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Paleosols and paleoenvironments of the middle Miocene, Maboko Formation, Kenya

The middle Miocene (15 Ma) Maboko Formation of Maboko Island and Majiwa Bluffs, southwestern Kenya, has yielded abundant fossils of the earliest known cercopithecoid monkey (*Victoriapithecus macinnesi*), and of a kenyapithecine hominoid (*Kenyapithecus africanus*), as well as rare proconsuline (*Simiolus leakeyorum*, cf. *Limnopithecus evansi*) and oreopithecine apes (*Mabokopithecus clarki*, *M. pickfordi*), and galagids (*Komba winamensis*). Specific habitat preferences can be interpreted from large collections of primate fossils in different kinds of paleosols (pedotypes). Fossiliferous drab-colored paleosols with iron-manganese nodules (Yom pedotype) are like modern soils of seasonally waterlogged depressions (dambo). Their crumb structure and abundant fine root-traces, as well as scattered large calcareous rhizoconcretions indicate former vegetation of seasonally wet, wooded grassland. Other fossiliferous paleosols are evidence of nyika bushland (Ratong), and early-successional riparian woodland (Dhero). No fossils were found in Mogo paleosols interpreted as saline scrub soils. Very shallow calcic horizons (in Yom, Ratong, and Mogo paleosols) and Na-montmorillonite (in Mogo) are evidence of dry paleoclimate (300–500 mm MAP=mean annual precipitation). This is the driest paleoclimate and most open vegetation yet inferred as a habitat for any Kenyan Miocene apes or monkeys. *Victoriapithecus* was abundant in dambo wooded grassland (Yom) and riparian woodland (Dhero), a distribution like that of modern vervet monkeys. *Kenyapithecus* ranged through all these paleosols, but was the most common primate in nyika bushland paleosols (Ratong), comparable to baboons and macaques today. *Mabokopithecus* was virtually restricted to riparian woodland paleosols (Dhero), and *Simiolus* had a similar, but marginally wider, distribution. Habitat preferences of *Mabokopithecus* and *Simiolus* were like those of modern colobus monkeys and mangabeys. A single specimen of *Komba* was found in dambo wooded grassland paleosol (Yom), a habitat more like that of the living Senegal bushbaby than of rainforest galagids. A shift to non-forest habitats may explain the terrestrial adaptations of *Victoriapithecus*, basal to the cercopithecoid radiation, and of *Kenyapithecus*, basal to the hominoid radiation. Both taxa are distinct from earlier Miocene arboreal proconsulines, oreopithecines and galagids.

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Introduction

The main excavation of Kenya's Maboko Island is famous for its abundant and well-preserved middle Miocene (15 Ma)

primate fossils, particularly the cercopithecoid *Victoriapithecus macinnesi* (Benefit & McCrossin, 1989; Benefit, 1993, 1994, 1999a), and hominoid *Kenyapithecus africanus* (Benefit & McCrossin, 1992, 1993;

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McCrossin & Benefit, 1994, 1997; McCrossin *et al.*, 1998). Based on a holotype from Maboko, *K. africanus* has recently been made the type species of the new genus "Equatorius" (Ward *et al.*, 1999). We think that all specimens of Maboko kenyapithecines represent a single species, which is linked with *K. wickeri*, the type species of *Kenyapithecus* (Leakey, 1962), by a variety of postcranial and dental characters (Benefit & McCrossin, 2000). "Equatorius" is thus a junior synonym of *Kenyapithecus* (Ishida *et al.*, 1999; Begun, 2000; Benefit & McCrossin, 2000; Kelley *et al.*, 2000). *Victoriapithecus* and *Prohylobates* are the oldest known representatives of the cercopithecoid evolutionary radiation (Benefit & McCrossin, 1997; Benefit, 1999a). *Kenyapithecus* is a sister taxon to the clade including living African great apes, australopithecines, and humans (McCrossin *et al.*, 1998). These taxa were the beginnings of evolutionary radiations into semiterrestrial habits different from those of earlier Miocene catarrhines, represented at Maboko by the proconsulines cf. *Limnopithecus evansi* and *Simiolus leakeyorum*, and the oreopithecines *Mabokopithecus clarki* and *M. pickfordi*. Also found at Maboko and nearby Majiwa are rare fossil bushbabies (*Komba winamensis* and another species), and a large fauna of other vertebrates, molluscs, myriapods and insects (Tables 1–3).

Here we examine paleosols yielding these taxa for clues to their paleoecology and evolutionary success. The Maboko–Majiwa fossil primate collections are sufficiently large to show significant differences in abundance of fossil primates within particular paleosols and sedimentary environments, and so offer the prospect of a statistically significant reconstruction of habitat preferences of these extinct primates. A χ^2 comparison of observed numbers of specimens compared with the expectation that they should be present in abundances comparable to that of the entire sample, shows very

remote probabilities that individual primate assemblages are the same, and, with the exception of rare bushbabies (*Komba*), that each taxon is proportionally distributed through each habitat (Table 1). These differences could represent taphonomic differences between paleosols and sedimentary environments, but, with the exception of one paleosol noted below, we think that unlikely for the following reasons. Virtually all the specimens, including very rare skulls, are disarticulated, stained, broken, gnawed, weathered and worn like attritional assemblages, rather than articulated and fresh like a catastrophic assemblage (Andrews *et al.*, 1981). While some of our specimens from Ratong paleosols (see Table 4 for definition) are surface collections from Majiwa where only those paleosols are exposed, our numbers for Yom and Dhero paleosols are all from specific levels of concentration in controlled excavations (Benefit, 1999a). Also from excavation is the assemblage from a lenticular green sand (Kent, 1944; Andrews, 1981a, plate 5), now completely excavated, which we interpret not as a paleosol, but as a deposit within a streamside swale or chute of the levee complex marginal to a stream. The lower yield from Ratong paleosols reflects less time and effort collecting, and is not related to obvious taphonomic biases, such as carbonate abundance or degree of development known to control vertebrate recovery from paleosols (Retallack, 1998). In contrast, lack of fossils from the Mogo paleosol is due to taphonomic bias, considering the markedly less calcareous and more saline nature of this profile. There is only one of these paleosols among hundreds examined at Maboko and Majiwa, and in rocks of the same age near Sondu (Wynn & Retallack, 2001), and the Mogo paleosol probably does not represent a widespread habitat. The Maboko–Majiwa fossil collections are outstanding samples of extinct primate populations.

Table 1 Observed fossil primate specimens from sediments and paleosols at Maboko and Majiwa compared with expected numbers if relative species abundance were uniform

Taxon	Swale		Dhero paleosol		Yom paleosol		Ratong paleosol		Σ	χ ² P
	Found	Expected	Found	Expected	Found	Expected	Found	Expected		
<i>Victoriapithecus</i>	840	872	1401	1430	538	463	1	17	2780	2.2 × 10 ⁻⁶
<i>Kenyapithecus</i>	120	90	132	147	19	48	16	2	287	1.6 × 10 ⁻³¹
<i>Proconsulines</i>	124	69	77	113	16	36	3	1	220	6.7 × 10 ⁻¹⁵
<i>Mabokopithecus</i>	5	58	177	96	4	31	1	1	187	2.6 × 10 ⁻³⁰
<i>Komba</i>	1	1	0	1	1	0	0	0	2	0.4572
Σ	1090	1090	1787	1787	578	578	21	21	3476	
χ ² P	1.2 × 10 ⁻²¹		4.5 × 10 ⁻¹⁷		1.4 × 10 ⁻¹³		4.5 × 10 ⁻²⁸			

Table 2 Percentages (and numbers of specimens) of mammal fossils from Maboko and Majiwa

Taxon	Species	Swale Bed 3	Dhero Bed 5b	Yom Bed 5w	Ratong SE 12	Ratong S 12	Ratong E13-16	Ratong Majiwa
Primates								
Galagidae	<i>Komba winamensis</i>	0.03 (1)	—	—	—	—	—	—
	<i>Komba</i> sp. nov.	—	—	0.6 (1)	—	—	—	—
Proconsuloidea	<i>Simiolus leakeyorum</i> and cf. <i>Limnopithecus evansi</i>	3 (124)	2 (77)	1 (16)	4 (3)	—	—	—
Hominoidea								
Oreopithecinae	<i>Mabokopithecus clarki</i> and <i>M.</i> <i>pickfordi</i>	0.1 (5)	5 (177)	0.2 (4)	—	8 (1)	—	—
Kenyapithecinae	<i>Kenyapithecus africanus</i>	3 (120)	4 (132)	1 (19)	16 (11)	8 (1)	—	44 (4)
Cercopithecoidea	<i>Victoriapithecus macinnesi</i>	24 (840)	39 (1401)	32 (538)	—	—	—	11 (1)
Insectivora								
Erinacidae	<i>Amphichinus rusingensis</i>	0.03 (1)	0.06 (2)	0.2 (3)	—	—	—	—
Family indet.	sp. indet.	0.1 (5)	—	0.2 (5)	—	—	—	—
Rodentia								
Thyromomyidae	cf. <i>Paraphiomys pigotti</i> , cf. <i>P.</i> <i>siromeri</i> , and <i>Paraulacodus</i> sp.n. genus indet.	0.06 (2)	—	0.06 (1)	—	—	—	—
	cf. <i>Diamantomys laederitzi</i>	0.1 (4)	0.03 (1)	0.06 (1)	—	—	—	—
Diamantomyidae	genus indet.	0.6 (2)	—	—	—	—	—	—
Bathyergidae	genus indet.	0.03 (1)	—	—	—	—	—	—
Pedetidae	<i>Megapedetes pentadactylus</i>	—	—	0.06 (1)	—	—	—	—
	<i>Pedetes</i> sp. indet.	0.4 (16)	0.1 (5)	—	1 (1)	—	—	—
Cricetidae	genus indet.	—	—	0.06 (1)	—	—	—	—
Family indet.	genus indet.	3 (110)	2 (87)	3 (46)	14 (10)	—	—	—
Lagomorpha								
Family indet.	genus indet.	0.08 (3)	—	0.06 (1)	—	—	—	—
Crocodonta								
Hyaenodontia	<i>Anasinopa leakeyi</i>	0.2 (7)	—	0.2 (4)	—	—	—	—
	<i>Dissopsalis pyroclasticus</i>	—	—	0.06 (1)	—	—	—	—
	cf. <i>Pterodon nyanzae</i>	0.03 (1)	0.03 (1)	—	—	—	—	—
	<i>Hyaenatourus</i> sp. indet.	0.4 (13)	—	0.6 (10)	—	—	—	—
Family indet.	genus indet.	0.08 (3)	—	0.06 (1)	—	—	—	—

Table 2 Continued

Taxon	Species	Swale Bed 3	Dhero Bed 5b	Yom Bed 5w	Ratong SE 12	Ratong S 12	Ratong E13-16	Ratong Majiwa
Carnivora								
Canidae	<i>cf. Cynelos eurydon</i>	0-03 (1)	—	—	—	—	—	—
Viverridae	<i>cf. Moprionodon</i> sp. genus indet.	0-03 (1) 0-01 (5)	—	—	—	—	—	—
Family indet.	genus indet.	3 (114)	1 (40)	3 (36)	—	8 (1)	4 (1)	—
Tubulidentata								
Orycteropidae	<i>Orycteropus chemeldoi</i>	0-3 (12)	0-08 (3)	0-06 (1)	—	—	—	—
Proboscidea								
Gomphotheriidae	<i>Protanancus macinnesi</i> <i>Choerolophodon kisumuensis</i> genus indet.	0-06 (2) — 0-8 (29)	— — —	— 0-06 (1) 0-2 (4)	— — 4 (3)	— — 8 (1)	— — 4 (1)	13 (1+) — —
Deinotheriidae	<i>Prodeinotherium hobleyi</i>	0-06 (2)	—	—	—	8 (1)	—	13 (1+)
Hyracoidea								
Phoryracidae	<i>Pachyhyrax championi</i> genus indet.	0-3 (14) 0-3 (12)	2 (54) 1 (16)	0-4 (6) 0-2 (4)	— —	— —	— —	— —
Perissodactyla								
Rhinocerotidae	<i>Brachypotherium heinzelini</i> and <i>Dicerorhinus leakeyi</i> genus indet.	6 (217) 0-03 (1)	0-5 (1) —	0-3 (9) —	7 (5) —	23 (3) —	24 (6) —	11 (1) —
Chalicotheriidae								
Artiodactyla								
Samitheriidae	<i>Samitherium nadirum</i> genus indet.	0-2 (7) 0-03 (1)	0-6 (13) —	0-1 (2) —	— —	— —	— —	— —
Tayassuidae	<i>cf. Kenyapotamus tenuis</i> genus indet.	0-2 (8) 0-3 (12)	0-08 (3) —	— —	1 (1) —	— —	8 (2) —	— —
Hippopotamidae	<i>Libycochoerus jeanelli</i> and <i>L. khamsisibirius</i>	0-2 (7)	—	—	1 (1)	—	—	—
Suidae	<i>Listriodon akaikubas</i> <i>Listriodon</i> sp. indet. <i>Lopholistriodon kidogasona</i> <i>Lopholistriodon moruoroi</i> <i>Lopholistriodon</i> sp. indet. genus indet.	0-3 (14) 0-3 (10) — 0-3 (9) — 2 (73)	— — 0-3 (6) 3 (71) 0-2 (4) 3 (102)	0-3 (5) 0-3 (5) — 0-5 (6) — 1 (19)	1 (1) — — — — 1 (1)	— — — — — —	8 (2) — — — — —	11 (1) — 11 (1) — — —

Table 2 Continued

Taxon	Species	Swale Bed 3	Dhero Bed 5b	Yom Bed 5w	Ratong SE 12	Ratong S 12	Ratong E13-16	Ratong Majiwa
Artiodactyla (continued)								
Tragulidae								
	<i>Dorcatherium parvum</i>	0.06 (2)	—	—	—	—	—	—
	<i>Dorcatherium pigotti</i>	5 (180)	4 (155)	5 (88)	—	—	—	—
	<i>Dorcatherium chappuisi</i>	2 (72)	0.3 (14)	1 (23)	6 (4)	—	—	—
	<i>Dorcatherium libiensis</i>	0.03 (1)	—	—	—	—	—	—
	<i>Dorcatherium</i> sp. indet.	5 (191)	21 (771)	8 (128)	9 (6)	23 (3)	8 (2)	—
Climacoceridae								
	<i>Climacocerus africanus</i>	16 (572)	2 (85)	10 (165)	22 (15)	31 (4)	16 (4)	—
	<i>Palaeotragus</i> sp.	0.4 (16)	—	—	1 (1)	—	4 (1)	—
	<i>Canthumeryx</i> sp.	—	—	0.06 (1)	—	—	—	—
Bovidae								
	<i>Eotragus</i> sp.	0.1 (4)	0.06 (2)	—	—	—	—	—
	<i>Nyanzameronyx pickfordi</i>	0.03 (1)	—	—	—	—	—	—
	<i>Gazella</i> sp.	0.03 (1)	—	0.06 (1)	—	—	—	—
	<i>Hypsodontinae</i> sp. indet.	—	0.03 (1)	—	—	—	—	—
	genus indet.	5 (178)	2 (46)	2 (23)	10 (7)	—	4 (1)	—
	genus indet.	9 (323)	4 (156)	18 (306)	4 (3)	—	16 (4)	—
	genus indet.	5 (162)	2 (68)	4 (159)	1 (1)	8 (1)	—	—
Total specimens		(2624)	(2249)	(1182)	(69)	(13)	(25)	(9)

Numbers shown are percentage for that collection and numbers of specimens (latter in parentheses). Bed numbers are those of Pickford (1984, 1986a) and McCrossin *et al.* (1998). Collections from swale green sand of Bed 3, Yom paleosol of white upper Bed 5 and Dhero paleosol of lower brown Bed 5 are from Maboko main excavations (by BRB and MLM) and do not include collections of Pickford (1984) or Andrews *et al.* (1981). Ratong paleosol collections from Maboko Bed 12 at the S and SE localities are small quarry samples (again only by BRB and MLM). Ratong paleosol collections from Majiwa and Maboko Cliffs Beds 13-16 are surface collections from Pickford (1984, 1986a). Other data are from Pickford (1982b, 1983, 1985), Thomas (1985), Cifelli *et al.* (1986), Benefit & McCrossin (1989), McCrossin (1992), Winkler (1992, 1994), McCrossin *et al.* (1998), Benefit (1999a).

