, TD trochlea depth. Curvature measurements (B). L articular length, D depth, H height. Curvature image adapted from Jungers et al., 1997.

Statistical Analyses

Statistical analyses were performed in R (version 3.5.3, R Core Team, 2019). Box-and-whisker plots were used to visually inspect for differences between taxa and groups (Figure 3,4). Descriptive statistics (mean, standard deviation, and maximum and minimum values) were calculated for both relative length and included angle values. Significant Tests for normality among relative length and included angle values were performed using the Shapiro-Wilks test

(Shapiro-Wilk, 1965), while tests for the equal variance among positional groups was performed using the Lavene's test for homogeneity of variances and visual inspection of the data. Relative length values are normally distributed, but variances are not equal between groups. A Welch's one-way ANOVA was performed for relative length to take into account heteroscedasticity. Included angle values satisfied assumptions of normality and homoscedasticity. Comparisons between positional groups were made by means of one-way analysis of variance (ANOVA).

Results

Relative Length

Summary statistics of relative length of manual intermediate phalanges for each locomotor category are shown in table 5. Welch's ANOVA reveals that there are statistical differences in mean relative length among extant locomotor groups (df=4, N=389; F= 112; $p< 0.001$). Post-hoc pairwise tests indicate most groups are statistically different from each other ($p< 0.001$). Knuckle-walkers and digitigrade cercopithecines are not statically different in mean relative length, nor are palmigrade anthropoids and the leaping colobines.

The box-and-whisker plots for relative length are shown in Figure 3. Summary statistics are listed in Table 6. Because some species are represented by a single individual, box-and-whisker plots display data collapsed into genera. Suspensors have the longest manual intermediate phalanges. Among the suspensory taxa sampled here, *Hylobates* has the longest phalanges and *Pongo* has the shortest. *Symphalangus* and *Ateles* have similar levels of elongation that are intermediate between those found in *Hylobates* and *Pongo*. The colobine species that are known for frequent leaping have elongated phalanges in comparison to knuckle-walkers, digitigrade cercopithecines, and most palmigrade anthropoids. Values for relative length of these leaping colobines overlap extensively with values of the suspensors, except for *Hylobates.*

Procolobus and *Trachypithecus* have the highest values among leaping taxa, and overlap with values found in *Ateles*, and the upper range of relative length values of *Pongo*. *Colobus* has the lowest relative length values of the leapers and overlaps with values of *Pongo*, the more arboreal palmigrade taxa, and *Pan*. Among palmigrade taxa, *Presbytis rubicunda* has the highest relative length values, which are similar to values of *Ateles* and *Symphalangus*. The median relative length values of *Nasalis* and *Alouatta* are similar and fall within the lower range of *Presbytis* values but are higher than values of *Cebus* and *Macaca*. *Cercopithecus mitis* has the shortest intermediate phalanges among palmigrade taxa with relative length values that overlap with values of *Mandrillus* and lower values of *Pan.* Knuckle-walkers and digitigrade cercopithecines have the shortest phalanges and lowest relative length values. *Gorilla* and *Papio* have the shortest phalanges of all taxa sampled. Among the knuckle-walkers, *Pan* phalanges are more elongated with higher relative length values and limited overlap with *Gorilla* values. Within the limited digitigrade sample, *Papio* individuals have shorter phalanges than the one *Mandrillus spinx* individual measured.

Among hominoids, the more arboreal species have longer intermediate phalanges. Further, among the most arboreal hominoids, there appears to be a pattern of decreasing relative phalangeal length with increasing body size. Among cercopithecoids, the colobine taxa have longer phalanges than the few cercopithecine taxa sampled here. However, *Colobus guereza* has similar relative length values as the arboreal and semi-terrrestrial *Macaca* species.

Among early Miocene catarrhines, Songhor phalanges KNM SO 974, KNM SO 35514, and KNM SO 1966 most closely resemble the elongated phalanges of *Pongo, Trachypithecus, Ateles*, *Nasalis* and *Symphalangus*. KNM SO 986 is less elongated and overlaps with relative length residual values found in *Pan*, *Macaca*, and *E. heseloni*. Intermediate phalanges from the late early Miocene taxa are less elongated with relative lengths similar to those of *Pan* and *Cercopithecus mitis*. The shortest phalanges from this time period belong to hand phalanges of *E. nyanzae*. *E. heseloni* phalanges are slightly relatively longer than *E. nyanzae* phalanges.

Intermediate phalanges of *Mabokopithecus* and the small bodied ape are even more elongated than the Songhor phalanges and overlap with the relative lengths of *Ateles, Presbytis*, and *Symphalangus*. KNM MB 35585 and KNM MB 38433 overlap in relative length with the lower bounds of relative length in *Hylobates* individuals. The large bodied hominoid intermediate phalanx from Maboko (MB 28393) has a short relative length, overlapping with values found in *Cercopithecus ascanius* and the lowest values for *Pan* and *Mandrillus*. TH 28860 from Kipsaramon has an intermediate relative length, overlapping with the median of *Pan*. TH 28860 is also similar in relative length to the phalanx attributed to *Afropithecus*. Overall, middle Miocene noncercopithecoid catarrhine taxa from Maboko and Kipsaramon display greater variation in relative phalangeal length then do noncercopithecoid catarrhine taxa from the early Miocene sites of Songhor, Rusinga and Kalodirr. This increase in variation is even more exaggerated when phalanges of *Victoriapithecus* are included, which overlap in relative length with those of *Gorilla* and *Papio*

Table 16. Summary statistics for intermediate phalangeal length residuals for each positional behavioral group.

Positional/Locomotor Group	N_i	N_p	Mean	SD	Min	Max
Digitigrade	7	13	-0.16	0.09	-0.29	-0.01
Knuckle-walker	32	85	-0.11	0.12	-0.30	0.18
Palmigrade	51	109	0.09	0.09	-0.17	0.29
Leaping	17	48	0.16	0.08	-0.10	0.26
Suspension	45	130	0.21	0.12	-0.16	0.46

N_i=number of individuals
N_p=number of phalanges

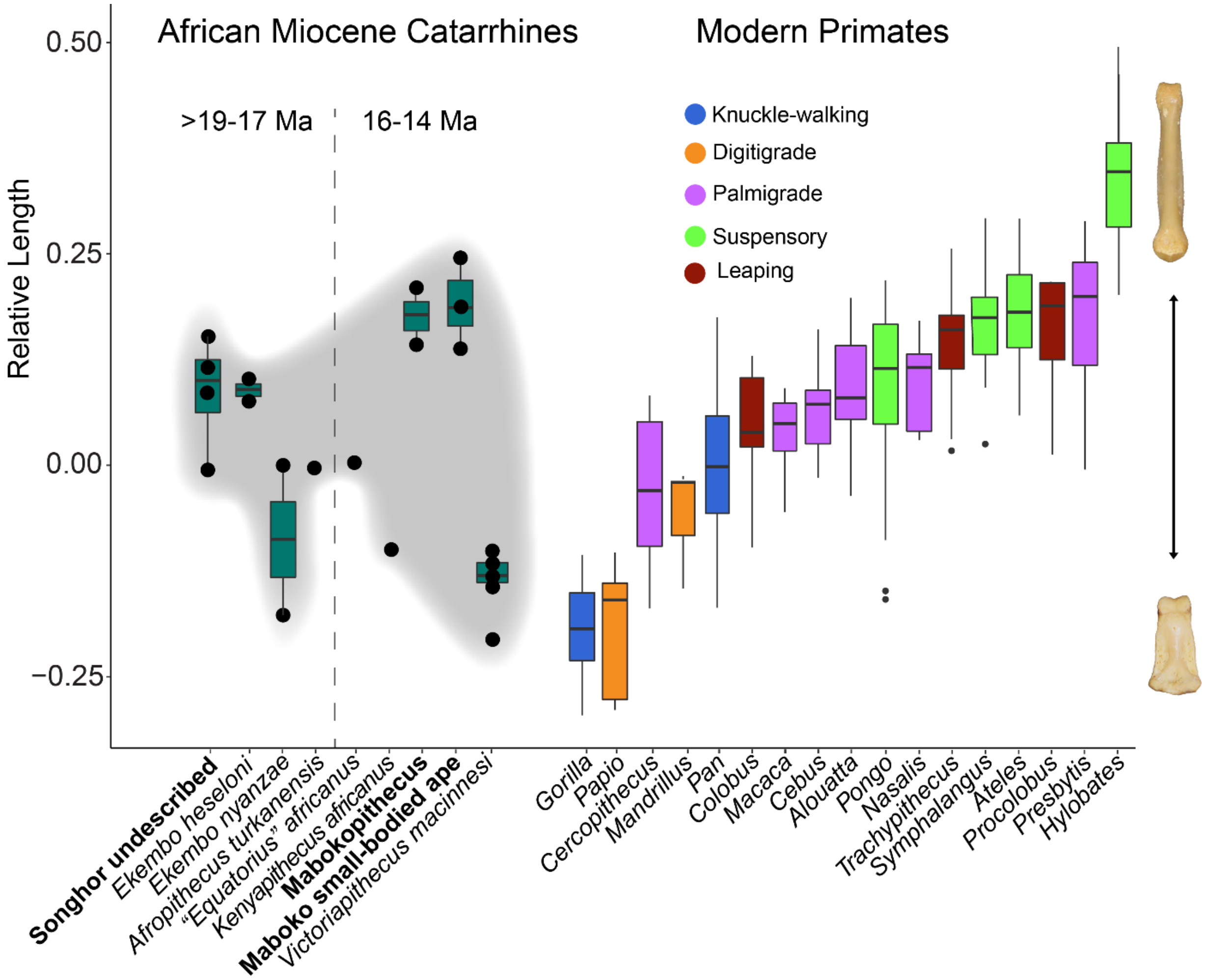

Figure 14. Bivariate plot of residuals of relative length. Residuals are computed as observed phalangeal length minus expected phalangeal length using an equation generated with raw data from *Pan troglodytes*. Horizontal lines represent the median values, whereas the boxes represent the 25% and 75% percentiles, and the whiskers the maximum-minimum ranges. Fossil specimens are on the left and arranged in chronological order. Extant anthropoid taxa (right) are arranged according to increasing median relative length and colored by locomotor category.

