

Stable Isotope Ecology of the Early Miocene Rusinga Island Mammalian Communities from the Hiwigi and Kulu Formations (Nyanza Province, Western Kenya)

David L. Fox ^{a,*}, Nicole D. Garrett ^{b,1}, Daniel J. Peppe ^c, Lauren A. Michel ^d, Kirsten Jenkins ^e, Thomas Lehmann ^f, Kieran P. McNulty ^{b,g}

^a Department of Earth & Environmental Sciences, University of Minnesota, John T. Tate Hall, 116 Church Street SE, Minneapolis, MN 55455, USA

^b Department of Anthropology, University of Minnesota, 395 Hubert H. Humphrey Center, 301 19th Ave S, Minneapolis, MN 55455, USA

^c Terrestrial Paleoclimatology Group, Department of Geosciences, Baylor University, One Bear Place #97354, Waco, TX 76798, USA

^d Department of Earth Sciences, Tennessee Tech University, 1 William L. Jones Dr., Cookeville, TN 38505, USA

^e Department of Social Sciences, Tacoma Community College, Tacoma, WA 98466, USA

^f Messel Research and Mammalogy Department, Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, Frankfurt am Main 60325, Germany

^g Department of Ecology, Evolution & Behavior, 140 Gortner Laboratory, 1479 Gortner Avenue, St. Paul, MN 55108, USA

ARTICLE INFO

Editor: Bing Shen

Keywords:

Stable carbon isotopes
Stable oxygen isotopes
Early Miocene
Paleodiet
Paleoclimate
Paleoenvironment
Hominoid evolution
Eastern Africa

ABSTRACT

Fossils from Rusinga Island, Kenya, provide an exceptional collection for understanding the evolution and diversification of Early Miocene mammals in Africa, preserving rich assemblages distributed across nearly 2 million years and a variety of habitats. Placing these mammal communities within clear ecological contexts is crucial to understanding the selection pressures that shaped individual taxa but also community composition through time. Although numerous paleoenvironmental reconstructions for these deposits have been suggested, they present conflicting interpretations, with reconstructed habitats for various lithostratigraphic units and/or fossil localities ranging from closed rainforests to open and semiarid environments. Here we present the first paleoenvironmental reconstructions based on carbon and oxygen isotope composition of fossil mammal tooth enamel from Rusinga Island's important fossil assemblages, focusing on specimens from the fossiliferous Hiwigi and Kulu Formations. Our results indicate that these Early Miocene mammals foraged on plants using the C₃ photosynthetic pathway in a range of habitats, including those experiencing light and/or water stress, and that habitats were differentially exploited by various species. Although the presence of a dense closed-canopy forest has been documented from at least one Hiwigi stratum, specimens sampled for our analysis exhibit only rare isotopic evidence for foraging within that habitat. Additionally, this study documents a significant difference in the oxygen isotope composition of meteoric water available to fauna found in the Hiwigi Formation versus the younger Kulu Formation. This signals a change in moisture source and/or transport path, or a climatic shift including an increase in mean annual temperature, an increase in aridity, and/or a decrease in mean annual precipitation from the Hiwigi to the Kulu Formation. These results suggest marked differences in paleoenvironmental conditions experienced by these two Early Miocene mammalian communities and underscore the need for more detailed and rigorous analyses of their taxonomic compositions, species abundances, and ecological structures.

1. Introduction

Early Miocene fossil sites in eastern Africa record an exciting period

in the evolution of African ecosystems. During this time, the abutment of African and Eurasian continental masses resulted in topographic, geographic, biogeographic, and climatic changes that triggered the

* Corresponding author at: Department of Earth & Environmental Sciences, University of Minnesota, 116 Church St. SE, John T. Tate Hall Room 150, Minneapolis, MN 55455, USA.

E-mail address: dlfox@umn.edu (D.L. Fox).

¹ Current address/affiliation: Critical Care Research Center, Regions Hospital, 640 Jackson Street, St Paul, MN 55101

transition from Paleogene ecosystems in Africa to the Neogene distribution of ecosystems that ultimately led to the configuration of modern habitats and animal communities (Jacobs et al., 2010; Rage and Gheerbrant, 2020; Couvreur et al., 2021). A major factor with regard to faunal community evolution was establishment of a terrestrial corridor that permitted migration of animals out of and into Africa via what is now the Arabian peninsula (e.g., Rögl, 1997, 1999; Stampfli et al., 2002; Golonka, 2004), creating new competitive interactions and ultimately driving substantial changes in organismal evolution and faunal community structures (Dercourt et al., 2000; Jacobs et al., 2010; Sen, 2013; Rage and Gheerbrant, 2020; Couvreur et al., 2021); eastern Africa, as the primary “gateway” to these exchanges, provides some of the earliest evidence of this. Also during this time, the East African Rift System (EARS) achieved significant topographic relief (e.g., Macgregor, 2015; Michon et al., 2022), facilitating the establishment of more heterogeneous landscapes (e.g., Peppe et al., 2023), and global temperatures were increasing toward the Mid-Miocene Climatic Optimum (Flower and Kennett, 1994; Zachos et al., 2001, 2008; Steinhorsdottir et al., 2021; Westerhold et al., 2020; Herbert et al., 2022), further influencing the evolution of African ecosystems.

Early Miocene fossil deposits on Rusinga Island, Kenya (Fig. 1), are one of the best places to recover evidence of the impact of these important events on eastern African ecosystems. With more than 90

years of paleontological and geological research conducted there, Rusinga has yielded an abundance of vertebrate (e.g., Van Couvering, 1972b; Pickford, 1986a; Werdelin and Sanders, 2010; Conrad et al., 2013; Černánský et al., 2020), invertebrate (e.g., Leakey, 1952; Verdcourt, 1963; Pickford, 1986a; Thackray, 1994), and plant remains (Chesters, 1957; Collinson et al., 2009; Maxbauer et al., 2013; Michel et al., 2014; Baumgartner and Peppe, 2021), plus a variety of paleo-ecological data that help fully characterize Early Miocene paleoenvironments (see, e.g., Michel et al., 2014, 2020; Peppe et al., 2023). Recent geochronological analyses indicate that Rusinga's fossil deposits record nearly 2 million years of biotic evidence, from ca. 18.7–17.0 Ma (Peppe et al., 2009; Peppe et al., 2017; Michel et al., 2023), which is substantially longer than any other highly fossiliferous site in eastern Africa. Additionally, a long history of stratigraphic research (Kent, 1944; Shackleton, 1951; Whitworth, 1953; Van Couvering, 1972a; Drake et al., 1988), including important recent revisions (Peppe et al., 2009; Michel et al., 2014, 2020, 2023), means that most fossil sites and paleoecological proxies can be confidently placed within a chronological sequence, often calibrated to geochronological markers.

In this paper, we briefly review the stratigraphy and geology of the Early Miocene Rusinga Group on Rusinga Island, summarize prior paleoecological reconstructions for the sequence, and present new paleoenvironmental and paleoclimatic information based on the stable

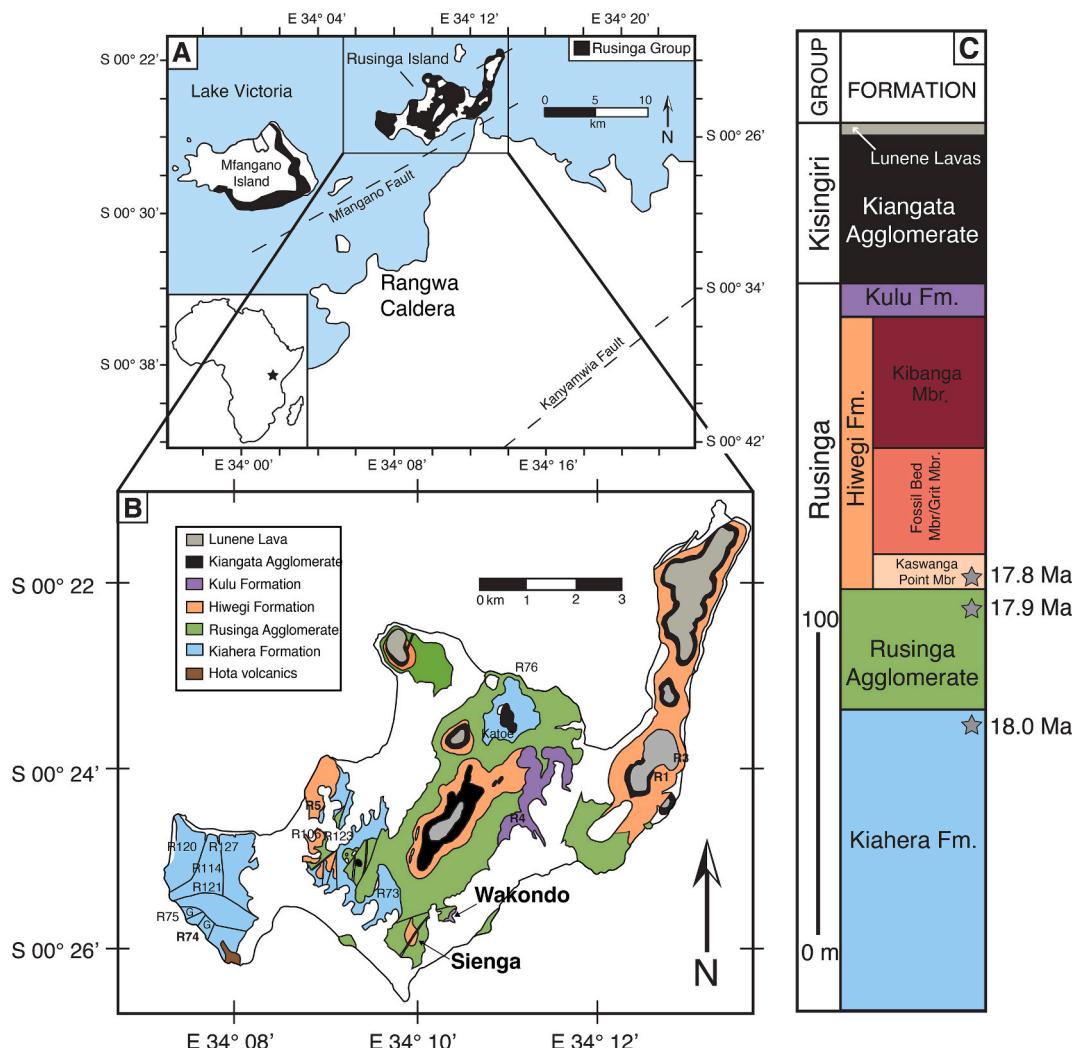


Fig. 1. (A) Location of Rusinga Island in Lake Victoria, western Kenya with outcrops of the Rusing Group indicated. (B) Geological map of Miocene strata on Rusinga Island with locations of some fossil localities indicated; sampled localities in bold. (C) Miocene stratigraphy on Rusinga Island. Figure based on Fig. 10 in Michel et al., 2023.

Table 1

Early Miocene fossil mammals from Rusinga and Mfangano Islands. Presences are indicated for the Hiwegi and Kulu Formations on Rusinga Island.

Order	Family	Species	Kulu	Hiwegi
Artiodactyla	Anthracotheriidae	<i>Brachyodus aequatorialis</i>	x	x
	Giraffidae	<i>Sivameryx africanus</i>	x	x
	Hippopotamidae	<i>Canthumeryx sirtensis</i>		x
	Sanitheriidae	<i>Kulutherium kenensis</i>	x	
	Suidae	<i>Diamantohyus africanus</i>	x	x
		<i>Kenyasus rusingensis</i>	x	x
		<i>Kubanochoerus archidens</i>		x
		<i>Nguruwe kijivium</i>	x	x
	Tragulidae	<i>Dorcatherium chappuisi</i>	x	x
		<i>Dorcatherium parvum</i>	x	x
		<i>Dorcatherium pigotti</i>	x	x
		<i>Dorcatherium songhorensis</i>		x
		<i>Propalaeoryx nyanzae</i>		x
		<i>Walangania africanus</i>	x	x
Carnivora	Amphicyonidae	<i>Cynelos euryodon</i>	x	x
	Barbourofelidae	<i>Cynelos macrodon</i>		x
	Felidae	<i>Afrosmilus africanus</i>		x
	Herpestidae	<i>Afrosmilus turkanae</i>		x
		<i>Asilfelinis coteae</i>		
		<i>Kichechia zamanae</i>		
		<i>Leptoplesictis mbitensis</i>		
		<i>Leptoplesictis rangwai</i>		
	Mustelidae	<i>Luogale rusingensis</i>		
	Ursidae	<i>Hemicyon sp.</i>		
	Viverridae	<i>Herpestides aequatorialis</i>		
		<i>Stenoplesictis muhoronii</i>		
Chiroptera	Megadermatidae	indet		x
	Molossidae	<i>Tadarida rusingae</i>		x
Hyaenodontidae	Hyaenodontidae	<i>Anasinopa leakeyi</i>		x
		<i>Isohyaenodon andrewsi</i>		x
		<i>Isohyaenodon matthewi</i>		x
		<i>Isohyaenodon pilgrimi</i>		x
		<i>Hyainailourus nyanzae</i>	x	x
		<i>Leakitherium hiwegi</i>	x	x
		<i>Metapterodon kaiseri</i>		x
		<i>Metapterodon zadoki</i>		x
		<i>Teratodon spekei</i>		x
Hyracoidea	Titanohyracidae	<i>Afrohyrax championi</i>	x	x
	Plioxyracidae	<i>Merohyrax bateae</i>		x
Lipotyphla	Erinaceidae	<i>Amphechinus rusingensis</i>	x	x
		<i>Galerix africanus</i>		x
		<i>Gymnurechinus leakeyi</i>	x	x
		<i>Gymnurechinus camplocephalus</i>		x
Lagomorpha	Ochotonidae	<i>Kenyalagomys minor</i>		x
Macroscelidea	Macroscelididae	<i>Kenyalagomys rusingae</i>	x	x
		<i>Hiwegicyon juvenalis</i>		x
		<i>Miorhynchocyon clarki</i>	x	x
		<i>Miorhynchocyon rusingae</i>		x
		<i>Myohyrax oswaldi</i>	x	x
Perissodactyla	Chalicotheriidae	<i>Butleria rusingensis</i>	x	x
	Rhinocerotidae	<i>Brachypotherium snowi</i>		x
		<i>Chilotheridium pattersoni</i>	x	
		<i>Rusingaceros leakeyi</i>	x	x
		<i>Turkanatherium acutirostratum</i>	x	x
		<i>Aceratheriini gen. & sp. indet.</i>		x
Primates	Dendropithecidae	<i>Dendropithecus macinnesi</i>	x	x
	Galagidae	<i>Komba minor</i>		x
		<i>Komba walkeri</i>	x	x
	Lorisidae	<i>Mioeuoticus bishopi</i>		x
		<i>Mioeuoticus shipmani</i>		x
	Chiromyiformes	<i>Propotto leakeyi</i>		
	incertae sedis	<i>Ekembo heseloni</i>	x	x
		<i>Ekembo nyanzae</i>	x	x
		<i>Linnopithecus legetet</i>		x
		<i>Nyanzapithecus vancouveringorum</i>		x
Proboscidea	Deinotheriidae	<i>Prodeinotherium hobleyi</i>	x	x
	Gomphotheriidae	Gomphotheriidae indet.	x	x
Ptolemaiida	Kelbidae	<i>Kelba quadremae</i>		
Rodentia	Anomaluridae	<i>Nonanomalous soniae</i>		x
		<i>Paranomalous bishopi</i>		
	Bathyergidae	<i>Paranomalous walkeri</i>		x
		<i>Bathyergoides neotertiarius</i>		x
		<i>Proheliophobius leakeyi</i>		
	Kenyamyidae	<i>Kenyamys mariae</i>		x

(continued on next page)

Table 1 (continued)

Order	Family	Species	Kulu	Hiwegi
	Myophiomyidae	<i>Simoniomys genovefae</i> <i>Elmerimys woodi</i> <i>Myophiomyss arambourgi</i>		x x x
	Nesomyidae	<i>Afrocricetodon songhorii</i> <i>Notocricetodon petteri</i> <i>Protarsomys macinnesi</i>		x
	Pedetidae	<i>Megapedetes pentadactylus</i> <i>Rusingapedetes tsujikawai</i>		x x
	Phiomidae	<i>Diamantomys luederitzii</i>		x
	Sciuridae	<i>Vulcanisciurus africanus</i>		x
	Thryonomyidae	<i>Epiphiomys coryndonii</i> <i>Paraphiomys pigotti</i> <i>Paraphiomys renelavocati</i>	x	x x
Tenrecoidea	<i>incertae sedis</i>	<i>Lavocatomys aequatorialis</i>		x
	Tenrecidae	<i>Parageogale aletris</i>	x	x
Tubulidentata	Orycteropodidae	<i>Protenre tricuspidis</i>		x
Incertae sedis	Prionogalidae	<i>Myorycteropus africanus</i>	x	x
		<i>Prionogale breviceps</i>		

carbon and oxygen isotope composition of Early Miocene fossil mammal teeth.

2. Geological background of Rusinga Island

Rusinga Island ($0^{\circ}24'S$, $34^{\circ}0'E$; Fig. 1A, B) on the eastern edge of Lake Victoria preserves a sequence of Early Miocene volcanic and volcanic-derived rocks in the Rusinga Group, comprising, from oldest to youngest, the Kihera Formation, Rusinga Agglomerate, Hiwegi Formation, and Kulu Formation (Fig. 1C). These strata record eruption and dormancy of the Kisingiri Volcano (Shackleton, 1951; McCall, 1958; Van Couvering, 1972a; LeBas, 1977; Pickford, 1986b; Bestland et al., 1995) through a series of tuffs, proximal volcaniclastic deposits and lahars, and lacustrine and fluvial strata with interbedded paleosols (fossilized soils; e.g.: Van Couvering, 1972a; Peppe et al., 2009, 2011; Michel et al., 2014, 2020, 2023). The hyperalkaline, volatile-rich debris from this volcano facilitated exceptional fossil preservation throughout the Rusinga Group, although the majority of fossils have been found in the Hiwegi Formation, with a large assemblage also known from the Kulu Formation (see Table 1 for a list of mammalian fauna). Mammal fossils from these two units are the focus of this study.

Faunal composition led early researchers on Rusinga to identify the fossil assemblages there correctly as belonging to the Burdigalian stage of the Early Miocene (Van Couvering and Miller, 1969; Andrews and Van Couvering, 1975; Pickford, 1986a), and early K-Ar dates similarly suggested an age between 23 and 16 Ma (Bishop et al., 1969; Van Couvering and Miller, 1969). Subsequent K-Ar analyses placed the Rusinga Group fossil assemblages at circa 17.8 Ma and, importantly, interpreted the deposition of the entire Rusinga Group to represent <0.5 My (Drake et al., 1988). In this scheme, the Kulu Formation was not included in the Rusinga Group and thought to be somewhat younger. This interpretation has been shown to be incorrect, however, by recent geochronological and magnetostratigraphic work, which indicates that the Rusinga Group formations, which includes the Kulu Formation, together accumulated over a much longer span, between ca. 18.7–17.0 Ma (Peppe et al., 2009, 2017, 2023).

Hiwegi Formation The Hiwegi Formation contains intercalated fluvial and palustrine deposits commonly dominated by reworked volcanic and volcaniclastic sediments, evaporites, weakly developed paleosols, and volcanic airfall tuff deposits (Van Couvering, 1972a; Pickford, 1986a; Drake et al., 1988; Retallack et al., 1995; Bestland et al., 1995; Bestland and Krull, 1999; Forbes et al., 2004; Conrad et al., 2013; Maxbauer et al., 2013; Michel et al., 2014, 2020). The Hiwegi Formation has historically been divided into four members: Kaswanga Point, Grit, Fossil Bed and Kibanga Members (Fig. 2; Van Couvering, 1972a; Drake et al., 1988). However, the Fossil Bed and Grit Members cannot be distinguished based on their sedimentology (Michel et al., 2020), and

our detailed lithostratigraphic analyses of the major exposures indicate that they are stratigraphically equivalent (Fig. 2). Thus, we do not recognize them as distinct members and herein refer to this middle section of the Hiwegi Formation as the Grit/Fossil Bed Member (see also Michel et al., 2020).