As we shall demonstrate, very shallow calcic horizons of paleosols and pedogenic Na-montmorillonite in the Maboko Formation formed under dry bushland (nyika) and represents the driest paleoclimate and most open vegetation of any known Miocene locality with fossil apes. Our interpretation supports early views that sites such as Rusinga Island (18 Ma) and Fort Ternan (14 Ma) were mosaics of wooded grassland, woodland and dry forest (Whitworth, 1953, 1958; Shipman *et al.*, 1981; Korlandt, 1983; Shipman, 1986). Subsequent reinterpretation of these sites favored forest habitats, especially rainforest, like those of great apes today: for example, faunal analyses of Andrews & Van Couvering (1975; Van Couvering, 1980; Andrews, 1992, 1996; Andrews & Humphrey, 1999), functional morphological studies of Kappelman (1991, 1993) and isotopic studies of Cerling *et al.* (1992, 1997a). In contrast, evidence for dry, open, nonforest vegetation during the middle Miocene has continued to come from studies of the taxonomy, taphonomy and functional morphology of fossil grasses, pollen (Retallack, 1992a, 1992b; Dugas & Retallack, 1993; Bonnefille, 1994), snails (Pickford, 1983, 1995) and mammals (Mihlbacher *et al.*, 1998), as well as from the isotopic composition of paleosols and mammals (Kingston *et al.*, 1994; Morgan *et al.*, 1994; Bestland & Krull, 1999; Kingston, 1999), sedimentological studies of evaporite and lacustrine deposits (Pickford, 1992; Renaut *et al.*, 1999), and from the petrographic and geochemical study of paleosols (Retallack *et al.*, 1990, 1995; Retallack, 1991a; Wynn & Retallack, 2001). This paper presents additional evidence from paleosols for habitats other than forest at 15 Ma in western Kenya.

Geological setting

Past research has focused on the extraordinarily fossiliferous main excavation on

Maboko Island (Figures 1–3), but the Maboko Formation extends 15 km northeast on the mainland. Lithologically the formation is diverse, with white to yellow carbonatite tuffs characteristic of the main exposures of Maboko Island, and orange conglomerates widespread on the mainland. Calcrete nodules are the most conspicuous features of the formation throughout its outcrop.

To the north, the Maboko Formation is only 44 m thick at Ombo, and it thins to nothing northward near Mariwa, where overlying Ombo Phonolite flowed directly over lateritized Nyanzian–Kavirondian–Bukoban metamorphic–granitic basement (Pickford, 1984, 1986a). Majiwa was evidently an east–west axial drainage, because it includes paleochannel conglomerates full of nephelinite clasts like those of the extinct (18 Ma) Tinderet volcanic center 70 km to the east (Retallack, 1991a). To the north was a hilly terrain to Precambrian basement and deeply weathered lateritic soils, which are now exposed on the Kakamega road south of Vihiga and near Mariwa (Saggerson, 1952). Inselbergs may have provided little-weathered crystals of microcline and metamorphic rock fragments in the parent material to Ratong paleosols at Majiwa. Some bedrock islands in Lake Victoria are fine-grained, Nyanzian rhyolites and cherty banded iron formations, distinct from widespread porphyritic granite (Saggerson, 1952), and may be exhumed inselbergs (Figure 1).

To the south, the Maboko Formation is thick (more than 50 m, base not seen) and fine grained on Maboko Island, which was a lowland depocenter. Toward the southwest, the alluvial plain sloped up toward the volcanic center of Kisingiri (most active ca. 18 Ma), near Rusinga Island some 60 km to the southwest (Bestland *et al.*, 1995). This source direction is indicated by northward paleocurrents from trough cross beds (Figure 2) and ripple drift cross

Table 3 Specimen numbers of non-mammal fossils from Maboko and Majiwa

Taxon	Species	Channel Bed 3	Yom Bed 5w	Ratong Maboko	Ratong Kaloma	Ratong Majiwa
Gastropoda	<i>Tropidophora miocenicum</i> (trochoidal)	—	—	—	10	—
	<i>Succinea</i> (rapidly expanding whorls)	—	—	—	1	—
	<i>Pupoides</i> (small, pupiform)	—	—	Many	1	—
	<i>Edouardia</i> sp. (trochoidal smooth)	—	2	—	1	—
	<i>Rachistia</i> sp. aff. <i>R. rhodotaenia</i> (small high spired)	—	—	650	Many	Many
	<i>Pseudoglessula</i> sp. (high spired)	—	—	—	—	1
	Subulinidae gen. indet.	—	—	34	20	—
	<i>Opeas</i> (high spired, rounded apex)	—	—	2	—	2
	<i>Nothapalimus</i> sp. (very high spired)	—	—	Many	—	—
	<i>Achatina</i> sp. cf. <i>A. leakeyi</i> (large)	—	—	2	—	—
	<i>Burtoa nilotica</i> (globose, high spired)	—	—	29	19	24
	<i>Limicolaria</i> sp. cf. <i>L. martensiana</i> (ovoid)	—	1	53	69	52
	Urocyclidae (slug plates)	—	—	66	2	—
	<i>Trochozonites</i> sp. (trochoidal, keeled)	—	—	—	2	—
	<i>Trochonanina</i> (low spired, keeled)	—	—	5	1	7
	<i>Zingis?</i> (trochoid, keeled)	—	—	2	1	9
	<i>Macrogonaxis</i> sp. (shortened pupiform)	—	—	1	—	4
	<i>Pseudogonaxis protocavalli</i> (pupiform)	—	—	—	1	—
	<i>Edentalina rusingensis</i> (large pupiform)	—	—	—	—	2
	<i>Prychotrema fusiforme</i> (long pupiform)	—	—	4	—	—
<i>Gulella</i> sp. (small pupiform, toothed)	—	—	6	2	—	
Myriapoda	Diplopoda gen. indet. (millipede)	—	—	—	—	X
Insecta	Coleoptera gen. indet. (beetle cocoon)	—	—	—	—	X
Amphibia	Anura gen. indet. (frog)	2	24	—	—	—
	Urodela gen. indet. (salamander)	—	1	—	—	—
Crocodylia	<i>Crocodylus</i> sp. (crocodile)	34	123	—	—	—
	<i>Euthecodon</i> sp. (gavial)	—	—	—	—	—
Chelononia	Pelomedusidae gen. indet. (terrapin)	—	—	—	—	X
	Trionychidae gen. indet. (soft-shelled turtles)	—	—	—	—	X
Lacertilia	gen. et sp. indet.	364	Many	—	1	6
	Varanidae gen. indet. (monitor lizard)	—	1	—	—	—
Amphisbaenia	Family indet.	3	9	—	—	—
	gen. indet. (wormlike reptiles)	—	1	—	—	—
Ophidea	Ophidea gen. indet. (snake)	—	2	—	—	—
	Pythoridae gen. indet. (python)	2	—	—	—	—
	Family indet.	—	2	—	—	—

Table 3 Continued

Taxon	Species	Swale Bed 3	Yom Bed 5w	Ratong Maboko	Ratong Kaloma	Ratong Majiwa
Aves	<i>Phalacrocorax</i> sp. (cormorant)	—	—	—	—	—
	<i>Anhinga</i> sp. (darter)	—	—	—	—	—
	<i>Pelecanus</i> sp. (pelican)	—	—	—	—	—
	aff. <i>Egretta</i> sp. (egret)	—	—	—	—	—
	aff. <i>Ciconia</i> sp. (stork)	—	—	—	—	—
	<i>Chlamydotis undulatus</i> (bustard)	—	—	—	—	—
	<i>Leakeyornis aethiopicus</i> (flamingo)	—	—	—	—	—
	Accipitridae gen. indet. (eagle)	—	—	—	—	—
	aff. <i>Francolinus</i> sp. (francolin)	—	—	—	—	—
	Rallidae gen. indet. (rails and coots)	—	—	—	—	—
	Anatidae gen. indet. (ducks)	—	—	—	—	—
	Jacaniidae gen. indet. (lily trotter)	—	—	—	—	—
	aff. <i>Himantopus</i> sp. (stilt)	—	—	—	—	—
	aff. <i>Burhinus</i> sp. (curlew)	—	—	—	—	—
	aff. <i>Tockus</i> sp. (hornbill)	—	—	—	—	—
	Passeriformes gen. indet. (songbird)	—	—	—	—	—

Sources: Numbers of specimens for Ratong paleosols include Kaloma, Majiwa and Urocyclid collections of Pickford (1984, 1986a, 1995), for channel bed 3 are Quarry 1 and for Yom paleosol are Quarry 2 of Andrews *et al.* (1981). Not included in this list are Pickford's records of freshwater oyster (*Etheria elliptica*), aquatic snails (*Melanoides turberculata*, *Pila ovata*, *Lanistes carinatus*, *L. purpureus*) and fish (*Protopterus*, *Polypterus*, aff. *Hydrocyon*, *Gymnarchus*, *Clarias*). Some of the fish specimens archived are weathered but unmineralized, and may have been modern. All these aquatic taxa still live in the area and have not been found in our excavations. Bird fossils are currently under study: this provisional list combines records of Rich & Walker (1983), Pickford (1984, 1986a) and McCrossin *et al.* (1998).

lamination in Maboko main excavation. Abundant fresh carbonatite ash in Maboko main excavation may also have come from Kisingiri or associated cinder cones still active (Bestland *et al.*, 1995), and less likely from distant volcanoes of Mt Elgon or Moroto, which also may have been active at 15 Ma (Simonetta & Bell, 1995; Pickford *et al.*, 1999). The Maboko-Nyakach depositional and structural basin can be considered a downwarp between the Tinderet and Kisingiri Volcanic centers, comparable to the modern Amboseli Basin flanking Kilimanjaro Volcano (Pickford, 1986b).

The Ombo phonolite capped and preserved the Maboko Formation. It flowed down a broad paleovalley from calderas on the margin of Gregory Rift (Lippard, 1973), and was ponded against the Kakamega Hills

to the north and the Kisii Hills to the south (Andrews *et al.*, 1981; Retallack, 1991a; Wynn & Retallack, 2001). The whole region was then faulted to produce the current Nyanza Rift scarps and numerous sympathetic faults (Pickford, 1982a, 1986b).

The fossil mammal fauna of the Maboko Formation is the best known example of faunal set IIIb, equivalent to European land mammal zone MN 4b, and dated at about 15 Ma (Pickford, 1981; Pickford & Morales, 1994; Sawada *et al.*, 1998). On Maboko Island, a carbonatite tuff (Bed 8 of Figures 4 and 5) has been radiometrically dated at 14.71 ± 0.16 Ma, and the Ombo Phonolite has been dated at 13.80 ± 0.04 Ma. Both dates are from single-crystal laser fusion $^{40}\text{Ar}/^{39}\text{Ar}$ on anorthoclase (Feibel & Brown, 1991). These dates are here preferred over

Table 4 Diagnosis and identification of paleosols in the middle Miocene Maboko Formation

Pedo-type	Luo	Diagnosis	U.S. taxonomy	FAO map	Australian handbook	Northcote key	South African
Dhero	Thin	Gray to brown, bedded carbonatite, tuffaceous sandstone or conglomerate with root traces and trunk casts	Endoaquent	Calcic Fluvisol	Gray-brown calcareous soil	Uc1.31	Namib beachwood
Mogo	Flour	White carbonatite ash with clayey iron-manganese and goethite spotted surface horizon, and subsurface calcareous (Bk) horizon	Aquisalid	Gleyic Solonchak	Solonchak	Gc1.21	Montagu baden
Ratong	Orange	Gray blocky-play structured surface (A) over orange nodular calcareous subsurface	Haplocalcid	Calcic Xerosol	Desert Loam	Gc1.12	Augrabies hefnaar
Yom	Soft	Brown (7.5 YR-2.5 Y) crumb-structured claystone with calcareous nodules and rhizoconcretions and iron-manganese nodules	Aquic Ustropept	Gleyic Cambisol	Wiesenboden	Uf6.11	Willowbrook ottawa

Soil classifications are from Soil Survey Staff (1999), FAO (1974, 1977), Stace *et al.* (1968), Northcote (1974) and Soil Classification Working Group (1991).