Table 17. Summary statistics for relative length residuals for modern (a) and fossil (b) intermediate manual phalanges.

a	Taxa	N_i	N_p	sex	mean	sd	min	max
	Modern							
	Alouatta belzebul	1	3	male	0.07	0.05	0.02	0.12
	Alouatta fusca	1	3	female	0.10	0.07	0.02	0.16
	Alouatta paliatta	5	15	?	0.09	0.05	-0.01	0.16
		2	5	female	0.08	0.08	-0.04	0.16
		1	3	male	0.09	0.03	0.07	0.13
	Ateles belzebuth	1	3	female	0.24	0.02	0.22	0.26
	Ateles fusciceps	4	12	female	0.16	0.04	0.11	0.23
		2	5	male	0.13	0.04	0.06	0.18
	Ateles geoffroyi	1	3	?	0.18	0.02	0.16	0.21
		3	11	female	0.24	0.03	0.18	0.29
		1	3	male	0.13	0.00	0.13	0.13
	Ateles paniscus	2	5	female	0.17	0.05	0.10	0.22
	Cebus albifrons	1	3	?	0.07	0.04	0.02	0.11
		4	11	female	0.06	0.05	-0.01	0.16
	Cebus capucinus	2	2		0.11	0.01	0.10	0.12
	Cercopithecus mitis	3	5	female	-0.02	0.09	-0.13	0.07
		3	7	male	-0.05	0.08	-0.17	0.08
	Colobus badius	2	4	female	0.15	0.10	0.01	0.22
	Colobus guereza	2	6	female	0.06	0.06	-0.03	0.13
		1	3	male	0.00	0.09	-0.10	0.07
	Gorilla beringei	2	6	female	-0.17	0.03	-0.20	-0.12
		3	7	male	-0.24	0.04	-0.29	-0.17
	Gorilla gorilla	6	18	female	-0.19	0.06	-0.31	-0.11
		7	10	male	-0.22	0.05	-0.30	-0.14
	Hylobates lar	8	24	female	-0.11	-	-0.11	-0.11
		7	19	male	-0.19	0.05	-0.25	-0.15
	Macaca fascicularis	4	9		0.34	0.06	0.20	0.46
		5	4	female	0.34	0.06	0.21	0.46
	Mandrillus spinx	1	3	male	0.00	0.07	-0.16	0.09
	Nasalis larvatus	5	10	female	0.06	0.03	0.03	0.09
		5	13	male	-0.06	0.07	-0.15	-0.01
	Pan pansicus	1	3	male	0.12	0.05	0.03	0.20
	Pan troglodytes	1	3	?	0.10	0.05	0.02	0.17
		6	13	female	0.01	0.09	-0.09	0.08
		6	9	male	0.01	0.08	-0.16	0.18
	Papio anubis	1	3	?	0.04	0.05	-0.02	0.07
		2	4	male	0.00	0.05	-0.09	0.10
	Papio cynocephalus	1	3	female	-0.03	0.12	-0.17	0.16

			3	male	-0.21	0.07	-0.30	-0.16
	Papio ursinus	1	3	female	-0.22	0.07	-0.29	-0.14
	Pongo abelli	4	12	female	-0.20	0.08	-0.29	-0.15
		1	3	male	-0.19	0.09	-0.29	-0.13
	Pongo pygmaeus	2	14	female	-0.17	0.09	-0.28	-0.10
		4	4	male	0.14	0.05	0.04	0.22
	Presbytis rubicunda	4	16	female	0.03	0.06	-0.05	0.09
		4	13	male	0.15	0.06	0.03	0.26
	Symphalangus syndactylus	3	9	female	0.14	0.06	0.00	0.20
		1	3	male	0.18	0.09	0.03	0.29
	Trachypithecus cristata	6	18	female	0.14	0.05	0.08	0.17
		6	17	male	0.09	0.11	-0.15	0.22
b	**Fossil**			Accession Number				
	Songhor			SO 1966	0.15	-	-	-
	Songhor			SO 35514	0.08	-	-	-
	Songhor			SO 974	0.12	-	-	-
	Songhor			SO 986	0.00	-	-	-
	Ekembo heseloni			PH 222	0.08	-	-	-
	Ekembo heseloni			PH 64	0.10			
	Ekembo nyanzae			RU 15100I	-0.09	-	-	-
	Ekembo nyanzae			RU 15100J	-0.18	-	-	-
	Afropithecus turkanensis			WK 18356B	0.00	-	-	-
	Equatorius africanus			TH 28861	0.00	-	-	-
	Kenyapithecus africanus			MB 28393	-0.14	-	-	-
	small bodied ape			MB 28430	0.14	-	-	-
	small bodied ape			MB 28433	0.24	-	-	-
	small bodied ape			MB 35585	0.21	-	-	-
	Nyanzapithecine			MB 32417	0.19	-	-	-
	Nyanzapithecine			MB 32420	0.14	-	-	-
	Victoriapithecus macinnesi			MB 11982	-0.21	-	-	-
	Victoriapithecus macinnesi			MB 12017	-0.10	-	-	-
	Victoriapithecus macinnesi			MB 340	-0.12	-	-	-
	Victoriapithecus macinnesi			MB12020	-0.14	-	-	-

Curvature

Summary statistics of included angle values for each locomotor category are shown in table 8. ANOVA reveals that there are statistical differences in mean included angle among extant locomotor groups (df=4, N=363; F= 75.88; $p< 0.001$). Post-hoc pairwise tests indicate most groups are statistically different from each other ($p< 0.001$). The only positional groups not statistically different with a p-value< 0.001 are palmigrade taxa and leaping colobines.

The box-and-whisker plots for included angle are shown in Figure 4. Included angle values of intermediate phalanges show overlap among taxa sampled here, but a clear pattern is still present, with terrestrial species having lower values (i.e. straighter shafts), more arboreal species displaying higher values, with the highest values (i.e most curved shafts) found in suspensory taxa.   Among suspensory taxa, the hylobatids have the highest included angle values with similar medians between *Hylobates* and *Symphalangus*. *Pongo* and *Ateles* included angle values are lower but still overlap with the range of included angle values found in hylobatids. The leaping colobines have included angle values that overlap extensively with values found in other positional behavioral groups. *Trachypithecus* and *Colobus* included angle values overlap with but are consistently higher than those of *Procolobus.* Within palmigrade taxa, included angle values are higher among the colobines and *Alouatta* than in arboreal cercopithecines and *Cebus*. The included angle values for knuckle-walking African ape taxa overlap extensively with each other and with the values of palmigrade taxa. Digitigrade taxa have the straightest phalangeal shafts. *Papio* individuals display the lowest included angle values that have limited overlap with all other anthropoid values, including values of *Mandrillus*.

Among hominoids, the Asian apes have more curved phalanges than the African apes. Hylobatid phalanges tend to be more curved than those of *Pongo*, but the former’s included angle values still fall within the range of the latter's included angle values. Among cercopithecoids, colobines have more curved phalanges with higher included angle values than cercopithecines, and arboreal cercopithecines have higher included values than those of terrestrial cercopithecines. In platyrrhines, the more general quadrupedal cebids have less curved phalanges than the slow climbing *Alouatta* species, while more suspensory atelines have more curved phalanges.

The level of curvature among the fossil intermediate phalanges varies greatly. Included angle values for Tinderet phalanges range from 28^{0} (KNM SO 1966) to 50.8^{0} (KNM SO 35514). KNM SO 974 and KNM SO 986 have included angle values of 35.0^{0} and 39.4^{0}. The straighter Songhor phalanx, KNM 1966, overlaps in included angle values with *Papio* and *Mandrillus,* despite being relatively elongated as shown above. KNM SO 986 and KNM SO 974 overlap in curvature with pronograde cercopithecines such as *Macaca* and *Cercopithecus* as well as the African apes. KNM SO 35514 has the highest curvature and its included angle overlaps with phalanges of *Hylobates* and *Symphalangus*. The phalanges of *Ekembo* and *Afropithecus* are less curved and overlap with the range of manual phalangeal curvature found in African apes, *Mandrillus*, *Cebus*, and *Macaca*.

The Maboko small and medium bodied catarrhine intermediate phalanges have similar levels of high curvature and range in included angle values from 43^{0} to 50^{0}. These included angle values overlap with the manual phalanges included angles of *Hylobates* and *Symphalangus* and the higher range of values for *Pongo*, *Ateles*, *Alouatta*, and leaping colobines. KNM TH 28861 is similar in curvature to *E. nyanzae* and overlaps with *Mandrillus*, *Cebus*, and *Gorilla*. KNM MB 28393 has the lowest curvature of the Miocene taxa included here and overlaps with the included angle values of *Victoriapithecus* and *Papio*. As with intermediate phalange relative length among fossil taxa, there appears to be an increase in curvature variation through time from early to middle Miocene catarrhines.

Table 18. Descriptive statistics for manual intermediate phalanx included angle values for each locomotor group.