Historically, paleontological and paleoenvironmental studies of the Hiwegi Formation have treated the major fossil mammal collecting sites as broadly contemporaneous (e.g., Van Couvering, 1972a; Nesbit Evans et al., 1981; Pickford, 1981; Bestland et al., 1995). However, lithostratigraphic correlations (Fig. 2) and magnetostratigraphy indicate that the fossil mammal localities do not represent a single, short period of deposition, but instead are distributed in three distinct stratigraphic intervals (McCollum et al., 2013; Peppe et al., 2017; Michel et al., 2014, 2020). As a result, historic collections typically represent time-averaged assemblages from multiple fossil-bearing units and levels. Conversely, collections made since the 1970s track the improvement of stratigraphic knowledge, such that most of these can be placed within a well-defined stratigraphic context.

The majority of specimens from this study were sampled from the Grit/Fossil Bed Member (exposed at sites R1, R5, and R106) and the Kibanga Member (exposed at R3; Fig. 2). The Grit/Fossil Bed Member exhibits sedimentary features indicative of fluvial processes, including cut and fill architecture, trough cross-bedding, and fining upward succession (Van Couvering, 1972a; Conrad et al., 2013; Maxbauer et al., 2013; Michel et al., 2020). The Grit/Fossil Bed Member preserves multiple strata with sedimentological evidence for high rates of evaporation during deposition, including salt hoppers, satin-spar calcite after gypsum, and teepee structures (Maxbauer et al., 2013; Michel et al., 2020). The unit also contains abundant fluvial and palustrine deposits and weakly developed paleosols. Based on the sedimentology of the Grit/Fossil Bed Member, preliminary taphonomic assessments of vertebrate fossils, and analyses of fossil plants remains, the interval is interpreted to be a warm and relatively dry and highly seasonal climate with open saline to hypersaline ponds and lakes surrounded by woodlands and riparian, tropical seasonal forests (Collinson et al., 2009; Conrad et al., 2013; Maxbauer et al., 2013; Michel et al., 2014, 2020; Jenkins, 2018; Baumgartner and Peppe, 2021).

The Kibanga Member exposed at R3 preserves fossils predominantly in two distinct stratigraphic units. At the base of the section is a poorly developed paleosol with rare mammal fossils in situ. Fossils from the upper stratigraphic unit come from a single paleosol that preserves a number of closely spaced tree-stump casts with a range of diameters, as well as many calcite-cemented root casts (Michel et al., 2014). Although the full spatial extent of this paleosol is unknown, it has been recognized in the same stratigraphic sequence at localities up to 4.3 km away and also preserves tree stump casts in those localities (Michel et al., 2014). This forest paleosol layer documents a period characterized by a

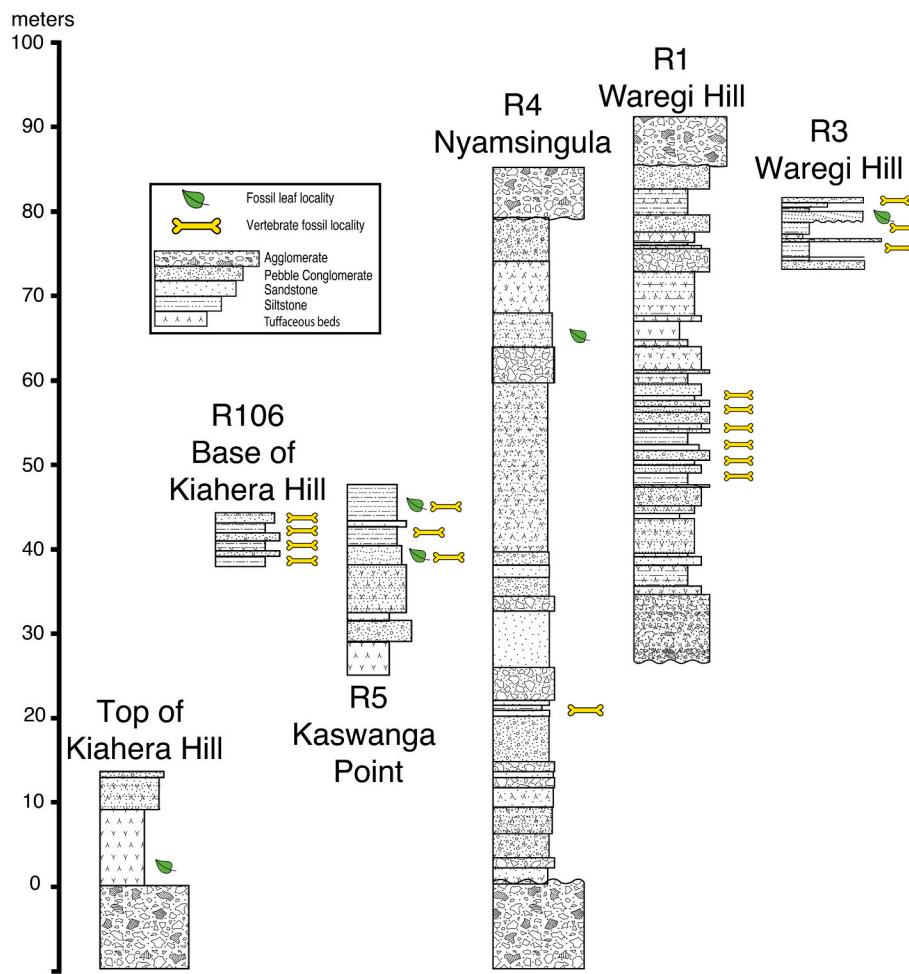


Fig. 2. Lithostratigraphy of the major fossil bearing localities in the Hiwigi Formation (see geographic location of sites in Fig. 1) with the stratigraphic position of fossil vertebrate sites and fossil leaf sites indicated. Based on lithostratigraphic correlations between sections, there are three major fossiliferous horizons, one near the base of the Grit/Fossil Bed Member, one from the middle to the top of the Grit/Fossil Bed Member, and one near the top of the Kibanga Member (right most panel).

widespread, multistoried, closed-canopy, tropical seasonal forest and a warm and seasonally wet climate (Michel et al., 2014, 2020; Baumgartner and Peppe, 2021).

Kulu Formation Although debate has surrounded the stratigraphic placement and age of the Kulu Formation (Shackleton, 1951; Van Couvering and Miller, 1969; Van Couvering, 1972a; Drake et al., 1988; Bestland, 1991; Peppe et al. (2009) recognized it as the youngest formation in the Rusinga Group with an age estimate for the unit of ca. 17 Ma. The Kulu Formation was deposited in a basin created by subsidence along a fault near the center of what is now Rusinga Island (Drake et al., 1988; Peppe et al., 2009) and comprises two distinct deposits: (1) a lacustrine unit of laminated shale, siltstone, and fine-grained sandstone beds that were occasionally incised by high-energy currents that deposited conglomerate lenses, and (2) a matrix-supported breccia and conglomerate that interfingers with the lacustrine unit, and was deposited by an alluvial fan or fan delta adjacent to the fault scarp, and includes clasts primarily from the underlying Hiwigi Formation and Rusinga Agglomerate (Van Couvering, 1972a; Bestland, 1991; Bestland and Krull, 1999; Peppe et al., 2009). The Kulu Formation yields abundant fossils of medium and large-sized mammals, but small-bodied mammals are rarely preserved. Most fossils analyzed in this study were found at the R4 collecting locality at Nyamsingula site (Peppe et al., 2009; see also Pickford, 1986a).

3. History of paleoecological reconstructions of Rusinga fossils

The long history of research on Rusinga Island has produced many and disparate paleoecological reconstructions for the fossils there. Table 2 and Fig. 3 summarize many of the more prominent reconstructions, which range across tropical rainforest (e.g., Chesters, 1957), closed forest (e.g., Andrews and Van Couvering, 1975; Pickford, 1985; Andrews and Kelley, 2007; Michel et al., 2014; Baumgartner and Peppe, 2021), closed woodlands and ecotones of forest and woodland (e.g., Collinson et al., 2009; Maxbauer et al., 2013), open woodlands (e.g., Bestland, 1990; Bestland and Retallack, 1993; Thackray, 1994; Retallack, 2002; Baumgartner and Peppe, 2021), rainforest (Verdcourt, 1963; Harris and Van Couvering, 1995), mosaic habitats (e.g., Andrews et al., 1979; Baumgartner and Peppe, 2021), and even semiarid environments (e.g., Bestland and Krull, 1999; Forbes et al., 2004).

Many of these discrepancies are related to differences in sites or strata sampled and/or the proxies used in different studies (Table 2, Fig. 3). A complicating factor, however, is that many samples in these studies, particularly in the older ones, had poor stratigraphic control and/or were broadly interpreted across time-averaged collections. Contributing to this latter problem was the assumption that most of Rusinga's fossils accumulated in a geologically short (< 0.5 Myr) period of time (Drake et al., 1988), which led to difficulty resolving conflicting paleoenvironmental interpretations throughout the Rusinga Group. This was further supported by seeming uniformity of faunal lists from various

Table 2

Previous paleoenvironmental reconstructions for Rusinga Island during the Early Miocene. Numbers for sources correspond to numbers for studies in Fig. 3. Formations (following Van Couvering, 1972; Peppe et al., 2009; Michel et al., 2020, 2023) are in boldface, members are italicized, and fossil localities are underlined. Geographic place names are in standard font. Note that the “Wayando Fm” was originally thought to be below the Kiahera Fm but is now considered equivalent to various parts of the Kiahera Fm. (Michel et al., 2023).

Source	Method	Stratigraphic extent or locality	Reconstruction
1. Chesters, 1957	Taxonomic uniformitarianism (plant macrofossils)	Rusinga Island from Kiahera and Hiwigi Fms	“gallery-type forest [proximal to forest margins] in which trees festooned with climbers overhung the water-courses” (p. 67)
2. Verdcourt, 1963	Taxonomic uniformitarianism (gastropods)	Rusinga Island from Kiahera , Hiwigi , and Kulu Fms	“The main type of vegetation present at the time most of the deposits were laid down was evergreen rain forest receiving a fairly heavy rainfall....There is some evidence that there were also some drier habitats, such as riverine forest and woodland cutting through areas of savanna” (p. 35)
3. Andrews and Van Couvering, 1975	Review, taxonomic uniformitarianism (plant macrofossils, vertebrate and invertebrate animals)	Hiwigi Fm, <i>Grit/Fossil Bed Mbr</i> , <u>R5</u>	Varying, with “lowland forest at or near Rusinga,” “waterside conditions, perhaps associated with forest,” and some “nonforest conditions of unknown type” (p. 98)
4. Andrews et al., 1979	Mammal ecological community structure (body size, diet, locomotor categories), sedimentology	Hiwigi Fm, <i>Grit/Fossil Bed Mbr</i> , <u>R5</u>	One “waterside community containing many small and large mammals” that “accumulated in flood plain conditions” and a “second faunal association included...forest indicator species [but] consisted entirely of small mammals, and so it is likely that it was both allochthonous and size sorted when it was transported to the flood plain environment.” (p. 200)
5. Pickford, 1985	Taxonomic uniformitarianism (gastropod)	Rusinga Island, not specified	“dry forest to woodland communities such as occur at Kibwezi in Kenya, characterized by 80–100 % tree cover with a single canopy” (p. 138)
6. Andrews, 1992	Review	Rusinga and Mfangano Islands, not specified + <u>R117</u> specifically	“at least three types of forest [in the area]: tropical evergreen, tropical semi-evergreen [including R117], and deciduous.” (p. 432)
7. Bestland and Retallack, 1993	Paleosol morphology and geochemistry	Kiahera Fm	“A landscape with a woodland along stream corridors is envisaged for the Okoto Series and grassy woodland for the Chido Series.” (p. 308)
8. Thackray, 1994	Taxonomic uniformitarianism (burrowing bees nest)	Hiwigi Fm, <i>Kibanga Mbr</i> , Waregi Hill area	“The nest suggests a subhumid to humid climate and angiosperm-dominated vegetation” (p. 795)
9. Harris and Van Couvering, 1995	Review + soil chemistry, sedimentology, taxonomic uniformitarianism (flora and fauna)	Rusinga Island, not specified	“Hyperalkalinity of the volcanic rocks and barrenness due to syneruptive sedimentology and geomorphology falsely suggest an arid to semiarid environment during the syneruptive phase, whereas the fossils that were preserved during the noneruptive, recovery phase represent humid successional and, in some cases, climax ecosystems.” (p. 595)
10. Retallack et al., 1995	Paleosol morphology and geochemistry	Hiwigi Fm, <i>Grit/Fossil Bed Mbr</i> at <u>R1</u> , <u>R3</u> , <u>R5</u> , and <i>Kibanga Mbr</i> at <u>R3</u>	“woodland with patches of dry forest, open early successional vegetation and local grassy woodland” (p. 84)
11. Bestland and Krull, 1999	Carbon isotope composition of paleosol organic matter and pedogenic carbonate	“Wayando,” Kiahera , and Hiwigi Fms	“We interpret the $\delta^{13}\text{C}$ values of the Rusinga Group paleosols as representative of an ancient C_3 vegetational mosaic with limited moisture availability.” (p. 968) “...associated fauna and flora inhabited a frequently disturbed landscape that experienced repeated catastrophic volcanic deposition in an overall semi-arid seasonal climate.” (p. 974)
12. Forbes et al., 2004	Paleosol geochemistry and organic matter carbon isotope composition	“Wayando” Fm (Gumba Beds on Rusinga, Karungu) (compared to B&K, 99 data for Kiahera and Hiwigi Fms)	“conditions changed from a stable landscape of a humid to sub-humid environment [during ‘Wayando’ deposition] to a landscape of decreased stability and greater aridity [during Kiahera and Hiwigi deposition].” (p. 77)
13. Andrews and Kelley, 2007	Review (some of the information for Rusinga is uncited)	Rusinga Island, not specified + Hiwigi Fm	“The general conclusion for the Mfwangano flora, which is located in the Kiahera [FM]..., is that it represents multi-canopied evergreen forest in large part, with areas of semi-evergreen forest.” (p. 336) “The conclusion from th[e Hiwigi Fm] flora...is that it represents disturbed woodlands bordering a large river, disturbance perhaps by volcanic activity. Structurally, the woodlands were single-canopied with a dense ground vegetation of herbs and bushes. It may also represent a river flood plain...” (p. 337)
14. Collinson et al., 2009	Plant macrofossils, Nearest Living Relative	Hiwigi Fm: <i>Grit/Fossil Bed Mbr</i> , <u>R117</u>	“The in situ R117 floras confirm the presence of closed woodland [at this site]” (p. 161)
15. Maxbauer et al., 2013	Plant macrofossils	Hiwigi Fm: <i>Grit/Fossil Bed Mbr</i> near <u>R5</u>	“riparian environment that supported a patchwork of woodland and forested biomes in a strongly seasonal, warm climate. This suggests both forested and woodland environments were important components of Rusinga’s Miocene ecosystem...” (p. 16–17)
16. Michel et al., 2014	Sedimentology, paleopedology, plant trace fossils, plant macrofossils, modern forestry	Hiwigi Fm: <i>Kibanga Mbr</i> , <u>R3</u> and equivalent	“widespread, dense, multistoried, closed-canopy tropical seasonal forest set in a warm and relatively wet, local climate” (p. 1)
17. Michel et al., 2020	Sedimentology, paleopedology, vertebrate paleontology	Hiwigi Fm: <i>Grit/Fossil Bed</i> and <i>Kibanga Mbrs</i> associated with <u>R1</u> and <u>R3</u>	“semi-arid to arid, possibly seasonal, climate [in the lower Grit/Fossil Bed Member] created a more open environment of woodlands and riparian forests. This contrasts with the upper Grit/Fossil Bed and Kibanga members...[and especially with the] closed-canopy forest environment during the deposition of the upper Kibanga Member.” (p. 3589–90)

(continued on next page)

Table 2 (continued)

Source	Method	Stratigraphic extent or locality	Reconstruction
18. Baumgartner and Peppe, 2021	Plant macrofossils	Hiwegi Fm: Kaswanga Point Mbr on Kiahera Hill, Grit/Fossil Bed Mbr at R5, Kibanga Mbr at R3	"temporal environmental heterogeneity [during the Hiwegi Fm] ... Kaswanga Point Member was a warm and wet, closed forest, followed by a relatively dry and open environment in the Grit/Fossil Bed Member at R5, and then a wetter and spatially heterogeneous forest at R3 in the Kibanga Member." (p. 11)
19. Peppe et al., 2023	Carbon isotope analyses of bulk soil organic matter, plant wax biomarkers, and pedogenic carbonates; phytolith assemblages	Rusinga Island generally, with data from Kiahera, Hiwegi, and Kulu Fms	Although it remains a challenge to differentiate spatial and temporal heterogeneity at a local level... temporally restricted horizons at Moroto and Rusinga document penecontemporaneous forested to grassy woodland microhabitats... suggesting that landscape-scale spatial heterogeneity contributed to the variable paleovegetation signals in our records." (p. 4) "...arboreal habitats of great variety were most likely available for chameleons. These varied from very large trees of the genus <i>Entandrophragma</i> to smaller forest trees (for instance of the genera <i>Celtis</i> and <i>Sterculia</i>) and shrubs, thorny plants and lianas, all of which have been recorded as present at or very near Rusinga/Mfangano fossil vertebrate sites (Chesters, 1957)."
20. Rieppel et al., 1992	Taxonomic uniformitarianism (fossil chameleon)	Hiwegi Fm, Grit/Fossil Bed Mbr, R107	"...arboreal habitats of great variety were most likely available for chameleons. These varied from very large trees of the genus <i>Entandrophragma</i> to smaller forest trees (for instance of the genera <i>Celtis</i> and <i>Sterculia</i>) and shrubs, thorny plants and lianas, all of which have been recorded as present at or very near Rusinga/Mfangano fossil vertebrate sites (Chesters, 1957)."

localities throughout the sequence (Pickford, 1981, 1984; Andrews et al., 1997; Peppe et al., 2009; Michel et al., 2014). However, three factors call this assumption into question. First, geochronological and magnetostratigraphic work by our group (Peppe et al., 2009, 2017) indicates that accumulation of the Rusinga Group occurred over a much longer span, increasing the likelihood of habitat and faunal change through time. Second, taxon presence/absence across Rusinga Group faunas may not equate with unchanging habitats, as such changes could impact taxon abundances and proportions rather than overall faunal lists (Jenkins, 2018; Hall et al., 2025). Third, the Hiwegi Formation includes multiple fossiliferous horizons, thus even the Hiwegi fauna alone does not represent a single time slice or environment, as was previously assumed (Van Couvering, 1972a; Bestland et al., 1995), but instead consists of different windows of time at different localities (Fig. 2; McCollum et al., 2013; Peppe et al., 2017; Jenkins, 2018; Michel et al., 2020).

Very few studies have tried to characterize the paleoenvironments of the Kulu Formation, but lack of consensus over its stratigraphic position further contributes to paleoecological uncertainty (compare Van Couvering, 1972a and Bestland, 1991 for alternative interpretations). However, detailed geologic analyses now confirm the position of the Kulu Formation stratigraphically above the Hiwegi Formation and below the Kiangata Agglomerate (Peppe et al., 2009; Fig. 1C). Different lithological facies of the Kulu Formation are interpreted as contemporaneous deposits, accumulating in a very short time span (Peppe et al., 2009), suggesting that, unlike the Hiwegi faunas, Kulu fossil assemblages may be reasonably interpreted as temporally constrained and approximately contemporaneous.

