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Authors:

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## Introduction

Cercopithecoidea is a diverse and successful clade that comprises the majority of living catarrhine primate species (Disotell 1996). Cercopithecoids have a wide geographic distribution over most of the Old World, encompassing a wide latitudinal gradient, and are found in diverse habitats such as tropical and subtropical forests, woodlands, savanna, and grasslands (Jablonski and Frost 2010). By contrast, today, non-cercopithecoid catarrhines, represented by modern apes and humans, are relatively taxon poor (Fleagle 1999). This pattern contrasts with the Early Miocene when non-cercopithecoid catarrhines were more taxonomically diverse than cercopithecoids (Fleagle 1999; Jablonski and Frost 2010) even though the two groups apparently began diverging by the Late Oligocene (Stevens *et al.* 2013). Moreover, although cercopithecoids are clearly well established in Africa by the Early Miocene (Miller *et al.* 2009), they are usually rare elements in the mammalian community at that time (Jablonski and Frost 2010).

Catarrhine paleocommunities during the Early and Middle Miocene of Africa (Table I) occupied a large diversity of habitats and exploited many niches, some quite different from those of modern apes and monkeys (Leakey *et al.* 2011). Early and Middle Miocene monkeys are usually viewed as members of the modern Cercopithecidae (Jablonski and Frost 2010). Recent work (Miller *et al.* 2009) demonstrates increased diversity within the Victoriapithecidae (the sister family of modern Cercopithecidae). This diversity serves to highlight the complexity of evolutionary history within the Cercopithecoidea. Early to Middle Miocene non-cercopithecoid catarrhines are sometimes viewed as members of the Hominoidea (Michel *et al.* 2014), or stem-Hominoidea (Stevens *et al.* 2013). Yet, some authorities prefer to place them in a broader radiation that includes the Dendropithecoidea and Proconsuloidea (Harrison 2010) and exclude most from the Hominoidea. Nevertheless, a broad division exists between cercopithecoid monkeys and the non-cercopithecoid catarrhines. Yet, despite their abundance in Africa during the Early Miocene, we cannot predict when apes and monkeys will be found together at a site, or when only one group is more likely to be present.

It is well recognized that community composition is often allied with environmental conditions, so that communities in localities with different habitats, e.g. forests vs. woodlands vs. deserts, will differ in taxonomic composition, species richness, and

Table I African catarrhine paleocommunities used in this study: Age, geographic location, and habitat reconstructions

Site (coordinates)	Age (Ma)	Non- cercopithecoid catarrhines	Cercopithecoidea	Habitat
<b>Early Miocene</b>				
<b>Eastern Uganda</b>				
Moroto (2°31'30.0" N, 34°46'21.0" E) <a href="http://en.wikipedia.org/wiki/Mount_Moroto#cite_note-2">http://en.wikipedia.org/wiki/Mount_Moroto#cite_note-2</a>	Aquitanian (20.6) (Gebo <i>et al.</i> 1997; cf. Pickford and Mein 2006 for an alternative view)	<i>Afropithecus turkanensis;</i> <i>Kogolepithecus morotoensis;</i> <i>Micropithecus</i> sp.	Cercopithecoidea indet	Thick woodland with grassy spaces
Napak (34°14' E; 02°05' N) (Bishop 1967)	Early Burdigalian (18.5–20) (Pickford <i>et al.</i> 2010)	<i>Proconsul major</i> <i>Proconsul africanus</i> <i>Dendropithecus macinnesi</i> <i>Limnopithecus legetet</i> <i>Micropithecus clarki</i> <i>Lomorupithecus harrisoni</i>	Cercopithecoidea indet	Forest – some grassy and more open areas may be present
<b>Tinderet Sequence – Western Kenya (Lake Victoria)</b>				
Koru 35°16' E; 00°09' S (Bishop 1967)	Early Burdigalian (19–20) (Bishop <i>et al.</i> 1969)	<i>Proconsul major</i> <i>Proconsul africanus</i> <i>Dendropithecus macinnesi</i> <i>Limnopithecus legetet</i> <i>Kalepithecus songhorensis</i> <i>Micropithecus clarki</i>	—	Forest
Songhor 35°13' E; 00°02' S (Bishop 1967)	19–20; Early Burdigalian (Bishop <i>et al.</i> 1969)	<i>Proconsul major</i> <i>Dendropithecus macinnesi</i> <i>Rangwapithecus gordoni</i> <i>Limnopithecus evansi</i> <i>Kalepithecus songhorensis</i>	—	Montane rain forest – may have some grassy more open areas present
<b>Kisingiri Volcano – Western Kenya (Lake Victoria)</b>				
Rusinga – Hiwigi 00°02' S; 35°13' E (Bishop 1967)	Early Burdigalian (≥18 Ma) (Peppe <i>et al.</i> 2011)	<i>Proconsul heseloni</i> <i>Proconsul nyanzae</i> <i>Dendropithecus macinnesi</i>	—	Numerous localities but forest conditions at least in some – evidence for more open conditions

Table I (continued)