Positional/Locomotor Group	N_i	N_p	Mean	SD	Min	Max
Digitigrade	6	18	23.15	9.18	5.46	36.79
Knuckle-walker	31	84	34.91	6.64	17.56	50.28
Palmigrade	46	113	40.32	8.65	10.15	62.86
Leaping	17	48	44.97	6.80	17.75	53.49
Suspension	36	105	50.51	8.21	22.50	61.92

N_i=number of individuals
N_p=number of phalanges

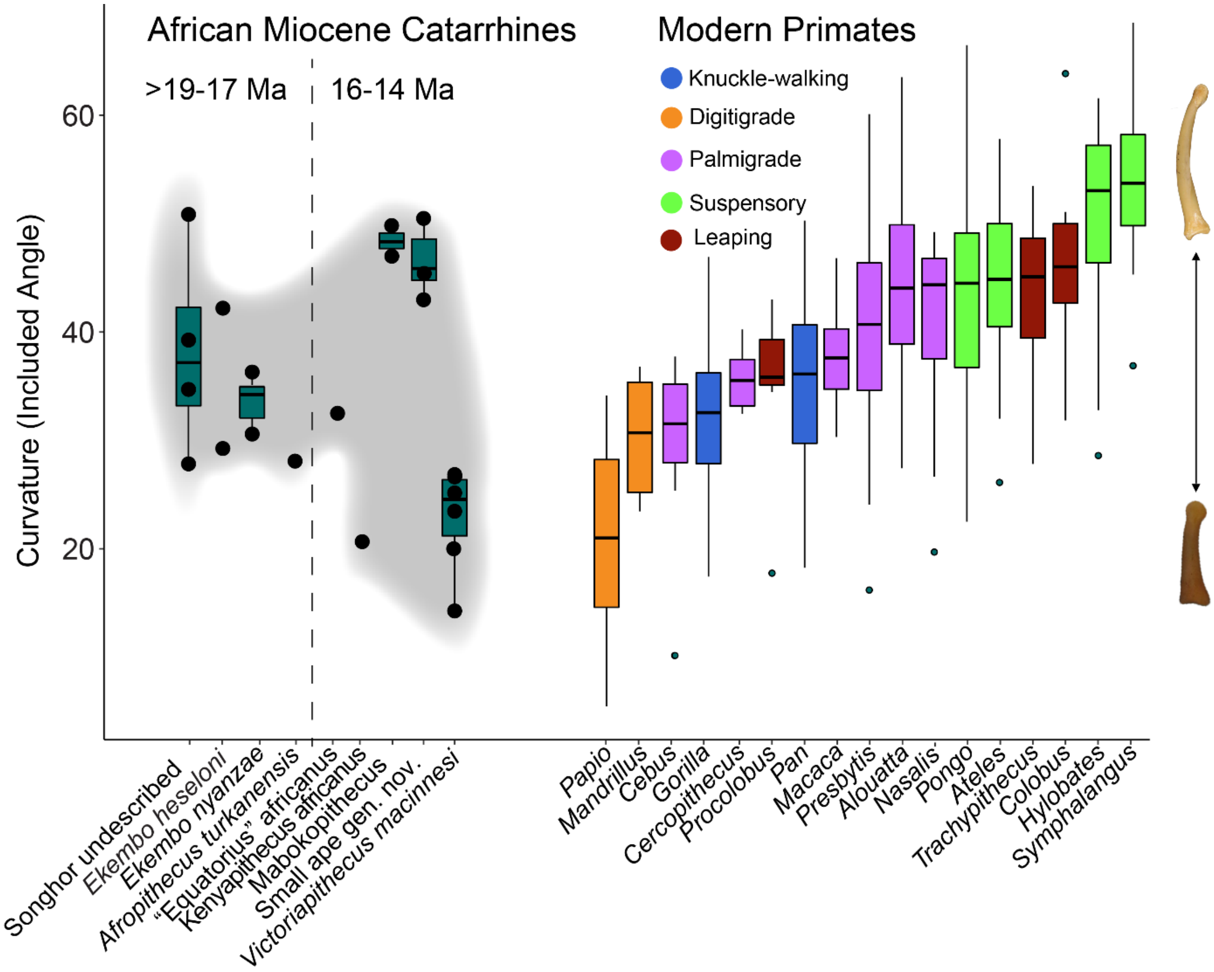

Figure 15. Box-and-whisker plot of intermediate phalange curvature as computed by the included angle. Extant anthropoid taxa (right) are arranged according to increasing median relative length and colored by locomotor category. Fossil specimens (left) are arranged chronologically.

Table 19. Summary statistics for curvature (IA) for modern (a) and fossil (b) phalanges.

a	Taxa	N_i	N_e	Sex	Mean	sd	min	max
	Modern							
	Alouatta belzebul	1	3	male	47.2	6.6	39.7	51.8
	Alouatta caraya	1	2	female	32.1	1.8	30.9	33.4
	Alouatta fusca	1	3	female	46.8	1.6	45.4	48.6
	Alouatta palliata	5	15	?	43.7	7.5	31.1	54.7
		1	3	female	59.4	3.2	56.7	62.9
		1	2	male	41.3	3.8	38.6	44.0
	Ateles fusciceps	4	12	female	46.7	7.7	36.0	57.8
		2	5	male	42.4	6.2	32.5	49.0
	Ateles geoffroyi	1	3	?	51.6	1.1	50.4	52.4
		2	6	female	46.7	5.9	38.7	54.8
	Ateles paniscus	1	3	female	50.7	2.2	48.2	51.9
	Cebus albifrons	2	5	female	27.7	10.9	10.1	37.7
		1	1	?	33.9	-	33.9	33.9
	Cebus capucinus	1	1	female	39.4	5.9	32.3	45.0
	Cercopithecus mitis	3	7	male	35.9	5.9	25.8	40.2
		3	5	female	33.9	11.4	17.7	43.0
	Colobus guereza	1	3	male	46.3	6.0	39.5	51.1
		2	6	female	42.4	9.3	31.9	49.3
	Gorilla beringei	3	7	male	34.9	3.8	29.9	41.9
		2	6	female	30.6	6.8	17.6	40.5
	Gorilla gorilla	6	17	male	36.5	4.5	29.7	45.2
		6	14	female	55.6	4.0	48.2	61.6
	Hylobates lar	7	19	male	53.5	4.7	44.7	59.3
		8	24	female	40.1	4.2	35.0	46.8
	Macaca fascicularis	5	9	male	36.9	3.8	30.9	41.1
		4	4	female	30.1	0.1	30.0	30.1
	Mandrillus spinx	1	3	male	39.8	8.6	19.7	48.7
	Nasalis larvatus	5	13	male	43.4	6.5	26.6	49.2
		5	10	female	45.8	4.3	41.6	50.3
	Pan pansicus	1	3	male	36.8	5.0	31.1	40.8
	Pan troglodytes	6	16	female	34.7	5.5	26.5	46.9
		6	18	male	35.4	7.8	19.3	47.1
		1	3	?	29.2	4.4	24.3	32.8
	Papio anubis	1	3	male	18.6	3.3	14.7	20.5
		1	3	?	21.2	11.5	9.7	32.7
	Papio cynocephalus	1	3	male	21.7	8.2	12.6	28.6
		1	3	female	15.9	11.4	5.5	28.1
	Papio ursinus	1	3	female	50.1	8.3	40.5	55.6

	Pongo abelli	1	3	male	56.6	3.6	54.3	60.8
		1	3	female	36.1	9.5	22.5	49.6
	Pongo pygmaeus	3	6	male	44.2	2.4	40.1	47.1
		3	9	female	45.4	6.1	28.1	53.4
	Presbytis rubicunda	2	8	male	36.8	7.8	24.1	47.8
		5	16	female	55.6	4.6	49.3	61.9
	Procolobus badius	2	4	female	43.3	4.8	37.6	50.7
	Symphalangus syndactylus	1	3	male	60.8	1.2	59.6	61.9
		3	9	female	55.6	4.6	49.3	61.9
	Trachypithecus cristata	6	17	male	47.5	4.7	36.8	53.5
		6	18	female	41.6	10.3	16.2	60.1
b	**Fossil**			Accession number	IA			
	Songhor			SO 1966	28.0	-	-	-
	Songhor			SO 35514	50.9	-	-	-
	Songhor			SO 974	34.9	-	-	-
	Songhor			SO 986	39.4	-	-	-
	Ekembo heseloni			PH 222	42.2	-	-	-
	Ekembo nyanzae			RU 15100I	36.3	-	-	-
	Ekembo nyanzae			RU 15100J	33.8	-	-	-
	Afropithecus turkanensis			WK 18356B	28.2	-	-	-
	Equatorius africanus			TH 28861	28.9	-	-	-
	Kenyapithecus africanus			MB 28393	20.7	-	-	-
	small bodied ape			MB 28430	42.9	-	-	-
	small bodied ape			MB 28433	50.5	-	-	-
	small bodied ape			MB 35585	45.9	-	-	-
	Nyanzapithecine			MB 32417	49.7	-	-	-
	Nyanzapithecine			MB 32420	48.7	-	-	-
	Victoriapithecus macinnesi			MB 11982	14.3	-	-	-
	Victoriapithecus macinnesi			MB 12017	26.9	-	-	-
	Victoriapithecus macinnesi			MB 340	25.6	-	-	-
	Victoriapithecus macinnesi			MB12020	26.6	-	-	-

Discussion

Positional behavior correlates

Results presented here are consistent with the intermediate manual phalanges preserving a positional behavioral signal. Previous studies that examined intermediate phalange length in less diverse datasets of modern taxa indicated taxa could be discriminated according to broad locomotor behaviors (Begun et al., 1994; McCrossin et al., 1998; Allen, 2008, Madar et al., 2002; Almécija et al., 2009). Positional groups differ statistically from another, except members of palmigrade quadrupeds and leapers do not differ from one another. Although leapers display some subtle anatomical differences compared to closely related non-leapers (Dunham et al., 2015, 2016; Wuthrich et al., 2019), there is also extensive overlap morphologically and behaviorally among pronograde arboreal taxa.