As studies became more closely tied to specific depositional units, the picture that emerged for the entire Rusinga Group was one that fit a broader narrative of Neogene ecological succession from older environments that were more closed and wet to drier, more open habitats (e.g., Andrews, 1992; Forbes et al., 2004; Andrews and Kelley, 2007). This is sharply contrasted by the most recent analyses of the Hiwegi Formation, however, which demonstrate that environments fluctuated from more closed habitats at the base, to more open habitats associated with some important mammal localities (R1, R105, R106, R107), back to closed habitats at the R3 locality, near the top of the formation (Michel et al., 2020; Baumgartner and Peppe, 2021). Likewise, Peppe et al. (2023) used stable carbon isotope measurements of soil carbonates and organic matter as well as fossil phytolith assemblages to show Early Miocene habitats in eastern Africa were heterogeneous and at times included quite open and grassy habitats, but they found no discernible trends of habitat change over time or space. In the Hiwegi Formation specifically, the carbon isotope composition of bulk organic matter in paleosol samples at multiple sites (range in $\delta^{13}\text{C}$ values: -31.5‰ to -17.1‰, $n = 139$) is consistent with relatively open modern habitats

such as woodlands, bushlands, and shrublands, but the sample with the highest $\delta^{13}\text{C}$ value (-17.1‰) is consistent with wooded grasslands that included grasses that used the isotopically distinct C₄ photosynthetic pathway (Peppe et al., 2023; see section 4.1 below for details of carbon isotope systematics). These isotopic data are corroborated by quantitative analyses of five samples from the Hiwegi Formation that had well preserved phytoliths (microscopic silica bodies with diverse morphologies that are produced by plants and that are taxonomically diagnostic). In all five productive samples, the abundance of forest-indicating phytoliths ranged from ca. 10%–40%, but 50% or more of the total identifiable phytoliths in each of these samples were diagnostic of the PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, Danthonioideae) grass clade, and four of these samples included fractions up to ca. 20% of phytoliths diagnostic specifically of the Chloridoideae, which today comprises exclusively C₄ grasses. Thus, the paleosol isotope and phytolith data suggest a heterogeneous mix of habitats on what is now Rusinga Island during deposition of the Hiwegi Formation with no apparent stratigraphic trends that were, at times, surprisingly open and grassy with a well-supported C₄ grass component (Peppe et al., 2023). These results provide important context for the interpretation of our isotopic data from fossil mammal tooth enamel.

4. Stable isotope composition of mammalian tooth enamel

The isotope composition of enamel apatite from large-bodied animals is thought to be generally resistant to diagenesis during the fossilization process due to its highly crystalline state and extremely low organic content (DeNiro and Epstein, 1978; Sullivan and Krueger, 1981; Tieszen et al., 1983; Ambrose and DeNiro, 1986; Lee-Thorp et al., 1989; LeGeros, 1991; Wang and Cerling, 1994; Cerling and Harris, 1999; Kohn et al., 1999; Lee-Thorp, 2000; Lee-Thorp and Sponheimer, 2013). The total time of enamel mineralization in a single tooth is finite and relatively short (months to a few years) compared to bone, which, due to the process of remodeling, is dynamic and will represent an average of an animal's diet over many years before death. As mammals typically move around the landscape, the spatial scale integrated in an enamel isotopic signal can be quite large for species with large home ranges (Kingston, 2007), providing a short temporal and large spatial snapshot of the animal's habitat.

4.1. Carbon isotopes

The $\delta^{13}\text{C}$ values of consumer tissues reflect the amount-weighted carbon isotope composition of diet during tissue synthesis and tissue specific isotope enrichments between ingested carbon and tissue carbon. Most plants, including most trees, shrubs, forbs, and cool growing-

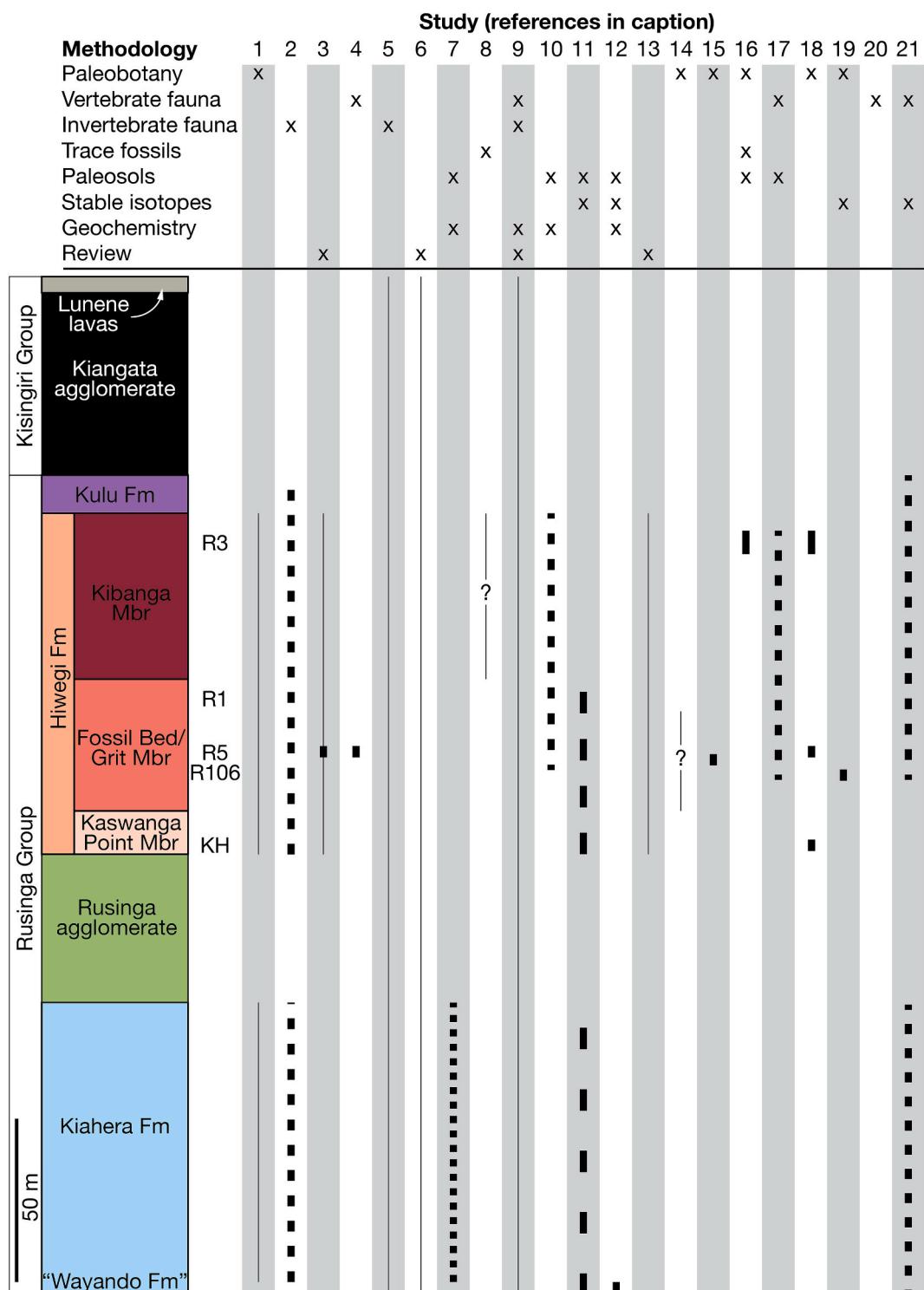


Fig. 3. Lower Miocene lithostratigraphy of Rusinga Island with stratigraphic intervals sampled or summarized and methodology of previous paleoenvironmental reconstructions for the Early Miocene of Rusinga Island, including this study. Key fossil localities are indicated beside the lithostratigraphy (KH is Kiahera Hill; R106 is at approximately the same level as R106 in the Fossil Bed/Grit Member of the Hiwagi Formation). Thin solid lines indicate range for studies in which specific intervals or localities are not specified; thin line with question mark indicates the specific sampled interval is not reported; thick lines indicate intervals sampled, with regular dashed lines indicating intermittent sampling stratigraphically through an interval either schematically (2, 7, 10, 20) or with the number of samples indicated (but not the exact stratigraphic level; 11, 17). Prior paleoenvironmental reconstructions are given in Table 2. References for studies: 1) Chesters, 1957; 2) Verdcourt, 1963; 3) Andrews and van Couvering, 1975; 4) Andrews et al., 1979; 5) Pickford, 1985; 6) Andrews, 1992; 7) Bestland and Retallack, 1993; 8) Thackray, 1994; 9) Harris and Van Couvering, 1995; 10) Retallack et al., 1995; 11) Bestland and Krull, 1999; 12) Forbes et al., 2004; 13) Andrews and Kelley, 2007; 14) Collinson et al., 2009; 15) Maxbauer et al., 2013; 16) Michel et al., 2014; 17) Michel et al., 2020; 18) Baumgartner and Peppe, 2021; 19) Peppe et al., 2023; 20) Rieppel et al., 1992; 21) this study.

season grasses, use the C₃ photosynthetic pathway, which strongly discriminates against ¹³CO₂ during fixation of atmospheric CO₂. Consequently, C₃ plants have low δ¹³C values relative to atmospheric CO₂ (mean modern C₃ = -27.4‰ ± 1.6‰; O'Leary, 1981; Passey et al., 2002; Cerling et al., 2003; Kohn, 2010; Diefendorf et al., 2010). Plants that use the C₄ photosynthetic pathway, which are primarily warm-growing season grasses and sedges, have anatomical and biochemical adaptations that act as a pump to concentrate intracellular CO₂ prior to final fixation, which reduces photorespiration and is energetically favorable over C₃ photosynthesis at low environmental CO₂ concentration and warmer temperatures (O'Leary, 1981; Sage, 2004). Net fractionation of atmospheric CO₂ by C₄ plants is less than that in C₃ plants, and C₄ plants have δ¹³C values that are closer to atmospheric CO₂ and non-overlapping with those of C₃ plants (mean modern C₄: -12.7‰ ± 1.1‰; O'Leary, 1981; Passey et al., 2002; Cerling et al., 2003; Kohn, 2010; Diefendorf et al., 2010). A small fraction of plants, primarily cacti and other succulents, use the Crassulacean Acid Metabolism (CAM) pathway that functionally allows for both C₃ and C₄ photosynthesis and results in δ¹³C values intermediate between and overlapping with those of C₃ and C₄ plants; as these plants do not generally constitute important food resources for large-bodied mammalian herbivores and were not likely abundant in the Early Miocene floras of Rusinga Island, we do not consider them further.

To interpret the δ¹³C values of fossil mammal tooth enamel in terms of diet and ecology, several factors must be considered. First, the δ¹³C of atmospheric CO₂ has changed through time in response to plate tectonic processes, changes in the rates of chemical weathering of silicates and burial of organic carbon, and long-term and anthropogenic perturbations to the global carbon cycle (Zachos et al., 2008; Tipple et al., 2010; Foster et al., 2017; Hönisch and The CenCO2PIP Consortium, 2023). The δ¹³C of atmospheric CO₂ in the Early Miocene was higher than modern, so the average C₃ and C₄ plant δ¹³C values would have been concomitantly higher. As described below, we use a constant offset for all of our data to address this.

The second factor is the isotope enrichment between ingested carbon and carbonate in tooth enamel hydroxyapatite. For fossil herbivores in this study (artiodactyls, perissodactyls, and proboscideans), we use +14.1‰ ± 0.5‰, which is the mean value for numerous large-bodied species of modern ruminant and non-ruminant artiodactyls and perissodactyls (Cerling and Harris, 1999). For higher level consumers with mostly or entirely animal-based diets (e.g., most large-bodied carnivores and, presumably, creodonts), the diet-enamel enrichment is not as well constrained as for herbivores, and it is beyond the scope of this paper to address this issue in detail. At least one recent paper has treated the diet-enamel enrichment as negligible for carnivorous mammals (Hopley et al., 2023), and we follow that here. However, given our results for carnivores and creodonts, even a modest diet-enamel enrichment for carnivores would not change our interpretations and conclusions about environments on Rusinga Island during the Early Miocene.

Finally, while non-overlapping, the δ¹³C values of C₃ and C₄ plants are quite variable, and for C₃ plants this variation has a large environmental component. In open habitats, high irradiance (hereafter referred to as light stress) and lower water availability (hereafter referred to as water stress) drive physiological and biochemical responses by C₃ plants to reduce water loss that reduce fractionation during uptake and fixation of CO₂, resulting in δ¹³C values that are shifted positively toward the C₄ endmember (Ehleringer and Cooper, 1988). Consequently, consumers in an open habitat with only C₃ vegetation would have enamel δ¹³C values that could be interpreted as including some fraction of carbon derived from C₄ plants. We use the δ¹³C value reported by Passey et al. (2002; -24.6 ± 1.1‰) for C₃ plants sampled in Kenya in 1988 during a drought to constrain this open habitat C₃ endmember. Conversely, in closed forests, photosynthetic recycling of plant respired CO₂ that has the low δ¹³C value characteristic of C₃ plants and lowered light intensity results in C₃ plant tissues with lower than average δ¹³C values and a vertical

gradient of δ¹³C with the most negative values near the ground and the highest values at the top of the canopy (the canopy effect; van der Merwe and Medina, 1991; Drucker et al., 2008; Bonafini et al., 2013). Thus, consumers with substantially lower than average δ¹³C values would be interpreted as feeding in closed forest habitats during tooth enamel formation. However, arboreal taxa that feed high in the canopy and at the top of the canopy would be eating leaves not subject to the canopy effect. If that were the dominant foraging site, such taxa would, in principle, have δ¹³C values consistent with foraging in non-closed canopy forest despite otherwise utilizing closed-canopy habitats. It is important to note that different studies use different methods and assumptions to establish end-member values for different foraging habitats, and thus some use different values than those we adopt here, including for closed-canopy feeding (e.g., Passey et al., 2002; Cerling et al., 2004; Cerling et al., 2015; Garrett et al., 2015).

4.2. Oxygen isotopes

The δ¹⁸O value of mammalian tooth enamel reflects the oxygen isotope composition of body water/fluids and the temperature dependent fractionation of oxygen isotopes during enamel formation, which for mammals occurs at a more or less constant temperature. The composition of mammalian body water is controlled by a combination of climate, diet, and physiology (Longinelli, 1984; Luz et al., 1984; Luz and Kolodny, 1985; Koch et al., 1989; Bryant and Froelich, 1995; Kohn, 1996; Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999). The oxygen isotope composition of mammalian tooth enamel primarily reflects the δ¹⁸O value of ingested water because mammals with a body mass > 1 kg have an approximately constant body temperature of ca. 37 °C, and enamel precipitation occurs in equilibrium with body water, which for many large-bodied mammals is dominated by ingested water (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Kohn et al., 1996). For herbivores that are not obligate drinkers (i.e., obtain their water from food sources such as leaves), the δ¹⁸O value of body water is more strongly influenced by leaf water, which is evaporatively enriched in ¹⁸O relative to meteoric water (Sternberg, 1989), so in the same habitat non-obligate drinkers will generally have high enamel δ¹⁸O values than obligate drinkers (Levin et al., 2006). In closed canopy forests, the relatively higher humidity levels in the understory result in ¹⁸O-depleted leaf water and increasing enrichment in ¹⁸O by preferential evaporation of ¹⁶H₂O from leaf water with increasing canopy height (Sternberg, 1989). This vertical gradient in leaf δ¹⁸O values has been correlated with canopy height habitat and feeding preferences in sympatric monkey species from the closed-canopy Tai Forest, Côte d'Ivoire (Krigbaum et al., 2013).

Reconstructing the average δ¹⁸O value of surface and plant water available at a site or in a region based on estimates of the δ¹⁸O of local meteoric water is often a key component of paleoclimatic reconstructions. Using oxygen mass balance models, Bryant and Froelich (1995) and Kohn (1996) found that large carnivores and obligate-drinking herbivores reliably track changes in meteoric water δ¹⁸O values. Extant proboscideans are obligate water drinkers that consume large volumes of surface water daily, and studies of fossil proboscidean enamel suggest that proboscideans faithfully record past meteoric water δ¹⁸O values (Ayliffe et al., 1992; Sánchez Chillón et al., 1994; Bryant et al., 1996; Reinhard et al., 1996; Koch, 1998; Fox and Fisher, 2001; Fox et al., 2007).

Based on spatial patterns in the δ¹⁸O of modern meteoric water (Rozanski et al., 1993), several processes could have changed the δ¹⁸O of average meteoric water through time at Rusinga Island. Increasing air temperature would lead to higher δ¹⁸O meteoric water based on the positive global correlation between meteoric water and surface temperature (Rozanski et al., 1993). Change in dominant vapor source to local air masses between the Atlantic and Indian Oceans would also change the δ¹⁸O of meteoric water because Atlantic moisture would be subjected to greater rainout along longer storm tracks than would Indian

Ocean moisture and so would deliver water with lower $\delta^{18}\text{O}$ due to preferential rainout of ^{18}O from vapor along the storm track. Finally, an increase in local storm intensity and duration over time would lead to a decrease in $\delta^{18}\text{O}$ of meteoric water through more complete rainout of ^{16}O (Rozanski et al., 1993).

5. Materials and methods

We sampled 105 fossil teeth from Early Miocene Rusinga faunas housed and curated at the National Museums of Kenya, Nairobi. Specimens were selected to document a wide range of taxa and represent many fossil sites on the island (Table S1). Of the 105 teeth, 37% ($n = 39$) were identifiable to genus and species, whereas the others were identified at the genus level or higher. Eighty-eight of the sampled teeth come from the Kiahera, Hiwegi, and Kulu Formations. The remaining 17 teeth do not have reliable site information and therefore cannot be placed into one of the Rusinga Group formations. Eighty-one teeth were associated with accurate and reliable provenience information from seven Rusinga localities in the Hiwegi and Kulu Formations, and two teeth were associated with the Hiwegi and Kulu Formations, respectively, without site information. Five samples were taken from mammal teeth collected from R74 (Fig. 1B), which has been variously considered to represent the Wayando (e.g., Pickford, 1986a), Kiahera (Whitworth, 1953; Michel et al., 2023), or possibly Kulu Formation (Drake et al., 1988). Based on the sedimentology of the site and its geographic position, R74 is now interpreted to be in the Kiahera Formation and the Wayando Formation is no longer thought to exist on Rusinga Island (Michel et al., 2023). However, this site is bounded by faults and surrounded by discontinuous exposures of the Kiahera Formation (Van Couvering, 1972a; Pickford, 1986a; Geraads et al., 2016; Michel et al., 2023), so assignment of the strata at R74 to a specific member of the Kiahera Formation is still uncertain, but the locality is likely relatively high in the Kiahera Formation (Michel et al., 2023). Of the 105 samples analyzed, the 17 specimens for which provenience in terms of lithostratigraphic unit and locality are unknown were included for two reasons. First, larger samples of individual taxa enabled us to assess variability within species. Second, ongoing research (e.g., Peppe et al., 2009; Michel et al., 2014, 2020, 2023) is helping to revise and improve the Rusinga stratigraphy, and isotope values from these specimens may gain interpretive value as our stratigraphic knowledge improves. Unprovenienced samples and samples from the Kiahera Formation are clearly identified in the results so that they do not influence interpretations of Hiwegi and Kulu faunas.

5.1. Laboratory analytical techniques

At the National Museums of Kenya, approximately 7 mg of tooth enamel were drilled from each specimen using a diamond bur. Care was taken to avoid diagnostic morphology while drilling; slow drill speeds were used to minimize heating and any resulting isotopic fractionation. Bulk samples were drilled from the buccal side of each tooth unless the enamel on that side was discolored or cracked, which could indicate alteration, in which case the lingual side was sampled. Samples were oriented as much as possible parallel to the direction of crown growth and extended along the tooth crown as far as possible so as to maximize time averaging within each sample and provide a time integrated dietary signal.

Sample powders were reacted with 1 M acetic acid with a 1 M calcium acetate buffer (pH = 5) for 24 h to remove any exogenous carbonate. Samples were rinsed three times with distilled, deionized water and then dried in a 60 °C oven for >48 h to remove any remaining water.

Primate specimens were analyzed at the Stable Isotope Laboratory in the Earth and Planetary Sciences at the University of California Santa Cruz using a Kiel automatic carbonate extraction device connected to a MAT 253 isotope ratio mass spectrometer; the non-primate specimens were analyzed at the Stable Isotope Laboratory in the Department of Earth Sciences at the University of Minnesota using a Kiel automatic

carbonate extraction device connected to a MAT 252 isotope ratio mass spectrometer. At each lab, the cleaned enamel samples were reacted with 100% phosphoric acid in the presence of ca. 2 cm of silver thread to react with any SO₂ generated during acid digestion of the enamel. Results are reported as conventional $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in parts per thousand (permil, ‰), where $\delta\text{X} = (\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1) * 1000$, X is ^{13}C or ^{18}O , R is $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$ respectively, and we report carbon isotope data relative to the Vienna Pee Dee Belemnite (V-PDB) scale and oxygen isotope data relative to the Vienna Standard Mean Ocean Water (V-SMOW) scale. Oxygen isotope data from tooth enamel are sometimes reported relative to the V-PDB scale, but the environmental parameter of interest is the $\delta^{18}\text{O}$ value of meteoric water, which is reported relative to the V-SMOW scale by convention, so here we use the V-SMOW scale for our oxygen isotope data. Corrections to the V-PBD and V-SMOW scales were based on repeated measurements of calibrated international standards (NBS-19) and commonly used materials (Carrera marble), and precision in both labs was better than 0.1‰.