Site (coordinates)	Age (Ma)	Non- cercopithecoid catarrhines	Cercopithecoid catarrhines	Habitat
Rusinga - Kulu 00°02 S; 35°13 E (Bishop 1967)	Late Burdigalian (15–17) (Peppe et al. 2009)	<i>Limnopithecus legetet</i> <i>Nyanzapithecus vancouveringorum</i> <i>Proconsul heseloni</i> <i>Proconsulnyanzae</i> <i>Dendropithecus macinnesi</i>	—	Lake and a forest – perhaps drier and more open than Hiwegi
<b>Turkana Region</b>				
Loperot (2°20' 0 N; 35°51' 0 E)	Early Burdigalian (ca. 19 Ma) (this article)	<i>Limnopithecus legetet</i> <i>Rangwapithecus gordoni</i>	<i>Noropithecus</i> sp. nov.	Large river, some evidence of forest and dense woodland, evidence of grass as well perhaps suggesting some open spaces
Kalodirr (3°20' N, 35°45' E) (Boschetto 1988)	Late Burdigalian (16.8–17.5 ± 0.3 Ma) (Boschetto 1988)	<i>Afropithecus turkanensis</i> <i>Turkanapithecus kalakolensis</i> <i>Simiolius enjessi</i>	—	Tropical woodland, seasonal, meandering streams
Moruorot (3°17' N, 35°50' E) (Boschetto 1988)	Late Burdigalian (16.8–17.5 ± 0.3 Ma) (Boschetto 1988)	<i>Afropithecus turkanensis</i> <i>Turkanapithecus kalakolensis</i> <i>Simiolius enjessi</i>	—	Tropical woodland, seasonal, meandering streams
Buluk (4°16' N, 36°36' E) (Harris and Watkins 1974)	Late Burdigalian (>17.2) (McDougal and Watkins 1985)	<i>Afropithecus turkanensis</i> <i>Simiolius enjessi</i>	<i>Noropithecus bulukensis</i> cf. <i>N. fleaglei</i>	Deciduous forest –Tropical woodland, seasonal, fluvial
<b>North Africa</b>				
Wadi Moghara, Egypt (38°20' N, 28°30' E) (Approximated from Figure 1.1 in Hasan 2013)	Late Burdigalian (17–18) (Miller 1999)	—	<i>Prohylobates tandyi</i> Gen. indet. <i>mogharensis</i>	Coastal fluvial, estuarine, lagoonal, low-lying swamps
Jebel Zelten, Libya (28°00' N, 20°30' E) (Approximate location of Wadi Shatirat	Early and Middle Miocene in at least three distinct horizons (Wessels et al. 2003)	—	<i>Zaltanpithecus simonsi</i>	Coastal fluvial, estuarine, lagoonal, low-lying swamps

Table I (continued)

Site (coordinates)	Age (Ma)	Non- cercopithecoïd catarrhines	Cercopithecoïd catarrhines	Habitat
in map of Wessels 2003)				
Middle Miocene				
Western Kenya – Lake Victoria				
Maboko Island (00°10' S; 34°36' 30" E) (Bishop 1967)	Langhian (ca. 15 Ma) (Retallack <i>et al.</i> 2002)	<i>Equatorius africanus</i> <i>Mabokopithecus clarki</i> <i>Nyanzapithecus pickfordi</i> <i>Micropithecus leakeyorum</i> <i>Limnopithecus evansi</i>	<i>Victoriapithecus macinnesi</i>	Riparian woodland, nyika bushland, seasonally wet wooded grassland
Fort Ternan (00°13' S; 35°21' E) (Bishop 1967)	Late Langhian or earliest Serravalian (13.7 ± 0.3– 13.8 ± 0.3) (Pickford <i>et al.</i> 2006)	<i>Kenyapithecus wickeri</i> <i>Simiolus</i> sp. <i>Proconsul</i> sp.	—	Closed to open woodland with possible grasslands

References for taxonomy: Cote 2008; Drake *et al.* 1988; Harrison 2010; Leakey *et al.* 2011; Michel *et al.* 2014; Miller *et al.* 2009; Patel and Grossman 2006; Peppe *et al.* 2009; Pickford 2002; as well as personal observation.

References for habitat reconstructions: Andrews 1992, 1996; Andrews and Van Couvering 1975; Andrews and Walker 1976; Andrews *et al.* 1979, 1981, 1997; Behrensmeyer *et al.* 2002; Cerling *et al.* 1991, 1992, 1997; Cote 2008; Gentry 1970; Grossman 2008; Hill *et al.* 2013; Kappelman 1991; Kortlandt 1983; Leakey *et al.* 2011; Madden 1972; Miller 1999; Michel *et al.* 2014; Miller and Wood 2010; Nesbit Evans *et al.* 1981; Peppe *et al.* 2009; Pickford 1981, 1983, 1987, 1995; Pickford and Andrews 1981; Pickford and Mein 2006; Pickford *et al.* 2003; Retallack 1991, 1992a,b; Retallack *et al.* 2002; Shipman 1986; Shipman *et al.* 1981; Ungar *et al.* 2012; Van Couvering and Van Couvering 1976; Van Damme and Gautier 1972.

abundance (Grossman 2008; Kamilar and Beaudrot 2013; Reed 1997). However, recognizing subtle environmental differences among fossil sites is often difficult or unreliable because of factors such as taphonomic biases, lack of abiotic context (geology, sedimentology, etc.) or incomplete samples. Nevertheless, we can test whether other factors, namely temporal differences and geographic distance, significantly affect similarities and differences in the taxonomic composition of the mammalian communities among our study sites. Simply stated, local habitats change over time through numerous local events combined with large-scale climatic and geologic events, all of which lead to effectively change community composition via extinction, speciation, migration, or immigration (Preston 1960). This means we can expect sites that are closest in age to have more similar community composition as long as they are in roughly similar habitats. Similarly, as geographical distance increases, the dispersal propensity of species lessens, possibly because of an increased chance of encountering geographic barriers or unsuitable habitat, which affects the similarity of community

composition (Beaudrot and Marshall 2011; Beaudrot *et al.* 2014; Kamilar 2009; Soininen *et al.* 2007). Thus, identifying the mammalian communities of Early and Middle Miocene catarrhine-bearing sites and comparing them across time and space will provide important information about the forces that shape the taxonomic composition of early catarrhine communities.

To address questions about the effects of geographic distance and temporal distance on community composition among Early and Middle Miocene sites we need a sample of sites from different locations over similar time spans. However, Early Miocene catarrhine-bearing sites are unevenly distributed in time and space. Catarrhine-bearing sites of appropriate age are limited to East Africa with a few also in North Africa (including the Arabian Peninsula). This is complicated further by the incompleteness of faunal records for some of the sites. However, one site that can contribute important information to our understanding is Loperot, in West Turkana, in Kenya (Grossman 2013). Our efforts have led to recovery of a number of mammalian taxa, some previously unknown at the site. Among the fossils found are remains of both cercopithecoid and non-cercopithecoid catarrhines. Unlike at most Early Miocene sites, cercopithecoid remains are much more abundant at Loperot than non-cercopithecoids. However, to include Loperot in a comparison among Early and Middle Miocene sites we must first determine its mammalian community and establish its age relative to that of other sites.

Thus, we aim to address the following questions:

- 1) What is the mammalian community, including the primates, of Loperot, and how does it compare with Early and Middle Miocene sites?
- 2) What is the age of the mammalian and primate community at Loperot as estimated from faunal comparisons with other Early and Middle Miocene sites?