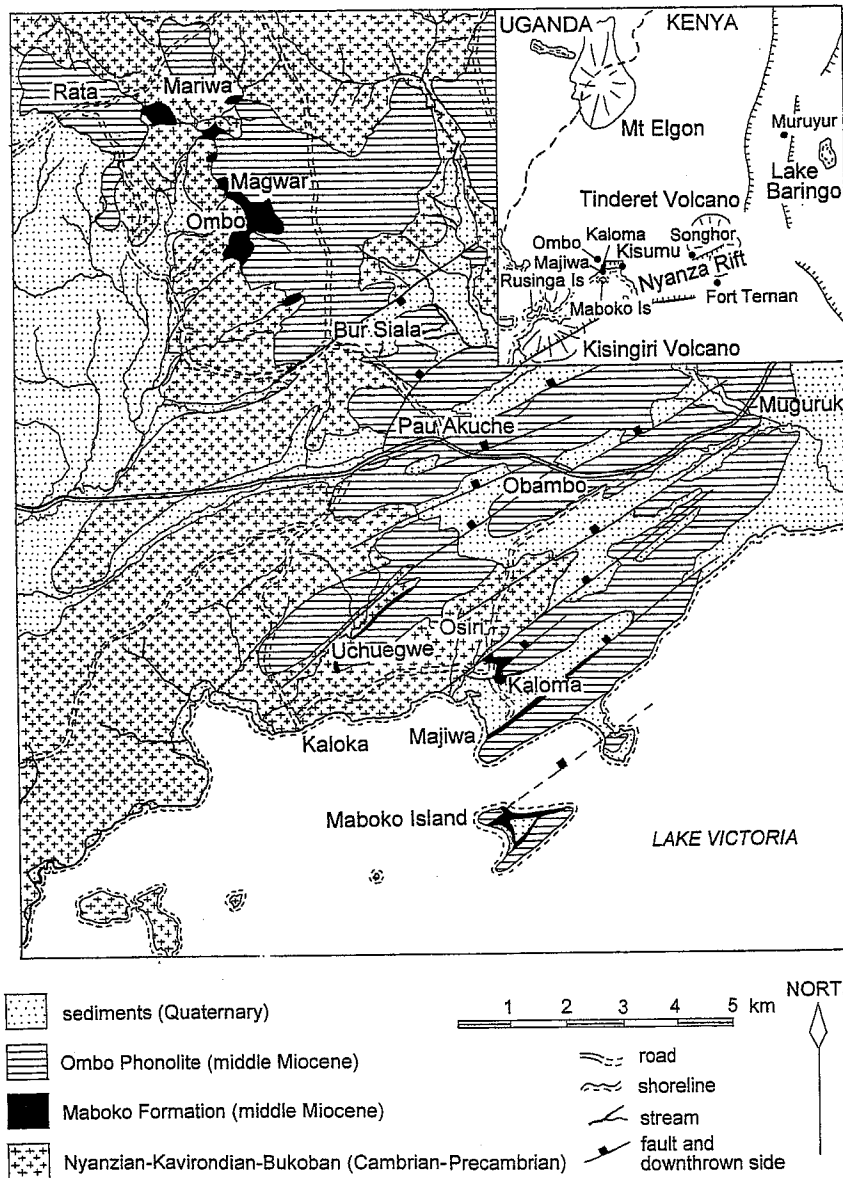


Figure 1. Geological map of the Maboko-Majiwa-Ombo area, Kenya (from Pickford, 1984).

earlier K/Ar dating of the Ombo Phonolite at Majiwa of 12–13 Ma (Andrews *et al.*, 1981). Majiwa is older than 13.80 Ma and probably younger than 14.71 Ma, because its conglomerates and caliches are similar to units high in the sequence on Maboko Island (Figure 4).

Materials and methods

Study of paleosols on Maboko Island in June 1997 made use of the excavation directed locally by Stephen Gitau. We made site plans and sketches, as well as detailed stratigraphic sections on Maboko Island and in

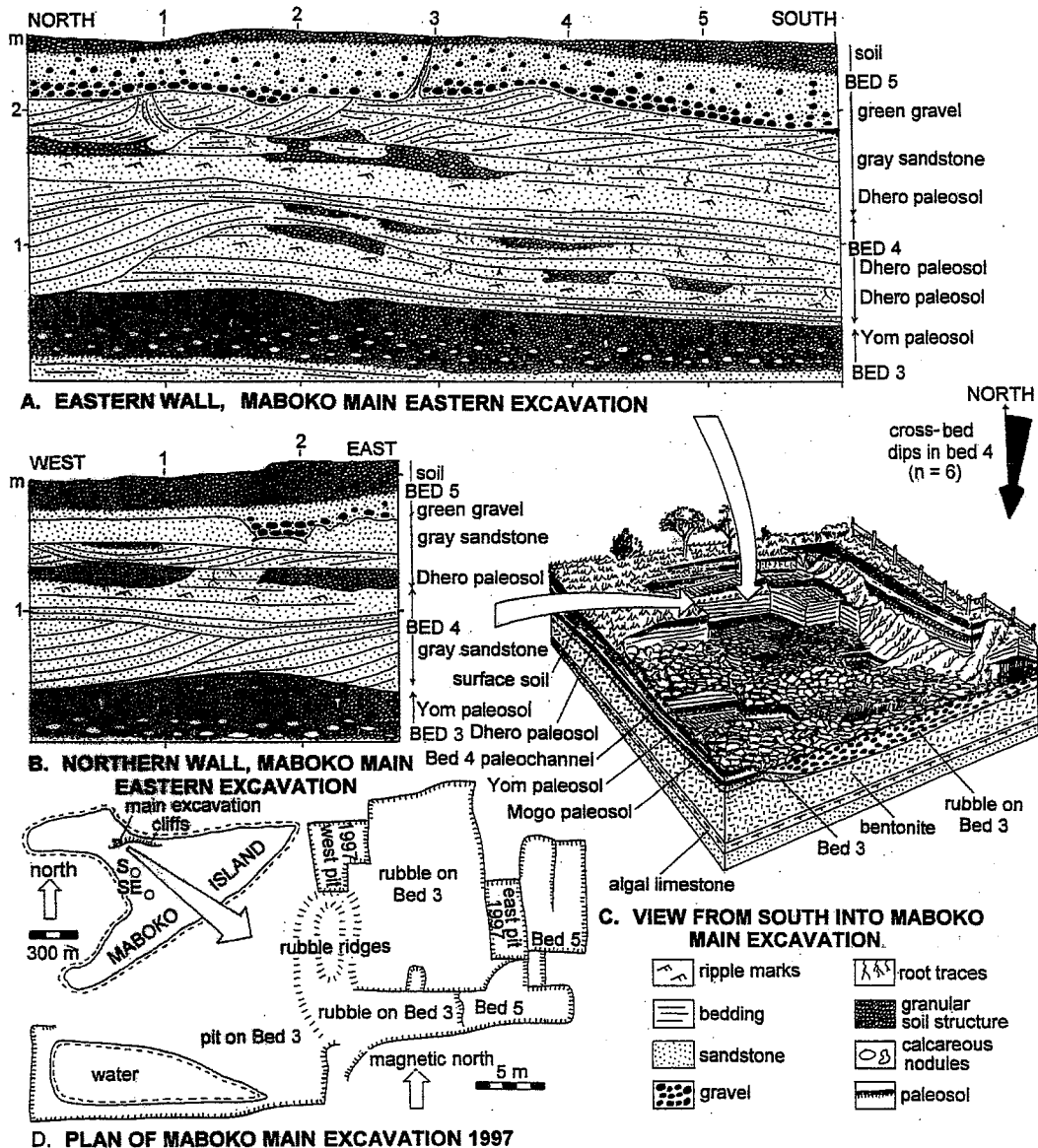


Figure 2. Sedimentological sketches, overview and plan of the Maboko main excavation in June 1997, Maboko Island, Kenya. Bed numbers are from Pickford (1984, 1986a).

Majiwa Bluffs (Figures 2, 5 and 6). Scales for acid reaction and degree of development of the paleosols are explained by Retallack (1997a). Color is from Munsell Color (1975). Pedotype names for the paleosols were taken from the local Luo language

(Gorman, 1972). Samples were cut and ground into petrographic thin sections, described using terminology of Brewer (1976), and point counted using a Swift automated stage and counter, to show both grain size and mineral composition of the



Figure 3. View from southwest of eastern pit of Maboko main excavation, Maboko Island, Kenya.

paleosols (Figure 7). Major and trace element geochemical analysis was by XRF in the commercial laboratory of Bondar-Clegg, Vancouver, Canada. Bulk density was estimated by the clod method, using paraffin (Retallack, 1997a). Clay mineral analysis was based on XRD traces using a Rigaku Miniflex instrument (Figure 8), and modal compositions calculated by the computer program *NEWMOD* (Reynolds, 1985). Rock specimens are stored in the Department of Palaeontology, National Museums of Kenya.

Although stable isotopic studies of carbon and oxygen in paleosols of East Africa have been revealing (Cerling *et al.*, 1992; Kingston *et al.*, 1994), they were not attempted with this study for several reasons. Such studies have been used to discriminate isotopically heavy carbon of C_4 plants (such as tropical grasses) from isotopically light carbon of C_3 plants (most trees and shrubs). A third group of plants with CAM physiology have carbon isotopic

composition intermediate between C_3 and C_4 end members, and are ignored in most studies because such plants are rare in well-drained subhumid to humid soils (Koch, 1998). Unfortunately both paleosols and fossil fauna on Maboko Island indicate seasonal waterlogging and aridity, conditions under which CAM plants thrive. There is also the difficulty, discovered at Fort Ternan and then other Miocene sites worldwide, of abundant tropical and warm temperate C_3 grasses before the late Miocene (7 Ma), thus undermining the utility of isotopic studies of paleosols for revealing tropical grasslands older than late Miocene (Cerling *et al.*, 1997b; Koch, 1998; MacFadden, 2000).

Description and classification of the paleosols

The paleosols were classified within both nongenetic, field-based pedotypes

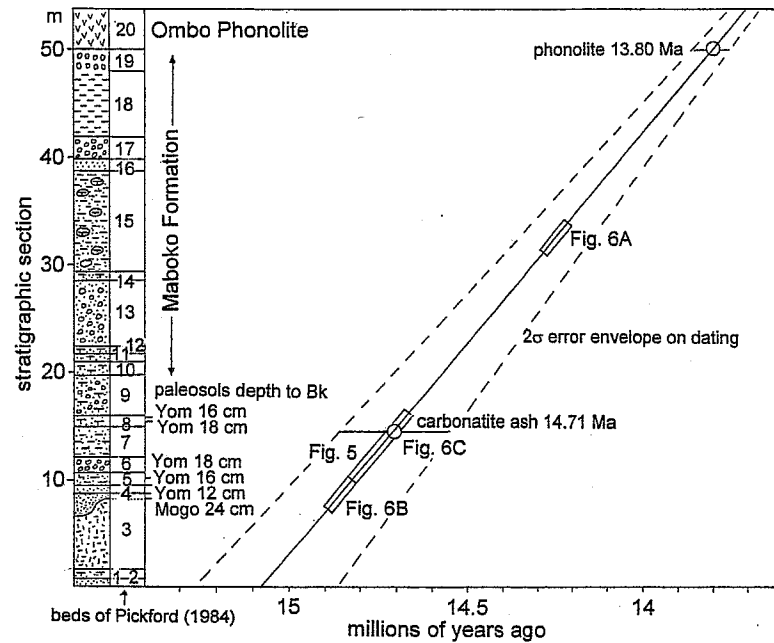


Figure 4. Graphical correlation of measured sections of the middle Miocene Maboko Formation to high-precision radiometric data of Feibel & Brown (1991).

(Retallack, 1994a), and genetic classifications of modern soils (Stace *et al.*, 1968; Northcote, 1974; Soil Classification Working Group, 1991; Soil Survey Staff, 1999). Pedotypes are named for convenience of field recognition (Figure 9), but identifications in modern soil classifications are interpretations based on both field and laboratory data (Figures 6 and 7).

Pedotype recognition

Four distinct pedotypes were recognized during fieldwork (Table 4). Thin, gray, crumb-textured Yom paleosols on Maboko Island are similar to those previously described from Rusinga Island (Retallack *et al.*, 1995), but have less reddish hue and finer soil structure than the single profile from Rusinga Island. Dhero paleosols on Maboko Island show little pedogenic modification beyond root traces in redeposited carbonatite ash, as for comparable profiles at Fort Ternan, but were not on lahars like some Dhero profiles at Fort Ternan

(Retallack, 1991a). Ratong paleosols of Maboko Cliffs and Majiwa Bluff are orange-brown in color with abundant, shallow, rounded, carbonate nodules, and sandy to conglomeratic, carbonatite parent materials, as for Ratong paleosols in the laterally equivalent Nyakach Formation at Kaimogool (Wynn & Retallack, 2001). The wide geographic and temporal distribution of these pedotypes in southwest Kenya is evident that they reflect local paleoenvironments, rather than temporal marker beds.

The only new pedotype recognized with this study is the Mogo clay paleosol, which is clayey and bentonitic, with nodular to tabular carbonate horizons. Only one example was found, forming a floor to the current main excavation on Maboko Island.

Pedotype classification

From the perspective of modern soil classifications, the abundant carbonate nodules at a shallow level (<1 m) in Ratong paleosols [Figure 9(a)] mark them as Aridisols of the

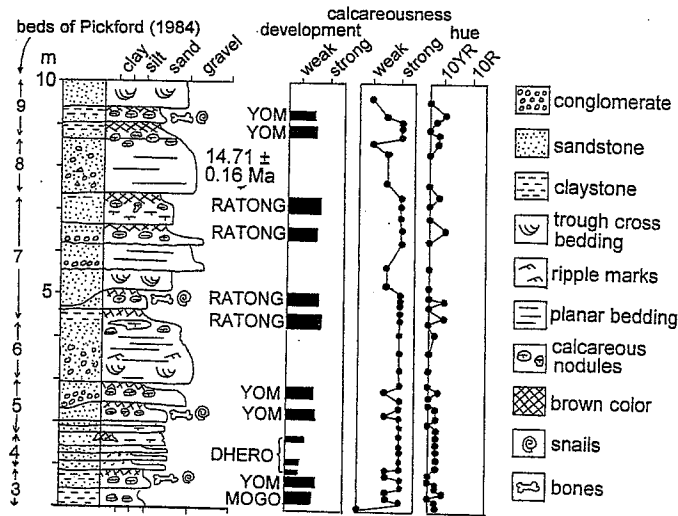


Figure 5. Geological section from Maboko main excavation eastward to Maboko Cliffs on Maboko Island, Kenya, showing position and variety of paleosols. Scales for degree of development of paleosols and calcareousness are from Retallack (1997a), and hue from Munsell Color (1975). Bed numbers are from Pickford (1984, 1986a).

U.S. taxonomy (Soil Survey Staff, 1999), and more specifically as Haplocalcids. In the FAO (1974) classification these are most like Calcic Xerosols. Other identifications shown in Table 4 are from the South African (Soil Classification Working Group, 1991) and Australian classifications (Stace *et al.*, 1968), and the Northcote (1974) key.