Using methods described in detail by Garrett et al. (2015), the $\delta^{13}\text{C}$ value of Early Miocene atmospheric CO₂ was estimated as $-6.0\text{\textperthousand} \pm 0.2\text{\textperthousand}$ (mean ± 2 s.d.; Zachos et al., 2001, 2008; Tipple et al., 2010), and fossil $\delta^{13}\text{C}$ values are expressed throughout in the text and figures as modern equivalent by shifting measured $\delta^{13}\text{C}$ values by $-2\text{\textperthousand}$ (assuming a modern atmospheric CO₂ $\delta^{13}\text{C}$ value of $-8.0\text{\textperthousand}$).

5.2. Statistical tests

The means of the aggregated $\delta^{18}\text{O}$ values of rhinocerotids and proboscideans from the Grit/Fossil Bed Member and Kibanga Member of the Hiwegi Formation and for the Kulu Formation were compared statistically using Student's *t*-tests calculated in JMP Pro 13.2 (SAS Institute Inc., Cary, NC, 1989–2021).

6. Results and interpretations

6.1. Carbon isotope results

The carbon isotope data are presented in Figs. 4–6 as the atmosphere adjusted, modern equivalent enamel values based on the assumed $-2\text{\textperthousand}$ difference in the $\delta^{13}\text{C}$ value of Early Miocene atmospheric CO₂ ($-6.0\text{\textperthousand} \pm 0.2\text{\textperthousand}$; see Section 5.1 above) relative to the $\delta^{13}\text{C}$ value of modern atmospheric CO₂ ($-8.0\text{\textperthousand}$). Measured $\delta^{13}\text{C}$ values, modern equivalent enamel $\delta^{13}\text{C}$ values, and modern diet equivalent $\delta^{13}\text{C}$ values assuming a diet-enamel enrichment of $+14.1\text{\textperthousand}$ for primates and ungulates (Cerling and Harris, 1999) and no diet-enamel enrichment for carnivores are reported in Table S1. All $\delta^{13}\text{C}$ values for fossils discussed below are the atmosphere adjusted, modern equivalent enamel values.

The carbon isotope compositions of the Rusinga mammalian enamel samples spans the entire range of diets based on modern C₃ vegetation. No individuals sampled have $\delta^{13}\text{C}$ values that require consumption of C₄-based resources under the C₃ and C₄ endmembers assumed here (Figs. 4–6, Table S1), but, given the results of Peppe et al. (2023), higher $\delta^{13}\text{C}$ values are permissive of some C₄ grass consumption in some cases and consistent with the interpretations of Peppe et al. (2023). The majority of specimens (75 of 105, or 71%) had diets that were within one standard deviation of mean modern C₃ vegetation ($-27.4\text{\textperthousand} \pm 1.6\text{\textperthousand}$, all means reported ± 1 standard deviation), indicating most sampled animals foraged in environments with neither light/water-stressed vegetation nor closed canopies.

Some specimens of herbivorous taxa sampled from the Hiwegi and Kulu Formations ($n = 18$), as well as some for which the formation is uncertain (i.e., "Wayando or Kulu") or unknown ($n = 8$), have $\delta^{13}\text{C}$ values more than one standard deviation higher than mean C₃ vegetation, consistent with foraging in more open habitats in which plants experienced some degree of light/water stress (hence higher than average $\delta^{13}\text{C}$ values for C₃ plants) or possibly inclusion of some C₄ grasses in the diet (given that no measured $\delta^{13}\text{C}$ values require C₄

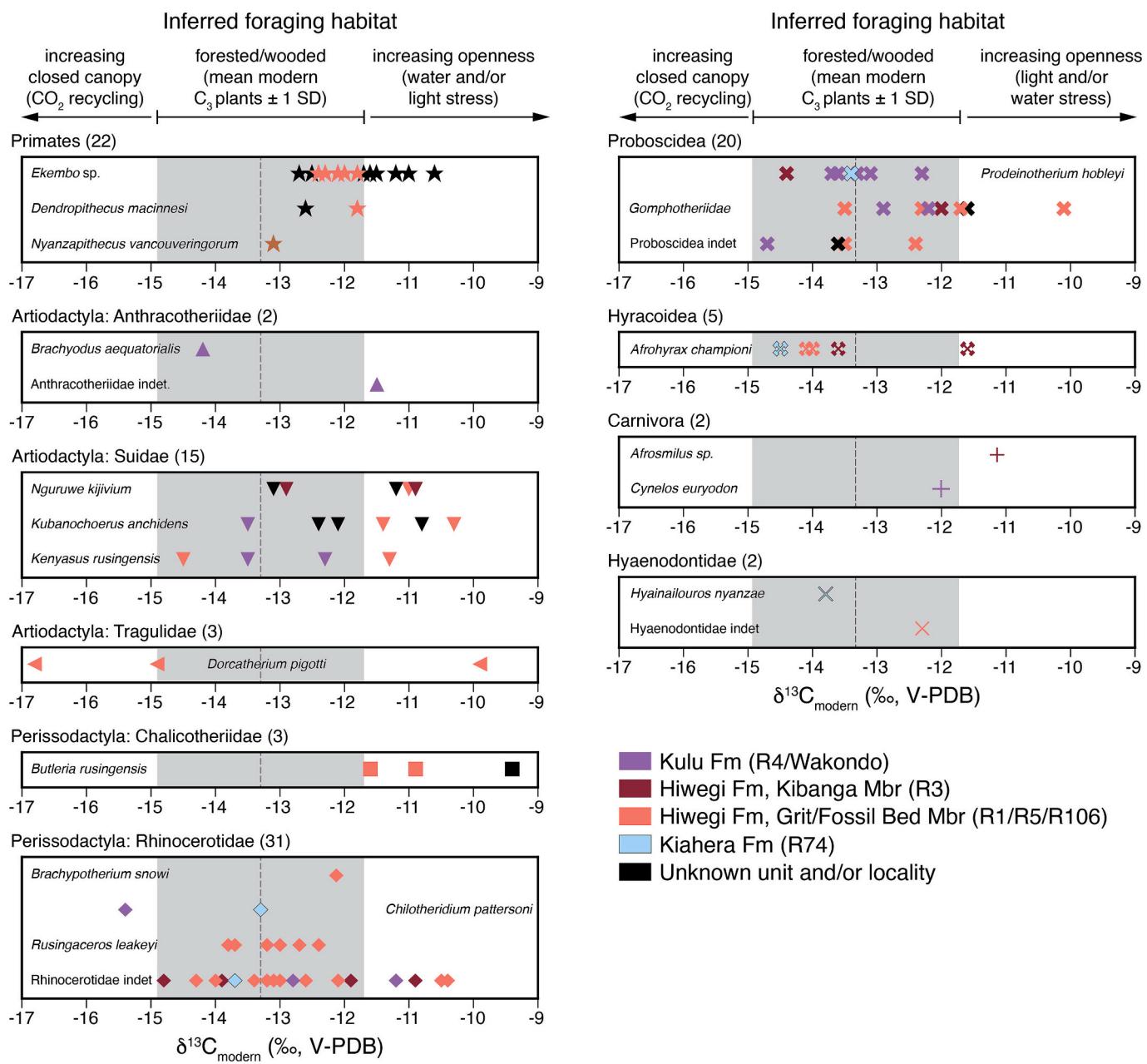


Fig. 4. Enamel carbon isotope composition by taxon. All $\delta^{13}\text{C}$ values have been corrected to modern atmospheric CO_2 (see text). The dark grey dashed line represents the corrected enamel $\delta^{13}\text{C}$ value consistent with diet of mean modern C_3 plants and the grey bar throughout represents the ranges of corrected enamel $\delta^{13}\text{C}$ values consistent with diets within ± 1 standard deviation of mean of modern C_3 plants. Animals with enamel $\delta^{13}\text{C}$ values within this range were foraging on plants experiencing neither CO_2 recycling nor light/water stress, interpreted to be wooded or forested habitats. Animals with enamel $\delta^{13}\text{C}$ values more negative than 1 SD below the mean of modern C_3 plants are interpreted as foraging in closed canopy forests that experienced CO_2 recycling. Animals with enamel $\delta^{13}\text{C}$ values less negative than 1 SD above the mean of modern C_3 plants are interpreted as foraging in more open habitats that experienced light and/or water stress.

consumption, we do not calculate percent C₄ in diets). However, only three specimens—two of the tragulid *Dorcatherium pigotti* from the Hiwegi Formation (KNM-RU 17229 and KNM-RU 71235) and one of the rhinocerotid *Chilotheridium pattersoni* from the Kulu Formation (KNM-RU 3024)—have δ¹³C values more than one standard deviation below mean C₃ vegetation, indicating foraging in a more closed-canopy forest. None of the Hiwegi Formation specimens sampled from the R3 site have δ¹³C values that specifically require the animals to have foraged in closed-canopy forests and instead indicate both mean and light/water-stressed C₃ vegetation. Below we discuss the results by higher taxon.

6.1.1. Primates

The $\delta^{13}\text{C}$ values for all 19 *Ekembo* specimens sampled from Rusinga

indicate they were foraging in habitats with either average C₃ vegetation or more open, light- and/or water-stressed habitats (-12.7‰ to -10.6‰; mean δ¹³C = -11.9‰ ± 0.6‰). Eight of the *Ekembo* specimens were reliably found within the Grit/Fossil Bed Member of the Hiwegi Formation; the δ¹³C values for only these individuals indicate they were consuming average C₃ vegetation (mean δ¹³C = -12.2‰ ± 0.2‰). Of the remaining 11 *Ekembo* specimens lacking reliable information about their provenience, six had ¹³C-enriched enamel values that indicate they were feeding in more open light- and/or water-stressed habitats. The δ¹³C values from the other two catarrhine species indicate they were consuming average C₃ vegetation: the δ¹³C values from the two specimens of *D. macinnesi* are -11.8‰ and -12.6‰ (midpoint = -12.2‰), and the δ¹³C value for the one *N. vancouveringorum* specimen was

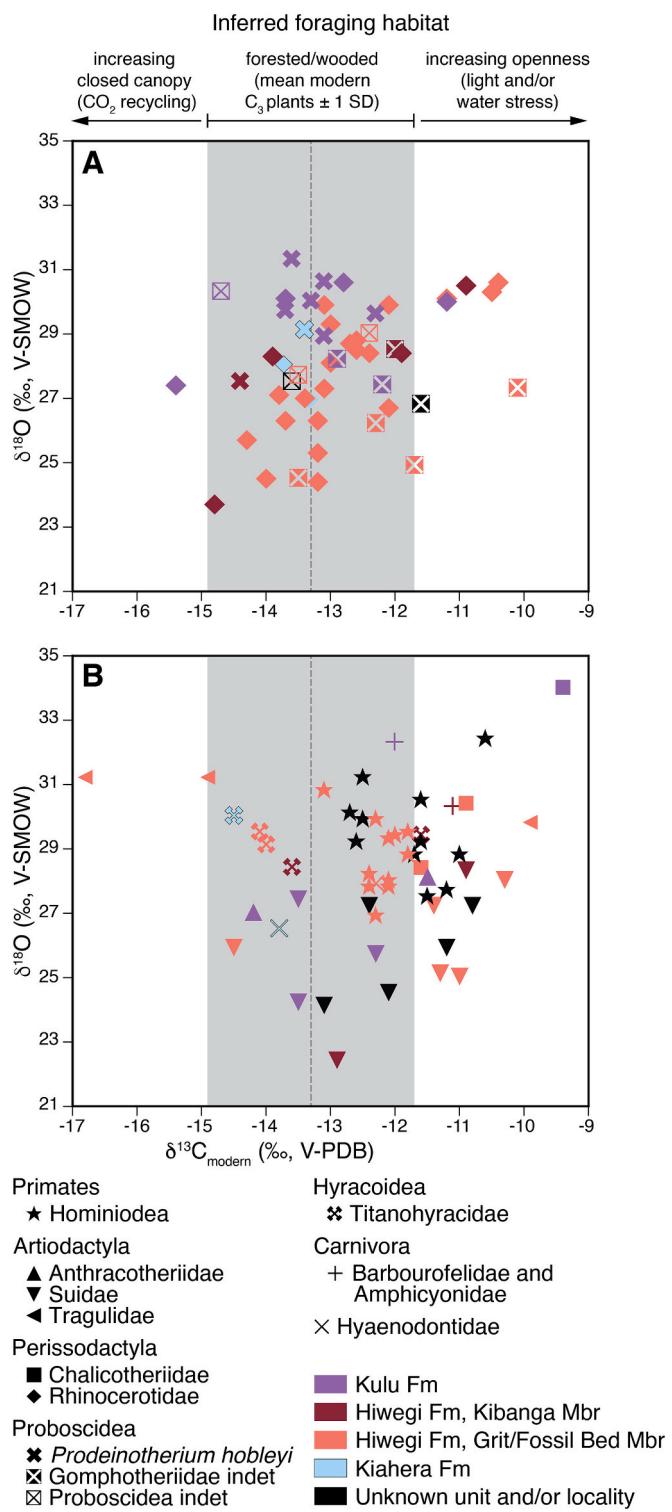


Fig. 5. Mammalian enamel carbon and oxygen isotope composition by taxon. (A) Enamel isotopic composition of all sampled rhinocerotids and proboscideans. (B) Enamel isotopic composition of all other taxa sampled. All $\delta^{13}\text{C}$ values have been corrected to modern atmospheric CO_2 (see text). The inferred foraging habitats are as in Fig. 4.

–13.1‰. If some or all of these species had foraging ecology like modern apes, then they may have foraged at least some of the time in closed-canopy forests. However, none of the Rusinga primates sampled have $\delta^{13}\text{C}$ values low enough to require consuming vegetation exclusively from the understory of closed-canopy forests, and the degree to which a

given $\delta^{13}\text{C}$ value could represent some feeding in the understory of closed-canopy forest would have to be balanced by either an equivalent reliance on a more open habitat or a greater reliance on typical wooded environments

In principle, the average to moderately high $\delta^{13}\text{C}$ values of the primates could reflect foraging at the top of the canopy of closed-canopy forest where CO_2 recycling is minimal and irradiance is high, yielding leaves and possibly fruits at the top of the canopy with average or even high $\delta^{13}\text{C}$ values for C_3 plants. However, Krigbaum et al. (2013) did not find any relationship between $\delta^{13}\text{C}$ values and foraging height in the canopy for seven sympatric modern species of cercopithecoid monkeys in the Taï Forest, Côte d'Ivoire, and thus the moderately high $\delta^{13}\text{C}$ values of many of the primates cannot be used to infer foraging at the top of closed-canopy forest. Krigbaum et al. (2013) did find a positive relationship between $\delta^{18}\text{O}$ values and foraging height for these species, presumably driven by evaporative enrichment of ^{18}O in food items for individuals feeding higher in and at the canopy top in closed-canopy forest. Twelve of the 19 *Ekembo* specimens and all three of the specimens of *D. macinnesi* and *N. vancouveringorum* we sampled have $\delta^{18}\text{O}$ values greater than the mean for all samples (28.2‰ V-SMOW), which could be consistent with some degree of foraging higher in the canopy of closed-canopy forest instead of in typical wooded habitats or more open habitats. *Ekembo* resembles extant apes in having mobility as well as strengthening and stability at the wrist (Sarmiento, 1988; Daver and Nakatsuka, 2015). Although *Ekembo* is regarded as an arboreal quadruped and did not exhibit the shoulder adaptations for suspensory behaviors (suspension, brachiation, orthograde climbing) found in extant hominoids, several postcranial features are indicative of climbing and clambering behaviors (Sarmiento, 1984; Langdon, 1986; Rose, 1992, 1993; Walker et al., 1993; Begun et al., 1994; Rose, 1994; Dunsforth, 2006) and enhanced joint mobility throughout the forelimb (Jenkins, 1973; Rose, 1988) and hindlimb (Rose, 1993, 1994; Ward, 1993; Ward et al., 1995; Ward, 1997; Bacon, 2001). While these features suggest at least some adaptations to forest habitats, such as those used by extant apes, *Ekembo* was likely not as capable in such habitats as the earlier *Morotopithecus* which, perversely, has been shown to live in a more open woodland at Moroto (MacLatchy et al., 2023).

None of the *Ekembo* specimens with secure provenience and higher than average $\delta^{18}\text{O}$ values is from the R3 locality, the only highly fossiliferous locality with evidence for a closed-canopy forest, so we infer that terminal branches at the canopy top were not the primary foraging location for *Ekembo*. Both *D. macinnesi* and *N. vancouveringorum* are smaller bodied than *Ekembo* and could have more easily foraged habitually high in or at the top of closed-canopy forest. However, little is known of the post-crural anatomy and locomotor capabilities of the two smaller primate species, and none of the specimens is from R3, so the isotopic data do not constrain inferences about their foraging habitats among the alternative possibilities.

6.1.2. Anthracotheriidae

The $\delta^{13}\text{C}$ values for two anthracotheres from the Kulu Formation are –14.2‰ and –11.5‰ (midpoint = –12.9‰). Although one of the Kulu Formation anthracothere specimens was consuming average C_3 vegetation, $\delta^{13}\text{C}$ values from the other suggests a diet of C_3 vegetation from more open, light- and/or water-stressed habitats, such as woodlands or wooded C_3 grasslands. Given the small sample size, it is hard to assess the range in values between these two specimens. It could be that Rusinga anthracotheres foraged in a range of habitats and consumed aquatic plants to a variable degree (Boisserie et al., 2005). Although most aquatic plants utilize the C_3 photosynthetic pathway, these plants receive their carbon from dissolved bicarbonate, which is generally ^{13}C enriched relative to atmospheric CO_2 (Keeley and Sandquist, 1992; Hayes, 1993; Chikaraishi and Naraoka, 2003). Animals consuming aquatic vegetation would consequently also have higher $\delta^{13}\text{C}$ enamel values. Notably, anthracotheres have been described as hydrophilic based on taphonomic (Pickford, 1983) and isotopic (Clementz et al.,

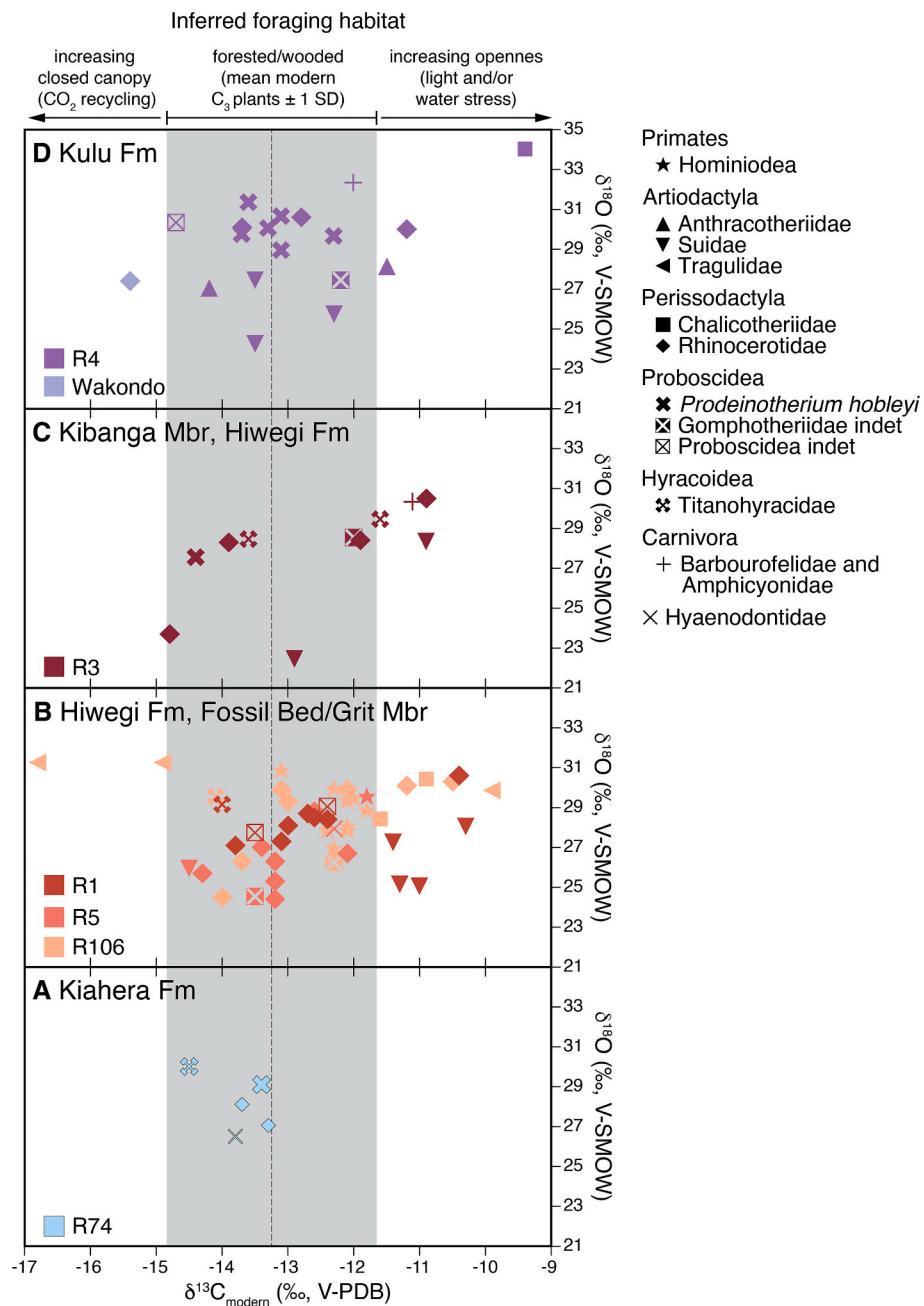


Fig. 6. Mammalian enamel carbon and oxygen isotope composition by stratigraphic unit and locality. Only specimens with secure provenience to locality are included in this figure. (A) Enamel isotopic composition of Kihera Formation fauna. (B) Enamel isotopic composition of the fauna from the Kibanga Member of the Hiwegi Formation. (C) Enamel isotopic composition of the fauna from Grit/Fossil Bed Member of the Hiwegi Formation. (D) Enamel isotopic composition of Kulu Formation fauna. All $\delta^{13}\text{C}$ values have been corrected to modern atmospheric CO_2 (see text). The inferred foraging habitats are as in Fig. 4.