Once the first two questions are answered we can use this information to address questions about factors affecting the degree of similarity among Early and Middle Miocene mammalian and primate communities in their taxonomic composition. More specifically we ask:

- 3) Do temporal distance and geographic distance affect the composition of the mammalian communities at catarrhine-bearing localities of the Early and Middle Miocene in Africa?

## Methods

### Description of the Loperot Site

The fossil-bearing site of Loperot ( $2^{\circ}20'0''$  North,  $35^{\circ}51'0''$  East) is located 90 km south of the Lothidok range at the headwaters of the Kalabata River, a tributary of the Keno River, which drains south–north to the southwestern shores of Lake Turkana (Fig. 1). This site is found within a larger area ( $2^{\circ}-2^{\circ}30'N$ ,  $35^{\circ}30'-36^{\circ}E$ ) with exposed Miocene rocks (Boschetto 1988; Boschetto *et al.* 1992; Joubert 1966). Previous

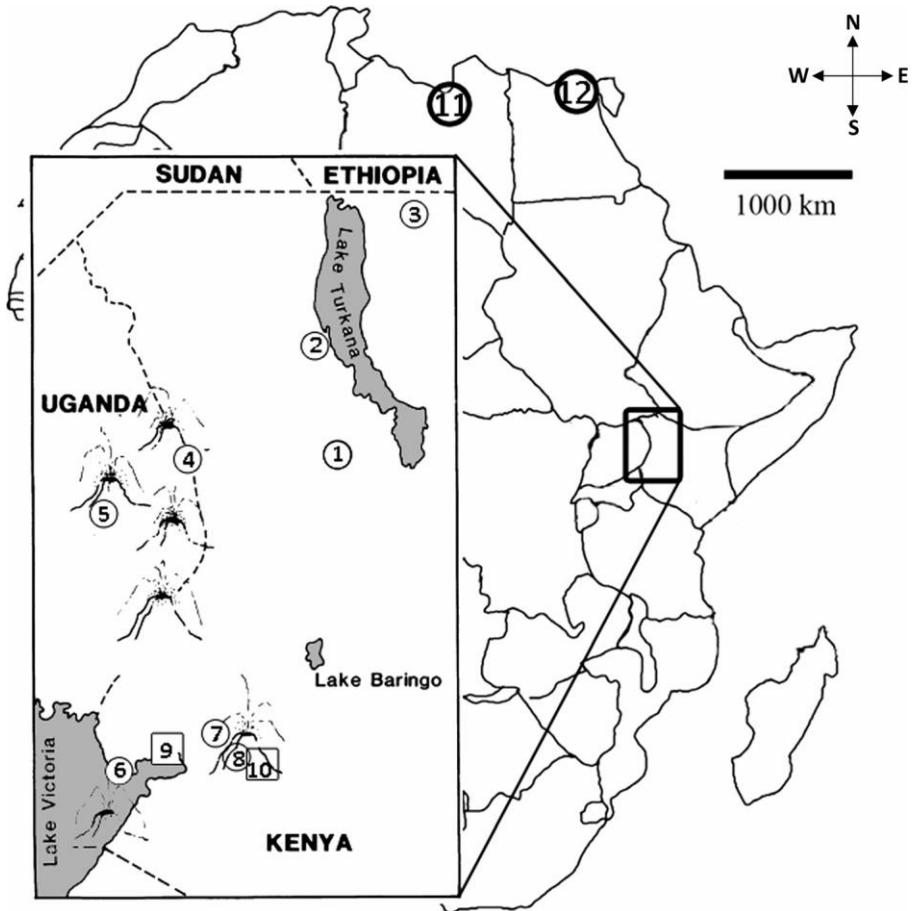


Fig. 1 Map of Africa showing the location of the sites used in this study. 1) Loperot; 2) Kalodirr and Moruorot; 3) Buluk 4) Moroto; 5) Napak; 6) Rusinga Island; 7) Songhor; 8) Koru; 9) Maboko; 10) Fort Ternan; 11) Wadi Moghra; 12) Gebel Zelten Circles = Early Miocene; Squares = Middle Miocene.

research at Loperot identified an Early or Middle Miocene fauna that included monkeys and perhaps apes as well as additional mammals (see Table II).

In June 2012, we conducted a research expedition to Loperot, identifying four localities (LpM1–LpM4) that yielded numerous vertebrate and invertebrate fossil remains.

#### Regional Geologic History of Loperot

*The Lokichar Basin* Loperot sits on the western side of modern-day Lake Turkana, a rift lake along the East African Rift System (EARS) situated between the Kenyan and Ethiopian domes (Feibel 2011; Morley *et al.* 1999a) (Fig. 2). As a result of Tertiary (as well as more recent) faulting, various different basins formed, including the Lokichar Basin, in which the site of Loperot sits (Feibel 2011). The Lokichar Basin is a north-south trending half graben that is ca. 60 km long by 30 km wide and is bound by an east-dipping border fault on the west (Morley *et al.* 1999b). The Lokichar Basin is

**Table II** Taxonomic list of the fauna found in the Early Miocene fossiliferous deposits at Loperot

Primates	indet
Victoripithecidae	Pliohyracidae
<i>Noropithecus</i> sp. nov.	cf. <i>Meroehyrax batae</i>
Proconsulidae	Perrisodactyla
<i>Rangwapithecus gordoni</i>	Rhinocerotidae
Family incertae sedis	<i>Chilotheridium pattersoni</i>
<i>Limnopithecus leteget</i> <sup>a</sup>	cf. <i>Brachypotherium</i> sp.
Rodentia	Artiodactyla
Thryonomyidae	Anthracotheriidae
<i>Paraphiomys stromeri</i>	<i>Brachyodus aequatorialis</i>
Diamantomyidae	<i>Afromeryx</i> cf. <i>zelteni</i> <sup>a</sup>
<i>Diamantomys leuderzi</i>	Tragulidae
Carnivora	<i>Dorcatherium pigotti</i>
Felidae	<i>Dorcatherium chappuisi</i>
Indet (small)	Giraffidae
Creodonta	cf. <i>Canthumeryx syrtensis</i>
Hyaenodontidae	Suidae
cf. <i>Hyainailouros</i>	cf. <i>Kenyasus rusingensis</i>
Indet (Medium-Small species)	Ziphidae
Proboscidea	indet
Deinotheriidae	
<i>Prodeinotherium hobleyi</i>	
Gomphotheriidae	
Indet	
<i>Platybelodon</i> sp. <sup>a</sup>	
cf. <i>Archaeobelodon</i>	
Hyracoidea	