Soil classification of other pedotypes on fresh carbonatite and phonolite volcanic ash requires chemical and petrographic data. Soil development on carbonatite and phonolite tuffs is distinct from that on other parent materials (Hay, 1978; Mizota & Chapelle, 1988; Mizota *et al.*, 1988; Retallack, 1991a; Bestland & Retallack, 1993; Retallack *et al.*, 1995). In summary, friable carbonatite tuffs weather to fertile clayey soils (Cambisols, Kastanozems, Luvisols of FAO, 1974) like those on calcareous beach sand, but vitric tuffs weather into low density soils with abundant noncrystalline colloids (Andosols of FAO, 1974). None of these orders is appropriate for Yom

or Mogo paleosols because of their drab colors and iron-manganese nodules that indicate substantial waterlogging, characteristic of Gleysols and Solonchaks. The Yom paleosol near the top of the Maboko main excavation (upper Bed 5 of Figures 2 and 4), has some slickensides, but these are not organized into lentil or wedge peds or lenticular subsurface horizons characteristic of Vertisols (Coulombe *et al.*, 1996). The iron-manganese stain of Yom paleosols marks them as Gleyic Cambisols and the high soda values (particularly soda/potash ratios of Figure 7) of the type Mogo clay paleosol is suggestive of Gleyic Solonchaks. Dhero paleosols include much fresh carbonatite ash, with abundant pyroxene and other easily weathered materials. Evidence of early cementation includes distinctive petrographic fabrics (vermiform and pervasively displacive calcite) and breccias around root traces, as in other carbonatite paleosols of southwest Kenya (Retallack, 1991a; Retallack *et al.*, 1995). Despite this, their

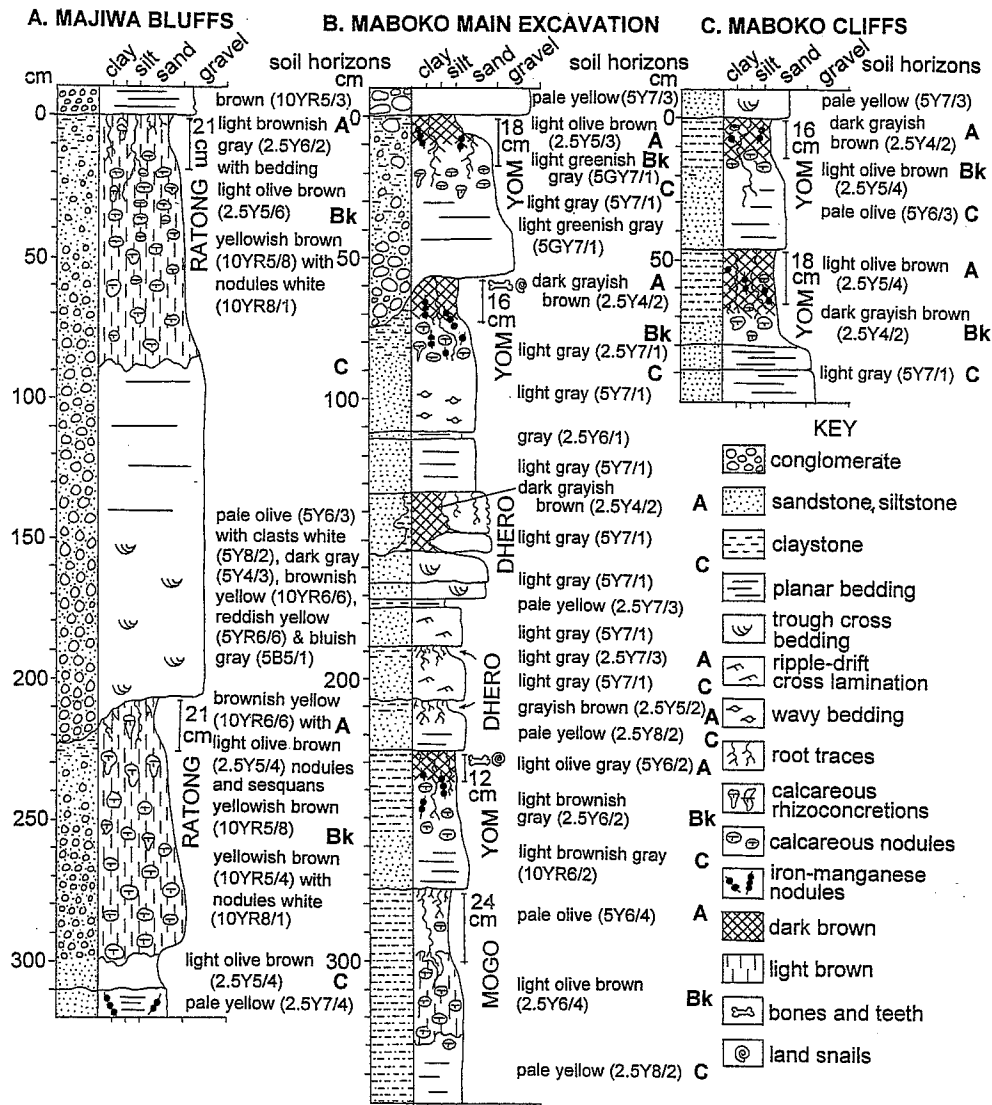


Figure 6. Detailed measured sections of paleosols at (right to left) Majiwa Bluff (A), Maboko main excavation (B) and eastern Maboko cliffs (C), Kenya.

strong alluvial association indicates that they were probably Calcaric Fluvisols in the FAO (1974) classification.

Within the U.S. soil taxonomy (Soil Survey Staff, 1999), Gleyic Solonchaks envisaged for Mogo paleosols are Aquisalids. There is also evidence from iron-manganese nodules and drab hue for

waterlogging in Dhero paleosols, which are here identified as Endoaquents. Yom paleosols lack mollic structure of sufficient depth (18 cm is needed) to qualify as Mollisols, and are only weakly differentiated like Inceptisols, such as Aquic Ustropepts. Identifications in other soil classifications are given in Table 4.

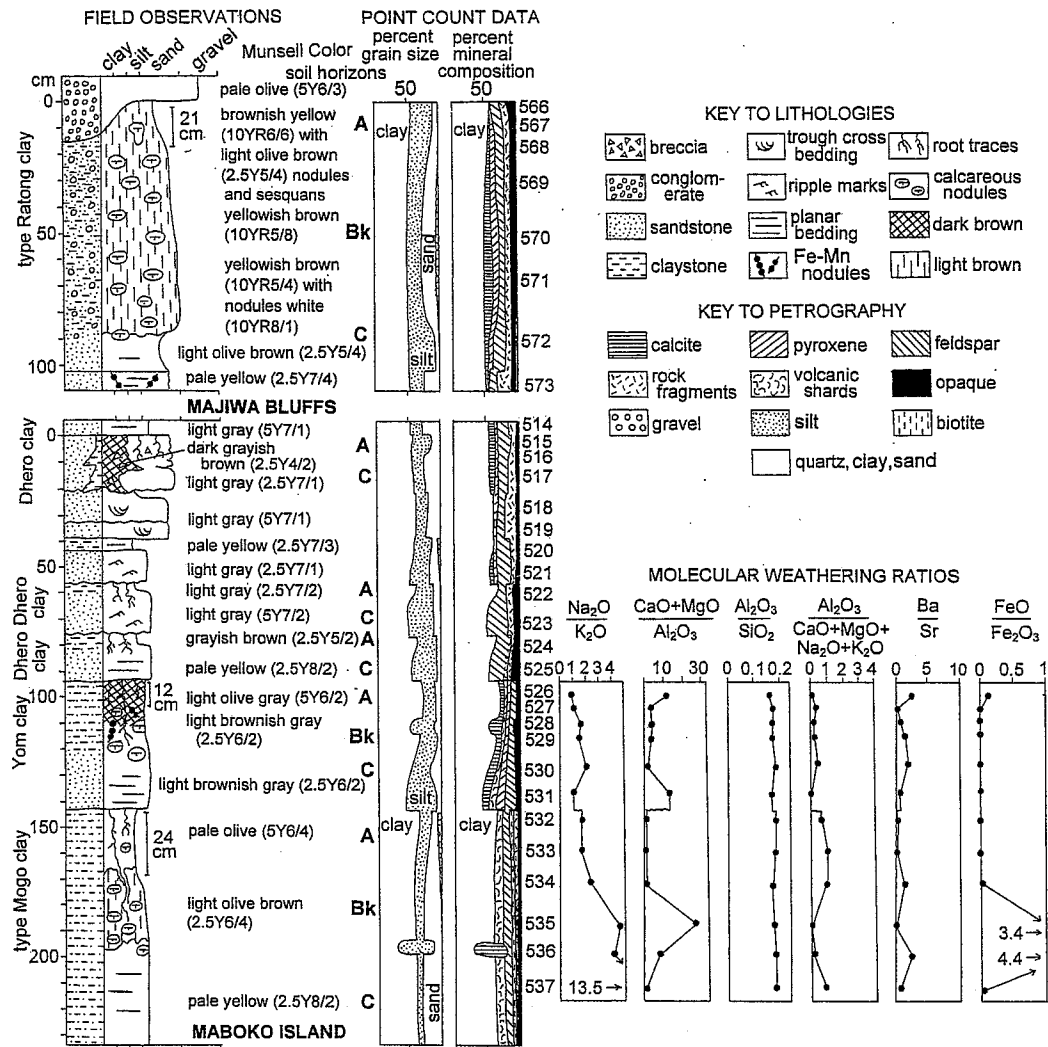


Figure 7. Measured section, Munsell colors, soil horizons, grain size, mineral compositions, and selected molecular weathering ratios of Dhero, Yom and Mogo paleosols in Maboko main excavation, middle Miocene, Maboko Formation.

Burial alteration constraints on paleosol interpretation

Before interpreting paleosols in the Maboko Formation, it is well to consider the degree to which they have been altered after burial. Decomposition of organic matter within all the paleosols is the most significant burial alteration, considering the absence of plant

fossils and scarcity of organic matter, despite the common large root traces filled with calcite.

There is no evidence of reddening of ferric hydroxide minerals during burial, because neither the gray to yellow paleosols on Maboko Island nor the orange paleosols of Majiwa are red. Burial gleization is unlikely for paleosols on Maboko Island, with their

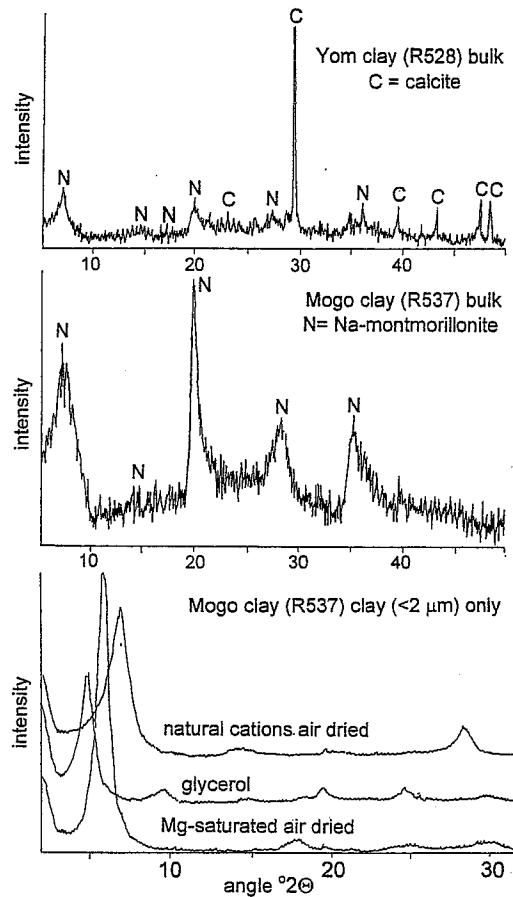


Figure 8. X-ray diffractometer traces of clays from Maboko main excavation, Maboko Island, Kenya: (a) bulk sample from Yom paleosol of upper Bed 3 (sample R528); (b) bulk sample from Mogo paleosol of lower Bed 3 (sample R537); (c) clay (<2 μm) fraction air dried with natural actions and fumigated with glycerol, showing expansion peak of montmorillonite.

prominent iron-manganese nodules like those of originally waterlogged soils. There are some drab-haloed, deeply penetrating root traces in the orange paleosols at Majiwa Bluff, but even here this burial gleization is not as prominent as at Songhor, Kenya (Retallack, 1991a).

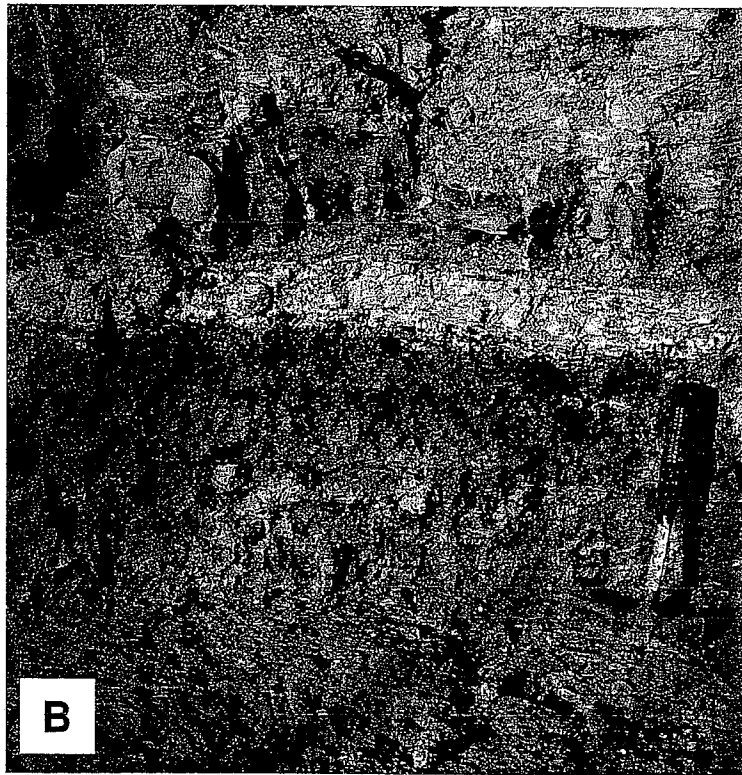
The depth of burial of the Maboko Formation was slight, with a maximum of 50 m within the formation, and no more

than 110 m of overlying phonolite (Pickford, 1982a). Furthermore, the abundance of volcanic pebbles and calcareous nodules at Majiwa and widespread carbonate cement on Maboko Island would render the paleosols resistant to burial compaction (Retallack, 1991b). At such shallow depths illitization or other burial alterations of clays would not be expected, and the broad peaks of clay in X-ray diffractograms confirm

Figure 9. Field photographs of (A) calcareous nodules in Ratong paleosol at Majiwa Bluffs; (B) crumb structured surface horizon of Yom paleosol and relict bedding of overlying Dhero paleosols in Maboko main excavation, Maboko Island.



A



B

lack of burial diagenetic modification (Figure 8).

Parent material constraints on paleosol interpretation

Parent material is the starting point against which soil formation is assessed. Four distinct parent materials in paleosols of the Maboko Formation correspond to geologically distinct source terrains: active carbonatite volcanoes, active phonolite volcanoes, extinct nephelinitic volcanic edifices and Kavirondian–Nyanzian–Bukoban crystalline rocks with lateritic paleosols. Only these last contributed inherited weathering products to the paleosols.

Yom, Dhero and Ratong paleosols are derived from carbonatite ash, because they contain abundant calcite, as rock fragments (alvikite), large crystalline clasts (sövite), calcite-filled spherules, accretionary lapilli, hexagonal pseudomorphs of nepheline, parallelogram pseudomorphs of nyerereite and acicular pseudomorphs of melilite, as is common in Kenyan Miocene paleosols (Retallack, 1991*a*). The accretionary lapilli could be confused with ooids or ministromatolites, but can be distinguished by their cores of angular pyroxene and other pyrogenic carbonatite minerals, their great range in size (1–5 mm), common broken rounds and re-coated fragments [see Wynn & Retallack, 2001, Figure 7(e)]. Isolated crystals of pyroxene are also common [Figure 10(c)], especially in Dhero paleosols. The core complex of Kisingiri Volcano is a carbonatite intrusion of about the right geological age (Le Bas, 1977; Drake *et al.*, 1988), and may have been cognate with an eruptive stage from parasitic cinder cones of what was by then a large shield volcano (Bestland *et al.*, 1995).