2008) evidence, and are likely therefore to be water-dependent similar to modern hippopotamids. Thus, it is plausible that the higher values are the result of aquatic plants in the diets of these anthracotheres.

6.1.3. Suidae

After enamel sampling, it was noted that a few suid enamel samples may have included dentine, which should be more susceptible to isotopic alteration than enamel. The suid samples that may have included dentin have notably more negative values than the others (Table S1, specific samples noted with # before $\delta^{13}\text{C}$ values), and it is possible that these values represent a mixture of pristine enamel and altered dentin. However, isotopic alteration could in principle change dentin values in either direction (i.e., higher or lower). Alternatively, inadvertently

sampled dentin could also be pristine but represent a different time in tooth formation, and therefore possibly different diet, than enamel. We did not sample any pure dentin from any specimens, and as the low suid values that could include dentine do not impact the overall conclusions, those samples have been included but need to be interpreted with caution.

The four suids sampled from the Grit/Fossil Bed Member at R1 indicate they were foraging in more open habitats with C_3 vegetation experiencing light- and/or water-stress (mean $\delta^{13}\text{C} = -11.0\text{‰} \pm 0.5\text{‰}$). The fifth suid from the Grit/Fossil Bed Member, from R5, has a distinctly lower $\delta^{13}\text{C}$ value, which could reflect feeding in a more closed habitat, although this sample may have included dentine. The one suid from the Kibanga Member of the Hiwegi Formation, *Nguruwe kijivium* KNM-RU-

2777 from R3, has a high $\delta^{13}\text{C}$ value suggesting light- and/or water-stressed habitats ($\delta^{13}\text{C} = -10.9\text{\textperthousand}$). The $\delta^{13}\text{C}$ values from three suids from the Kulu Formation (two *Kenyasus rusingensis* and one *Kubanochoerus anchidens*) indicate these individuals were consuming average C₃ vegetation (mean $= -13.1\text{\textperthousand} \pm 0.7\text{\textperthousand}$); two of these samples may have included dentine and yet do not have notably low $\delta^{13}\text{C}$ values. The five specimens from the Rusinga collections that lack site data show a similar distribution, with three consuming average C₃ vegetation, and two foraging in more open habitats ($\delta^{13}\text{C}$ enamel range $= -13.1\text{\textperthousand}$ to $-10.8\text{\textperthousand}$).

6.1.4. Tragulidae

The $\delta^{13}\text{C}$ values from the three *Do. pigotti* from the Grit/Fossil Bed Members of the Hiwegi Formation (mean $\delta^{13}\text{C} = -13.9\text{\textperthousand} \pm 3.5\text{\textperthousand}$) indicate a wide range of foraging habitats. Interestingly, two tragulids from the Grit/Fossil Bed Member are the only two specimens of any taxa from the Hiwegi Formation with $\delta^{13}\text{C}$ values that indicate foraging in a closed-canopy habitat; conversely, the remaining Grit/Fossil Bed Member tragulid has a $\delta^{13}\text{C}$ value ^{13}C -enriched enough ($-9.9\text{\textperthousand}$) to indicate foraging in light- and/or water-stressed habitats. Microwear analysis on the Rusinga tragulids indicated *Do. pigotti* was a mixed feeder with microwear textures close to modern grazers/generalists (Ungar et al., 2012). The $\delta^{13}\text{C}$ values from three *Do. pigotti* specimens span a range equivalent to that of modern C₃ plants ($-24.0\text{\textperthousand}$ to $-30.9\text{\textperthousand}$) and corroborate reconstruction of a forested/woodland habitat with the possibility of some grass or open habitat browse included in the diet.

6.1.5. Chalicotheriidae

The two chalicotheres from the Grit/Fossil Bed Member of the Hiwegi Formation had $\delta^{13}\text{C}$ values of $-11.6\text{\textperthousand}$ and $-10.9\text{\textperthousand}$, whereas the chalicothere from the Kulu Formation had a $\delta^{13}\text{C}$ value of $-9.4\text{\textperthousand}$. The $\delta^{13}\text{C}$ enamel values from all *Butleria rusingensis* fossils sampled (both from the Grit/Fossil Bed Member and the Kulu Formation) indicate herbivorous diets from habitats that include some light/water-stressed areas.

6.1.6. Rhinocerotidae

The carbon isotope composition from the sampled Rusinga rhinocerotids ($-15.4\text{\textperthousand}$ to $-10.4\text{\textperthousand}$) spans the entire range of C₃ vegetation. The mean $\delta^{13}\text{C}$ for the 21 samples from the Grit/Fossil Bed Member of the Hiwegi Formation is $-12.7\text{\textperthousand} \pm 1.0\text{\textperthousand}$; the four from the Kibanga Member of the Hiwegi Formation have a mean of $-12.9\text{\textperthousand} \pm 1.8\text{\textperthousand}$. The four from the Kulu Formation have a mean of $-13.3\text{\textperthousand} \pm 1.8\text{\textperthousand}$, whereas values for the two rhinocerotid specimens from R74 in the Kiahera Formation are $-13.7\text{\textperthousand}$ and $-13.3\text{\textperthousand}$. Six rhinocerotids that could not be identified to genus have $\delta^{13}\text{C}$ values high enough to indicate foraging in more open habitats in which C₃ vegetation was under light- and/or water-stress: one from the Kulu Formation (R4 site; $\delta^{13}\text{C} = -11.2\text{\textperthousand}$), two from the Kibanga Member (R3; $\delta^{13}\text{C}$ values $= -10.9\text{\textperthousand}$, and $-11.9\text{\textperthousand}$), and three from the Grit/Fossil Bed Member (R1 and R106 localities; $\delta^{13}\text{C}$ values $= -10.4\text{\textperthousand}$, $-10.5\text{\textperthousand}$, and $-11.2\text{\textperthousand}$).

6.1.7. Proboscidea

Eight deinotheriid specimens were included in this analysis: six from the Kulu Formation (mean $\delta^{13}\text{C} = -13.2\text{\textperthousand} \pm 0.5\text{\textperthousand}$), one from the Kibanga member of the Hiwegi Formation ($\delta^{13}\text{C} = -14.4\text{\textperthousand}$), and one from R74 in the Kiahera Formation ($\delta^{13}\text{C} = -13.4\text{\textperthousand}$). Eight gomphotheriid specimens were sampled: four from the Grit/Fossil Bed Member of the Hiwegi Formation (mean $\delta^{13}\text{C} = -11.9\text{\textperthousand} \pm 1.4\text{\textperthousand}$), one from the Kibanga Member of the Hiwegi Formation ($\delta^{13}\text{C} = -12.0\text{\textperthousand}$), one from the Hiwegi Formation (without specific member information; $\delta^{13}\text{C} = -11.6\text{\textperthousand}$), and two from the Kulu Formation ($\delta^{13}\text{C} = -12.9\text{\textperthousand}$ and $-12.2\text{\textperthousand}$). Four proboscideans, without identification to family, were also sampled: two from the Grit/Fossil Bed Member of the Hiwegi Formation ($\delta^{13}\text{C} = -13.5\text{\textperthousand}$ and $-12.4\text{\textperthousand}$), one from the Kulu Formation ($\delta^{13}\text{C} = -14.7\text{\textperthousand}$), and one from an unknown Rusinga site ($\delta^{13}\text{C} = -13.6\text{\textperthousand}$).

Irrespective of their provenience, all but one *Prodeinotherium* specimens have $\delta^{13}\text{C}$ values lower than $-13\text{\textperthousand}$ (the exception is KNM-RU 71245 from R4), whereas all but one gomphotheriid specimens have $\delta^{13}\text{C}$ values higher than $-13\text{\textperthousand}$ (the exception is RU 1050 '84 from R5). The proboscidean specimen KNM-RU 71239 from the Grit/Fossil Bed Member of the Hiwegi Formation could not be conclusively identified but shows some morphological similarities with Gomphotheriidae; its $\delta^{13}\text{C}$ value was $-12.4\text{\textperthousand}$. All remaining unidentified proboscideans sampled have low $\delta^{13}\text{C}$ values ($<-13\text{\textperthousand}$).

6.1.8. Hyracoidea

The hyracs (*Afrohyrax championi*) from the Grit/Fossil Bed Member ($\delta^{13}\text{C} = -14.1\text{\textperthousand}$ and $-14.0\text{\textperthousand}$), the Kibanga Member ($\delta^{13}\text{C} = -13.6\text{\textperthousand}$), and the Kiahera Formation ($\delta^{13}\text{C} = -14.4\text{\textperthousand}$) fall within the standard deviation of mean modern C₃ plants and do not indicate foraging in a closed-canopy habitat. Moreover, one specimen (KNM-RU 71234) from the Kibanga Member of the Hiwegi Formation, whose position relative to the forest paleosol at R3 cannot be determined, shows a rather high $\delta^{13}\text{C}$ value ($-11.6\text{\textperthousand}$), which indicates a somewhat open, wooded habitat with C₃ vegetation experiencing a moderate degree of light- and/or water-stress.

6.1.9. Carnivora and Hyaenodontidae

The $\delta^{13}\text{C}$ value for the large *Afrosmilus* sp. from the Kibanga Member of the Hiwegi Formation sampled is $-11.1\text{\textperthousand}$ and for the small *Cynelos euryodon* from the Kulu Formation sampled is $-12.0\text{\textperthousand}$. The relatively high $\delta^{13}\text{C}$ value for the *Afrosmilus* sp. indicates its prey was consuming C₃ vegetation from more open C₃ habitats. The indeterminate hyaenodontid specimen sampled from the Grit/Fossil Bed Member (R5) of the Hiwegi Formation has a $\delta^{13}\text{C}$ value of $-12.3\text{\textperthousand}$. Finally, the large *Hyainailouros nyanzae* sampled from R74 (Kiahera Formation) has a $\delta^{13}\text{C}$ value of $-13.8\text{\textperthousand}$.

6.2. Oxygen isotope results

The Rusinga fauna exhibits a wide range in enamel $\delta^{18}\text{O}$ values (22.4‰ to 34.0‰ V-SMOW; Figs. 5–7, Table S1), indicating considerable variation in the oxygen isotope compositions of water sources for these animals, evaporative effects on drinking or plant water, species thermophysiological adaptations, and/or canopy height habitat and feeding preferences. Overall, the data suggest a weak, positive relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the specimens ($r = 0.19$, $p = 0.06$, Fig. 5). Of the groups with larger sample sizes, suids ($r = 0.42$) and rhinocerotids ($r = 0.65$) exhibit this trend from weak to moderately strong degrees, although only the correlation for rhinocerotids is statistically significant ($p = 0.001$). These positive correlations suggest some taxa obtained both food and water, either by obligate drinking or via their food, in the same habitat, with those individuals with higher $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values feeding and obtaining water in more open habitats subject to light and/or water stress. Other groups with larger sample sizes (proboscideans, primates) have weak or very weak correlations between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values that are not statistically significant (and in the case of proboscideans the correlation is negative). This may suggest no association between habitats in which proboscideans and primates were feeding and those in which they obtained water. For the remaining groups, sample sizes are too small to assess the relationships between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values.

For the proboscideans, rhinocerotids, and suids, specimens from the Kulu Formation have relatively higher $\delta^{18}\text{O}$ values than those of the same taxa from the Hiwegi Formation (Fig. 5). This trend is apparent even though the $\delta^{13}\text{C}$ values do not show any ^{13}C depletion or enrichment relationship to formation for these three taxa, suggesting there is a difference in meteoric water $\delta^{18}\text{O}$ values between the Kulu and Hiwegi Formations (Figs. 5–7).

Whereas $\delta^{18}\text{O}$ values from several taxa should closely reflect meteoric water $\delta^{18}\text{O}$ values based on our understanding of their biology, specifically the large body mass and physiological need for large

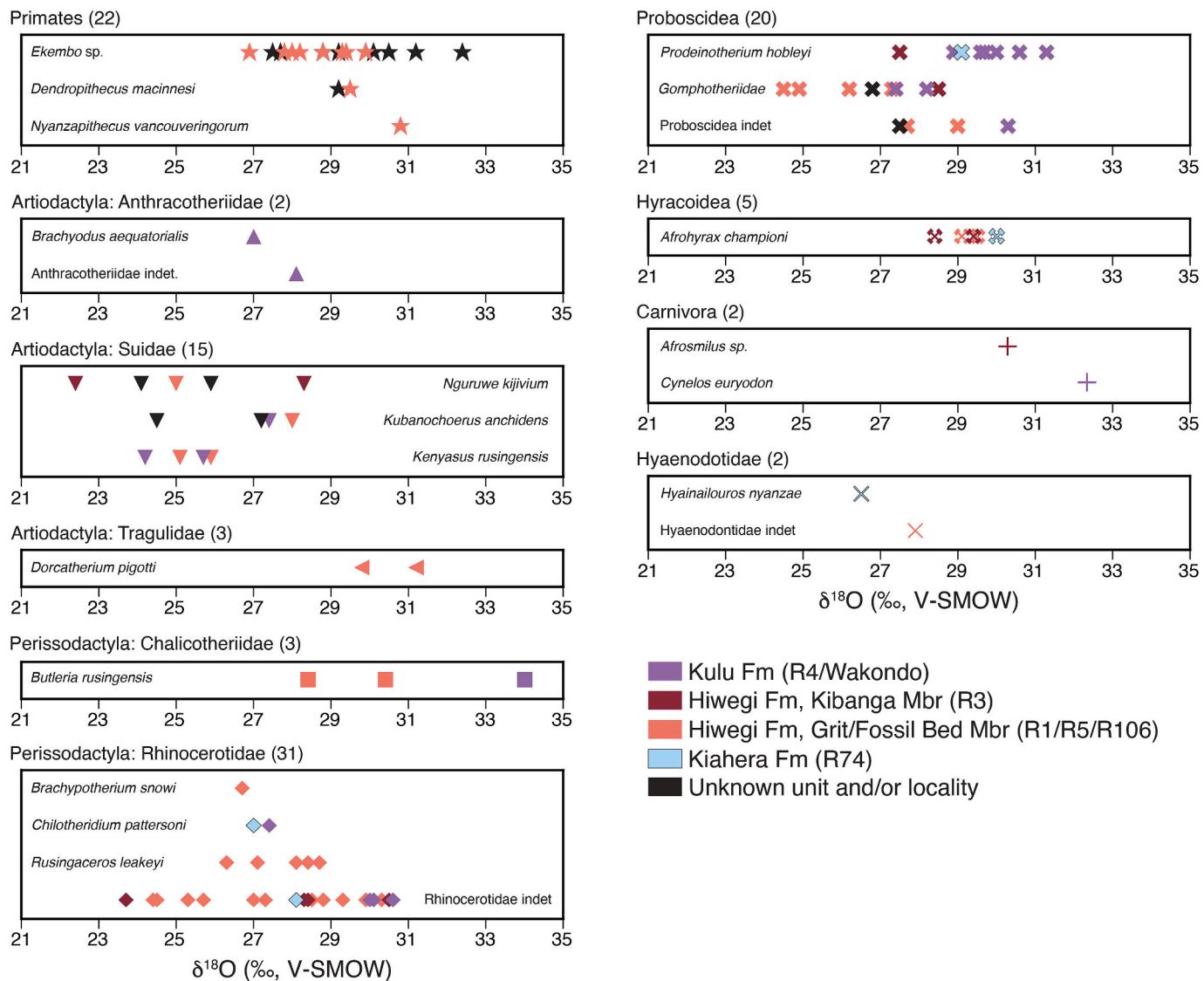


Fig. 7. Enamel oxygen isotope composition by taxon.

volumes of ingested water (i.e., proboscideans and rhinocerotids; Bryant and Froelich, 1995; Kohn, 1996), determining whether any of the remaining taxa are evaporation sensitive or insensitive in the sense of Levin et al. (2006) is not possible without assuming taxonomic uniformitarianism for their behavior from extant relatives. As such, applying an aridity index, such as the method of Levin et al. (2006), would be speculative. However, treating proboscideans and rhinocerotids as evaporation insensitive taxa, it is possible to determine whether there were trends or changes in meteoric water across Rusinga Group strata using Student's *t*-tests to compare the $\delta^{18}\text{O}$ values of the Rusinga proboscideans and rhinocerotids that can be reliably placed into the Grit/Fossil Bed Member and Kibanga Member of the Hiwegi Formation, or the Kulu Formation (Table 3). Grit/Fossil Bed Member proboscideans and rhinocerotids ($n = 27$) have $\delta^{18}\text{O}$ values that range from 24.4‰ to 30.6‰ and the distribution of values cannot be distinguished statistically from normal based on a Shapiro-Wilkes test ($p = 0.23$); the Kibanga Member proboscideans and rhinocerotids ($n = 6$) have $\delta^{18}\text{O}$ values that range from 23.7‰ to 30.5‰, but the sample size is too small to determine whether the values are normally distributed; and the Kulu Formation proboscideans and rhinocerotids ($n = 13$) have $\delta^{18}\text{O}$ values that range from 27.4‰ to 31.3‰ and the distribution of values cannot be distinguished statistically from normal based on a Shapiro-Wilkes test ($p = 0.08$). Hence, the $\delta^{18}\text{O}$ values of proboscideans and rhinocerotids from

Table 3

Results of Student's *t*-test used to compare the $\delta^{18}\text{O}$ values of the rhinocerotids and proboscideans from the Grit/Fossil Bed Member of the Hiwegi Formation, the Kibanga Member of the Hiwegi Formation, and the Kulu Formation. Significant differences in mean values are indicated in bold.

Member; Formation	$\delta^{18}\text{O}$ mean	SD	n	df	t-value	p-value
Grit/Fossil Bed; Hiwegi	27.5	1.9	27			
Kibanga; Hiwegi	27.8	2.2	6	31	0.34	0.73
Kibanga; Hiwegi	27.8	2.2	6			
Kulu	29.5	1.2	13	17	2.19	0.04
Grit/Fossil Bed; Hiwegi	27.5	1.9	27			
Kulu	29.5	1.2	13	36	3.50	0.001

the Grit/Fossil Bed Member and the Kibanga Member of the Hiwegi Formation are statistically indistinguishable in these samples. The Kulu Formation proboscideans and rhinocerotids, however, are significantly more ^{18}O -enriched than those from both the Grit/Fossil Bed Member and Kibanga Member of the Hiwegi Formation (Table 3).