<sup>a</sup>Taxa published previously but not seen by authors.  
Based on personal observations and the following references: Andrews 1978; Black 1978; Geraads 2010; Gingerich 2010; Guérin 2000; Harrison 1982, 2010; Hooijer 1971; Lavocat 1978; Maglio 1969; Mead 1975; Pickford 1991; Sanders et al. 2010; Savage and Williamson 1978; Simons and Delson 1978.

separated from the neighboring Kerio Basin by a topographic high of gneissic basement (the Lokone Horst) (Hendrie *et al.* 1994; Morley *et al.* 1999b). Sediment infill of the Lokichar Basin is on the order of 7 km and thickens to the west near the border fault (Feibel 2011; Morley *et al.* 1999b). Analysis of the basin sediments indicates Eocene through Late Miocene strata (Boschetto *et al.* 1992; Joubert 1966; Morley *et al.* 1999a).

*Stratigraphy* Basin-fill sediments below the Auwerwer Basalts were known previously as the Turkana Grits (Joubert 1966). These sediments are now subdivided into the Lokone and Auwerwer Formations (Morley *et al.* 1999b). The Lokone Formation (Paleogene–Early Miocene) consists of fluvio-deltaic, arkosic sandstones intercalated with two lacustrine shale units (the older Loperot Shale Member and the younger Lokone Shale Member) (Morley *et al.* 1999b). Fluvial and lacustrine environments are confirmed by the presence of crocodile, tortoise, oyster, and fish fossils within these sediments (Feibel 2011;

### Regional Map Of LpM Sites

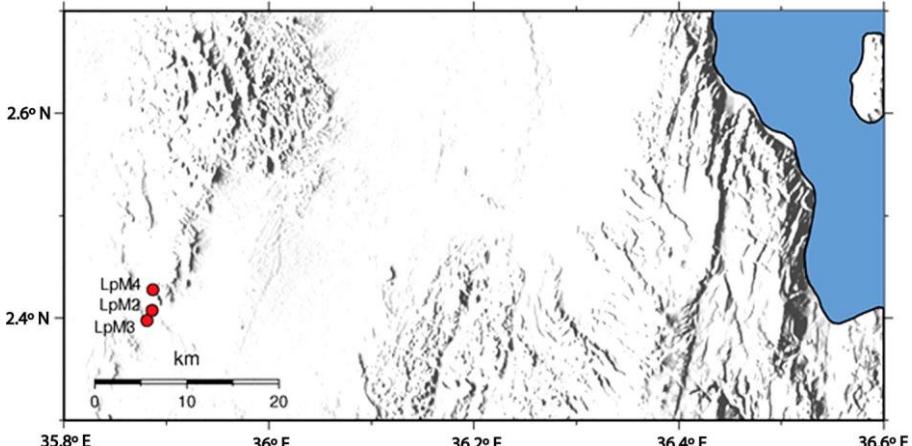


Fig. 2 Shaded relief map of the southwestern side of Lake Turkana and the location of three of the LpM sites visited in 2012. The sites sit to the west of the Lokone Horst (oblong topographic feature *ca.* 10 km to the east of the LpM sites that strikes NE-SW).

Joubert 1966). The Auwerwer Sandstone Formation (Middle Miocene) overlies the Lokone Member, and contains considerable volcaniclastic sediments including reworked tuffs (Morley *et al.* 1999b). The Auwerwer Basalt directly overlies the Awerwer Sandstone Formation. It is *ca.* 300 m thick and gives an age of 12.5–10.7 Ma (Morley *et al.* 1999b).

*Fossil-Bearing Sediments Near Loperot* Three primary sites (LpM2, LpM3, and LpM4) were identified as potential fossil localities during 2012 fieldwork (Fig. 2), with LpM4 being the most fossiliferous. At LpM4 we were able to find the location where M. Leakey and her team found monkey remains in the past.

*Sedimentology and Depositional Environments* A brief description of the sedimentology at each fossil locality is provided in Table III. The presence of aquatic species, such as crocodiles, fish, and various invertebrates, coupled with the cross-bedding, climbing ripples, and fining-up sequences of the fossil-bearing quartz-rich sand units at all three sites indicate fluvial deposition. Thin, fining-up sequences found at LpM4 suggest shallow, quick (braided) stream flow (with coarse bedload), at least at that site. Red to green silts/sands above and below the fossil-bearing layers represent paleosols, as noted by the ped structure, rhizoconcretions, abundant plant microfossils, and the presence of gypsum and gibbsite. Preliminary identification of pollen grains we found at site LpM4 indicates an abundance of grass (*unpublished data*). No lacustrine units (dark gray-black shales) were identified at any of the sites.

The sedimentology therefore indicates a fluvial depositional environment, suitable (large enough, perennial) to sustain crocodiles, fish, and oysters. Paleosols, however, indicate periods of stability on the land surface, long enough for the sediments (likely floodplain silts and fine sands) to alter to soils. It is difficult to know at this time whether the change from a fluvial environment (the

Table III Summary of sedimentological features seen in samples from LpM sites, collected in 2012

Sample	Color	Grain size	Composition	Texture	Structures	Environmental interpretation
LpM2 Unit 1.1	Beige to yellow	Fine sand to silt	Quartz, feldspar, calcite, mafics, mica	Poorly sorted, coarse skewed		Fluvial
LpM2 Unit 1.2	Red	Medium to coarse sand	Quartz, calcite, gibbsite, mafics, mica	Poorly sorted	Peds, rhizoconcentrations, carbonate nodules	Paleosol/Floodplain
LpM3 Unit 2.1	Brown	Medium to coarse sand	Quartz, minor feldspar	Poorly sorted	Contains bone fragments and invertebrates	Fluvial
LpM3 Unit 2.2	Red/Green (mottled)	Fine sand to silt	Quartz, feldspar, calcite, gibbsite	Poorly sorted, coarse skewed	Peds?	Paleosol/Floodplain
LpM3 Unit 3.1	Beige	Medium to coarse sand	Quartz, feldspar, mafics	Moderately sorted	Rhizoconcentrations	Fluvial (flow to SW)
LpM3 Unit 3.2	Red	Medium to coarse sand	Quartz, feldspar, calcite, mafics, mica	Poorly sorted, fine skewed		Paleosol/Floodplain
LpM4 Unit 4.1	Beige to yellow	Fine to medium sand	Quartz, feldspar, mafics	Poorly sorted	Bones, crossbeds, 5–10 cm fining up sequences, grass pollen	Fluvial (possibly braided streams)
LpM4 Unit 4.2	Red	Fine sand	Quartz, feldspar, mica, calcite, gibbsite, gypsum	Poorly sorted	Platy peds, gypsum crystals, plant microfossils	Paleosol/Floodplain

quartz sands) to the more stable land surface (paleosols) was due to a climate change, e.g., climate dries and the river ceases to flow, or more simply a change in the river's course, e.g., anastomosing.