The type Mogo clay paleosol capping the bentonite at the base of the Maboko main excavation (Figure 2; Table 5) includes numerous pseudomorphs of volcanic shards

replaced by Na-montmorillonite [Figures 8 and 10(d)]. This bentonite has retained a bulk geochemical composition, including very elevated values of Ba, most like Kenyan Miocene phonolites and a Pliocene (4 Ma) tuff from Laetoli, Tanzania (Tables 6, 7). The parent ash of this Maboko bentonite may represent an early phase of middle Miocene Plateau Phonolite eruptions, which include the Kericho Phonolites at Fort Ternan and Nyakach, and the Ombo and Kisumu Phonolites near Maboko Island (Lippard, 1973; Baker, 1987). Some of the earliest of these phonolite flows near their source vents to the east are coeval with deposition of the Maboko Formation. For example the Baraget Phonolite at Fort Ternan has been dated at 15.0 ± 0.1 Ma using $^{39}\text{Ar}/^{40}\text{Ar}$ degassing (Hooker & Miller for Shipman *et al.*, 1981).

Ratong paleosols at Majiwa contain a few clasts of nephelinite lava which could be derived either from the Kiangata Agglomerate of Kisingiri Volcano (20–18 Ma) some 60 km to the south, or (more likely) from the Kapurtay Agglomerate of Tinderet Volcano (18–16 Ma) some 70 km to the east (Retallack, 1991*a*; Bestland *et al.*, 1995).

Ratong paleosols also contain quartz, feldspar and metamorphic rock fragments derived from Nyanzian–Kavirondian–Bukoban basement rocks, as well as hematitic claystone clasts from erosion of earlier Miocene lateritic paleosols developed on these basement rocks (Retallack, 1991*a*). A moderately hilly terrane of inselbergs, rocks and relict soils extended northward from the Maboko–Nyakach basin.

Implications of paleosols for sediment accumulation and age

The duration of paleosol formation inferred by comparison with Quaternary soils is relevant to both geological age and sediment accumulation rates and gaps. Ratong

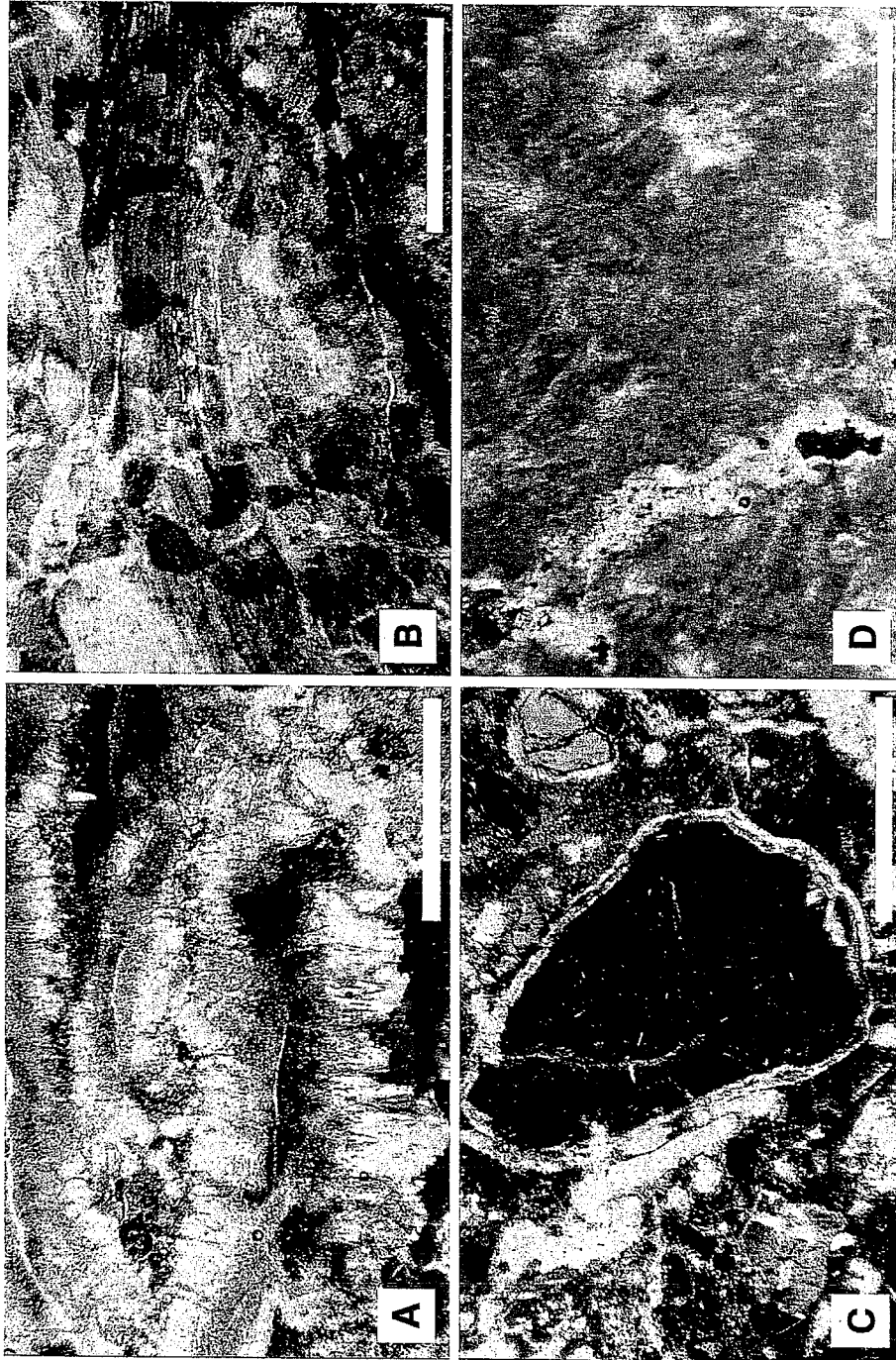


Figure 10. Photomicrographs viewed under crossed nicols of Maboko Island travertines, paleosols and volcanic ashes: (A) fibrous calcite growth from skeins of cyanobacteria in algal limestone (Bed 2 of Figure 4, specimen R575); (B) banded clay skin (argillan) from algal limestone (Bed 2 of Figure 4, specimen R575); (C) pedogenic alteration of carbonatite with circumgranular cracks and root traces filled with sparry calcite (Majiwa specimen R570); (D) altered shards of phonolithic vitric tuff (upper bed 3 of Figure 4, specimen R537). Scale bars all 1 mm.

Table 5 Description of type Mogo clay paleosol in Maboko main excavation, Kenya

Top (cm)	Horizon	Rock type	Prominent colors	Other	Microfabric	Contact
+ 17	Above	Fine-grained sandstone	Light brownish gray (10 YR6/2)	Faint relict bedding, manganese stain very dark gray (10 YR3/1), small mottles of yellowish brown (10 YR5/6); strongly calcareous	Porphyroskelic calciasepic: opaque mottles, calcite spherules, biotite, feldspar, sovite	Abrupt smooth to
0	A	Claystone	Pale olive (5 Y6/4)	Rhizoconcretions (up to 7 mm diameter) and veins of calcite white (2.5 Y8/1), mottles yellow (2.5 Y7/6); coarse granular ped; weakly calcareous	Porphyroskelic skeimosepic; clay skins (argillans) with 2-3 bands; volcanic shards	Irregular gradual to
- 23	Bk	Silty claystone	Light olive brown (2.5 Y6/4)	Common calcite nodules (up to 5 cm diameter) of white (2.5 Y8/1); weak coarse blocky structure defined by sesquans yellowish brown (10 YR5/6) and mangans very dark gray (10 YR3/1); strongly calcareous	Porphyroskelic skeimasepic in clayey matrix, porphyroskelic calciasepic with vermiciform displace calcite in nodules; volcanic shards	Irregular gradual to
- 50	C	Fine-grained sandstone	Pale yellow (2.5 Y8/2)	Massive, with sand-sized grains of yellow (2.5 Y7/6) and very dark gray (2.5 Y3/1); strongly calcareous	Porphyroskelic clinobimasepic with common volcanic shards	Base not seen

Table 6 Major element composition (weight %) of paleosols from Maboko Island, Kenya

Paleosol	Hz	#	SiO ₂	TiO ₂	Al ₂ O ₃	Fe ₂ O ₃	FeO	MnO	MgO	CaO	Na ₂ O	K ₂ O	P ₂ O ₅	LOI	Total
Yom	A	526	19.35	0.50	5.51	2.91	0.16	0.43	1.63	32.93	1.03	1.57	0.48	31.58	98.50
	A	527	34.71	0.65	10.31	4.04	<0.05	0.51	2.97	15.10	1.57	2.22	0.54	25.67	98.59
	Bk	528	32.87	0.51	9.74	4.43	<0.05	0.61	2.98	15.65	1.72	1.61	0.82	26.53	98.72
	Bk	529	31.87	0.50	9.49	3.95	<0.05	0.37	2.85	17.49	1.62	1.59	0.64	27.19	98.05
	C	530	44.04	0.39	13.80	3.61	<0.05	0.16	3.63	6.02	1.67	1.15	0.10	24.05	98.86
Mogo	C	531	17.47	0.33	5.03	2.74	<0.05	0.89	1.75	34.48	0.71	0.94	0.70	33.59	98.86
	A	532	45.52	0.40	14.69	3.65	<0.05	0.23	3.52	4.67	1.57	1.33	0.28	23.06	99.05
	A	533	49.15	0.40	15.98	3.84	<0.05	0.23	3.82	0.93	1.66	1.39	0.27	21.36	99.18
	Bk	534	48.72	0.46	15.99	3.83	0.13	0.11	3.74	0.49	1.79	1.13	0.06	21.95	98.66
	Bk	535	9.96	0.06	3.20	0.31	0.48	0.03	1.15	44.75	0.50	0.16	0.04	38.87	99.54
	Bk	536	24.88	0.19	8.06	0.59	1.16	0.05	2.19	28.12	1.19	0.42	0.04	32.48	99.57
	C	537	49.94	0.34	15.57	3.96	0.13	0.06	3.92	0.41	2.57	0.29	0.04	22.92	100.26
Error			0.77	0.044	0.23	0.20	—	0.001	0.04	0.04	0.02	0.05	0.015	—	1.19
Phon.	—	Bak.	51.7	0.9	19.3	3.9	2.4	0.2	1.1	4.1	8.9	4.6	0.3	2.6	100.0
Neph.	—	Bak.	46.2	1.6	18.6	6.0	3.5	0.2	2.3	7.3	9.3	4.2	0.5	1.0	100.7
Mela.	—	Bak.	41.5	2.7	11.9	6.6	5.7	0.2	6.1	14.6	5.7	2.6	0.9	1.8	100.3
tuff	—	Hay	51.42	0.70	15.93	5.25	0.99	0.15	1.93	1.22	3.26	5.44	0.87	13.75	100.68

Analyses of Kenyan phonolites, nephelinites and melanephelinites for comparison are from Baker (1987), and a Tanzanian phonolitic tuff analysis is from Hay (1978).

Table 7 Trace elements (ppm) and bulk density (g cm^{-3}) of paleosols from Maboko Island, Kenya

Paleosol	Hz	Spec.#	Cr	Ba	Sr	Y	Nb	Zr	Rb	Density
Yom	A	526	<1000	3286	835	25	141	122	26	1.67
	A	527	<1000	1030	1229	46	238	365	73	1.68
	Bk	528	<1000	1015	840	58	218	268	58	1.70
	Bk	529	<1000	2889	1415	45	202	258	57	1.63
	C	530	<1000	1390	445	33	154	315	58	1.56
	C	531	<1000	955	999	59	112	154	22	1.75
Mogo	A	532	<1000	270	485	59	133	285	59	1.56
	A	533	<1000	219	681	56	153	311	66	1.59
	Bk	534	<1000	1523	508	24	186	335	58	1.49
	Bk	535	<1000	<10	198	27	<5	63	7	1.54
	Bk	536	<1000	1408	349	26	42	144	17	1.74
	C	537	<1000	356	289	19	81	377	26	1.69
Error	—	—	50	50	0.6	1	3	0.6	7	0.08
Phonolite	—	Baker	—	1240	1190	28	—	840	130	—
Nephelinite	—	Baker	—	1650	2260	29	—	703	116	—
Melaneph.	—	Baker	—	915	1160	31	—	263	63	—

Analyses of Kenyan phonolites, nephelinites and melanephelinites for comparison are from Baker (1987).

paleosols have abundant, small calcareous nodules comparable to those of moderately developed soils (Gile *et al.*, 1980). Comparable development of carbonate nodules in tropical dry soils is seen in Bhalwal Series soils dated at 10–20 ka near Lahore, Pakistan (Ahmad *et al.*, 1977).

Paleosols of carbonatite affiliation (i.e., Yom and Dhero) of Maboko Island can be compared with soils under dry shrublands around the carbonatite volcano Oldoinyo Lengai, in northern Tanzania. Here calcite-cemented hardpans like those of some Dhero paleosols form within 600 years, weakly developed soils like Yom paleosols are found on 2–30 ka Gray Tuffs and Agglomerates, and moderately developed soils like Mogo paleosols are found on 30–400 ka Yellow Tuffs and Agglomerates (Hay, 1989). In slightly wetter grasslands (400–600 mm MAP) of the eastern Serengeti Plains near Olduvai Gorge, Tanzania, also dusted with carbonatite ash, comparable nodules and pans to those of the Mogo paleosol are found in the 3–9 ka Naisiusiu Beds (Hay & Reeder, 1978).

Taking 500 years for Dhero paleosols, 40,000 years for Mogo and 20,000 years for

Yom and Ratong paleosols, the amount of time represented by paleosols in the main fossiliferous sequence (beds 3–9 of Figure 4) on Maboko Island is 301,500 years for an accumulation rate of 0.31 mm/yr. This estimate is compatible with estimates from radiometric dating (by Feibel & Brown, 1991) of the phonolite (13.80 Ma) and a carbonatite ash (Bed 8–14.71 Ma) extrapolated backward to 14.86 ± 0.17 Ma for the base of the main excavation (upper bed 3 of Figure 4). From this, a duration for deposition and soil formation of beds 3–9 is 210,000 years for an accumulation rate of 0.45 mm/yr. Maboko Formation rates of sediment accumulation are more than inferred from paleosols of the laterally equivalent Nyakach Formation (0.4–0.24 mm/yr at ca. 15 Ma) along the margin of the Maboko–Nyakach depositional basin to the south (Wynn & Retallack, 2001). The Maboko rates are also greater than rates (0.11 mm/yr at ca. 18 Ma) for paleosols in redeposited volcanoclastics of the Fossil Bed Member of the Hiwegi Formation on Rusinga Island (Retallack *et al.*, 1995; Bestland & Krull, 1999), and greater than rates (0.14 mm/yr at ca. 14 Ma) from

paleosols at Fort Ternan where ash and lahars accumulated on upland phonolite plateaus (Retallack, 1991a). The Maboko Formation accumulated in a depocenter at a time of active volcanism.