Patterns of variability for the included angle of the intermediate manual phalanges are similar to those found by Matarrazzo (2008), with suspensory taxa having the highest levels of curvature, pronograde quadrupeds with moderate to high levels, and knuckle walkers having moderate to low levels of curvature. However, the curvature data here, with the inclusion of colobines and *Alouatta*, demonstrates statistical differences between terrestrial, arboreal, and more suspensory taxa. Colobines with high instances of leaping and climbing behaviors have phalanges as elongated and curved as those of the suspensory *Ateles* and *Symphalangus* but not as long and curved as in *Hylobates*. Some colobine phalanges are also more gracile and curved than those of *Pongo*. *Pongo* is considered a quadrumanous climber and differs from Hylobatids and Atelines in body size and amount of suspension (Cant, 1986, 1987; Thorpe and Crompton, 2006; Youlatos and Guillot, 2015: Nowak and Reichard, 2016). The larger size of Pongo coupled with its extremely elongated metacarpals and proximal phalanges (Susman, 1979; Almécija et al., 2009), could provide enough hand and digit surface area to properly grip arboreal substrates. However, phalangeal curvature studies have yet to examine the relationship between phalangeal length, curvature, body size, and support size (Congdon, 2012).

Locomotor diversity change in fossil taxa

Intermediate phalangeal relative length and curvature both display a pattern of increasing morphological variation from the early to the middle Miocene among catarrhine taxa (Figure 3, 4). This pattern still holds when *Victoriapithecus* intermediate phalanges are excluded. If the amount of variation in relative length is represented as the percent difference between the highest and lowest values of relative length within a time period, early Miocene phalanges across all taxa presented here have a percent difference of 37%, while middle Miocene phalanges have a value of 41%, excluding *Victoriapithecus*. Including *Victoriapithecus* phalanges, the percent difference between the highest and lowest relative length residual in the middle Miocene increases to 45%. For included angle values the percent difference among early Miocene taxa is 82%. For middle Miocene taxa the percent difference among middle Miocene fossils is 144% without *Victoriapithecus* specimens. With *Victoriapithecus* specimens the percent difference of included angle values among middle Miocene taxa is 253%. This increase in anatomical variation from the early to middle Miocene is the result of two trends: 1) more elongated and curved phalanges among the small-medium sized catarrhines (which are assumed to sample noncercopithecoid catarrhines including nyanzapithecines but not other hominoids (see below)) and 2) shorter, straighter phalanges among the large bodied hominoids and cercopithecoids (*Victoriapithecus*).

Implications for fossil catarrhine evolution

Nine of the phalanges listed in Table 4 (four from Songhor and five from Maboko) are undescribed and have been tentatively assigned to taxonomic identifications based on comparisons of linear dimensions with extant taxa. The width of the larger specimen, KNM SO 974, is similar in size to widths found in female *Nasalis* and male *Hylobates* (5.9 -9.2 kg; Table 2). Candidate taxa in this size range include *P. africanus* or *R. gordoni*. KNM SO 974 is thus most likely attributable to one of these two species. KNM SO 1966 is much smaller and similar in size to *Presbytis* (6.2 -6.3 kg) suggesting a likely attribution to *cf. D. macinnesi*. KNM SO 986 and KNM SO 35514 are the smallest of the Songhor phalanges and overlap in width dimensions with males of *Cebus albifrons* and *C. mitis* (3.3 to 5.8 kg) and could be attributed to either *L. evansi* or *K. songhorensis*. The lack of associated postcranial material for Songhor catarrhines hinders more specific identifications. Unassociated phalanges from Maboko can be assigned to either *Mabokopithecus* or *Micropithecus "Simiolus" leakeyorum* based on differences in size. The larger specimens, KNM MB 32417 and KNM MB 32420 can be attributed to Mabokopithecus, while smaller specimens (KNM MB 28433, KNM MB 35585, and KNM MB 28430) are attributed to *Micropithecus "Simiolus" leakeyorum.*

The results presented here support previous studies that suggest African Miocene catarrhines, specifically small and medium bodied stem catarrhines, evolved additional positional behavioral capacities other than generalized above branch arboreal quadrupedalism (Simons and Fleagle, 1973; Rose, 1992, 1993; Wuthrich, 2019). The presence of relatively longer intermediate phalanges at Songhor compared to those attributed to *E. heseloni* from Rusinga suggests that a Songhor catarrhine may have had enhanced grasping during arboreal locomotion relative to *E. heseloni*, whose postcrania suggest adaptations primarily for above branch arboreal quadrupedalism and some climbing (Corruccini et al., 1975; Morbeck 1975; Walker and Pickford, 1983; Rose, 1983; Begun et al., 1994; Ward, 1998; Dunsworth, 2006; Rein et al., 2011). KNM SO 974 and KNM SO 1966, though they differ in size, are similar in morphology and relatively longer than *E. heseloni* intermediate phalanges. The different morphologies of the similar sized KNM SO 986 and KNM SO 35514 suggest they belong to different taxa. The greater curvature of KNM SO 35514 suggests the animal utilized more habitual grasping postures. The shorter KNM SO 986 suggests it came from a more generalized arboreal quadruped. Results indicate small to medium sized catarrhines at Songhor were more variable in their locomotor and positional behaviors than previously documented. This is in line with qualitative comparisons of Tinderet capitates, which are indicative of the presence of generalized and more specialized arboreal catarrhines at Tinderet localities (Wuthrich et al., 2019).

Maboko small and medium sized phalanges are similar in morphology to one another, but relative length and curvature exceed those found in most Songhor phalanges, and most closely resemble the gracile and highly curved phalanges of the acrobatically arboreal and leaping colobines. This also suggests that the small and medium sized catarrhines at Maboko likely used more specialized arboreal hand postures. Proximal phalanges length and curvature has been shown to accurately predict suspensory behaviors in extant taxa (Rein et al., 2011). The accentuated features of the Maboko intermediate phalanges could suggest more frequent below branch grasping for suspensory locomotion. However, more research is necessary to determine the utility of intermediate phalange length of curvature for predicting extant anthropoid locomotor behaviors.

It is also interesting to note that phalanges at Maboko indicate the likely absence of a general pronograde arboreal quadruped like *Ekembo heseloni*. Nakatsukasa and colleagues (2003) has also noted similar relative lengths of intermediate phalanges between KNM MB 28393 and *E. nyanzae* specimens KNM RU 15100I and suggests the relative lengths or robustness is not a strong indicator of terrestriality in the large bodied hominoid from Maboko as suggested by

McCrossin (1994) and McCrossin and colleagues (1998). However, the straighter shaft of KNM MB 28393 compared to the more curved shaft of *E. nyanzae* does support more terrestrial locomotion for the LBHM. Other large bodied hominoid postcranial elements, such as a proximal humerus, first metatarsal, and patella, from Maboko further support the interpretation of a semi-terrestrial component to the positional behavior of the Maboko hominoid (McCrossin, 1994; McCrossin and Benefit., 1997; McCrossin et al., 1998; Allen, 2008; Pina et al., 2014).

The increase in phalangeal anatomical variation form the early to the middle Miocene is concordant with a trend of increasing molar functional variation (see chapter 3), which together support a much broader-scale adaptive shift (i.e. characterized by increasing ecological specialization) among catarrhines from the early to the middle Miocene than previously recognized. However, as discussed in Chapter 2, δ^{13}C values from early and middle Miocene catarrhine localities do not support a major environmental shift from closed canopied forests to more open canopied forests and woodlands, as previously hypothesized, during this time period. Further research is thus necessary to more fully contextualize the shift in catarrhine adaptive diversity from the early to the middle Miocene.

Conclusion

In an attempt to examine morphological adaptations in a single element across multiple African Miocene taxa and localities, comparative analyses of extant anthropoid manual intermediate phalanges were performed. The relative length and curvature for 21 fossil specimens from five localities were assessed, including nine previously undescribed phalanges from the early Miocene site of Songhor and the middle Miocene site of Maboko. Elongation and curvature of phalanges from some fossil specimens from both of these sites are comparable to levels found in extant taxa that use below branch grasping including hylobatids, atelids and colobines. At Maboko, some phalanges were shorter and less curved, with relative length and included angle values overlapping with those of terrestrial anthropoid taxa. Other undescribed phalanges were longer and highly curved overlapping in morphology with phalanges of *Ateles* and *Symphalangus*. When compared chronologically, the amount of variation in length and curvature increases through time. Phalanges from Maboko indicate increased specialization compared to early Miocene phalanges.