7. Discussion

7.1. Dietary implications for Rusinga mammals

Resolving the habitats present on Rusinga Island during deposition of the Rusinga Group is important for understanding the environmental context of early ape evolution and, more generally, the habitats used by terrestrial vertebrates during the Early Miocene in eastern Africa. *Ekembo* exhibits synapomorphies that directly link it to extant hominoids, such as lack of tail (Ward et al., 1991, 1999; Ward, 1997), as well as features in the hand (Walker et al., 1993), wrist (Daver and Nakatsukasa, 2015), elbow (Rose, 1988), and ankle (Dunsworth, 2006). New research indicates that *Ekembo* shared with extant apes a high degree of mobility and strengthening and stability at the wrist (Daver and Nakatsukasa, 2015; see also Sarmiento, 1988). Although *Ekembo* engaged in quadrupedalism and did not exhibit the adaptations for orthograde behaviors (suspension, vertical climbing) found in extant hominoids (e.g., Ward et al., 1993; Rose, 1994; Begun, 2007; but see Daver and Nakatsukasa, 2015), several postcranial features are indicative of extensive climbing and clambering (Langdon, 1986; Rose, 1992, 1993, 1994; Walker et al., 1993; Begun et al., 1994; Dunsworth, 2006) and of enhanced joint mobility throughout the forelimb (Jenkins, 1973; Rose, 1988) and hindlimb (Rose, 1993, 1994; Ward, 1993; Ward et al., 1995; Ward, 1997; Bacon, 2001). This combination of features makes this taxon an excellent model for understanding the ancestral condition from which locomotor specializations exhibited by later apes evolved (McNulty, 2010; McNulty et al., 2015), and, given the anatomical evidence for some degree of arboreality in *Ekembo*, highlights the need for a better understanding of Early Miocene habitats on Rusinga Island.

Many of the primate specimens we analyzed have $\delta^{13}\text{C}$ values similar to the rest of the Rusinga fauna, which are generally higher than expected for closed-canopy forest animals (e.g., modern ungulates and primates in the Ituri Forest, Democratic Republic of Congo, Cerling et al., 2004; modern hominoids from various sites, MacLatchy et al., 2023). This implies that early hominoids in the area of what is now Rusinga Island did not exclusively inhabit closed-canopy forests and that they likely consumed vegetation from more open environments, indicating adaptations to a wider range of habitats than just closed-canopy forests. This is consistent with the conclusions of Peppe et al. (2023) about the episodic appearance of more open habitats across multiple localities in eastern Africa during the Early Miocene and consistent with the hypotheses of MacLatchy et al. (2023) that morphological adaptations of early apes may have been for foraging in broken canopies and more open environments.

Our results for several other clades warrant further discussion. Extant eastern African suids exhibit the full range of enamel $\delta^{13}\text{C}$ values, from C₃ hyper-browsers consuming vegetation from the floor of closed-canopy forests (e.g., *Hylochoerus meinertzhageni*), to C₄ hyper-grazers (e.g., *Phacochoerus africanus*; Cerling et al., 2004; Codron et al., 2007). None of the Rusinga suids exhibits low $\delta^{13}\text{C}$ values indicating closed canopy browsing, but rather typical C₃ browsing in mixed habitats (including light/water-stressed C₃ habitats), most similar to extant *Potamochoerus larvatus*.

The fossil chalicotheres are an unusual group of perissodactyls having dentition adapted for herbivory (specifically browsing) and claws on their digits rather than the hooves typical of other perissodactyls. Moreover, the hook-like manual digits found especially in Miocene forms (like *Butleria* from Rusinga), could have served for pulling branches down and gaining access to food (e.g., leaves, fruits), or even for stripping bark from trees (Coombs, 1983; Semprebon et al., 2011). Chalicotheres have thus often been used as an indicator taxon, suggesting the presence of at least some trees and shrubs in the nearby habitat (Coombs and Cote, 2010). Microwear analyses of a variety of chalicothere species from Asia, Europe, and North America indicate that all of these taxa were browsers with no significant grass in their diets (Schulz et al., 2007; Semprebon et al., 2011). If Eocene forms appear to

have been leaf and fruit browsers, many Miocene species potentially included hard food objects such as fibrous fruits, seeds, nuts, pits, bark/twig, and roots (Schulz et al., 2007; Semprebon et al., 2011). The Chalicotheriinae, of which *Butleria* is probably a basal representative (Anquetin et al., 2007), have the highest degree of enamel abrasion among chalicotheres (Semprebon et al., 2011). It is important to note, that to date no microwear analysis has been performed on African chalicotheres. Our isotopic analysis of the Rusinga chalicotheres further distance these animals from a strict leaf-eating (browsing) diet and rekindles the discussion about the nature of the abrasive dietary component seen by dental wear studies. The tooth enamel $\delta^{13}\text{C}$ values suggest that at least *Butleria rusingensis* consumed a diet from more open habitats, consistent with a degree of habitat heterogeneity during the Early Miocene across what is now Rusinga Island.

Modern rhinocerotids exhibit both C₃-browsing and C₄-grazing, and carbon isotope compositions of the two African species suggests dietary niche partitioning, with *Diceros bicornis* consuming a C₃-dominated diet with a mean $\delta^{13}\text{C}$ value of ca. -10.5‰ and *Ceratotherium simum* consuming a C₄-dominated diet with a mean $\delta^{13}\text{C}$ value of ca. 0.0‰ (Kingston and Harrison, 2007). Although all of the Rusinga rhinocerotids were probably consuming pure C₃ diets, a small number of them (19%) appear to be thriving in more open habitats. The only rhinocerotid specimen from Rusinga that has a $\delta^{13}\text{C}$ value low enough to indicate foraging in closed canopy habitats (-15.4‰) is assigned to *Chilotheridium pattersoni* and is from the Wakondo site in the Kulu Formation. The other specimen of *Chilotheridium* sampled for this study was found at the Kihera Formation locality R74 and has a somewhat higher $\delta^{13}\text{C}$ value (-13.3‰). Both specimens are fragments of relatively high crowned (hypodont) rhinoceros teeth and were identified as *Chilotheridium* mostly on that basis (Geraads, 2010). This hypodonty is at odds with the low $\delta^{13}\text{C}$ value found for the Wakondo specimen, as high crowned teeth are usually associated with grazing. The presence among the other rhinocerotids from the Kulu Formation (R4, Ks unit of Peppe et al., 2009) of at least one specimen with a $\delta^{13}\text{C}$ value consistent with foraging in a more open habitat ($\delta^{13}\text{C} = -11.2\text{\textperthousand}$) could indicate spatial or temporal heterogeneity in habitats in the upland catchment of the lake represented by the Kulu Formation deposits (but see below). Yet, as the *Chilotheridium* tooth is the only specimen sampled from Wakondo, additional specimens from this site would be required to evaluate the total variation in habitats captured by the Kulu Formation.

Rhinocerotids are very difficult to identify by their teeth only, which is why 21 of the rhinocerotid samples could not be identified to genus. According to Geraads (2010), the Hiwegi and Kulu Formations record the same species (*Rusingaceros leakeyi*), but they differ in the exclusive presence of *Brachypotherium snowi* in the Hiwegi Formation and *Turkanatherium acutirostratum* in the Kulu Formation. The former is characterized by a brachydont dentition, whereas the latter shares the tendency to hypodonty with *Chilotheridium* (Geraads, 2010). The $\delta^{13}\text{C}$ values found for the only identified *B. snowi* specimen in our sample (-12.1‰) and the mean value found for all the Hiwegi Rhinocerotidae indet. (-12.7‰ ± 1.0‰) are consistent with the brachydont dentition of these animals, usually associated with browsing. Likewise, the presence in the Kulu deposits of brachydont (*Rusingaceros*) as well as hypodont taxa could explain the observed heterogeneity of $\delta^{13}\text{C}$ values measured.

Two of the rhinocerotids from R3 have notably low $\delta^{13}\text{C}$ values (-13.9‰ and -14.7‰). Although there is no available information about the exact stratigraphic origin of these specimens, the presence at R3 of a distinct closed-canopy forest paleosol (Michel et al., 2014) offers a potential explanation for these low $\delta^{13}\text{C}$ values if the animals foraged within the forest environment.

Modern African elephants have a predominantly C₃ diet, with only those from the Amboseli and Tsavo regions of Kenya consuming a significant amount (> 20%) of C₄ vegetation (Codron et al., 2012). Although modern African elephants are predominantly browsers, previous studies (Cerling et al., 1999, 2005) showed that fossil

proboscideans had a greater range of dietary variation: deinotheres consistently consumed C₃ vegetation from the Early Miocene through the Early Pleistocene, whereas many other proboscideans, including gomphotheres, started consuming considerable amounts of C₄ vegetation from the late Miocene onwards. Harris (1978) suggested that deinotheres preferred jungle and densely vegetated gallery forest habitats (at least for foraging). Our results indicate that Early Miocene *Prodeinotherium hobleyi* at Rusinga were consuming an average C₃ diet, hence predominantly foraged in forested or wooded habitats (but not in closed-canopy forest) and not in more open areas, which is consistent with the previous isotopic studies of fossil proboscideans from eastern Africa (e.g., Cerling et al., 2005). Conversely, our sample of gomphotheres, which have more complex tooth crowns than deinotheres (Sanders et al., 2010; Sanders, 2024), appear to have foraged in a wider range of environments, including more open habitats subject to increased light- and/or water-stress. This greater range could presage the later shift to greater reliance on C₄ grasses in open habitats documented by Cerling et al. (1999, 2005). It may also be an early indication for dietary and habitat niche separation between deinotheres and gomphotheres on Rusinga, the latter starting to be less restrictive in its habitat than the former. Gomphothere teeth have been recovered in the forest paleosol at R3 (Michel et al., 2014, 2020), although none were sampled for this study.

Extant hyraxes are small herbivorous mammals with limbs with digits bearing broad, flat hoof-like nails and plantigrade locomotion (Shoshani et al., 2013). The three living genera range from tree-dwelling, herbivorous species with brachydont teeth to open habitat grazers with hypsodont teeth. However, during the Paleogene, Hyracoidea were the dominant small- to medium-sized mammalian herbivores in Afro-Arabia and showed a greater morphological disparity than their modern counterparts (e.g., Schwartz et al., 1995; Rasmussen and Gutierrez, 2010). *Afrohyrax*, which is fairly common in Early Miocene sites in eastern Africa, is a holdover from these archaic forms and survived for some time after the faunal interchange with Eurasia at the Oligocene-Miocene boundary, when many African species were replaced by immigrant artiodactyls and perissodactyls (Kappelman et al., 2003). *Afrohyrax* was cursorial, thought to inhabit at least partially open environments, and had brachydont teeth suggesting adaptations to folivory (Rasmussen and Gutierrez, 2010). However, the presence of *Afrohyrax* in the forest paleosol at R3 (Michel et al., 2014) indicates that this species did not completely avoid closed-canopy forest environments. Our isotopic results are consistent with a diet for Afrohyrax of C₃ plants with average δ¹³C values, consistent with foraging in habitats without closed canopies despite occurring in the forest paleosol at R3. Thus, *Afrohyrax* appears to have used both more open and more closed environments.

7.2. Paleoenvironments on Rusinga

The range of enamel δ¹³C values from the Rusinga mammalian fauna suggests habitat variability in both space and time during deposition of the Rusinga Group, which would have included a temporally and/or spatially dynamic mixture of open-canopy forests/woodlands and more open habitats (such as shrublands, bushlands, or woody grasslands—i.e., habitats with less than 80% woody cover; White, 1983; Cerling et al., 2011), and more closed, forested habitats. This heterogeneity is consistent with regional patterns described by Peppe et al. (2023) across multiple sites in eastern Africa during the Early Miocene, including Rusinga. Unfortunately, without higher temporal and spatial resolution of sampling, it is currently not possible to tell the difference between temporal variability and spatial variability because the animals sampled here likely derive from multiple habitats, but the fossils sampled were collected from different depositional environments, which means that the samples were somewhat time-averaged based on their depositional environments and any spatial heterogeneity in the landscape is unresolvable. Further, the historical collections are stratigraphically

averaged within fossil localities, also preventing assessments of spatial or temporal patterns of variability. Additionally, some of the higher δ¹³C values, specifically those from the semiaquatic anthracotheres (e.g., RU2009–1016 with an atmosphere adjusted δ¹³C value of –11.5‰), may indicate the consumption of some aquatic C₃ plants, rather than light- and/or water-stressed vegetation. However, consumption of aquatic plants is considered unlikely for other specimens of other species with somewhat elevated δ¹³C values sampled here, including the primates.

Some lineages of C₄ grasses evolved during the late Paleogene (Sage, 2004; Christin et al., 2008; Vicentini et al., 2008; Edwards et al., 2010; Sage et al., 2011; Christin and Osborne, 2014) and therefore could be present in eastern Africa during the Early Miocene. Indeed, Peppe et al. (2023) and MacLatchy et al. (2023) presented isotopic and phytolith evidence for the presence of C₄ grasses at some Early Miocene localities in eastern Africa, including Rusinga. Modern C₄ ecosystems are dominated by C₄ monocotyledonous species, including grasses, but it is possible that C₄ dicotyledonous plants including shrubs and trees, which are relatively uncommon in C₄ ecosystems today (Ehlertinger et al., 1997), were present within the Early Miocene Rusinga habitats. If such non-analog habitats (i.e., those with relatively abundant C₄ dicotyledonous plants) were present, consumption of C₄ plants could explain the δ¹³C-enriched enamel values without necessarily indicating light- and/or water-stressed vegetation, as could ingestion of small fractions of C₄ grasses when and where those were present. However, C₄ plants were not consumed by any species or individuals in sufficient abundance to leave an unambiguous isotopic signature in their enamel.

There do not appear to be any overall trends in carbon isotopic composition within the Hiwegi Formation or between the Hiwegi and Kulu Formations, but rather the entire dataset suggests predominately average C₃ habitats with some more open and/or light/water-stressed habitats and rare evidence for closed-canopy habitats. The lack of evidence for closed-canopy habitats is interesting in light of the reconstruction of the tree stump casts with densities indicating an interlocking and therefore closed-canopy forest at R3 (Michel et al., 2014). Based on the scale, density, and distribution of tree stump casts over almost 5 km of outcrops at multiple localities (R1, R2, and R3; Michel et al., 2014), it seems unlikely that the forest habitat during the R3 paleosol deposition was not extensive enough for the canopy effect to manifest in mammalian consumers. However, in addition to evidence for the closed-canopy forest, there is also considerable evidence for spatial heterogeneity in the environment. Fossils leaves and phytoliths collected from different locations across the R3 site indicate there were more open areas on the landscape that document evidence for both plant taxa that live in habitats with fluctuating water levels (i.e., standing water to damp soil without standing water) and C₄ grasses (Baumgartner and Peppe, 2021; Peppe et al., 2023). Further, paleobotanical evidence indicates a seasonal tropical forest with both evergreen and deciduous taxa (Michel et al., 2014, 2020; Baumgartner and Peppe, 2021). Thus, it is possible that during drier periods the deciduous taxa would have lost their leaves creating more open patches within the forest. This evidence suggests that the R3 forest paleosol was not a uniform, closed-canopy forest, and instead was a mixture of habitats ranging from multi-storyed closed canopy to more open patches with abundant C₄ vegetation, which is a forest structure common in eastern Africa and equatorial African forests today. Considering these environmental interpretations, the tooth enamel isotopic data could reflect dietary preference, the total environmental heterogeneity, or unintentional sampling bias. Given the range of habitats that existed at the R3 site, the tooth enamel isotopic data could indicate that the animals sampled consumed vegetation primarily on the ecotone boundaries or a mixture of vegetation from both the more closed and more open parts of the landscape. However, the provenance information is not detailed enough to determine which specimens in this study derive from the forested layer or from the underlying ravine layer at R3 (see Michel et al., 2020) or where they were sampled across the preserved forest landscape (i.e., open vs. closed

areas). The mixture of more open and closed forest environments and seasonal climate at R3 could also result in a shift toward higher than expected $\delta^{13}\text{C}$ values of the plants within the forest (e.g., a seasonally dry tropical forest). This in turn would cause the relative ^{13}C enrichment in the R3 fauna. It is also possible that the data from R3 are the result of some taphonomic and sampling artifact. For example, some individuals sampled may have foraged in multiple habitats during tooth formation (i.e., some specimens collected at R3 may have foraged elsewhere earlier in life) but died and were buried at R3 or individuals that foraged within the closed-canopy habitats were inadvertently not included in this study.

Regardless of the explanation for the tooth enamel data at R3, our isotopic data demonstrate the presence of both average C_3 habitat (such as open-canopy woodlands) as well as light- and/or water-stressed habitats in the same horizon as the fossilized tree stump and root casts at the R3 site. Notable in this regard is the observation that at least some modern sympatric cercopithecoid primate species from closed-canopy forests do not exhibit correlations between the $\delta^{13}\text{C}$ values of enamel and canopy height habitat and feeding preferences (Krigbaum et al., 2013). Although our enamel $\delta^{13}\text{C}$ values provide little evidence for closed canopy feeding, differences among taxa in $\delta^{18}\text{O}$ values may be due, in part, to canopy height feeding preferences. For example, the suids (mean $\delta^{18}\text{O} = 26.0\% \pm 1.5\%$, $n = 15$) as a group have the lowest $\delta^{18}\text{O}$ values, conceivably due to foraging within the forest understory, compared to the primates (mean $\delta^{18}\text{O} = 29.2\% \pm 1.3\%$, $n = 22$) with relatively ^{18}O -enriched values that could be due to feeding higher in the forest canopy or perhaps at the end of branches in more light/water stressed environments.

The mean $\delta^{18}\text{O}$ values of rhinocerotids and proboscideans indicates a change in the oxygen isotope composition of local meteoric water during accumulation of the Hiwegi and the Kulu Formations. The statistically higher $\delta^{18}\text{O}$ values of rhinocerotids and proboscideans in the Kulu Formation relative to those in the Hiwegi Formation indicates either an increase in mean annual temperature, an increase in aridity (evaporation), a decrease in mean annual precipitation, or some combination of these three climatic factors. Regardless of which climatic factor drove the increase in local $\delta^{18}\text{O}$ values, this was a noticeable shift that may have impacted the Kulu Formation fauna and may therefore explain differences in faunal community composition. Several taxa found in the Hiwegi Formation deposits are missing from the Kulu Formation (Table 1), and these changes in faunal composition could be directly related to climatic differences, rather than differences in sampling and/or preservation. The climatic changes may be directly related to increasing global temperatures leading up to the Mid-Miocene Climatic Optimum (Flower and Kennet, 1994; Zachos et al., 2001, 2008; Westerhold et al., 2020; Steinhorst et al., 2021; Herbert et al., 2022). Alternatively, higher $\delta^{18}\text{O}$ values of mammals from the Kulu Formation may be associated with the Early Miocene closure of the Tethys and a resulting change in source water for precipitation in western Kenya. A change from a moisture source in the Tethyan realm ("Mediterranean") or the Atlantic Ocean during Hiwegi Formation deposition to the Indian Ocean during Kulu Formation deposition would shorten the distance from the moisture source and potentially cause less rain out of ^{18}O along the path of air masses, resulting in isotopically heavier meteoric water in the region. Future climate reconstructions from paleosol geochemistry or paleobotanical analyses may help to establish the basis of the change in the $\delta^{18}\text{O}$ value of meteoric water inferred from the tooth enamel data.

Many of the previous paleoenvironmental reconstructions for Rusinga have yielded a wide range of often conflicting results and interpretations, indicating habitats ranging from closed forests, woodland, or rainforest to mosaic habitats of both open and closed habitats and even semiarid environments (Table 2). Our results refute previous paleoenvironmental analyses and interpretations of a spatially and temporally homogeneous habitat (e.g., Chesters, 1957; Andrews and Van Couvering, 1975; Andrews et al., 1979; Pickford, 1983, 1985; Bestland, 1990; Bestland and Retallack, 1993; Retallack, 2002; Forbes et al., 2004). Instead, it is clear from our data that these Early Miocene

faunal communities inhabited a spatially heterogeneous habitat that changed through time, as was the case at other Early Miocene sites in the region (MacLatchy et al., 2023; Peppe et al., 2023). This implies that the previous, seemingly disparate, paleoenvironmental reconstructions may, in part, reflect spatial and temporal heterogeneity in the Early Miocene Rusinga ecosystem rather than the product of conflicting results from sampling different sites and/or using different proxies.