Paleotopographic implications of the paleosols

Paleosols in the Maboko Formation show evidence of seasonal waterlogging expected in a lowland fluvial basin, but not fully lacustrine facies (Pickford, 1982b). The thickly bedded carbonatite tuffs (Bed 4) have ripple marks and trough cross beds indicating that they were redeposited, rather than accumulating from airfall into water. Furthermore this sequence was periodically colonized by trees, as indicated by large root traces and stump casts in Dhero paleosols. The thick bentonite (also Bed 3) below this paleochannel and Mogo paleosol also lacks lacustrine varves and graded bedding, and is a massive phonolitic tuff altered to Na-montmorillonite (Figure 8, Tables 5-7). The other pedotype of Maboko (Yom) was better drained with more oxidized, brown colors, more deeply penetrating root traces, and a mollic surface indicating substantial permanent ground cover. There is evidence from iron-manganese nodules and spots, persistence of reduced iron and pervasively drab colors that these paleosols were seasonally saturated (Rahmatullah *et al.*, 1990; McDaniel & Buol, 1991). On the other hand, carbonate nodules and deeply reaching root traces are evidence of a dry season, during which water table, streams and lakes fell to low levels and gained salinity.

A thin (<1 m) lens of clayey green sands in bed 3 (Kent, 1944; Andrews, 1981a, plate 5), has now been completely excavated because of its rich fossil content. We interpret it as a streamside swale. Such elongate depressions are common within the levee complex of streams as conduits for floodwaters downstream and feeding into

crevasse splays (Davis, 1983; Miall, 1996). The lower surface of this green sand swale was the impermeable montmorillonite clays of the Mogo paleosol, and it is likely that perched water persisted here for animals long after it disappeared from sandy stream beds during the dry season.

There are also hints of local standing water from limestone at the base of the Maboko Formation (Bed 2 of Figure 4). The basal limestone is distinct from the Maboko calcretes and carbonatites in its surface texture like skeins of cyanobacteria and its appearance in thin section of fenestral fabric of sparry calcite in the interstices defined by palisades of radial fibrous calcite growing in both directions from a network of planar surfaces [Figure 10(a)]. This kind of fibrous calcite growth around skeins of cyanobacteria is characteristic of travertine and tufa (Julia, 1983; Chafetz & Guidry, 1999). This fabric differs fundamentally from superficially similar pervasively displacive carbonate of pedogenically altered carbonatites (Retallack, 1991a; Retallack *et al.*, 1995) in that it does not appear to displace clayey matrix, but instead grows from organic substrates into open cavities. There is also a cavity-filling, equant, sparry calcite, probably meteoric carbonate cement formed during weathering and subsequent burial of the bed (compare photomicrographs of Adams & Mackenzie, 1998). This distinctive nonpedogenic limestone is not well exposed, but can be traced for several hundred meters west of Maboko main excavation as a flat-lying bed with no discernible relief. The surface shows only cyanobacterial filaments, and sparse root traces with banded clayskins [Figure 10(b)]. There are no fossils such as the twigs, leaves and charophytes common in travertines and tufas, nor rimstone dams, pools or cascades. Presumably it was a broad spring mound or mudflat marginal to a lake, rather than a speleothem, tufa mound or hot spring (Eugster & Kelts, 1983). Comparable

travertines form today around alkaline lakes within Ngorongoro Crater, Tanzania, and also have been found within lower Bed II (1.8 Ma) in the Plio-Pleistocene sequence of Olduvai Gorge, Tanzania (Ashley, 2000). Soda lakes of East Africa are commonly choked by near-monospecific algal blooms of cyanobacteria (*Spirulina platensis*) harvested by flocks of flamingos (Melack, 1996).

Sediments from deeper parts of these lakes may yet be discovered in the subsurface Maboko Formation to the south and east of Maboko Island. Analcime-rich varved shales with well-preserved fossil fish have been found in the Tambach Formation, near Muruyur in the Baringo Basin, roughly coeval (15 Ma) with the Maboko Formation (Renaut *et al.*, 1999). Fossiliferous lacustrine shales also are known from the earlier Miocene (18 Ma) Kulu Member on Rusinga Island (Bestland, 1991) and the late Miocene (9 Ma) Ngorora Formation near Baringo (Renaut *et al.*, 1999).

Paleoclimate

A variety of observations indicate a surprisingly dry middle Miocene (15 Ma) paleoclimate for Maboko and Majiwa. These include not only the depth to calcic horizon, clay minerals, iron-manganese nodules and modern comparison of paleosols, but evidence for seasonally dry paleochannels, for open vegetation and for water stressed plants and animals.

Depth to paleosol calcic horizon

Depth to calcic horizon has been found to show a clear relationship to mean annual precipitation in soils, provided competing factors such as topographic position and degree of development of the calcic horizon are considered (Royer, 1999; Retallack, 2000; Wynn & Retallack, 2001). Yet

another important variable is evapotranspiration, which is high in tropical regions, and limited available soil moisture. Wynn & Retallack (2001) have taken only tropical African data to derive the following transfer function for depth to calcic horizon (d) and mean annual precipitation (P) from African lowland soils of moderate development on sedimentary parent materials:

$$P = [d / (0.0267 + 0.00102d)] - 32.3$$

($\sigma = \pm 161$ mm; $r = 0.59$; $r^2 = 0.35$; $n = 58$). Correction was made for reduction in depth to calcic horizon due to compaction of overburden, using the compaction equation of Sheldon & Retallack (2001) for Inceptisols. Granular soil structure and calcareous rhizonecretions in the upper horizons of the paleosols are evidence that they were not appreciably eroded before burial. No correction was made for changing atmospheric composition, because Miocene change in CO_2 partial pressure was too small to significantly affect depth to calcic horizons (Ekart *et al.*, 1999; Pagani *et al.*, 1999; Retallack, 2001a).

Another potential problem with interpretation of calcic horizons on Maboko Island is the pitfall of "mock aridity", a false impression of dry climate created by rapid deposition, zeolites, and abundant carbonates of active carbonatite-nephelinite volcanism (Harris & Van Couvering, 1995; Bestland & Krull, 1999). We have taken pains not to infer paleoclimate from zeolites or volcanoclastic depositional features. The problem of carbonate inheritance from carbonatite is circumvented by comparing the Maboko paleosols only with soils on carbonatite volcanics. Soils developed on carbonatite ash were completely decalcified in less than 4000 years under MAP 1444 mm at Fort Portal, Uganda (Harrop, 1960; Osmaston, 1967). Soils on carbonatite ash around Basotu Craters and in the western Serengeti Plains, Tanzania [mean annual precipitation

(MAP) >600 mm], have calcareous nodules developed to a degree comparable with Yom and Ratong paleosols of the Maboko Formation, indicating a comparable time for soil development, yet the calcic horizon is deeper within the soils around Basotu Craters (Fenger *et al.*, 1986) and the western Serengeti Plains (Jager, 1982). Soils developed in a dry climate (<400 mm MAP) around Oldoinyo Lengai carbonatite volcano and eastern Serengeti Plains, Tanzania (de Wit, 1978; Hay, 1978, 1989) have abundant carbonate, in part due to times for formation of as much as 400 ka, but their pedogenic carbonate is shallower in the profile than in paleosols of the Maboko Formation. These soils were included in our depth-precipitation relationship (see Wynn & Retallack, 2001). Decalcification and depth to carbonate horizons of soils on carbonatites is not unusual, and these comparisons also suggest MAP of 400–600 mm during deposition of the Maboko Formation.

Compaction-corrected depths to the calcic horizon in paleosols of Maboko Island give MAP of $278\text{--}369 \pm 161$ mm (for Yom paleosols) and 439 ± 161 mm (for Mogo), which in round numbers is some 150–600 mm MAP. Ratong paleosols at Majiwa both gave 404 ± 161 mm, or roughly 250–550 mm MAP. In the agro-climatic classification of the Kenyan Soil Survey (Sombroek *et al.*, 1982) these are all arid.

Paleosol clay mineralogy

Another line of evidence for dry climate comes from the Na-montmorillonite clays of Yom and Mogo paleosols (Figure 8), which indicate very limited weathering and leaching of clay (Weaver, 1989). In East Africa, such smectite clays are found in ashy soils forming under less than 1200 mm MAP (Mizota & Chapelle, 1988; Mizota *et al.*, 1988). Clays of the paleosols on Maboko Island are more base-rich than those of soils around the Basotu Craters of Tanzania

(605 mm MAP; Fenger *et al.*, 1986), but are less base-rich than soils with palygorskite, phillipsite and gaylussite around the volcano Oldoinyo Lengai, Tanzania (<400 mm MAP: Hay, 1978, 1989). Among Kenyan Miocene paleosols, the clays of Maboko paleosols are more base-rich than those of any paleosols yet recorded from Fort Ternan (Retallack, 1991a) or Rusinga Island (Retallack *et al.*, 1995), interpreted from recalibrated depth to calcic horizon to have formed in climate no drier than 386 ± 161 mm MAP (Chogo at Fort Ternan) or 443 ± 161 mm MAP (Yom on Rusinga Island). The fibrous clay palygorskite and the zeolites gaylussite and phillipsite are common in lakes and soils of very arid (<300 mm MAP) regions (Weaver, 1989; Calvo *et al.*, 1999; Renaut *et al.*, 1999), but were not detected in paleosols on Maboko Island (Figure 8). The absence of the zeolites could be blamed on alteration after burial, but palygorskite is locally common in paleosols, some of them as ancient as Permian (Watts, 1976; Calvo *et al.*, 1999). Thus, a dry but not desertic paleoclimate is indicated by clay mineralogy for Maboko Island during the middle Miocene.

Paleosol iron-manganese nodules

Seasonal waterlogging of Yom and Mogo paleosols is indicated by iron manganese nodules and drab colors (Rahmatullah *et al.*, 1990; McDaniel & Buol, 1991), yet occasional deeply penetrating calcareous rhizoconcretions and clay-filled root traces remain, indicating dry seasons. Clay skins in the paleosols show banding, but the bands are not strongly iron stained [Figure 10(b)] compared with clay skins in monsoonal tropical soils and paleosols (Retallack, 1991a). Calcareous rhizoconcretions are mostly filled with sparry calcite, and do not show the fine ferric-calcareous banding seen in Miocene paleosols and modern soils of such monsoonal tropical regions as Pakistan (Tandon & Narayan, 1981;

Retallack, 1991a). Although slickensided, none of the paleosols at Maboko is a Vertisol, with the deep and systematic cracking patterns found in modern soils of the Kano Plain near Kisumu (Thorp *et al.*, 1960), or an alluvial flats near Majiwa and Kaloma (Saggerson, 1952), or in Miocene–Pleistocene paleosols of northwest Kenya (Wynn & Feibel, 1995; Wynn, 2000; Retallack, 2001b). Thus, there were dry seasons during the middle Miocene, but dry seasons did not last so many weeks or involve such a moisture deficit as Kenyan dry seasons since the late Miocene.

Analogous modern soils

Another way of inferring paleoclimate in paleosols is to consider the paleoclimate of analogous modern soils (Table 4). The FAO classification is especially useful because East African soils have been mapped using this scheme (FAO, 1977; Sombroek *et al.*, 1982). There are no comparably calcareous soils in southwest, highland or coastal Kenya today, because these areas have high rainfall, which leaches carbonate from soils. Nor were there any soluble salts or their pseudomorphs in the Maboko paleosols, as in desert soils of northeast Kenya today. Landscapes dominated by Calcic Xerosols with inclusions of Solonchak are found today in three separate areas extending from Kora National Reserve on the Tana River almost to Maralal in Kenya (FAO, 1977, map unit X7-2ab; Sombroek *et al.*, 1982, map unit Pf2), around Lodwar to the west of Lake Turkana in Kenya (FAO, 1977, map unit Xk19-2a), and also in Ethiopia on the fringes of the Afar depression from Awash east to Waruf and from Awash north to Tendaho (Xk20-2a). There are also similar soils near the Tsavo River, 20 km east of Ngulia lodge in Tsavo National Park, Kenya, although most of this area has a more deeply-weathered red soil remaining from long-term Cenozoic weathering of Precambrian basement rocks (Sombroek

et al., 1982), comparable to lateritic paleosols on the Kavirondian–Nyanzian–Bukoban basement rocks underlying the Maboko Formation (Saggerson, 1952; Retallack, 1991a). Another comparable modern soilscape is around Lotigipi Swamp of northwest Kenya and the nearby Kobowen and Kenamuke Swamps of Sudan (map unit Gm 15-2a, with inclusions of Fluvisols and Solonchaks, of FAO, 1977).

At Voi in Tsavo National Park, Kenya, MAP is 538 mm, with peak rainfall (96–126 mm average) in November–December, another wet season (73–92 mm average) in March–April, and dry seasons in January (30 mm average) and June–August (3–8 mm average per month). Mean annual temperature at Voi is 30°C, with little fluctuation in monthly means (28–32°C) throughout the year. Average annual evapotranspiration is high (2148 mm: Griffiths, 1972). For other comparable modern soilscares, such as Lokichokio near Lopitipi Swamp in northwest Kenya, MAP is 524 mm (Walsh & Dodson, 1969), and for Kora National Preserve it is between 500 and 380 mm (Coe, 1985). Although middle Miocene climate was seasonally dry, hot, and isothermal, dry seasons as long and dry as those of today are unlikely.

Sedimentary evidence for dry paleoclimate

Another line of evidence for dry seasons is the distinctive sedimentary architecture of the gray sandstones (Bed 4) in Maboko main excavation (Figures 2 and 3). In the eastern side of the pit are shallowly dipping, heterolithic, cross-bedded sandstones, and thin very weakly developed paleosols (Dhero pedotype). These pass laterally to the north into trough cross-bedded sandstones and conglomeratic lag deposits. This bed lacks claystone clasts, unlike lunette dune deposits (Bowler, 1973; Goudie & Thomas, 1983). It also lacks conduits, travertines or fully aquatic facies of spring mounds (Eugster & Kelts, 1983). There also are

problems with interpreting it as a levee, crevasse-splay or channel (Davis, 1983; Miall, 1996): for example, its lateral gradation from heterolithic to trough cross bedding without erosional truncation or channelization. Dhero paleosols remained spotted with iron-manganese nodules and retained much pyroxene, unlike oxidation and weathering expected during the dry season on a tropical fluvial levee-crevasse system. Also unusual for levees is soft-sediment deformation and shallow holes in the carbonatite sands filled with gray-brown claystone (Figure 2). These anomalous features are better explained as trample marks and waterholes excavated by mammals in an ephemeral stream bed, or lugga, in East African parlance (Coe, 1985). During the wet season this was a raging torrent, creating large sand waves, but in the dry season, the stream became a chain of ponds with wind-rippled sand over moist sand just below the surface. Interpreted in this way, the dry season water table would have been shallower than in the Turkana and Kora regions of Kenya today, where water is dug from several meters below dry washes at the height of the dry season.