**Age** Radiometric age dating of the basalt unit at LpM4 is currently in progress. Even so, the fossil-bearing units at all three primary sites are quartz- and feldspar-rich sands (arkosic composition). This suggests that they belong to the Lokone Formation and are Paleogene–Early Miocene in age (Morley *et al.* 1999b). Baker *et al.* (1971) provide an age range of 18.0–16.2 Ma for basalts at Loperot. Hooijer (1971) provides a radiometric age date of  $18.0 \pm 0.9$  Ma on a lava situated stratigraphically higher, e.g., younger, than rhinoceros fossils at a Loperot location  $<2$  km from the LpM3 site. However, Mead (1975) provides an approximate age of 17.1 Ma for Loperot. Boschetto *et al.* (1992) provide age determinations of  $13.9 \pm 0.2$  Ma and  $15.0 \pm 0.2$  Ma for Loperot but argue that these dates are too young because of Argon loss in their samples. These reports, coupled with radiometric age dates of tuffaceous strata to the north, led Brown and McDougall (2011) to suggest that mammalian fossils found at Loperot are Early Miocene, while refraining from constraining Loperot within a specific time range.

Following our fieldwork at Loperot, we compiled a revised faunal list (Table II). This list includes our discoveries of taxa previously unknown from Loperot combined with reanalysis of previously published materials. To compare the Loperot material to other sites in East Africa (Fig. 1), we compare the mammalian assemblage of Loperot with the faunal assemblage of 10 other fossil sites (see Electronic Supplementary Material Table SI).

### Age Determination for Loperot Using Simpson's Faunal Resemblance Index

We use Simpson's Faunal Resemblance Index (FRI) to compare among all localities that have a taxonomically sufficient faunal list (Table IV). Simpson's FRI is defined as:  $FRI (\%) = (Nc / N1) \times 100$ , where  $Nc$  is the number of identified taxa shared by two faunas, and  $N1$  is the number of identified taxa in the smaller of the two faunas (Simpson 1960). Simpson's FRI conservatively measures the similarity among two assemblages by simultaneously minimizing the use of samples of uneven size, and is very common in paleontological research (Holroyd and Ciochon 1994; Miller 1999; Nakaya 1994; Tsubamoto *et al.* 2004). Also, when the taxonomic lists of faunal assemblages at different sites have large differences in size, Simpson's FRI minimizes the effects of this difference (Miller 1999; Tsubamoto *et al.* 2004). We perform this analysis at the generic level because, typically, genus-level data are more taxonomically stable and robust than species-level data (Alroy 1996; Cifelli 1981; Tsubamoto *et al.* 2004).

### Testing the Significance of Geographic Distance and Temporal Distance in Explaining Taxonomic Composition Differences Among Sites

**Cluster Analysis** We use a hierarchical Unpaired Group Mean Average (UPGMA) cluster analysis (Rohlf 1970) to determine whether the sites in our analysis form discrete groups. We performed the analysis by converting our similarity matrix of 11 sites to a dissimilarity matrix ( $1 - FRI$ ) using the genus-level FRI

Table IV Results of the Simpson's Faunal Resemblance Index examining faunal resemblance at the genus level among a set of Early and Middle Miocene sites

Site	Loperot	Kalodirr	Moruorot	Rusinga–Hiwegi	Rusinga–Kulu	Songhor	Koru	Napak	Moroto	Maboko	Fort Ternan
Loperot	19	42.1	42.1	63.2	36.8	36.8	21.1	47.4	26.3	15.8	31.6
Kalodirr	8	32	91.3	65.6	53.8	31.3	12.5	28.1	17.2	31.3	18.8
Moruorot	8	21	23	60.9	43.5	26.1	8.7	30.4	17.4	39.1	34.8
Rusinga–Hiwegi	12	21	14	68	96.2	66.7	67.6	67.9	48.3	41.9	45.7
Rusinga–Kulu	7	14	10	25	26	61.5	38.5	69.2	19.2	30.8	46.2
Songhor	7	10	6	42	16	63	91.2	69.8	51.7	20.9	34.3
Koru	4	4	2	23	10	31	34	73.5	34.5	26.5	23.5
Napak	9	11	7	36	18	37	25	53	51.7	34.9	37.1
Moroto	5	5	4	14	5	15	10	15	29	24.1	24.1
Maboko	3	10	9	18	8	17	9	15	7	43	45.7
Fort Ternan	6	10	8	16	12	12	8	13	7	16	35

values. We performed this analysis using the SPSS statistics package (IBM release 2009).

*Partial Mantel Tests* We performed two partial Mantel tests (Mantel 1967; Ossi and Kamilar 2006; Smouse *et al.* 1986) using the Vegan package (Oksanen *et al.* 2013) for R (R Core Team 2014) to examine the relative importance of temporal distance and geographic distance between sites. Age estimates and location data are provided in Table I. The first partial Mantel test looked at the correlation between taxonomic distance (converting the FRI values to dissimilarity matrix 1 – FRI) and temporal distance while controlling for geographic distance. The second looked at the correlation between taxonomic distance and geographic distance while controlling for temporal distance.