Chapter 4 References

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Supplementary Material

Table 20. Summary statistics for total length of modern (a) and fossil (b) specimens.

a	taxa	N_i	N_p	sex	Mean	sd	min	max
	Modern							
	Alouatta belzebul	1	3	male	17.4	1.3	16.0	18.6
	Alouatta fusca	1	3	female	17.1	1.5	15.4	18.1
	Alouatta palliata	5	15	?	20.0	1.8	16.1	21.9
		2	5	female	18.8	1.8	16.3	20.2
		1	3	male	19.7	2.4	18.0	21.4
	Ateles belzebuth	1	3	female	27.5	1.9	25.4	28.8
	Ateles fusciceps	4	12	female	26.0	1.8	23.4	28.5
		2	5	male	24.0	2.4	20.9	27.2
	Ateles geoffroyi	1	3	?	25.9	2.0	23.7	27.5
		3	11	female	25.6	2.2	22.1	28.6
		1	3	male	24.2	1.8	22.1	25.4
	Ateles paniscus	2	5	female	26.4	3.3	21.3	28.9
	Cebus albifrons	1	3	?	14.8	1.0	13.7	15.9
		4	11	female	13.0	0.8	11.4	13.7
	Cebus capucinus	2	2	?	14.1	0.2	13.9	14.2
	Cercopithecus mitis	3	5	female	13.7	2.0	11.4	15.5
		3	7	male	14.6	2.4	11.3	17.5
	Colobus guereza	2	6	female	19.2	2.5	15.5	21.2
		1	3	male	19.4	3.4	15.4	21.6
	Gorilla beringei	2	6	female	32.4	3.5	27.5	37.1
		3	7	male	38.3	3.1	33.2	41.4
	Gorilla gorilla	6	18	female	34.4	3.8	26.1	39.8
		7	10	male	41.6	4.8	32.7	47.8
	Hylobates lar	8	24	female	29.6	2.9	25.1	34.8
		7	19	male	30.9	2.7	26.9	36.0
	Macaca fascicularis	4	9	female	13.3	0.6	12.5	14.0
		5	4	male	14.4	1.4	12.1	15.9
	Mandrillus spinx	1	3	male	22.3	3.1	18.7	24.4
	Nasalis larvatus	5	10	female	23.7	2.1	20.1	27.1
		5	13	male	28.3	3.3	22.4	31.4
	Pan pansicus	1	3	male	33.1	5.1	27.2	36.8
	Pan troglodytes	1	3	?	34.3	4.4	29.5	38.2
		6	13	female	37.0	5.1	28.7	44.7
		6	9	male	40.2	5.9	29.3	48.7
	Papio anubis	1	3	?	18.3	2.1	15.9	20.0
		2	4	male	19.6	2.9	16.9	22.4
	Papio cynocephalus	1	3	female	15.3	1.9	13.1	16.5
		1	3	male	17.8	2.3	15.2	19.2

	Papio ursinus	1	3	female	19.1	2.4	16.3	20.8
	Pongo abelli	4	12	female	45.5	4.1	36.7	50.1
		1	3	male	55.1	5.6	48.6	58.4
	Pongo pygmaeus	2	14	female	41.7	4.4	33.9	46.4
		4	4	male	49.3	6.6	42.3	59.7
	Presbytis rubicunda	4	16	female	19.2	3.4	14.0	22.5
		4	13	male	20.9	3.3	14.7	23.6
	Procolobus badius	2	4	female	20.1	4.2	13.7	22.4
	Symphalangus syndactylus	3	9	female	30.1	3.2	25.0	34.5
		1	3	male	27.6	3.3	23.9	30.4
	Trachypithecsu cristatus	6	18	female	18.4	2.5	14.4	21.4
		6	17	male	18.8	2.4	15.0	21.3
b	**Fossil**			Accession Number				
	Songhor			SO 1966	22.7	-	-	-
	Songhor			SO 35514	18.3	-	-	-
	Songhor			SO 974	26.7	-	-	-
	Songhor			SO 986	15.9	-	-	-
	Ekembo heseloni			PH 222	23.2	-	-	-
	Ekembo heseloni			PH 63	19.2	-	-	-
	Ekembo heseloni			PH 64	21.0	-	-	-
	Ekembo nyanzae			RU 15100I	29.7	-	-	-
	Ekembo nyanzae			RU 15100J	22.4	-	-	-
	Afropithecus turkanensis			WK 18356B	32.1	-	-	-
	LBHK			TH 28861	20.1	-	-	-
	LBHM			MB 28393	29.5	-	-	-
	small bodied ape			MB 28430	15.9	-	-	-
	small bodied ape			MB 28433	18.7	-	-	-
	small bodied ape			MB 35585	18.1	-	-	-
	Nyanzapithecine			MB 32417	23.0	-	-	-
	Nyanzapithecine			MB 32420	18.3	-	-	-
	Victoriapithecus macinnesi			MB 11982	10.7	-	-	-
	Victoriapithecus macinnesi			MB 12017	11.1	-	-	-
	Victoriapithecus macinnesi			MB 340	11.9	-	-	-
	Victoriapithecus macinnesi			MB 9433	11.1	-	-	-
	Victoriapithecus macinnesi			MB12020	13.9	-	-	-

Table 21. Base mediolateral width for rays 2-4 of extant anthropoids and fossil specimens.

a	taxa	N_i	N_p	sex	mean	sd	min	max
	Modern							
	Alouatta belzebul	1	3	male	5.1	0.2	5.0	5.4
	Alouatta fusca	1	3	female	4.9	0.1	4.8	5.0
	Alouatta palliata	5	15	?	5.7	0.3	5.1	6.4
		2	5	female	5.5	0.3	5.0	5.8
		1	3	male	5.7	0.3	5.4	5.9
	Ateles belzebuth	1	3	female	7.4	0.4	7.0	7.7
	Ateles fusciceps	4	12	female	7.3	0.6	6.3	8.1
		2	5	male	7.0	0.4	6.5	7.5
	Ateles geoffroyi	1	3	?	6.8	0.6	6.1	7.1
		3	11	female	6.5	0.5	5.6	7.1
		1	3	male	7.1	0.6	6.4	7.5
	Ateles paniscus	2	5	female	7.2	0.6	6.3	7.6
	Cebus albifrons	1	3	?	5.0	0.2	4.8	5.3
		4	11	female	4.0	0.2	3.7	4.3
	Cebus capucinus	2	2	?	4.3	0.1	4.2	4.4
	Cercopithecus mits	3	5	female	5.2	0.6	4.6	5.8
		3	7	male	5.2	0.6	4.8	5.6
	Colobus guereza	2	6	male	6.5	0.6	5.8	7.0
		1	3	female	6.1	0.7	5.3	6.9
	Gorilla beringei	2	6	female	14.0	0.9	13.0	15.4
		3	7	male	18.0	1.1	16.6	19.2
	Gorilla gorilla gorilla	6	18	female	15.3	1.7	12.2	17.7
		7	10	male	20.0	1.5	17.5	21.9
	Hylobates lar lar	8	24	female	6.7	0.6	5.6	7.6
		7	19	male	7.1	0.7	5.6	8.2
	Macaca fascicularis	4	9	female	4.5	0.1	4.3	4.6
		5	4	male	5.1	0.3	4.7	5.5
	Mandrillus spinx	1	3	male	8.1	0.5	7.6	8.4
	Nasalis larvatus	5	10	female	7.3	0.4	6.7	7.9
		5	13	male	8.7	0.7	7.3	9.9
	Pan pansicus	1	3	male	12.4	1.1	11.2	13.4
	Pan troglodytes	1	3	?	12.3	1.1	11.2	13.5
		6	13	female	13.2	1.6	10.4	16.5
		6	9	male	14.3	1.6	12.0	17.3
	Papio anubis	1	3	?	7.9	0.4	7.5	8.2
		2	4	male	8.3	0.7	7.4	8.8
	Papio cynocephalus	1	3	female	6.8	0.3	6.4	7.0
		1	3	male	7.8	0.5	7.2	8.1
	Papio ursinus	1	3	female	7.9	0.4	7.4	8.2
	Pongo abelli	4	12	female	14.0	0.7	13.0	14.9

		1	3	male	15.6	1.0	14.5	16.3
	Pongo pygmaeus	2	14	female	13.1	1.2	11.1	15.0
		4	4	male	16.5	1.2	14.8	17.9
	Presbytis rubicunda	4	16	female	5.4	0.6	4.7	6.1
		4	13	male	6.0	0.7	4.9	6.7
	Procolobus badius	2	4	female	5.4	0.6	4.6	5.8
	Symphalangus syndactylus	3	9	female	8.0	0.5	7.2	8.8
		1	3	male	7.6	0.2	7.4	7.9
	Trachypithecus cristata	6	18	female	5.3	0.5	4.6	6.2
		6	17	male	5.6	0.5	4.8	6.2
b	**Fossil**			Accession number				
	Undescribed			SO 1966	6.1	-	-	-
	Undescribed			SO 35514	5.1	-	-	-
	Undescribed			SO 974	7.5	-	-	-
	Undescribed			SO 986	5	-	-	-
	E. heseloni			PH 222	6.7	-	-	-
	E. heseloni			PH 64	6	-	-	-
	E. nyanzae			RU 15100I	11.3	-	-	-
	E. nyanzae			RU 15100J	8.3	-	-	-
	A. turkanensis			WK 18356B	10.3	-	-	-
	LBHM			MB 28393	11	-	-	-
	Undescribed			MB 28430	4.6	-	-	-
	Undescribed			MB 28433	4.8	-	-	-
	Undescribed			MB 32417	5.5	-	-	-
	Undescribed			MB 32420	5.2	-	-	-
	Undescribed			MB 35585	4.7	-	-	-
	LBHK			TH 28861	6.4	-	-	-
	V. macinnesi			MB 11982	4.4	-	-	-
	V. macinnesi			MB 12017	4.3	-	-	-
	V. macinnesi			MB 20220	3.5	-	-	-
	V. macinnesi			MB 9433	4.2	-	-	-
	V. macinnesi			MB 12020	5.4	-	-	-
	V. macinnesi			MB 340	4.4	-	-	-

Table 22. Summary statistics for base dorsoplantar depth for modern (a) and fossil (b) phalanges.