Paleontological evidence for dry climate

Paleobotanically-based maps of early and middle Miocene vegetation of East Africa (Retallack, 1991a; Pickford, 1992; O'Brien & Peters, 1999) show much drier conditions than the extensive rain forest envisaged by Andrews & Van Couvering (1975). Dry conditions during deposition of the Maboko Formation are confirmed by a small fossil flora in the laterally equivalent Nyakach Formation at Kaimogool (Wynn & Retallack, 2001). Fossil land snails of Maboko, Majiwa and Kaloma are most like snails of nyika bushland and gallery woodland of the central Tana River with MAP <500 mm (Pickford, 1995). Dry and open vegetation is also indicated by the most common of the large terrestrial mammals

in Yom paleosols, the antlered giraffoid *Climacoceras africanus* (Thomas, 1985), and by the prominent size gap in the cenogram of body-size distribution for the fauna as a whole (Mihlbacher *et al.*, 1998).

A quantitative approach to paleoclimatology from fossils uses transfer functions between mammalian faunal composition and mean annual rainfall, for example the transfer function of Reed (1998) for percent arboreal mammals in African faunas yields a mean annual precipitation of $896-1017 \pm 419$ mm for the Maboko assemblage, depending in whether there are two or one species of proconsuline and oreopithecine. One of us (Retallack) has derived similar transfer functions from faunal data of Andrews *et al.* (1979) and Evans *et al.* (1981). The most significant of these ($r^2=0.48$) is

$$P=52R-273$$

where P is mean annual precipitation (mm) and R is percent rodent species. This transfer function applied to the Maboko fauna gives mean annual precipitation of 645 ± 414 mm.

Seasonality of rainfall is indicated by Maboko snails similar to living *Limicolaria martensiana*, which aestivates during two drought periods per year (Pickford, 1995). Other indications of seasonality come from perikymata bands in molars of *Victoriapithecus* from Maboko Island (Benefit, 1993).

The fossil snail assemblage from Maboko (15 Ma) is also evidence for hot paleotemperature, as for earlier snail assemblages of Rusinga Island and karungu (18 Ma), but unlike cool, upland, fossil snails of Fort Ternan (14 Ma: Pickford, 1985).

Local or regional paleoclimate change?

Miocene, like modern climate in East Africa, probably varied considerably with local topographic, maritime, lacustrine and

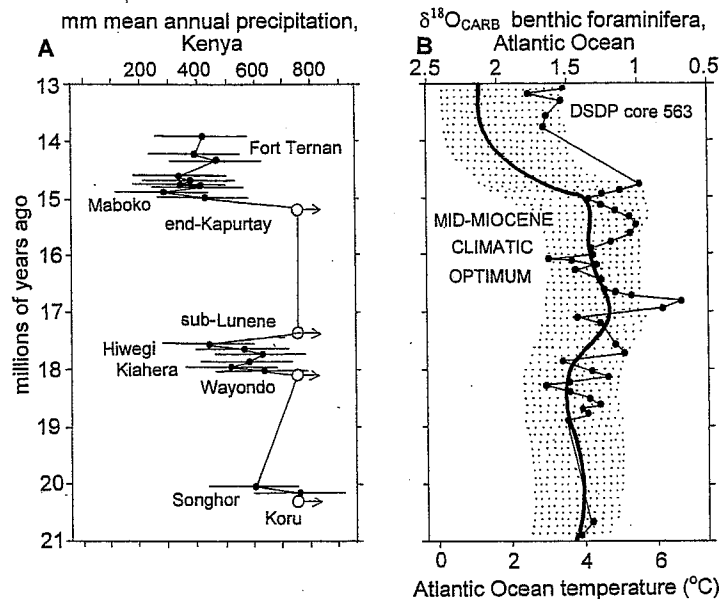


Figure 11. Miocene paleoprecipitation for southwest Kenya inferred from depth to calcic horizon and decalcification of paleosols (Retallack, 1991a; Bestland & Retallack, 1993; Retallack *et al.*, 1995; Wynn & Retallack, 2001) compared with the oxygen isotopic curve from deep sea cores as generalized for the Atlantic Ocean (bold line and shaded error from Miller *et al.*, 1987) and from Atlantic Ocean site 563 (from Wright *et al.*, 1992). Open symbols with arrows represent minimum paleoprecipitation from decalcified paleosols; closed symbols with standard error bars are estimates from depth to calcic horizon.

other effects. Could the paleosols of Maboko represent a local rain shadow? Dry climate was at least basin-wide, because comparable paleoclimate is evident from the same suite of paleosols in the Nyakach Formation (15 Ma), 50 km to the southeast, near Sondu, Kenya (Wynn & Retallack, 2001). Independent indications of arid, seasonal, tropical paleoclimate also come from analcime-bearing, lacustrine, varved shales of the Tambach Formation (15 Ma) near Muruyur in the Baringo Basin of Kenya (Pickford, 1988; Renaut *et al.*, 1999), and gypsiferous lacustrine shales in the Kisegi Formation (11–14 Ma) of western Uganda (Pickford, 1992). Rainforest, Afromontane and coastal wet climates did not disappear, but were reduced in area as dry climate and vegetation spread through many lowland basins of East Africa.

A Miocene rainfall history for southwest Kenya can be reconstructed from the depth to calcic horizon in paleosols (Retallack, 2001b; Wynn & Retallack, 2001), supplemented with evidence from decalcified paleosols (Figure 11), which in Africa represent climates with a MAP >750 mm (Yaalon, 1983). Paleosols of the Maboko and laterally equivalent Nyakach Formations have the shallowest calcic horizons seen in the southwest Kenyan Miocene. As is typical in paleosol sequences (Retallack, 1998), each rock unit also shows paleoclimate drying-upward trends. The wettest paleoclimates are represented by decalcified red soils at several levels: Wayondo Beds on Rusinga Island (ca. 18.1 Ma; Bestland *et al.*, 1995), sub-Lunene Lava paleosol on Rusinga Island (ca. 17 Ma; Thackray, 1994; Bestland

et al., 1995) and uppermost Kapurtay Agglomerate at Fort Ternan (ca. 18–15 Ma: Retallack, 1991a).

A shift to dry climate at 15 Ma was not only widespread in East Africa, but global. The oxygen isotopic composition of foraminifera in deep sea cores has been used as a proxy for global temperature and ice volume (Miller *et al.*, 1987; Wright *et al.*, 1992; Zachos *et al.*, 2001), and shows a marked peak in the middle Miocene at about 16 Ma, preceded by fluctuating levels, and followed by a profound drop nearer to modern levels (Figure 11). Pickford (1995) argued for correlation of Maboko with a global oxygen isotopic and temperature maximum at 16.5 Ma, but radiometric dating of the Maboko Formation (Fiebel & Brown, 1991) indicates a better correlation with the oxygen-isotopic temperature minimum at 15 Ma. By this correlation, Fort Ternan corresponds with a slight rebound to warmer and wetter conditions at 14 Ma, and paleoclimate fluctuations apparent from paleosols in the sequence of Rusinga Island correlate with oxygen isotopic evidence for high but fluctuating temperature from 19–17 Ma. In Wyoming and southern France, the terminal Paleocene climatic warm-spike coincides with deeply weathered, humid-climate paleosols (Koch *et al.*, 1995; Koch, 1998). A comparable middle Miocene warm-wet climatic spike, followed by cooling and drying, has been documented from evidence of fossil foraminifera, plants, and soils in Germany, Japan, South Australia and Oregon (Retallack, 1997a, 2001a; Schwarcz, 1997), and now also southwest Kenya (Figure 11).

Ancient vegetation

One of the surface disruptions of the upper Dhero paleosol in Maboko main eastern excavation is a cast of a tree trunk 12 cm in diameter (Figure 2). Scaling relations

between trunk diameter at breast height and height of tropical trees (Pole, 1999), can be used to predict that this tree was no taller than 16 m, as the presumed diameter at breast height used for this calculation would be smaller than the diameter preserved. The spar-filled interiors of calcareous rhizoconcretions in Yom paleosols are as much as 18 mm in diameter, and were probably formed by the rotting and fill of woody roots of that diameter. Such observations indicate individual trees or bushes, but not necessarily forest.

Limits to stature and spacing of trees during deposition of the Maboko Formation come from the iron-manganese nodules and drab colors of Dhero, Yom and Mogo paleosols and the highly alkaline soil chemistry needed to preserve Na-montmorillonite in the type Mogo clay. Yom paleosols have in addition a dark, crumb soil structure and abundant fire (1–2 mm) root traces [Figures 7 and 9(b)], which are characteristic of sod grassland soils (Retallack, 1991a, 1997b).

Considering also their shallow calcic horizons as indicators of aridity, these paleosols probably supported seasonally waterlogged wooded grassland, of the kind widely called dambo and vlei in Africa (White, 1983; O'Brien & Peters, 1999). Dhero paleosols on the other hand show relict bedding [Figures 2, 7 and 9(b)] and well-preserved pyroxene and other easily weathered minerals, as evidence of a short time for formation. Dhero paleosols probably supported woodland early in the ecological succession to colonize stream margins. Mogo paleosols show greater oxidation in their orange stain, but were much more clayey and sodic than either Yom or Dhero paleosols. Highly alkaline dry season conditions could also explain the lack of fine soil structure and sparseness of calcareous rhizoconcretions in Mogo paleosols. Their vegetation can be envisaged as salt scrub of woody bushes, with little herbaceous cover of ground with seasonal salt efflorescences.

Ratong paleosols at Majiwa and Kaloma also supported woody vegetation with little herbaceous or grassy cover, as indicated by their calcareous rhizoconcretions and surface horizons with blocky to platy structure. Grassland was unlikely, because these create dense root mats and pervasive fine crumb structure. The shallow calcic horizons of Ratong paleosols indicate an arid climate in which trees are no taller than about 6 m and bushes common (Swift *et al.*, 1996). This distinctive dry shrubland and woodland of East Africa is called nyika, a coastal Swahili word also used to describe regions and tribal groups associated with such vegetation (Coe, 1985; Pickford & Senut, 1988). Holocene soils comparable with Ratong paleosols can be seen in the distal levee of the Tsavo River, 20 km east of Ngulia Lodge, Tsavo National Park, Kenya, where nyika bushland grades into streamside gallery woodland of thorn tree (*Acacia* spp.) and Doum palm (*Hyphaene coriacea*; Figure 12). Another area of comparable climate, soils and nyika vegetation is the Kora National Reserve along the central Tana River, Kenya, which has been the subject of comprehensive recent ecological studies (Coe, 1985).

Former animal life

Maboko Island has yielded collections of fossils large enough to reasonably infer habitat preferences from fossil abundance in particular paleosol types (Table 1). Numerous fossils have been excavated from Yom (white upper bed 5) and Dhero (lower brown bed 5) paleosols of the main excavation on Maboko Island (Tables 1–3). Collections from quarry 2 of Andrews *et al.* (1981) are of uncertain provenance. Their report of vertical bones not found in subsequent digging by us may reflect partial excavation of earlier spoil piles. Collections from Bed 3 and Quarry 1 of Andrews *et al.* (1981) are not from a paleosol, but from a highly

fossiliferous green sand, which we interpret as a streamside swale deposit. There are small quarry collections from Ratong paleosols in bed 12 at the S and SE localities (Figure 2). Less certain is the provenance of surface collections in steep slopes of beds 13–16 at Maboko Cliffs, Majiwa and Kaloma, reported by Pickford (1984, 1986a). No fossils were found in Mogo paleosols.

Large collections from Maboko main excavation demonstrate well the difference between faunas of dambo wooded grassland (Yom pedotype) and riparian woodland (Dhero pedotype). As expected, the wooded grassland (Yom) nonprimate fauna is dominated by giraffoids (*Climacoceras*) and bovids (*Eotragus*, *Nyanzameri*, *Gazella*), with gomphotheres and deinotheres (*Protanancus*, *Choerolophodon*, *Deinotherium*), rhinos (*Brachypotherium*, *Dicerorhinus*) and pigs (*Libycochoerus*, *Listriodon*). The riparian woodland (Dhero) nonprimate fauna on the other hand is dominated by chevrotains (*Dorcatherium*) and other pigs (*Lopholistriodon*). Among rare animals, the dambo wooded grassland had more semiaquatic mammals (*Sanitherium*, *Kenyapotamus*) and aardvarks (*Orycteropus*) and riparian woodlands had more hyraxes (*Pachyhyrax*). The nonprimate fauna of nyika bushland (Ratong pedotype) is poorly known, but dominated by giraffoids (*Climacoceras*) and proboscideans. Comparable paleosols of the laterally equivalent Nyakach Formation reveal similar faunal differences, but are represented by smaller fossil collections (Wynn & Retallack, 2001).