### Taphonomic and Collection Biases

Taphonomic and collecting biases affect the species composition of fossil assemblages as well as the resulting perceived structure of the community. We include in our study only fossil assemblages that include mammals of all size classes and where we cannot *a priori* identify particular biases that would require exclusion of these sites from the analysis. Therefore, we exclude the Early Miocene sites of Buluk, Wadi Moghara, and Gebel Zelten, from this analysis even though these important sites preserve fossil monkeys. Buluk (Anemone *et al.* 2005) and Wadi Moghara (Miller 1999) have no rodents or other micromammals published. This biases the composition of the assemblages sufficiently to exclude these sites from the Simpson's FRI analysis. Gebel Zelten preserves a large number of micromammals that indicate the assemblage is a time-average of at least four different time zones (Wessels *et al.* 2003), making it unusable. We exclude an important Middle Miocene catarrhine-bearing site, Kipsaramon, from our analysis. Although a small number of recently published specimens from Kipsaramon assigned to Victoriapithecidae genus et species indet. are from sediments

estimated to be 15.83–15.59 Ma (Gilbert *et al.* 2010), most of the cercopithecoid materials described from Kipsaramon were assigned to cf. *Noropithecus* (Miller *et al.* 2009) and are assigned an approximate age of *ca.* 14.5 Ma (Pickford and Kunimatsu, 2005) further confounding the issue. At present it is unclear whether these two different articles represent parts of a single primate community or several different ones. In addition, fauna from Kipsaramon are not fully described limiting utility of the site for our analysis.

## Results

We present the revised list of taxa found at Loperot (Table II) as a single fauna even though the new fossils we discovered in 2012 are from four different loci within the larger Loperot site and other fossils may be from slightly different localities. We feel confident that they form a single assemblage because there is substantial overlap between the fauna found at most localities. Overall, the fauna from Loperot are primarily taxa that are known elsewhere in the Early Miocene of East Africa. Still, as mentioned previously, some taxa are known only from Loperot.

Overall, Loperot is most similar to the Hiwegi Formation of Rusinga Island (Table IV; FRI = 63.2). Next, Loperot is most similar to Napak (FRI = 47.4). Following that, Loperot is most similar to Kalodirr and Moruorot, the other two sites in West Turkana.

The Early and Middle Miocene are separate clusters (Fig. 3). The Early Miocene cluster is split into two distinct clusters. One cluster includes Loperot, Kalodirr, and Moruorot. The second includes all the other Early Miocene sites in our study. In the first cluster, Loperot is quite distantly linked to a distinct cluster that includes Kalodirr and Moruorot. In the second Early Miocene cluster, the two Rusinga assemblages form a distinct cluster, as do Koru and Songhor. Napak is nestled in a cluster with Koru and

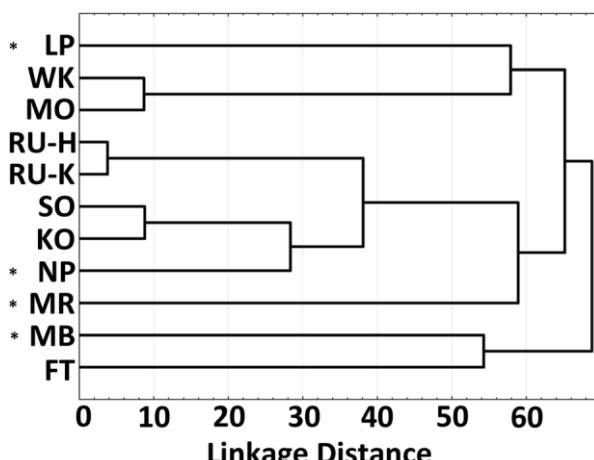


Fig. 3 A dendrogram showing the results of an Unpaired Group Mean Average (UPGMA) cluster analysis of the 1-FRI dissimilarity matrix for sites used in the FRI analysis. LP Loperot; WK Kalodirr; MO Moruorot; RU-H Rusinga-Hiwegi Fm.; RU-K Rusinga-Kulu Fm., SO Songhor; KO Koru; NP Napak; MR Moroto; MB Maboko; FT Fort Terman.

Songhor, Moroto is distantly linked to all the sites in the second cluster. The Middle Miocene sites, although forming a distinct cluster, are not closely linked either.

In the first partial Mantel test there is a significant correlation between taxonomic distance and temporal distance while controlling for geographic distance (Mantel statistic  $r$ : 0.5468;  $P = 0.001$ ). In the second partial Mantel test there is a significant correlation between taxonomic distance and geographic distance while controlling for temporal distance (Mantel statistic  $r$ : 0.3105;  $P = 0.022$ ).

## Discussion

### Age of Loperot as Indicated by the Fauna

As demonstrated by the Simpson's FRI, Loperot's best match ( $FRI = 63.2$ ) is to the Hiwegi Formation of Rusinga Island (Rusinga–Hiwegi in Table IV). The Rusinga–Hiwegi fauna is the largest and many other sites also have FRI values in the 60–70 range with Rusinga, e.g., Kalodirr, Moruorot, Songhor, Koru, and Napak. This could suggest that the Rusinga–Hiwegi faunal assemblage may skew the results of this analysis. However, Kalodirr and Moruorot are most similar to each other ( $FRI = 91.3$ ), Songhor and Koru are most similar to each other ( $FRI = 91.2$ ), and Napak is also most similar to Koru ( $FRI = 73.5$ ). In fact, only Loperot and Rusinga–Kulu are most similar to Rusinga–Hiwegi. However, Loperot and Rusinga–Kulu are not very similar ( $FRI = 36.8$ ). Therefore, it is unlikely that the Hiwegi Formation fauna from Rusinga dominates the FRI analysis enough to hide real patterns in the data.

The results of the FRI analysis support the placement of Loperot in the Early Miocene rather than the Middle Miocene, in accordance with Brown and McDougall (2011). Until recently, the Hiwegi Formation of Rusinga was dated to 17.8 Ma (Drake *et al.* 1988). Peppe *et al.* (2011) provide new information that suggests that the Hiwegi Formation is in fact older ( $\geq 18.0$  Ma based on text and Fig. 2 of Michel *et al.* 2014) than previously thought, but still not as old as Songhor and Koru (*ca.* 19.6 Ma; Bishop *et al.* 1969; Hill *et al.* 2013) and Napak (*ca.* 19.6; Bishop *et al.* 1969; Senut *et al.* 2000). The latter sites may be age equivalent with the older Wayando Formation of Rusinga Island and Mfangano (Peppe *et al.* 2011).