a	Taxa	N_i	N_p	sex	Mean	sd	min	max
	Modern							
	Alouatta belzebul	1	3	male	2.6	0.1	2.6	2.8
	Alouatta fusca	1	3	female	2.6	0.1	2.5	2.7
	Alouatta palliata	5	15	?	2.9	0.2	2.6	3.4
		2	5	female	2.3	0.2	2	2.5
		1	3	male	2.9	0.2	2.8	3.1
	Ateles belzebuth	1	3	female	2.8	0.3	2.5	3
	Ateles fusciceps	4	12	female	3	0.3	2.5	3.4
		2	5	male	2.9	0.3	2.6	3.3
	Ateles geoffroyi	1	3	?	3	0.2	2.8	3.1
		3	11	female	2.7	0.3	2.3	3
		1	3	male	2.9	0.3	2.6	3.1
	Ateles paniscus	2	5	female	3	0.2	2.7	3.3
	Cebus albifrons	1	3	?	2.1	0.1	2	2.3
		4	11	female	1.9	0.1	1.7	2.1
	Cebus capucinus	2	2	?	2	0	2	2
	Cercopithecus mitis	3	5	female	2.1	0.2	2	2.4
		3	7	male	2.3	0.2	2	2.5
	Colobus guereza	2	6	female	2.7	0.3	2.3	3
		1	3	male	3.1	0.1	2.9	3.2
	Gorilla beringei	2	6	female	6	0.5	4.9	6.5
		3	7	male	6.9	0.8	6	8.1
	Gorilla gorilla	6	18	female	5.8	0.6	4.7	6.9
		7	10	male	6.9	0.8	5.9	8.4
	Hylobates lar	8	24	female	2.8	0.2	2.5	3.1
		7	19	male	3	0.3	2.5	3.7
	Macaca fascicularis	4	9	female	1.7	0.1	1.6	2
		5	4	male	2.2	0.1	2	2.3
	Mandrillus spinx	1	3	male	3.8	0.3	3.4	4
	Nasalis larvatus	5	10	female	2.8	0.2	2.6	3.1
		5	13	male	3.7	0.2	3	3.9
	Pan pansicus	1	3	male	4.7	0.3	4.4	5
	Pan troglodytes	1	3	?	4.2	0.3	4	4.5
		6	13	female	5	0.6	4	6.4
		6	9	male	5.8	0.7	4.1	6.9
	Papio anubis	1	3	?	3.5	0.1	3.5	3.6
		2	4	male	3.8	0.4	3.4	4.3
	Papio cynocephalus	1	3	female	2.9	0	2.9	3

	1	3	male	3.2	0.1	3.1	3.3
Papio ursinus	1	3	female	3.5	0.1	3.4	3.6
Pongo abelli	4	12	female	4.9	0.3	4.2	5.5
	1	3	male	6.5	0.1	6.4	6.6
Pongo pygmaeus	2	14	female	5.1	0.7	4.3	6.4
	4	4	male	6.5	0.7	5.4	7.9
Presbytis rubicunda	4	16	female	2.3	0.2	2	2.7
	4	13	male	2.5	0.2	2.1	2.9
Procolobus badius	2	4	female	2.6	0.4	2.1	2.9
Symphalangus syndactylus	3	9	female	3.3	0.4	2.9	3.8
	1	3	male	3.4	0	3.4	3.4
Trachypithecus cristatus	6	18	female	2.4	0.2	2	2.8
	6	17	male	2.4	0.3	2.1	3

b	Taxa	Accession number	Mean	sd	min	max
	Fossil					
	Songhor	SO 1966	2.9	-	-	-
	Songhor	SO 35514	2.9	-	-	-
	Songhor	SO 974	3.3	-	-	-
	Songhor	SO 986	2.6	-	-	-
	Ekembo heseloni	PH 222	3.1	-	-	-
	Ekembo heseloni	PH 63	3	-	-	-
	Ekembo heseloni	PH 64	2.8	-	-	-
	Ekembo nyanzae	RU 15100I	5.1	-	-	-
	Ekembo nyanzae	RU 15100J	4.4	-	-	-
	Afropithecus turkanensis	WK 18356B	5.1	-	-	-
	LBHK	TH 28861	3.3	-	-	-
	LBHM	MB 28393	5.3	-	-	-
	small bodied ape	MB 28430	1.6	-	-	-
	small bodied ape	MB 28433	2.1	-	-	-
	small bodied ape	MB 35585	2	-	-	-
	Nyanzapithecine	MB 32417	2.9	-	-	-
	Nyanzapithecine	MB 32420	2.3	-	-	-
	Victoriapithecus macinnesi	MB 11982	2.2	-	-	-
	Victoriapithecus macinnesi	MB 12017	1.9	-	-	-
	Victoriapithecus macinnesi	MB 340	2.1	-	-	-
	Victoriapithecus macinnesi	MB 9433	2	-	-	-
	Victoriapithecus macinnesi	MB12020	2.6	-	-	-

Table 23. Summary statistics for midshaft mediolateral width.

a	Taxa	N_i	N_p	sex	Mean	sd	min	max
	Modern							
	Alouatta belzebul	1	3	male	3.8	0.3	3.6	4.1
	Alouatta fusca	1	3	female	3.4	0	3.4	3.5
	Alouatta palliata	5	15	?	4.2	0.4	3.6	4.7
		2	5	female	3.6	0.4	3	3.9
		1	3	male	4	0.6	3.6	4.4
	Ateles belzebuth	1	3	female	5	0.1	4.9	5.1
	Ateles fusciceps	4	12	female	5.4	0.5	4.7	6
		2	5	male	5.1	0.5	4.6	5.5
	Ateles geoffroyi	1	3	?	4.8	0.7	4	5.3
		3	11	female	4.7	0.5	3.8	5.4
		1	3	male	4.9	0.6	4.2	5.2
	Ateles paniscus	2	5	female	5.4	0.6	4.6	6
	Cebus albifrons	1	3	?	3.2	0.2	2.8	3.3
		4	11	female	2.7	0.1	2.5	2.9
	Cebus capucinus	2	2	?	2.8	0	2.8	2.8
	Cercopithecus mitis	3	5	female	3.2	0.3	2.7	3.4
		3	7	male	4	0.4	3.4	4.4
	Colobus guereza	1	3	female	4.1	0.5	3.4	4.7
		2	6	male	4.6	0.5	4.1	5.1
	Gorilla beringei	3	7	female	9.7	0.9	8.3	11
		6	18	male	13.7	1.6	11.8	15.6
	Gorilla gorilla	7	10	female	10.7	1.2	8.6	12.4
		8	24	male	14.3	1.4	11.9	16.3
	Hylobates lar lar	7	19	female	4.8	0.5	3.9	5.9
		4	9	male	5	0.5	4.2	5.8
	Macaca fascicularis	5	4	female	3.1	0.1	3	3.2
		1	3	male	3.5	0.2	3.3	4
	Mandrillus spinx	5	10	male	5.8	0.4	5.4	6
	Nasalis larvatus	5	13	female	5.2	0.5	4.5	6.2
		1	3	male	6.4	0.7	5.1	7.3
	Pan pansicus	1	3	male	8.3	1.1	7.3	9.6
	Pan troglodytes	6	13	?	7.5	0.9	6.7	8.5
		6	9	female	8.8	1.5	6	11.7
		1	3	male	10	1.4	6.9	12.8
	Papio anubis	2	4	?	6.2	0.3	6	6.5
		1	3	male	6.2	0.6	5.3	6.6
	Papio cynocephalus	1	3	female	4.4	0.2	4.3	4.6
		1	3	male	5.5	0.2	5.4	5.7
	Papio ursinus	4	12	female	6.3	0.4	5.9	6.6
	Pongo abelli	1	3	female	8.4	0.7	7	9.4

	2	14	male	10.9	0.6	10.1	11.3
Pongo pygmaeus	4	4	female	8.4	0.7	7.7	9.7
	4	16	male	10.2	1	8.5	11.8
Presbytis rubicunda	3	9	female	3.4	0.3	2.9	4
	1	3	male	3.8	0.4	3.3	4.4
Procolobus badius	2	6	female	3.8	0.8	2.8	4.6
Symphalangus syndactylus	6	18	female	6.3	0.7	5	7.2
	6	17	male	6.5	0.3	6.3	6.8
Trachypithecus cristatus	4	13	female	3.9	0.4	3.4	4.4
	2	4	male	4.1	0.5	3.1	4.8

b	Taxa	Accession Number	Mean	sd	min	max
	Fossil					
	Songhor	SO 1966	4.4	-	-	-
	Songhor	SO 35514	4.3	-	-	-
	Songhor	SO 974	5.4	-	-	-
	Songhor	SO 986	4	-	-	-
	Ekembo heseloni	PH 222	5.4	-	-	-
	Ekembo heseloni	PH 63	4.9	-	-	-
	Ekembo heseloni	PH 64	4.5	-	-	-
	Ekembo nyanzae	RU 15100I	8.5	-	-	-
	Ekembo nyanzae	RU 15100J	7.2	-	-	-
	Afropithecus turkanensis	WK 18356B	7.9	-	-	-
	LBHK	TH 28861	5.3	-	-	-
	LBHM	MB 28393	8.7	-	-	-
	small bodied ape	MB 28430	3.6	-	-	-
	small bodied ape	MB 28433	3.6	-	-	-
	small bodied ape	MB 35585	3.4	-	-	-
	Nyanzapithecine	MB 32417	4.6	-	-	-
	Nyanzapithecine	MB 32420	3.8	-	-	-
	Victoriapithecus macinnesi	MB 340	3.2	-	-	-
	Victoriapithecus macinnesi	MB 9433	3	-	-	-
	Victoriapithecus macinnesi	MB12020	3.8	-	-	-
	Victoriapithecus macinnesi	MB 11982	2.9	-	-	-
	Victoriapithecus macinnesi	MB 12017	2.7	-	-	-