Placement of the Rusinga primate community within these spatially and temporally varied habitats indicates they were able to cope and even thrive within this dynamic landscape by inhabiting both closed and more open habitats. Importantly, the placement of an early hominoid, *Ekembo*, in habitats ranging beyond the dense, closed- and interlocking-canopy forests, such as the one reconstructed for R3 (Michel et al., 2014), complicates interpretations of the locomotor adaptations of this early hominoid as related to habitual use of a single, specific habitat. Features such as a high degree of hallux flexion and powerful forelimb and hindlimb grasping (Langdon, 1986; Rose, 1992, 1993, 1994; Walker et al., 1993; Begun et al., 1994; Dunsworth, 2006) and enhanced joint mobility throughout the forelimb (Jenkins, 1973; Rose, 1988) and hindlimb (Rose, 1993, 1994; Ward, 1993, 1997; Ward et al., 1995; Bacon, 2001) must be interpreted within a broader context of environmental and ecosystem fluctuations. Likewise, the results presented here suggest the possibility that habitat flexibility may be a primitive characteristic for all hominoids. A more comprehensive evaluation of the dietary ecology of Rusinga's catarrhine primates would help to better evaluate variation and possible differences in their diets, including the possibility of niche separation.

8. Conclusions

The aim of this study was to assess paleoenvironments on Rusinga Island during the Early Miocene based on stable isotope data from fossil mammals and to compare those data with earlier paleoenvironmental reconstructions and more recent geological and paleontological observations. Many previous paleoenvironmental studies on Rusinga interpreted seeming stability of the taxonomic composition of mammalian assemblages as an indication of long-term uniformity of environments (e.g., Pickford, 1981, 1986a; Andrews et al., 1997; Peppe et al., 2009). However, recent studies have indicated that more geological complexity is present than previously recognized and shown evidence for spatial and temporal paleoenvironmental variability including both open, drier woodland habitats and a dense closed-canopy forest (Maxbauer et al., 2013; Michel et al., 2014, 2020; Baumgartner and Peppe, 2021; Peppe et al., 2023).

The carbon isotope composition of the Rusinga Group mammalian fauna suggests a high degree of spatial variability in both the Kulu and Hiwegi Formation habitats throughout the Early Miocene succession on Rusinga. The range of C_3 foods actively exploited by the mammals in this study included a significant number of plants experiencing light- and/or water-stress and do not preclude consumption of small fractions of C_4 grasses, the presence of which are indicated by other lines of isotopic evidence and the composition of phytolith assemblages (Peppe et al., 2023). Evidence for exploitation of plant resources from closed-canopy forests experiencing CO_2 recycling was rare, however. Finally, the oxygen isotope composition of the Rusinga Group mammals documents either changes through time in some combination of climatic factors such as an increase in mean annual temperature, an increase in aridity, a decrease in mean annual precipitation in the Kulu Formation relative to the Hiwegi Formation or a change in the source of air masses and moisture delivered to the region, which would imply larger scale reorganization of climate beyond eastern Africa.

CRediT authorship contribution statement

David L. Fox: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation,

Funding acquisition, Data curation, Conceptualization. **Nicole D. Garret:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Daniel J. Peppe:** Writing – review & editing, Investigation, Funding acquisition. **Lauren A. Michel:** Writing – review & editing, Investigation. **Kirsten Jenkins:** Investigation, Writing – review & editing, Conceptualization. **Thomas Lehmann:** Writing – review & editing, Investigation, Data curation. **Kieran P. McNulty:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to the curators and staff at the National Museums of Kenya for their care and management of the fossil collections, and thank especially Fredrick Manthi, Emma Mbua, and Tom Mukhuyu for their assistance with this research. We are grateful to Holly Dunswoth and Will Harcourt-Smith for their efforts in establishing and maintaining field research on Rusinga, and for their encouragement and support of this project. We thank Susanne Cote for her generous assistance with faunal identifications over the years, and specifically for help with a handful of difficult specimens in this study. We are grateful to Irisa Arney and Maire Malone, who helped sample some of the specimens analyzed here. The manuscript was improved by the comments of two anonymous reviewers. The Rusinga project was conducted with permission from the Kenyan government, under research permits issued to N.D. G. (NACOSTI/P/14/2987/698), D.J.P. (NCST/RCD/12B/012/07), L.A. M. (NACOSTI/P/18/73655/17421, T.L. (NCST/RRI/12/1/BS011/15, NACOSTI/P/15/4710/4716), and K.P.M. (e.g., NACOSTI/P/15/9092/4745, NACOSTI/P/18/9092/23264). Exploration/excavation licenses (e.g., NMK/GVT/2) were granted by the Ministry of Sports and Heritage. Sample powders were exported by permit from the Kenyan government. This study was funded by grants from the Leakey Foundation, and National Science Foundation (BCS 0852609, BCS 1241807, BCS 1241812), and is publication no. 18 in support of Research of East African Catarrhine and Hominoid Evolution (REACHE).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2025.113248>.

Data availability

I have shared the data file at the Attach File step.

References

- Ambrose, S.H., DeNiro, M.J., 1986. The isotopic ecology of East African mammals. *Oecologia* 69, 395–406.
- Andrews, P., 1992. Community evolution in forest habitats. *J. Hum. Evol.* 22, 423–438.
- Andrews, P., Kelley, J., 2007. Middle Miocene dispersals of apes. *Folia Primatol.* 78, 328–343.
- Andrews, P., Van Couvering, J.A.H., 1975. Paleoenvironments in the East African Miocene. In: Szalay, F. (Ed.), *Approaches to Primate Paleobiology*. Kargel, Basel, pp. 62–103.
- Andrews, P., Lord, J., Nesbit Evans, E.M., 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol. J. Linn. Soc.* 11, 177–205.
- Andrews, P., Begun, D., Zylstra, M., 1997. Interrelationships between functional morphology and paleoenvironments in Miocene hominoids. In: Begun, D., Ward, C., Rose, M. (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, pp. 29–58.
- Anquetin, J., Antoine, P.-O., Tassy, P., 2007. Middle Miocene Chalicotheriinae (Mammalia, Perissodactyla) from France, with a discussion on chalicotherine phylogeny. *Zool. J. Linnean Soc.* 151, 577–608.
- Ayliffe, L.K., Lister, A.M., Chivas, A.R., 1992. The preservation of glacial-interglacial climatic signatures in the oxygen isotopes of elephant skeletal phosphate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 99, 179–191.
- Bacon, A.M., 2001. La Locomotion des Primates du Miocene d'Afrique et d'Europe. Analyse Fonctionnelle des os Longs du Membre Pelvien et Systematique, CNRS, Paris.
- Baumgartner, A., Peppe, D.J., 2021. Paleoenvironmental changes in the Hiwegi Formation (lower Miocene) of Rusinga Island, Lake Victoria, Kenya. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 574, 110458.
- Begun, D.R., 2007. Fossil record of Miocene hominoids. In: Henke, W., Tattersall, I. (Eds.), *Handbook of Palaeoanthropology*, Primate Evolution and Human Origins, vol. 2. Springer, Berlin, pp. 921–977.
- Begun, D.R., Teaford, M.F., Walker, A., 1994. Comparative and functional anatomy of *Proconsul* phalanges from the Kaswanga Primate Site, Rusinga Island, Kenya. *J. Hum. Evol.* 26, 89–165.
- Bestland, E.A., 1990. Miocene Volcaniclastic Deposits and Paleosols of Rusinga Island, Kenya. Ph.D. Dissertation, University of Oregon.
- Bestland, E.A., 1991. A Miocene Gilbert-type fan-delta from a volcanically influenced lacustrine basin, Rusinga Island, Lake Victoria, Kenya. *J. Geol. Soc. Lond.* 1067–1078.
- Bestland, E.A., Krull, E.S., 1999. Palaeoenvironments of Early Miocene Kisingiri volcano *Proconsul* sites: evidence from carbon isotopes, paleosols, and hydromagmatic deposits. *J. Geol. Soc. Lond.* 156, 965–976.
- Bestland, E.A., Retallack, G.J., 1993. Volcanically influenced calcareous paleosols from the Miocene Kihiera Formation, Rusinga Island, Kenya. *J. Geol. Soc. Lond.* 150, 293–310.
- Bestland, E.A., Thackray, G.D., Retallack, G.J., 1995. Cycles of doming and eruption of the Miocene Kisingiri volcano, southwest Kenya. *J. Geol.* 103, 598–607.
- Bishop, W.W., Miller, J.A., Fitch, F.J., 1969. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *Am. J. Sci.* 267, 669–699.
- Boisserie, J.-R., Zazzo, A., Merceron, G., Blondel, C., Vignaud, P., Likius, A., Mackaye, H.T., Brunet, M., 2005. Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 221, 153–174.
- Bonafini, M., Pellegrini, M., Ditchfield, P., Pollard, A.M., 2013. Investigation of the ‘canopy effect’ in the isotope ecology of temperate woodlands. *J. Archaeol. Sci.* 40, 3926–3935.
- Bryant, J.D., Froehlich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. *Geochim. Cosmochim. Acta* 59, 4523–4537.
- Bryant, J.D., Froehlich, P.N., Showers, W.J., Genna, B.J., 1996. Biologic and climatic signals in the oxygen isotopic composition of Eocene-Oligocene equid enamel phosphate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 126, 75–89.
- Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120, 347–363.
- Cerling, T.E., Harris, J.M., Leakey, M.G., 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Oecologia* 120, 364–374.
- Cerling, T.E., Harris, J.M., Passey, B.H., 2003. Diets of East African Bovidae based on stable isotope analysis. *J. Mammal.* 82, 456–470.
- Cerling, T.E., Hart, J.A., Hart, T.B., 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* 138, 5–12.
- Cerling, T.E., Harris, J.M., Leakey, M.G., 2005. Environmentally driven dietary adaptations in African mammals. In: Ehleringer, J.R., Dearing, R.D., Cerling, T.E. (Eds.), *History of Atmospheric CO₂ and its Effects on Plants, Animals, and Ecosystems*. Springer-Verlag, New York, pp. 258–272.
- Cerling, T.E., Wynn, J.G., Andanje, S.A., Bird, M.E., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remini, C.H., 2011. Woody cover and hominin environments in the past 6 million years. *Nature* 476, 51–56.
- Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., Harris, J.M., Hart, J.A., Kirera, F.M., Kaleme, P., Leakey, L.N., Leakey, M.G., Levin, N.E., Manthi, F.K., Passey, B.H., Uno, K.T., 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *Proc. Natl. Acad. Sci. USA* 112, 11467–11472. [www.pnas.org/cgi/doi/10.1073/pnas.1513075112](https://doi.org/10.1073/pnas.1513075112).
- Černánský, A., Herrel, A., Kibibi, J.M., Anderson, C.V., Boistel, R., Lehmann, T., 2020. The only complete articulated early Miocene chameleon skull (Rusinga Island, Kenya) suggests an African origin for Madagascar's endemic chameleons. *Sci. Rep.* 10, 109. <https://doi.org/10.1038/s41598-019-57014-5>.
- Chesters, K.I.M., 1957. The Miocene flora of Rusinga Island, Lake Victoria, Kenya. *Palaeontographica* 101, 30–67.
- Chikaraishi, Y., Naraoka, H., 2003. Compound-specific δD and δ¹³C analyses of n-alkanes extracted from terrestrial and aquatic plants. *Phytochemistry* 63, 361–371.
- Christin, P.-A., Osborne, C.P., 2014. The evolutionary ecology of C₄ plants. *New Phytol.* 204, 765–781.
- Christin, P.-A., Besnard, G., Samaritani, E., Duvall, M.R., Hodkinson, T.R., Savolainen, V., Salamin, N., 2008. Oligocene CO₂ decline promoted C₄ photosynthesis in grasses. *Curr. Biol.* 18, 37–43.
- Clementz, M.T., Holroyd, P.A., Koch, P.L., 2008. Identifying aquatic habits of herbivorous mammals through stable isotope analysis. *Palaeos* 23, 574–585.
- Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D., Sealy, J., Grant, R., Fourie, N., 2007. Diets of savanna ungulates from stable carbon isotope composition of faeces. *J. Zool.* 273, 21–29.

- Codron, J., Condron, D., Sponheimer, M., Kirkman, K., Duffy, K.J., Raubenheimer, E.J., Mélice, J.-L., Grant, R., Clauss, M., Lee-Thorp, J.A., 2012. Stable isotope series from elephant ivory reveal lifetime histories of a true dietary generalist. *Proc. R. Soc. B* 279, 2433–2441.
- Collinson, M., Andrews, P., Bamford, M.K., 2009. Taphonomy of early Miocene flora, Hiwegi Formation, Rusinga Island, Kenya. *J. Hum. Evol.* 57, 149–162.
- Conrad, J.L., Jenkins, K., Lehmann, T., Manthi, F.K., Peppe, D.J., Nightingale, S., Cossette, A., Dunswoth, H.M., Harcourt-Smith, W.E.H., McNulty, K.P., 2013. New specimens of '*Crocodylus*' *pigotti* (*Crocodylidae*) from Rusinga Island, Kenya, and generic reallocation of the species. *J. Vertebr. Paleontol.* 33, 629–646.
- Coombs, M.C., 1983. Large mammalian clawed herbivores: a comparative study. *Trans. Am. Philos. Soc.* 73, 1–96.
- Coombs, M.C., Cote, S.M., 2010. Chalicotheriidae. In: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 659–668.
- Couvreur, T.L., Dauby, G., Blach-Ovgaard, A., Deblauwe, V., Dessein, S., Droissart, V., Hardy, O.J., Harris, D.J., Janssens, S.B., Ley, A.C., Mackinder, B.A., 2021. Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna. *Biol. Rev.* 96, 16–51.
- Daver, G., Nakatsukasa, M., 2015. *Proconsul heseloni* distal radial and ulnar epiphyses from the Kaswanga Primate Site, Rusinga Island, Kenya. *J. Hum. Evol.* 80, 17–33.
- DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* 42, 495–506.
- Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, M., 2000. Atlas Peri-Tethys, *Palaeogeographical maps*. In: CGGM/CWM Paris: 24 maps and explanatory notes: I–XX, pp. 2–269.
- Diefendorf, A.F., Mueller, K.E., Wing, S.L., Koch, P.L., Freeman, K.H., 2010. Global patterns in leaf ^{13}C discrimination and implications for studies of past and future climate. *Proc. Natl. Acad. Sci. USA* 107, 5738–5743.
- Drake, R.E., Van Couvering, J.A., Pickford, M.H., Curtis, G.H., Harris, J.A., 1988. New chronology for the early Miocene mammalian faunas of Kisingiri, Western Kenya. *J. Geol. Soc. Lond.* 145, 479–491.
- Drucker, D.G., Bridault, A., Hobson, K.A., Szuma, E., Bocherens, H., 2008. Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 266, 69–82.
- Dunswoth, H.M., 2006. Proconsul Heseloni Feet from Rusinga Island Kenya. Ph.D. Dissertation. Pennsylvania State University.
- Edwards, E.J., Osborne, C.P., Stromberg, C.A.E., Smith, S.A., Bond, W.J., Christin, P.-A., Cousins, A.B., Duvall, M.R., Fox, D.L., Freckleton, R.P., Ghannoum, O., Hartwell, J., Huang, Y., Janis, C.M., Keeley, J.E., Kellogg, E.A., Knapp, A.K., Leakey, A.D.B., Nelson, D.M., Saarela, J.M., Sage, R.F., Sala, O.E., Salamin, N., Still, C.J., Tipple, B., 2010. The origins of C_4 grasslands: integrating evolutionary and ecosystem science. *Science* 328, 587–591.
- Ehleringer, J.R., Cooper, T.A., 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76, 562–566.
- Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997. C_4 photosynthesis, atmospheric CO_2 , and climate. *Oecologia* 112, 285–299.
- Flower, B.P., Kennett, J.P., 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 108, 537–555.
- Forbes, M.S., Bestland, E.A., Krull, E.S., Dicker, D.G., 2004. Palaeoenvironmental mosaic of *Proconsul* habitats: geochemical and sedimentological interpretation of Kisingiri fossil sites, Western Kenya. *J. Afr. Earth Sci.* 39, 63–79.
- Foster, G.L., Royer, D.L., Lunt, D.J., 2017. Future climate forcing potentially without precedent in the last 420 million years. *Nat. Commun.* 8, 14845.
- Fox, D.L., Fisher, D.C., 2001. Stable isotope ecology of a late Miocene population of *Gomphotherium* (Mammalia, Proboscidea) from Port of Entry Pit, Oklahoma: diet, climate and diagenesis. *Palaearctos* 16, 279–293.
- Fox, D.L., Fisher, D.C., Vartanyan, S., Tikhonov, A.N., Mol, D., Buigues, B., 2007. Paleoclimatic implications of oxygen isotopic variation in late Pleistocene and Holocene tusks of *Mammuthus primigenius* from northern Eurasia. *Quat. Int.* 169–170, 154–165.
- Garrett, N.D., Fox, D.L., McNulty, K.P., Faith, J.T., Peppe, D.J., Van Plantinga, A., Tryon, C.A., 2015. Stable isotope paleoecology of late Pleistocene Middle Stone Age humans from the Lake Victoria Basin, Kenya. *J. Hum. Evol.* 82, 1–14.
- Geraads, D., 2010. Rhinocerotidae. In: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 669–684.
- Geraads, D., Lehmann, T., Peppe, D.J., McNulty, K.P., 2016. New Rhinocerotidae from the Kisingiri localities (lower Miocene of Western Kenya). *J. Vertebr. Paleontol.* 36, e1103247.
- Golonka, J., 2004. Plate tectonic evolution of the southern margin of Eurasia in the Mesozoic and Cenozoic. *Tectonophysics* 381, 235–273.
- Hall, A.S., Jenkins, K.E.H., Lehmann, T., Michel, L.A., Muteti, S.N., Peppe, D.J., McNulty, K.P., 2025. The ecological context of early hominoid evolution: evidence from the Early Miocene mammalian assemblages of the Kihiera Formation, Rusinga Island, Kenya. *Am. J. Biol. Anthropol.* 186, 66–66.
- Harris, J.M., 1978. Deinotherioidea and Barytherioidea. In: Maglio, V.J., Cooke, H.B.S. (Eds.), *Evolution of African Mammals*. Harvard University Press, Cambridge, pp. 315–332.
- Harris, J., Van Couvering, J., 1995. Mock aridity and the paleoecology of volcanically influenced ecosystems. *Geology* 23, 593–596.
- Hayes, J.M., 1993. Factors controlling ^{13}C contents of sedimentary organic compounds: principles and evidence. *Mar. Geol.* 113, 111–125.
- Herbert, T.D., Dalton, C.A., Liu, Z., Salazar, A., Si, W., Wilson, D.S., 2022. Tectonic degassing drive global temperature trends since 20 Ma. *Science* 377, 116–119.
- Hönisch, B., The CenCO2PIP Consortium, 2023. Toward a Cenozoic history of atmospheric CO₂. *Science* 382, eadis15177. <https://doi.org/10.1126/science.adis15177>.
- Hopley, P.J., Cerling, T.E., Crété, L., Werdelin, L., Mwebi, O., Manthi, F.K., Leakey, L.N., 2023. Stable isotope analysis of carnivores from the Turkana Basin, Kenya: evidence for temporally-mixed fossil assemblages. *Quat. Int.* 650, 12–27.
- Jacobs, B.F., Pan, A.D., Scotese, C.R., Werdelin, L., Sanders, W.J., 2010. A review of the Cenozoic vegetation history of Africa. In: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 57–72.
- Jenkins, F.A., 1973. The functional anatomy and evolution of the mammalian humero-ulnar articulation. *Am. J. Anat.* 137, 281–297.
- Jenkins, K., 2018. Taphonomy on Rusinga Island, Kenya. Ph.D. Dissertation. University of Minnesota, retrieved from the University Digital Conservancy. <https://hdl.handle.net/11299/201179>.
- Kappelman, J., Rasmussen, D.T., Sanders, W.J., Feseha, M., Bown, T., Copeland, P., Crabaugh, J., Fleagle, J., Glantz, M., Gordon, A., Jacobs, B., Maga, M., Muldoon, K., Pan, A., Pyne, L., Richmond, B., Ryan, T., Seiffert, E.R., Sen, S., Todd, L., Wiemann, M.C., Winkler, A., 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. *Nature* 426, 549–552.
- Keeley, J.E., Sandquist, D.R., 1992. Carbon: freshwater plants. *Plant Cell Environ.* 15, 1021–1035.
- Kent, P.E., 1944. The Miocene beds of Kavirondo, Kenya. *Q. J. Geol. Soc.* 100, 85–118.
- Kingston, J.D., 2007. Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. *Yearb. Phys. Anthropol.* 50, 20–58.
- Kingston, J.D., Harrison, T., 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: implications for early hominin paleoecology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 243, 273–306.
- Koch, P.L., 1998. Isotopic reconstruction of past continental environments. *Annu. Rev. Earth Planet. Sci.* 26, 573–613.
- Koch, P.L., Fisher, D.C., Dettman, D., 1989. Oxygen isotope variation in the tusks of extinct proboscideans – a measure of season of death and seasonality. *Geology* 17, 515–519.
- Kohn, M.J., 1996. Predicting animal $\delta^{18}\text{O}$: accounting for diet and physiological adaptation. *Geochim. Cosmochim. Acta* 60, 4811–4829.
- Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C_3 plants as indicators of (paleo)ecology and (paleo)climate. *Proc. Natl. Acad. Sci. USA* 107, 19691–19695.
- Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochim. Cosmochim. Acta* 60, 3889–3896.
- Kohn, M., Schoeninger, M., Barker, W., 1999. Altered states: effects of diagenesis on fossil tooth chemistry. *Geochim. Cosmochim. Acta* 63, 2737–2747.
- Krigbaum, J., Berger, M.H., Daegling, D.J., McGraw, W.S., 2013. Stable isotope canopy effects for sympatric monkeys at Tai Forest, Côte d'Ivoire. *Biol. Lett.* 9, 1–5.
- Langdon, J., 1986. Functional morphology of the Miocene hominoid foot. *Contrib. Primatol.* 22, 1–225.
- Leakey, L.S.B., 1952. Lower Miocene invertebrates from Kenya. *Nature* 169, 624–625.
- LeBas, M.J., 1977. Carbonite-nepheline Volcanism. *J. Wiley and Sons*, London.
- Lee-Thorp, J.A., 2000. Preservation of biogenic carbon isotopic signals in Plio-Pleistocene bone and tooth mineral. In: Ambrose, S.H., Katzenberg, M.A. (Eds.), *Biogeochemical Approaches to Paleodietary Analysis*. Kluwer Academic/Plenum Publishers, New York, pp. 89–114.
- Lee-Thorp, J.A., Sponheimer, M., 2013. Hominin ecology from hard-tissue biogeochemistry. In: Sponheimer, M., Lee-Thorp, J.A., Reed, K.E., Ungar, P.S. (Eds.), *Early Hominin Paleooecology*. University Press of Colorado, Boulder, pp. 281–324.
- Lee-Thorp, J.A., Sealey, J.C., de la Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *J. Archaeol. Sci.* 16, 585–599.
- LeGeros, R.Z., 1991. *Calcium Phosphates in Oral Biology and Medicine*. Karger Publishers, Paris.
- Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. *Proc. Natl. Acad. Sci. USA* 103, 11201–11205.
- Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? *Geochim. Cosmochim. Acta* 48, 385–390.
- Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites. IV. Mammal teeth and bones. *Earth Planet. Sci. Lett.* 75, 29–36.
- Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. *Geochim. Cosmochim. Acta* 48, 1689–1693.
- Macgregor, D., 2015. History of the development of the East African Rift System: a series of interpreted maps through time. *J. Afr. Earth Sci.* 101, 232–252.
- MacLatchy, L.M., Cote, S.M., Deino, A.L., Kitto, R.M., Mugume, A.A.T., Rossie, J.B., Sanders, W.J., Cosman, M.N., Driesse, S.G., Fox, D.L., Freeman, A.J., Jansma, R.J.W., Jenkins, K.E.H., Kinyanjui, R.N., Lukens, W.E., McNulty, K.P., Novello, A., Peppe, D.J., Stromberg, C.A.E., Uno, K.T., Winkler, A.J., Kingston, J.D., 2023. The evolution of hominoid locomotor versatility: evidence from Moroto, a 21 Ma site in Uganda. *Science* 380. <https://doi.org/10.1126/science.abq2835>.
- Maxbauer, D.P., Peppe, D.J., Bamford, M., McNulty, K.P., Harcourt-Smith, W.E.H., Davis, L.E., 2013. A morphotype catalog and paleoenvironmental interpretations of early Miocene fossil leaves from the Hiwegi Formation, Rusinga Island, Lake Victoria, Kenya. *Palaeontol. Electron.* 16, 16.3.28A.
- McCall, G.J.H., 1958. Geology of the Gwasi Area. Geological Survey of Kenya Report 45. In: Ministry of Commerce and Industry, Geological Survey of Kenya, Government Printer, Nairobi.