It is therefore intriguing that Loperot shares two taxa with Songhor to the exclusion of Rusinga–Hiwegi or any other sites. The primates at Loperot include *Rangwapithecus gordoni*, previously only known from Songhor (Hill *et al.* 2013) and the nearby and age-equivalent Lower Kapurtay locality (Cote *et al.* 2014). Both sites are within the Kapurtay Agglomerates Formation of the Tinderet Sequence (Pickford and Andrews 1981), and all the fauna found at Lower Kapurtay are also known from Songhor (Cote *et al.* 2014). Finding *Rangwapithecus gordoni* at Loperot is a remarkable range extension for this species. The other taxon that Loperot shares only with Songhor is a proboscidean d4 (KNM-LP 53749: cf. *Archaeobelodon* in Table II) that is almost identical to KNM-SO 1237 from Songhor. Both these specimen are more primitive than any amebelodontine proboscideans currently known from Rusinga–Hiwegi. This is evident by such features as thinner enamel, lack of posterior accessory cuspules, and relatively small size. Both of these taxa suggest that Loperot may be older than Rusinga–Hiwegi, although more data are needed to test this idea. At Loperot, there

are no taxa currently recognized that indicate an age younger than 18 Ma, which is in agreement with the fauna and the radiometric ages published by Hooijer (1971). Therefore, we estimate the age of Loperot as older than 18 Ma and perhaps closer to 19 Ma.

### Effects of Temporal Distance and Geographic Distance on Community Composition

Although a cursory look at the dendrogram presented in Fig. 3 may suggest a regional grouping pattern, this may be true only for sites that are very close geographically, i.e., the Rusinga sites from two different formations, Koru and Songhor, and Kalodirr and Moruorot. Even though Napak is geographically closest to Moroto, Napak is nestled in a cluster with Songhor and Koru, and then within a larger cluster that includes the Rusinga localities. Both Moroto and Loperot are linked only distantly to the other sites in the study. In fact, looking at the sites in Turkana and the sites from Uganda, it appears that temporal distance is more likely to explain the distances in linkage between sites from different times. Our estimates for Loperot indicate that it is older than Kalodirr and Moruorot, while Moroto is older than Napak. Napak actually clusters closer to contemporaneous localities (Songhor and Koru) that are geographically more distant than Moroto.

Given the results of the cluster analysis, combined with the unusual primate community and unique fauna at Loperot, we wanted to determine what factors are of primary importance in determining the composition mammalian community of Early Miocene sites. Habitat reconstructions for Loperot are quite preliminary, so we examined two other factors that may contribute to determining the similarity in the composition of mammalian communities: temporal distance and geographical distance. The partial Mantel tests indicate that both time and geographic location have an effect on taxonomic distance. However, at least in our data, temporal differences are more important. Therefore, we divide the Early Miocene sites in our study into three subperiods to allow for more detailed examination. Moroto is the only site within the Aquitanian (23.03–20.44 Ma; Cohen *et al.* 2013). We can divide the Burdigalian (20.44–15.97 Ma; Cohen *et al.* 2013) into Early Burdigalian ( $\geq ca.$  18 Ma; Rusinga-Hiwigi, Napak, Koru, Songhor, and Loperot) and Late Burdigalian (*ca.* 18 Ma–15.97 Ma; Kalodirr, Moruorot, Rusinga-Kulu). Maboko and Fort Ternan are both Middle Miocene sites but interestingly represent the two ends of the Langhian (15.97–13.82 Ma; Cohen *et al.* 2013).

Moroto is the oldest site and is indeed quite separate in its faunal composition from the other Early Miocene localities (highest FRI = 51.7 with Napak and Songhor). Koru, Songhor, and Napak are contemporaneous (*ca.* 19.5 Ma, Bishop 1969) and indeed we can see how they form a distinct group in the cluster analysis (Fig. 3). Within this cluster we see that Napak, geographically more distant, is also separate from a cluster that includes only Koru and Songhor.

Given the greater correlation and significance of temporal distance we expected Rusinga-Hiwigi and Loperot to cluster together and nestle within a larger cluster of early Burdigalian sites, while we expected Rusinga-Kulu to cluster with Kalodirr and Moruorot in a Late Burdigalian cluster. Indeed, Moruorot and Kalodirr cluster together, but the two Rusinga assemblages and Loperot do not cluster as expected. The faunas of the Hiwigi Formation and the Kulu Formation are very similar, as evidenced by their

low linkage distance (Fig. 3), while Loperot is almost as distant from Kalodirr and Moruorot as Moroto is distant from the two Rusinga assemblages (see Fig. 3).

Comparing the two Rusinga assemblages, only one genus, *Turkanatherium acutirostratum*, is reportedly present at Kulu (Peppe *et al.* 2009) but is not present in the Hiwigi assemblage. However, Geraads (2010) argues that *Turkanatherium acutirostratum* cannot be identified anywhere but Moruorot (he had no access to the Kalodirr fossils at that time), which would then make the two Rusinga assemblages identical at the genus level. The similarities among the two sites may be a result of sampling size (Kulu = 26 genera; Hiwigi = 68 genera), but may also be the result of historically treating the many localities at Rusinga Island as a single time-averaged fauna (Michel *et al.* 2014). It seems unlikely that two faunal assemblages a million or more years apart (Peppe *et al.* 2009, 2011) will be identical and perhaps there is a need for reanalysis of the Rusinga faunas, especially given the importance of these localities to understanding of the Early Miocene, as demonstrated by Michel *et al.* (2014).

The small size of the Loperot assemblage (19 genera) may affect the analysis. However, despite being most similar to Rusinga–Hiwigi in its FRI analysis (SI = 63.2), Loperot does not cluster closely to Rusinga–Hiwigi or any other sites. It is only distantly clustered with other sites in Turkana. Although Loperot is most similar to Rusinga–Hiwigi, other sites such as Rusinga–Kulu (SI = 96.2), Songhor (SI = 66.7), and others are even more similar to Rusinga–Hiwigi. This affects the cluster analysis and provides a likely explanation to why Loperot is not close to Rusinga–Hiwigi in the cluster analysis. Loperot clustering with Kalodirr and Moruorot is likely also the result of other sites being more similar to each other and not any indication of much similarity among the West Turkana sites. This is reflected in the very large linkage distance of Loeprot from Kalodirr/Moruorot. Loperot differs from other early Burdigalian sites in its geographic location and from other sites in West Turkana by its age. As both temporal differences and geographic differences affect faunal composition, Loperot's linkage distance on the cluster analysis from the rest of the Early Miocene sites may very well be a real phenomenon resulting from its unique interaction of geography and time.