Table 24. Summary statistics for midshaft depth for modern (a) and fossil (b) phalanges.

a	Taxa	sex	Mean	sd	min	max
	Modern					
	Alouatta belzebul	male	2.6	0.1	2.6	2.8
	Alouatta fusca	female	2.6	0.1	2.5	2.7
	Alouatta palliata	?	2.9	0.2	2.6	3.4
		female	2.3	0.2	2	2.5
		male	2.9	0.2	2.8	3.1
	Ateles belzebuth	female	2.8	0.3	2.5	3
	Ateles fusciceps	female	3	0.3	2.5	3.4
		male	2.9	0.3	2.6	3.3
	Ateles geoffroyi	?	3	0.2	2.8	3.1
		female	2.7	0.3	2.3	3
		male	2.9	0.3	2.6	3.1
	Ateles paniscus	female	3	0.2	2.7	3.3
	Cebus albifrons	?	2.1	0.1	2	2.3
		female	1.9	0.1	1.7	2.1
	Cebus capucinus	?	2	0	2	2
	Cercopithecus mitis	female	2.1	0.2	2	2.4
		male	2.3	0.2	2	2.5
	Colobus guereza	female	2.7	0.3	2.3	3
		male	3.1	0.1	2.9	3.2
	Gorilla beringei	female	6	0.5	4.9	6.5
		male	6.9	0.8	6	8.1
	Gorilla gorilla	female	5.8	0.6	4.7	6.9
		male	6.9	0.8	5.9	8.4
	Hylobates lar	female	2.8	0.2	2.5	3.1
		male	3	0.3	2.5	3.7
	Macaca fascicularis	female	1.7	0.1	1.6	2
		male	2.2	0.1	2	2.3
	Mandrillus spinx	male	3.8	0.3	3.4	4
	Nasalis larvatus	female	2.8	0.2	2.6	3.1
		male	3.7	0.2	3	3.9
	Pan pansicus	male	4.7	0.3	4.4	5
	Pan troglodytes	?	4.2	0.3	4	4.5
		female	5	0.6	4	6.4
		male	5.8	0.7	4.1	6.9
	Papio anubis	?	3.5	0.1	3.5	3.6
	Papio anubis	male	3.8	0.4	3.4	4.3
	Papio cynocephalus	female	2.9	0	2.9	3
		male	3.2	0.1	3.1	3.3
	Papio ursinus	female	3.5	0.1	3.4	3.6
	Pongo abelli	female	4.9	0.3	4.2	5.5

	male	6.5	0.1	6.4	6.6
Pongo pygmaeus	female	5.1	0.7	4.3	6.4
	male	6.5	0.7	5.4	7.9
Presbytis rubicunda	female	2.3	0.2	2	2.7
	male	2.5	0.2	2.1	2.9
Procolobus badius	female	2.6	0.4	2.1	2.9
Symphalangus syndactylus	female	3.3	0.4	2.9	3.8
	male	3.4	0	3.4	3.4
Trachypithecus cristata	female	2.4	0.2	2	2.8
	male	2.4	0.3	2.1	3

b	Taxa	Accession number	Mean	sd	min	max
	Fossil					
	Songhor	SO 1966	2.9	-	-	-
	Songhor	SO 35514	2.9	-	-	-
	Songhor	SO 974	3.3	-	-	-
	Songhor	SO 986	2.6	-	-	-
	Ekembo heseloni	PH 222	3.1	-	-	-
	Ekembo heseloni	PH 63	3	-	-	-
	Ekembo heseloni	PH 64	2.8	-	-	-
	Ekembo nyanzae	RU 15100I	5.1	-	-	-
	Ekembo nyanzae	RU 15100J	4.4	-	-	-
	Afropithecus turkanensis	WK 18356B	5.1	-	-	-
	LBHK	TH 28861	3.3	-	-	-
	LBHM	MB 28393	5.3	-	-	-
	small bodied ape	MB 28430	1.6	-	-	-
	small bodied ape	MB 28433	2.1	-	-	-
	small bodied ape	MB 35585	2	-	-	-
	Nyanzapithecine	MB 32417	2.9	-	-	-
	Nyanzapithecine	MB 32420	2.3	-	-	-
	Victoriapithecus macinnesi	MB 11982	2.2	-	-	-
	Victoriapithecus macinnesi	MB 12017	1.9	-	-	-
	Victoriapithecus macinnesi	MB 340	2.1	-	-	-
	Victoriapithecus macinnesi	MB 9433	2	-	-	-
	Victoriapithecus macinnesi	MB12020	2.6	-	-	-

Table 25. Summary statistics for trochlear width for modern (a) and fossil (b) phalanges.

a	Taxa	Ni	Np	sex	mean	sd	min	max
	Modern							
	Alouatta belzebul	1	3	male	4.1	0.4	3.6	4.4
	Alouatta fusca	1	3	female	3.9	0.2	3.7	4.1
	Alouatta palliata	5	15	?	4.5	0.4	3.7	5.1
		2	5	female	4.3	0.3	4.1	4.6
		1	3	male	4.2	0.4	4	4.5
	Ateles belzebuth	1	3	female	5.8	0.4	5.4	6.2
	Ateles fusciceps	4	12	female	5.5	0.5	4.8	6.4
		2	5	male	5.6	0.2	5.3	5.8
	Ateles geoffroyi	1	3	?	5.5	0.2	5.4	5.7
		3	11	female	5.1	0.4	4.4	5.9
		1	3	male	5.6	0.3	5.3	5.8
	Ateles paniscus	2	5	female	5.9	0.4	5.2	6.3
	Cebus albifrons	1	3	?	3.5	0.3	3.2	3.8
		4	11	female	3.1	0.2	2.8	3.3
	Cebus capucinus	2	2	?	3.3	0.1	3.2	3.3
	Cercopithecus mitis	3	5	female	3.7	0.1	3.6	3.8
		3	7	male	4	0.4	3.5	4.4
	Colobus guereza	2	6	female	4.8	0.4	4.3	5.2
		1	3	male	5.2	0.5	4.6	5.7
	Gorilla beringei	2	6	female	10.6	0.5	10.1	11.5
		3	7	male	13.3	0.9	12	14.6
	Gorilla gorilla	6	18	female	10.9	1.1	8.8	12.7
		7	10	male	14.1	1.2	11.5	16
	Hylobates lar	8	24	female	5.3	0.3	4.8	5.8
		7	19	male	5.5	0.5	4.7	6.4
	Macaca fascicularis	4	9	female	3.6	0.2	3.4	3.9
		5	4	male	4.2	0.3	3.7	4.8
	Mandrillus spinx	1	3	male	6.1	0.2	5.8	6.2
	Nasalis larvatus	5	10	female	5.5	0.2	5	5.8
		5	13	male	6.5	0.5	5.5	7
	Pan pansicus	1	3	male	7.6	0.5	7.3	8.1
	Pan troglodytes	1	3	?	8.2	0.6	7.6	8.9
		6	13	female	9.2	1.2	7.5	11.2
		6	9	male	9.7	1.2	7.9	12.2
	Papio anubis	1	3	?	6.3	0.4	6	6.7
		2	4	male	7	0.6	6.3	7.7
	Papio cynocephalus	1	3	female	5.4	0.5	4.9	5.9
		1	3	male	6.4	0.3	6.1	6.6
	Papio ursinus	1	3	female	6.5	0.1	6.4	6.5
	Pongo abelli	4	12	female	10.6	0.6	9.4	11.5

		1	3	male	12.1	0.5	11.5	12.5
	Pongo pygmaeus	2	14	female	9.7	1.2	8.5	12.4
		4	4	male	11.3	0.9	10	12.7
	Presbytis rubicunda	4	16	female	4.2	0.4	3.6	4.7
		4	13	male	4.7	0.4	4	5.1
	Procolobus badius	2	4	female	4.4	0.5	3.8	5
	Symphalangus syndactylus	3	9	female	6	0.5	5.6	6.9
		1	3	male	5.9	0.2	5.6	6.1
	Trachypithecus cristatus	6	18	female	3.8	0.4	3.3	4.5
		6	17	male	4	0.3	3.4	4.4
b	Taxa			Accession	Mean	sd	min	max
	Fossil							
	Songhor			SO 1966	5.3	-	-	-
	Songhor			SO 35514	4.3	-	-	-
	Songhor			SO 974	6.6	-	-	-
	Songhor			SO 986	4.1	-	-	-
	Ekembo heseloni			PH 222	6	-	-	-
	Ekembo heseloni			PH 63	5.1	-	-	-
	Ekembo heseloni			PH 64	5.3	-	-	-
	Ekembo nyanzae			RU 15100I	8.8	-	-	-
	Ekembo nyanzae			RU 15100J	7.5	-	-	-
	Afropithecus turkanensis			WK 18356B	8	-	-	-
	LBHK			TH 28861	5	-	-	-
	LBHM			MB 28393	8.1	-	-	-
	small bodied ape			MB 28430	3.8	-	-	-
	small bodied ape			MB 28433	3.3	-	-	-
	small bodied ape			MB 35585	3.8	-	-	-
	Nyanzapithecine			MB 32417	5.2	-	-	-
	Nyanzapithecine			MB 32420	4.1	-	-	-
	Victoriapithecus macinnesi			MB 11982	3.9	-	-	-
	Victoriapithecus macinnesi			MB 12017	3.6	-	-	-
	Victoriapithecus macinnesi			MB 340	4	-	-	-
	Victoriapithecus macinnesi			MB 9433	3.5	-	-	-
	Victoriapithecus macinnesi			MB12020	4.8	-	-	-