- McCollum, M.S., Peppe, D.J., McNulty, K.P., Dunsworth, H.M., Harcourt-Smith, W.E.H., Andrews, A.L., 2013. Magnetostratigraphy of the early Miocene Hiwegi Formation (Rusinga Island, Lake Victoria, Kenya). *Geol. Soc. Am. Abstr. Programs* 45, 12.
- McNulty, K.P., 2010. Apes and Tricksters: the Evolution and diversification of Humans' Closest Relatives. *Evol. Educ. Outreach* 3, 322–332.
- McNulty, K.P., Begun, D.R., Kelley, J., Manthi, F.K., Mbua, E., 2015. A systematic revision of *Proconsul* with the description of a new genus of early Miocene hominoid. *J. Hum. Evol.* 84, 42–61.
- Michel, L.A., Peppe, D.J., Lutz, J.A., Driese, S.G., Dunsworth, H.M., Harcourt-Smith, W.E.H., Horner, W.H., Lehmann, T., Nightingale, S., McNulty, K.P., 2014. Remnants of an ancient forest provide ecological context for Early Miocene fossil apes. *Nature Comm.* 5, 3236.
- Michel, L.A., Lehmann, T., McNulty K.P., Driese, S.G., Dunsworth, H. Fox, D.L., Harcourt-Smith, W.E.H., Jenkins, K., and Peppe, D.J., 2020. Sedimentological and Palaeoenvironmental Study from Waregi Hill in the Hiwegi Formation (Early Miocene) on Rusinga Island, Lake Victoria, Kenya. *Sedimentology*.
- Michel, L.A., Peppe, D.J., Cheng, K.D., Summers, H., Leimer, H.H., Lehmann, T., Muteti, S., McNulty, K.P., 2023. Stratigraphic revision of the early Miocene Kihera Formation from Rusinga Island, Lake Victoria, Kenya. *J. Afr. Earth Sci.* 200, 104877.
- Michon, L., Famin, V., Quidelleur, X., 2022. Evolution of the East African Rift System from trap-scale to plate-scale rifting. *Earth Sci. Rev.* 231, 104089.
- Nesbit Evans, E.M., Van Couvering, J.A.H., Andrews, P., 1981. Palaeoecology of Miocene sites in Western Kenya. *J. Hum. Evol.* 10, 99–116.
- O'Leary, M.H., 1981. Carbon isotope fractionation in plants. *Phytochemistry* 20, 553–567.
- Passey, B.H., Cerling, T.E., Perkins, M.E., Voorhies, M.R., Harris, J.M., Tucker, S.T., 2002. Environmental change in the Great Plains: an isotopic record from fossil horses. *J. Geol.* 110, 123–140.
- Peppe, D.J., McNulty, K.P., Cote, S.M., Harcourt-Smith, W.E.H., Dunsworth, H.M., Van Couvering, J.A., 2009. Stratigraphic interpretation of the Kulu Formation (early Miocene, Rusinga Island, Kenya) and its implications for primate evolution. *J. Hum. Evol.* 56, 447–461.
- Peppe, D.J., Deino, A.L., McNulty, K.P., Lehmann, T., Harcourt-Smith, W.E.H., Dunsworth, H.M., Fox, D.L., 2011. New age constraints on the early Miocene faunas from Rusinga and Mfangano Islands (Lake Victoria, Kenya). *Am. J. Phys. Anthropol.* 144, 237.
- Peppe, D.J., Cote, S.M., Deino, A.L., McNulty, K.P., McCollum, M.S., Mitchell, A.L., Driese, S.G., Dunsworth, H.M., Fox, D.L., Harcourt-Smith, W.E., Jenkins, K.E., Lehmann, T., Michel, L.A., 2017. Revised Geochronology of the Early Miocene Faunas from Rusinga Island and Mfangano Island (Lake Victoria, Kenya). In: Implications for Miocene Hominoid Evolution and Faunal Succession. American Association of Physical Anthropologists, Conference Program, p. 313.
- Peppe, D.J., Cote, S.M., Deino, A.L., Fox, D.L., Kingston, J.D., Kinyanjui, R.N., Lukens, W. E., MacLatchy, L.M., Novello, A., Strömborg, C.A.E., Driese, S.G., Garrett, N.D., Hillis, K.R., Jacobs, B.F., Jenkins, K.E.H., Kityo, R., Lehmann, T., Manthi, F.K., Mbua, E.N., Michel, L.A., Miller, E.R., Mugume, A.A.T., Muteti, S.N., Nengo, I.O., Oginga, K.O., Phelps, S.R., Polissar, P., Rossie, J.B., Stevens, N.J., Uno, K.T., McNulty, K.P., 2023. Oldest evidence of abundant C₄ grasses and habitat heterogeneity in eastern Africa. *Science* 280. <https://doi.org/10.1126/science.abq2834>.
- Pickford, M., 1981. Preliminary Miocene mammalian biostratigraphy for Western Kenya. *J. Hum. Evol.* 10, 73–97.
- Pickford, M., 1983. On the origins of Hippopotamidae together with descriptions of two new species, a new genus, and a new subfamily from the Miocene of Kenya. *Geobios* 16, 193–217.
- Pickford, M.H., 1984. Kenya Palaeontology Gazetteer, 1. National Museums of Kenya, Dept. of Sites and Monuments Documentation.
- Pickford, M., 1985. A new look at *Kenyapithecus* based on recent discoveries in western Kenya. *J. Hum. Evol.* 14, 113–144.
- Pickford, M., 1986a. Cainozoic palaeontological sites of western Kenya. *Münchener Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie* 8, 1–151.
- Pickford, M., 1986b. Sedimentation and fossil preservation in the Nyanza Rift system, Kenya. In: Frostick, L.D., Renaut, R.W., Reid, I., Tiercelin, J.J. (Eds.), *Sedimentation in the African Rifts*. Geological Society Special Publications, London, pp. 345–362.
- Rage, J.C., Gheerbrant, E., 2020. Island Africa and vertebrate evolution: a review of data and working hypotheses. In: Prasad, G.V.R., Patnaik, R. (Eds.), *Biological Consequences of Plate Tectonics: New Perspectives on Post-Gondwana Break-up—A Tribute to Ashok Sahni*. Springer, pp. 251–264.
- Rasmussen, D.T., Gutierrez, M., 2010. Hyracoidea. In: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 123–146. <https://doi.org/10.1525/california/9780520257214.003.0013>.
- Reinhard, E., de Torres, T., O'Neil, J., 1996. ¹⁸O/¹⁶O ratios of cave bear tooth enamel: a record of climate variability during the Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 126, 45–59.
- Retallack, G.J., 2002. Soils of the Past: An Introduction to Paleopedology, 2nd ed. Blackwell Science, London.
- Retallack, G., Bestland, E.A., Dugas, D.P., 1995. Miocene paleosols and habitats of *Proconsul* on Rusinga Island, Kenya. *J. Hum. Evol.* 29, 53–91.
- Rieppel, O., Walker, A., Odhiambo, I., 1992. A preliminary report on a fossil chamaeleoninae (Reptilia: Chamaeleoninae) skull from the Miocene of Kenya. *J. Herpetol.* 26, 77–80. <https://www.jstor.org/stable/1565027>.
- Rögl, F., 1997. Paleogeographic Considerations from Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Ann. des Naturhistorischen Museums Wien. Ser. A für Mineral.*
- Rögl, F., 1999. Circum-mediterranean Miocene paleogeography. In: Rössner, G., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Dr. Fritz Pfeil Verlag, Munich, pp. 39–48.
- Rose, M.D., 1988. Another look at the anthropoid elbow. *J. Hum. Evol.* 17, 193–224.
- Rose, M.D., 1992. Kinematics of the trapezium-1st metacarpal joint in extant anthropoids and Miocene hominoids. *J. Hum. Evol.* 22, 255–266.
- Rose, M.D., 1993. Locomotor anatomy of Miocene hominoids. In: Gebo, G.L. (Ed.), *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois University Press, DeKalb, pp. 252–272.
- Rose, M.D., 1994. Quadrupedalism in some Miocene catarrhines. *J. Hum. Evol.* 26, 387–411.
- Rozanski, K., Araguás-Araguás, L., Gonfiantini, R., 1993. Isotopic patterns in modern global precipitation. In: Swart, P.K., Lohmann, K.C., McKenzie, J.A., Savin, S.M. (Eds.), *Climate Change in Continental Isotopic Records*. Wiley Online Library, pp. 1–36. <https://doi.org/10.1029/GM078p0001>.
- Sage, R.F., 2004. The evolution of C₄ photosynthesis. *New Phytol.* 161, 341–370.
- Sage, R.F., Christin, P.-A., Edwards, E.K., 2011. The C₄ plant lineages of planet Earth. *J. Exp. Bot.* 62, 3155–3169.
- Sánchez Chillón, B., Alberdi, M.T., Leone, G., Bonadonna, F.P., Stenni, B., Longinell, A., 1994. Oxygen isotopic composition of fossil squid tooth and bone phosphate: an archive of difficult interpretation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 107, 317–328.
- Sanders, W.J., 2024. Evolution and Fossil Record of African Proboscidea. CRC Press, Boca Raton, FL, USA.
- Sanders, W.J., Gheerbrant, E., Harris, J.M., Saegusa, H., Delmer, C., 2010. Proboscidea. In: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 161–251.
- Sarmiento, E.E., 1988. Anatomy of the hominoid wrist joint: its evolutionary and functional implications. *Int. J. Primatol.* 9, 281–345.
- Schulz, E., Fahlke, J.M., Merceron, G., Kaiser, T., 2007. Feeding ecology of the Chalicotheriidae (Mammalia, Perissodactyla, Ancylopoda). Results from dental micro- and mesowear analyses. *Verhandlungen des naturwissenschaftlichen Vereins Hamburg* 45, 5–31.
- Schwartz, G.T., Rasmussen, D.T., Smith, R.J., 1995. Body-size diversity and community structure of fossil hyracoids. *J. Mammal.* 76, 1088–1099.
- Semprebon, G.M., Sise, P.J., Coombs, M.C., 2011. Potential bark and fruit browsing as revealed by stereomicrowear analysis of the peculiar clawed herbivores known as chalicotheres (Perissodactyla, Chalicotherioidea). *J. Mamm. Evol.* 18, 33–55.
- Sen, S., 2013. Dispersal of African mammals in Eurasia during the Cenozoic: Ways and whys. *GeoBios* 46, 159–172.
- Shackleton, R.M., 1951. A contribution to the geology of the Kavirondo Rift Valley. *Q. J. Geol. Soc. Lond.* 106, 345–392.
- Shoshani, J., Bloomer, P., Seiffert, E.R., 2013. Order Hyracoidea - Family Procaviidae. In: Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., Kalina, J. (Eds.), *Mammals of Africa, Introductory Chapters and Afrotheria*, vol. 1. Bloomsbury Publishing, London, pp. 148–151.
- Sponheimer, M., Lee-Thorp, J.A., 1999. Oxygen isotopes in enamel carbonate and their ecological significance. *J. Archaeol. Sci.* 26, 723–728.
- Stampfli, G.M., Borel, G.D., Marchant, R., Mosar, J., 2002. Western Alps geological constraints on western Tethyan reconstructions. *J. Virtual Explor.* 8, 77–106.
- Steinhorsdottir, M., et al., 2021. The Miocene: the future of the past. *Paleoceanogr. Paleoclimatol.* 36 e2020PA004037.
- Sternberg, L.S.L., 1989. Oxygen and hydrogen isotope ratios in plant cellulose: Mechanisms and applications. In: Rundel, P.W., Ehleringer, J.R., Nagy, K.A. (Eds.), *Stable Isotopes in Ecological Research: Ecological Studies: Analysis and Synthesis*. Springer-Verlag, New York, pp. 124–141.
- Sullivan, C.H., Krueger, H.W., 1981. Carbon isotope analysis of separate chemical phases in modern and fossil bone. *Nature* 292, 333–335.
- Thackray, G.D., 1994. Fossil nest of sweat bees (Halictinae) from a Miocene paleosol, Rusinga Island, Kenya. *J. Paleontol.* 68, 795–800.
- Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., Slade, N.A., 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for the ¹³C analysis of diet. *Oecologia* 57, 32–37.
- Tipple, B.J., Meyers, S.R., Pagani, M., 2010. Carbon isotope ratio of Cenozoic CO₂: a comparative evaluation of available geochemical proxies. *Paleoceanography* 25, PA3202.
- Ungar, P.S., Scott, J.R., Curran, S.C., Dunsworth, H.M., Harcourt-Smith, W.E.H., Lehmann, T., Manthi, F.K., McNulty, K.P., 2012. Early Neogene environments in East Africa: evidence from dental microwear of tragulids. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 342–343, 84–96.
- Van Couvering, J.A., 1972a. Geology of Rusinga Island and Correlation of the Kenya Mid-Tertiary Fauna. Ph.D. Dissertation. Cambridge University.
- Van Couvering, J.A.H., 1972b. Palaeontology and Comparative Osteology of some African Cichlid Fishes. Unpubl. Ph.D. thesis. Cambridge, England.
- Van Couvering, J.A., Miller, J.A., 1969. Miocene stratigraphy and age determinations, Rusinga Island, Kenya. *Nature* 221, 628–632.
- van der Merwe, N.J., Medina, E., 1991. The canopy effect, carbon isotope ratios, and foodwebs in Amazonia. *J. Archaeol. Sci.* 18, 249–259.
- Verdcourt, B., 1963. z. *Palaeontographica* 121A, pp. 1–37.
- Ventimini, A., Barber, J.C., Aliscioni, S.S., Giussani, L.M., Kellogg, E.A., 2008. The age of the grasses and clusters of origins of C-4 photosynthesis. *Glob. Chang. Biol.* 14, 2963–2977.
- Walker, A., Teaford, M.F., Andrews, M.P., 1993. A new species of *Proconsul* from the early Miocene Rusinga/Mfangano Islands, Kenya. *J. Hum. Evol.* 25, 43–56.

- Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 107, 281–289.
- Ward, C.V., 1993. Torso morphology and locomotion in *Proconsul nyanzae*. *Am. J. Phys. Anthropol.* 92, 291–328.
- Ward, C.V., 1997. Functional anatomy and phyletic implications of the hominoid trunk and hindlimb. In: Begun, D., Ward, C.V., Rose, M.D. (Eds.), *Miocene Hominoid Fossils: Functional and Phylogenetic Implications*. Plenum Press, New York, pp. 101–130.
- Ward, C.V., Walker, A., Teaford, M.F., 1991. *Proconsul* did not have a tail. *J. Hum. Evol.* 21, 215–220.
- Ward, C.V., Walker, A., Teaford, M.F., Odhiambo, I.N., 1993. Partial Skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. *Am. J. Phys. Anthropol.* 90, 77–111.
- Ward, C.V., Ruff, C.B., Walker, A., Teaford, M.F., Rose, M.D., Nengo, I.O., 1995. Functional morphology of *Proconsul* patellas from Rusinga Island, Kenya, with implications for other Miocene-Pliocene catarrhines. *J. Hum. Evol.* 29, 1–19.
- Ward, C.V., Leakey, M.G., Brown, B., Brown, F., Harris, J., Walker, A., 1999. South Turkwel: a new Pliocene hominid site in Kenya. *J. Hum. Evol.* 36, 69–95.
- Werdelin, L., Sanders, W.J., 2010. *Cenozoic Mammals of Africa*. University of California Press, Berkeley, California.
- Westerhold, T., et al., 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science* 369, 1383–1387. <https://doi.org/10.1126/science.aba6853>.
- White, F., 1983. *The Vegetation of Africa*, vol. 20. United Nations Scientific and Cultural Organization, Paris.
- Whitworth, T., 1953. A contribution to the geology of Rusinga Island, Kenya. *Q. J. Geol. Soc. Lond.* 109, 75–92.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.
- Zachos, J.C., Dickens, G.R., Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451, 279–283.