### Composition of Catarrhine Communities in Space and Time

Loperot shares its non-cercopithecoid catarrhines with Early Burdigalian sites (Songhor, Rusinga–Hiwigi, Koru, and Napak) rather than Late Burdigalian sites (Kalodirr, Moruorot, and Hiwigi–Kulu), even though Kalodirr and Moruorot are geographically closer to Loperot than any other sites. This is in accordance with the greater influence of temporal difference on mammalian community structure indicated by the partial Mantel tests. More importantly, this strongly suggests that the *Afropithecus–Turkanapihtecus–Simiolus* catarrhine community present in other younger Early Miocene sites in Lake Turkana (Leakey *et al.* 2011) very likely replaced a catarrhine community that primarily comprised taxa shared with other older sites also found in other regions.

In addition to the cercopithecoid specimens at Loperot, a single upper molar from Napak (either M1 or M2), UMP 62-21, was described (although not illustrated) with damaged mesial and buccal margins but intact cusps (Pilbeam and Walker 1968). A frontal was published together with the tooth but has since been assigned to

*Micropithecus clarki* (Fleagle and Simons 1978). It is possible that reanalysis of the molar may remove it from the Cercopithecoidea as well. At Moroto, a right lower canine and the lower p3 and p4 of a single individual were assigned to *Prohylobates macinnesi* (Pickford *et al.* 2003). A recent revision by Miller *et al.* (2009) erected a number of new genera and species and placed this specimen in *Victoriapithecus macinnesi*. The cercopithecid remains from Moroto would also benefit from reexamination, particularly given the large temporal gap between Moroto and Maboko. Although Loperot may share the presence of cercopithecid taxa with Moroto, at present these differ generically and the two sites do not share any non-cercopithecid catarrhine taxa.

Cercopithecid taxa in our studied sites do not follow the results of the partial Mantel tests. Loperot does not share *Noropithecus* sp. with any of the sites in the study. However, monkeys are known from three Late Burdigalian sites that we excluded from the study owing to taphonomic biases: Buluk ( $16.4 \pm 0.2$ - $17.4 \pm 1.6$  Ma: McDougall and Watkins 2006), Wadi Moghara (17–18 Ma: Miller 1999), and Gebel Zelten 18–15 Ma (Wessels *et al.* 2003). The only catarrhines currently known from the North African sites, Wadi Moghara and Gebel Zelten, are cercopithecid taxa, *Prohylobates tandyi* and *Zaltanpithecus simonsi* respectively (Miller *et al.* 2009), different from *Noropithecus* sp. from Loperot. Interestingly, *Noropithecus* was erected for the cercopithecid found at Buluk (Miller *et al.* 2009). *Noropithecus* differs from all other cercopithecid taxa in having more bunodont lower molar cusps, and greater degree of molar flare due to mesial and distal cusp tips being more closely approximated (Miller *et al.* 2009). A formal description of the Loperot cercopithecid material is outside the scope of this article and is the subject of an ongoing study; still, we place the monkey from Loperot in the genus *Noropithecus*, albeit a different species than *N. bulukensis* from Buluk (see Table I) because it is similar to *N. bulukensis* in its bunodont lower molar cusps and close approximation of mesial and distal cusps, leading to a high degree of molar flare. However, Buluk shares non-cercopithecid catarrhines with Kalodirr and Moruorot and not Early Burdigalian sites. Two other sites may also have *Noropithecus* present. Nabwal (<17.2 Ma; Fleagle *et al.* 1997) preserves cf. *Noropithecus fleaglei*, and Kipsaraman (14.5 Ma; Pickford, 1981) preserves cf. *N. kipsaramanensis* (Miller *et al.* 2009; Pickford and Künimatsu 2005). Whether these are two species of *Noropithecus* or not, they are apparently part of a “*Noropithecus*” group. Loperot may well represent the oldest member of this group.

During the Middle Miocene *Victoriapithecus macinnesi* is very well known at Maboko, (Benefit 1999), but is not present at Fort Ternan. Miller *et al.* (2009) recognize *Victoriapithecus macinnesi* at three Early Miocene sites: Napak, Moroto, in Uganda, and Loperot in Kenya, and several Middle Miocene sites: Maboko Island, Majiwa, Nachola, Nyakach, Ngorora, and Ombo, all in Kenya. As mentioned previously, we reassigned the material from Loperot to *Noropithecus* sp., and argue that the very minimal material from Moroto (one canine and two premolars from a single individual), and single incomplete upper molar from Napak, require reanalysis. Therefore, we suggest that it is currently best to treat *Victoriapithecus macinnesi* as a Middle Miocene taxon only. It is important to note that *Noropithecus* may have survived into the Middle Miocene as cf. *N. kipsaramensis*.

At present it is difficult to evaluate why some sites preserve monkeys along with apes, whereas most preserve only one or the other. In the case of the two North African

sites, one can postulate some barrier to the migration of non-cercopithecoids, as only cercopithecoids are identified in North Africa or the Arabian Peninsula before the early Middle Miocene when *Heliopithecus* is found at Ad-Dabtia in Saudi Arabia (Andrews and Martin 1987; Andrews *et al.* 1978; Harrison 2010). However, no such barrier has been demonstrated.

Temporal differences account for much of the difference in community composition between sites. Loperot shares non-cercopithecoids with the similar-age Hiwegi fauna of Rusinga (Michel *et al.* 2014) and with maybe even older Songhor and Lower Kapurtay (Cote *et al.* 2014). The presence of a monkey at Loperot may be the result of geographical differences in the distribution of monkeys, perhaps also suggested by the lack of any monkeys in any sites near Lake Victoria. However, such an idea would require a much greater sampling of catarrhine habitats than is currently available. The differences between the catarrhine communities of the Early Burdigalian and Late Burdigalian sites in East Africa are in agreement with the combined effect of both temporal difference and geographical difference.

## Conclusions

Our analyses indicate that both time differences and spatial distance affect the similarity of community composition in Early Miocene sites. Our study shows that catarrhine communities generally follow that pattern. Our results indicate possible turnover in catarrhine communities over time. Our results also indicate that geographic differences also played a role in differentiating mammalian and catarrhine communities. Further studies are necessary to determine if Loperot is unusual in some aspects of its ecology or environments to explain why certain taxa and not others are shared among Loperot and other sites, and why it shares taxa with sites that incorporate a large range of time.

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