Table 26. Summary statistics for trochlea depth for modern (a) and fossil (b) phalanges.

a	taxa	Ni	Np	sex	mean	sd	min	max
	Modern							
	Alouatta belzebul	1	3	male	2.7	0.2	2.4	2.8
	Alouatta fusca	1	3	female	2.5	0.1	2.5	2.6
	Alouatta palliata	5	15	?	3.1	0.2	2.9	3.6
		2	5	female	2.9	0.1	2.8	3
		1	3	male	3	0.1	2.9	3.1
	Ateles belzebuth	1	3	female	3.4	0.2	3.2	3.7
	Ateles fusciceps	4	12	female	3.7	0.2	3.3	4.1
		2	5	male	3.4	0.2	3.2	3.6
	Ateles geoffroyi	1	3	?	3.8	0	3.8	3.8
		3	11	female	3.4	0.2	3.1	3.6
		1	3	male	3.7	0.2	3.5	3.8
	Ateles paniscus	2	5	female	3.6	0.2	3.2	3.8
	Cebus albifrons	1	3	?	2.3	0.2	2.2	2.5
		4	11	female	2.2	0.1	1.9	2.5
	Cebus capucinus	2	2	?	2	0.1	2	2
	Cercopithecus mitis	3	5	female	2.3	0.1	2.1	2.4
		3	7	male	2.3	0.3	2	2.6
	Colobus guereza	2	6	female	2.8	0.2	2.6	3.2
		1	3	male	2.9	0.3	2.6	3.1
	Gorilla beringei	2	6	female	6	0.6	5.1	7
		3	7	male	7.9	0.6	7	8.6
	Gorilla gorilla	6	18	female	6.5	0.7	5.2	7.7
		7	10	male	8.2	0.6	7.1	9.3
	Hylobates lar	8	24	female	3.4	0.2	3	3.9
		7	19	male	3.5	0.3	3.1	4
	Macaca fascicularis	4	9	female	1.9	0.1	1.8	2.1
		5	4	male	2.3	0.2	2.1	2.5
	Mandrillus spinx	1	3	male	4.1	0.3	3.8	4.2
	Nasalis larvatus	5	10	female	3.4	0.4	3	4.3
		5	13	male	3.9	0.3	3.1	4.4
	Pan pansicus	1	3	male	5.2	0.3	4.9	5.5
	Pan troglodytes	1	3	?	5.4	0.3	5	5.7
		6	13	female	6.3	0.8	4.9	7.8
		6	9	male	6.6	0.8	5.2	7.7
	Papio anubis	1	3	?	3.6	0	3.6	3.7
		2	4	male	4.3	0.4	3.7	4.7
	Papio cynocephalus	1	3	female	3.1	0.2	3	3.3
		1	3	male	3.6	0.2	3.4	3.8
	Papio ursinus	1	3	female	3.4	0	3.4	3.4
	Pongo abelli	4	12	female	6.7	0.3	6.2	7.2

	1	3	male	8.1	0.3	7.7	8.3
Pongo pygmaeus	2	14	female	6.5	0.7	5.5	7.9
	4	4	male	7.6	0.5	6.9	8.3
Trachypithecus cristatus	4	16	female	2.5	0.3	2.1	3.2
	4	13	male	2.6	0.3	2.1	3.2
Presbytis rubicunda	2	4	female	2.5	0.3	2.1	3
	3	9	male	3	0.4	2.4	3.7
Procolobus badius	1	3	female	2.8	0.3	2.4	3
Symphalangus syndactylus	6	18	female	4.2	0.3	3.7	4.7
	6	17	male	4.4	0.3	4.1	4.6

b	Taxa	Accession	Mean	sd	min	max
	Fossil					
	Songhor	SO 1966	3.4	-	-	-
	Songhor	SO 35514	2.5	-	-	-
	Songhor	SO 974	4.2	-	-	-
	Songhor	SO 986	2.7	-	-	-
	Ekembo heseloni	PH 222	3.5	-	-	-
	Ekembo heseloni	PH 63	3.1	-	-	-
	Ekembo heseloni	PH 64	3	-	-	-
	Ekembo nyanzae	RU 15100I	5	-	-	-
	Ekembo nyanzae	RU 15100J	4.5	-	-	-
	Afropithecus turkanensis	WK 18356B	5.7	-	-	-
	LBHK	TH 28861	3.3	-	-	-
	LBHM	MB 28393	5.4	-	-	-
	small bodied ape	MB 28430	2.4	-	-	-
	small bodied ape	MB 28433	2.4	-	-	-
	small bodied ape	MB 35585	2.6	-	-	-
	Nyanzapithecine	MB 32417	3.2	-	-	-
	Nyanzapithecine	MB 32420	2.6	-	-	-
	Victoriapithecus macinnesi	MB 11982	2.4	-	-	-
	Victoriapithecus macinnesi	MB 12017	2.1	-	-	-
	Victoriapithecus macinnesi	MB 340	2.3	-	-	-
	Victoriapithecus macinnesi	MB 9433	2.3	-	-	-
	Victoriapithecus macinnesi	MB12020	2.7	-	-	-

Chapter 5

Conclusion

This dissertation explores the relationship between catarrhine adaptive ecology and environmental change from the early to the middle Miocene. Environmental change was assessed from a sample of mammalian tooth enamel $\delta^{13}C$ values. The inferred feeding ecologies of the fossil mammals from nine early and middle Miocene localities do not support a shift from closed canopied forests to open forest and woodland habitats. Enamel $\delta^{13}C$ values from the early Miocene reflect a variable landscape of C_3 dominated open forests/woodlands. Rusinga is the only early Miocene locality where enamel $\delta^{13}C$ values support mammalian foraging in a closed canopied forest. Enamel $\delta^{13}C$ values from middle Miocene localities followed previous paleoenvironmental reconstructions for open forests/woodlands but also indicated possibly drier and open woodland with significant C_4 biomass at Kipsaramon. Most of the enamel $\delta^{13}C$ values for Kipsaramon gomphotheres, Afrochoerodon kisumuensis and Protanancus macinnesi, overlap with modern mixed C_3/C_4 feeders. This amount of mixed feeding at 15.6 Ma is contra to past studies that propose C_4 biomass was not incorporated into herbivore diets until after 10 Ma (Cerling et al., 1999, 2003; Uno et a., 2011). These results also have implications for vegetation changes in the fossil record and the evolution of C_4 biomass.

Habitat inferences for Kipsaramon should be considered preliminary due to the limited number of taxa sampled (proboscideans and rhinos). While Kipsaramon's herbivore fauna is much more diverse (Behrensmeyer et al., 2002), the number of taxa with teeth available for isotopic sampling was sparse. Hopefully, additional research on the Kipsaramon fauna can provide additional dental remains for isotopic sampling.

Despite little evidence of environmental change from closed canopy forests to open forests and woodland, catarrhine primates display evidence of increased specialization in dietary and locomotor adaptations through time. Lower second molar shear quotient values from catarrhines of the middle Miocene were compared to an expanded sample of early Miocene SQ values. The total range of shear quotient values increased from the early to the middle Miocene, suggesting an increase in dietary diversity among middle Miocene catarrhines. This increase is driven by a decrease in molar shear crest development in large bodied hominoids and an increase in shear crest development among nyanzapithecines. The sampled hominoids did not show evidence for folivory in the middle Miocene, while nyanzapithecine shear quotients suggest they evolved more specialized folivory. There was no discernable pattern of change in shear quotient values for the small bodied primitive catarrhines.

Lastly, the postcranial functional diversity of early and middle Miocene catarrhines was examined through the quantification of intermediate phalangeal morphology. The relative length and curvature of manual intermediate phalanges II-IV were measured in 30 extant anthropoid taxa. Each taxon was assigned to a positional behavioral group based on the literature. Relative length values of manual intermediate phalanges were greatest in suspensory taxa, followed by anthropoids practicing either palmigrade arboreal quadrupedalism or frequent leaping, followed by anthropoids practicing either knuckle-walking or digitigrady. A similar pattern was found when comparing curvature among anthropoids, except that knuckle-walkers had more curved manual phalanges than did digitigrade taxa. While this study confirms the presence of a functional signal in the relative length and curvature of intermediate phalanges, more research is necessary to further tease apart the interaction between intermediate phalange length, curvature, positional behavior, locomotion, body size, and phylogeny. Relative length and curvature were also assessed in 20 fossil catarrhine intermediate phalanges from the early and middle Miocene. The range of variation in both relative length and curvature in the fossil intermediate phalanges increases over time, indicating an increase in morphological diversity, and hence likely positional behavioral diversity, through time. This increase in morphological diversity is driven by a decrease in relative length and curvature through time among large bodied hominoids and cercopithecoids and an increase in relative length and curvature among small to medium bodied non-cercopithecoid catarrhines.

The molar and phalangeal morphological evidence suggests greater dietary and locomotor specialization among middle Miocene catarrhines of East Africa relative to early Miocene taxa. This is interesting because this greater variation in the middle Miocene taxa is captured in a smaller sample size of fossils that span a shorter period of time than those from the early Miocene. However, understanding why catarrhines increase their morphological specialization remains challenging, given the lack of enamel stable carbon isotopic support for a large-scale regional vegetation shift from closed canopied forests to open forests and woodland. However, this study documents, for the first time, an increase in habitat heterogeneity through time, from open forests, closed forests and woodlands in the early Miocene, to environments that maintain forest and woodland elements, but also include C4 biomass, in the middle Miocene. Future investigations exploring the association between catarrhine adaptive morphological change and environment can incorporate this new framework.