Among primates, *Victoriapithecus macinnesi* is by far the most abundant (Tables 1 and 2). It is most abundant in riparian woodland (Dhero), marginally less abundant in dambo wooded grassland (Yom), and rare to absent elsewhere. *Kenyapithecus africanus* is also common, but is more widely distributed than *Victoriapithecus*. It is well represented in all pedotypes but the

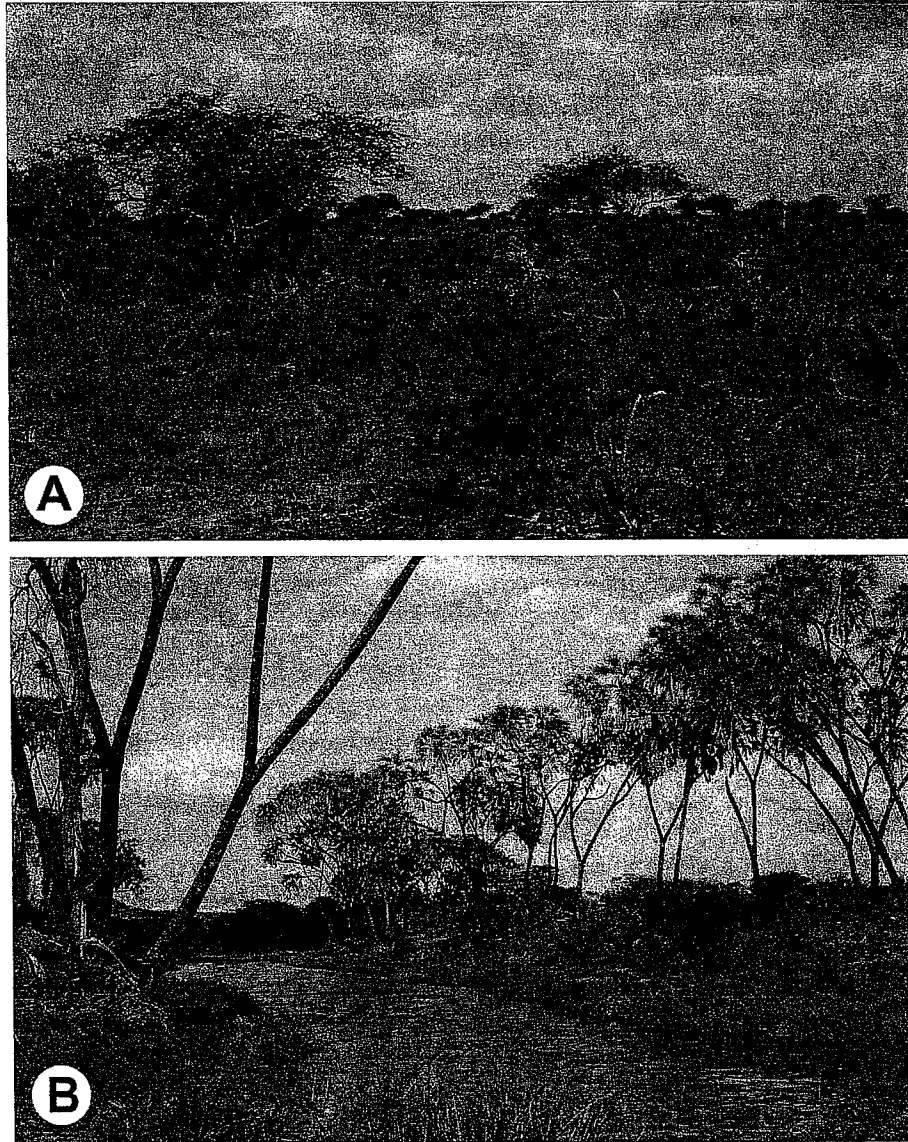


Figure 12. Comparable modern environment to middle Miocene of Majiwa Bluffs in Tsavo East National Park, Kenya: (A) nyika bushland (*Acacia* and *Commiphora*), near Crocodile Camp, on the Galana River, and (B) Doum palm (*Hyphaene coriacea*), thorn tree (*Acacia* spp.) and riparian marsh along the Tsavo River.

unfossiliferous Mogo, and is the most abundant primate in nyika bushland paleosols (Ratong). *Mabokopithecus clarki* and *M. pickfordi* are locally common, and with few exceptions derive from riparian woodland

(Dhero) paleosols. *Simiolus leakeyorum* had similar habitat preferences, though less strictly confined to a single pedotype. Another proconsuline (cf. *Limnopithecus evansi*) was not found in our excavations (or

tallies of Tables 1 and 2), and is of uncertain provenance. Only two specimens of bushbabies were found: the holotype of *Komba winamensis* from the green sand swale of Bed 3, and another species of *Komba* (undescribed) from a dambo wooded grassland paleosol (Yom).

Miocene Maboko compared with modern Kora

The Kora ecological reserve along the upper Tana River (Coe, 1985) shows instructive similarities and differences with our reconstruction of Maboko and Majiwa during the middle Miocene (Figure 13). The Tana River is flanked by a riparian fringe of thorn-tree (*Acacia tortilis*, *A. elatior*), tamarind (*Tamarindus indicus*), poplar (*Populus ilicifolia*) and Doum palm (*Hyphaene coriacea*), broadly comparable to vegetation envisaged for the upper Dhero paleosol of the main excavation at Maboko. Alkaline sandy soils of luggas, as envisaged here for other Dhero paleosols, support dense bushes of toothbrush tree (*Salvadora persica*) and edapal (*Dobera glabra*), which latter is known to preferentially accumulate iron-manganese nodules (Retallack *et al.*, 2000). Gray clayey soils of Monune lugga support seasonally waterlogged wooded grassland, with open grassy glades and isolated trees of myrrh (*Commiphora* spp.) and thorn tree (*Acacia* spp.), similar to vegetation envisaged for Yom paleosols. Saline seeps, like those envisaged here for Mogo paleosols, support thickets of saltbush (*Sueda monoica*). Well-drained soils of elevated floodplains, comparable to Ratong paleosols, support nyika wooded bushland and thicket, including thorn tree (*Acacia* spp.) and myrrh (*Commiphora* spp.) with little grassy cover. Shallow rocky soils around prominent inselbergs of Precambrian migmatites as Kora also support nyika wooded bushland of thorn tree (*Acacia senegal*), myrrh (*Commiphora africana*), and frankincense

(*Boswellia neglecta*), with occasional baobab (*Adansonia digitata*), mwangi (*Delonix elata*), lannea (*Lannea alata*) and spiny terminalia (*Terminalia spinosa*). Physiognomically comparable vegetation may have colonized degraded earlier Miocene lateritic paleosols and inselbergs of the metamorphic-granitic hills to the north during deposition of the Maboko Formation (Retallack, 1991a). Generally comparable vegetation can be envisaged for the paleosols at Maboko and Majiwa, but paleosols do not reveal floristic and ecological details. For example, a fossil flora from a Dhero paleosol in the middle Miocene (15 Ma) Nyakach Formation (Wynn & Retallack, 2001) indicates that the middle Miocene flora was probably less spinose, and that the grasses were less wiry than typical for modern vegetation of Kora.

Grassland currently occupies mainly the clayey luggas, which are a small proportion of the total area of the Kora Reserve. Coe (1985) argues that drought and fire recurring at intervals of tens to thousands of years allows flushes of grassland, followed by progressive invasion of woody and spiny shrubs that eventually dominate nyika. Such cycles are compatible with the pattern of paleosol superposition in the Maboko Formation, because Yom and Dhero paleosols have fine root traces and crumb structure of grasses and are more weakly developed than Ratong paleosols which lack any evidence of herbaceous grassy cover. Well-drained, sod grasslands are uncommon at Kora, and there is no evidence of them in the Maboko Formation (15 Ma), although they are evident from fossil soils and grasses at Fort Ternan and Kapsibor (14 Ma; Pickford, 1984, 1986a; Retallack, 1991a, 1992b).

Despite the small and scattered areas of grassland within bushland and thicket, Kora mammals include forms much more clearly adapted to grassland than any fossils from Maboko Island. Wooded grassland mammals at Kora include zebra (*Equus quagga burchelli*), giraffe (*Giraffa camelopardis*),

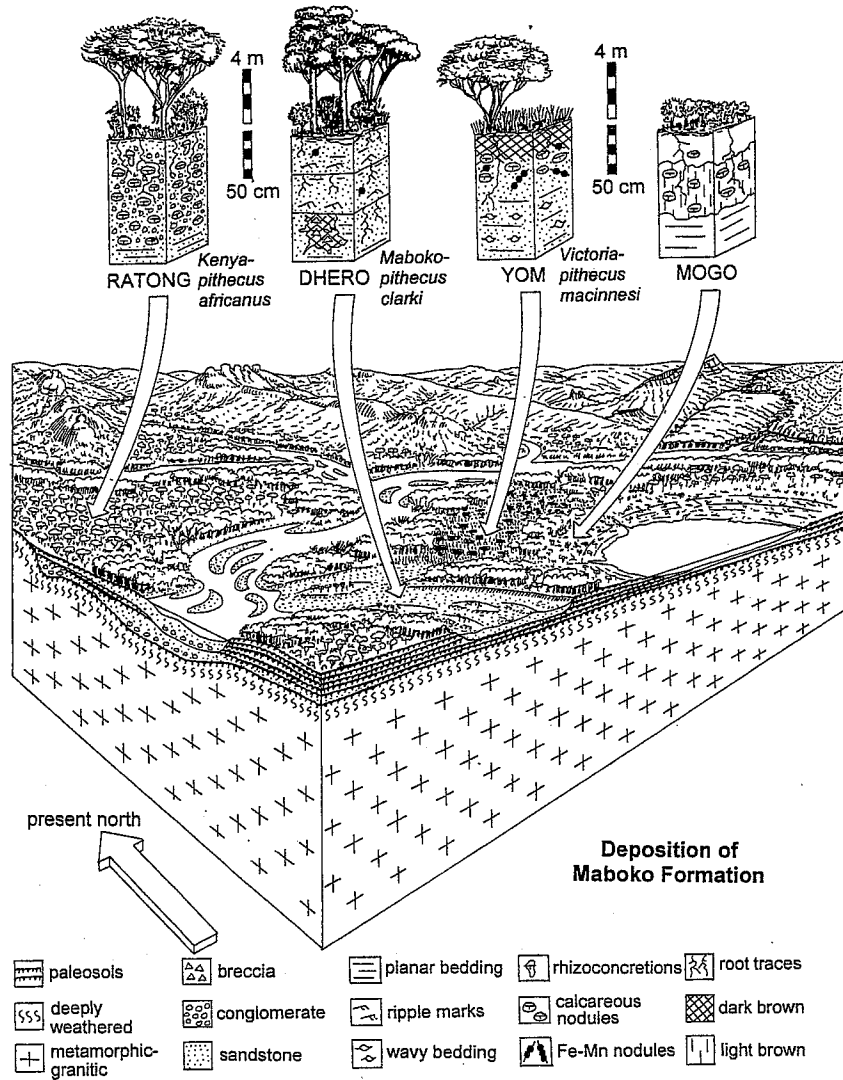


Figure 13. Interpreted paleoenvironments, soils and vegetation of the Maboko Formation, southwestern Kenya during the middle Miocene (15 Ma). While *Mabokopithecus* is virtually restricted to Dhero paleosols, *Victoriapithecus* is common in both Dhero and Yom, and *Kenyapithecus* ranged through all but Mogo paleosols.

gazelle (*Gazella granti petersi*), warthog (*Phacochoerus aethiopicus*) and cheetah (*Acinonyx jubatus*). The Maboko and laterally equivalent Nyakach Formations include the earliest giraffids and bovids in East Africa (Thomas, 1985; Pickford & Morales, 1994). Similar bovids of Fort Ternan

(Gentry, 1970; Kappelman, 1991) are less cursorial and hypsodont than the modern gazelles and giraffes of Kora. Semiaquatic mammals of Kora, such as hippo (*Hippopotamus amphibius*) are much larger and better adapted for prolonged submergence than semiaquatic *Sanitherium* and

Kenyapotamus of the Maboko Formation, which are found in near-stream (Dhero) paleosols. The hyraxes of Kora (*Procavia johnstoni* and *Heterohyrax brucei*) are small, and their preference for rocks and trees (respectively) is probably different from the larger hyrax (*Pachyhyrax championi*) of Maboko, which also was part of the near-stream (Dhero) fauna. Proboscideans of the middle Miocene included three distinct taxa, hoe tuskers (*Deinotherium hobleyi*), shovel tuskers (*Protanancus macinnesi*) and four tuskers (*Choerolophodon kisumuensis*: MacInnes, 1942), but there is only one elephant species today at Kora (*Loxodonta africanus*). The living aardvark (*Orycteropus afer*) is only a little less fossorial and slender than the Miocene aardvark (*Orycteropus chemeldoi*). The living dik-dik of Kora (*Madoqua kirkii*) is more gracile, but is the only small ungulate comparable with the Miocene chevrotain (*Dorcatherium pigotti*), which was most common in riparian woodland (Dhero) paleosols, but also found in dambo wooded grassland (Yom) and nyika bushland (Ratong). The living waterbuck of Kora (*Kobus ellipsiprymnus*) is comparably cursorial, but more hypsodont, than the common Miocene giraffoid (*Climacoceras africanus*), found in dambo wooded grassland (Yom) and nyika bushland (Ratong) paleosols. The Miocene gavial *Euthecodon* was an extinct sawtooth form (Buffetaut, 1979), and other Miocene crocodiles were larger, but similar to living crocodiles (*Crocodylus niloticus*) at Kora.

Among primates of Kora today, bushbabies (*Galago senegalensis*) are smaller, but similar to the Miocene species (*Komba winamensis* and *Komba* sp.), which are rare in a streamside swale and dambo wooded grassland (Yom), respectively. The living vervet (*Cercopithecus aethiops*) of Kora ranges not too far from streams, and is comparable in size and some semi-terrestrial adaptations to the Miocene monkey (*Victoriapithecus macinnesi*: Benefit, 1999a), found mainly in

riparian and dambo paleosols (Dhero and Yom). Kora has in addition two subspecies of wide-ranging baboons, the olive (*Papio cynocephalus anubis*) and yellow (*P. cynocephalus cynocephalus*), which are not especially similar to the Maboko kenyapithecine, but like it, range through most soils and vegetation. In locomotor adaptations, *K. africanus* has been compared with chimpanzees, but especially with macaques, such as the Barbary macaque (*Macaca sylvana*) of North Africa (McCrossin & Benefit, 1997; McCrossin *et al.*, 1998). Like baboons, Barbary macaques range very widely through a variety of habitats from high altitude cedar forests, to oak forests and lowland shrublands of *Olea*, *Ceratonia* and *Pistacia* (Fa, 1984). Some species of macaques are "weedy" in the sense that they flourish with human disturbance (Richard *et al.*, 1989), but the Barbary macaque is not one of these species. The Maboko riparian woodland (Dhero) proconsulines (cf. *Limnopithecus evansi*, *Simiolus leakeyorum*) and oreopithecines (*Mabokopithecus clarki* and *M. pickfordi*) are unmatched at Kora, although broadly comparable with red colobus monkey (*Colobus badius rufomitrans*) and mangabey (*Cercocebus galeritus galeritus*) common in gallery forest of the lower Tana River, near Hewani, Kenya (Andrews *et al.*, 1975; Kinnaird, 1992). Near Hewani, there are also vervets and baboons, and baboons range more widely into grassland and shrubland, especially during the dry season, than do vervets, mangabeys and colobus monkeys (Andrews *et al.*, 1975; Wahungu, 1998).

Nyika and dambo are not good habitats for colobines and mangabeys, and, as shown here from paleosol evidence, did not support arboreal proconsulines (*Simiolus*) and oreopithecines (*Mabokopithecus*), which remained in riparian woodlands most like forested habitats of early Miocene apes (Retallack, 1991a; Retallack *et al.*, 1995). But for semi-terrestrial monkeys (*Victoriapithecus*) and apes (*Kenyapithecus*),

nyika would have offered abundant small fruits and scattered shelter trees. Dambo habitats also offer scattered shelter trees, a large array of fruits, and abundant tubers, fowl and fish (O'Brien & Peters, 1999). Nyika and dambo remain good habitats for primates, such as the bushbabies, vervets and baboons of Kora (Coe, 1985).

Conclusions

Paleosols at Maboko and Majiwa with their shallow calcic horizons and pedogenic Na-montmorillonite indicate the driest paleoclimate and most open vegetation found at a fossil or living ape locality. Among the living great apes, the common chimpanzee (*Pan troglodytes*) is at the driest end of its range at Mt Assirik, Senegal, where mean annual precipitation is 954 mm, with a range of 854–1224 mm. Most chimpanzee habitats receive 1400–1870 mm/yr (Kappelman, 1993). Maboko–Majiwa paleosols were clearly much drier than Songhor–Koru paleosols (20 Ma), and discernibly drier than both Rusinga Island (18 Ma) and Fort Ternan (14 Ma) paleosols (Retallack, 1991a; Retallack *et al.*, 1995; Bestland & Krull, 1999). Even within the Rusinga Island record, paleosols of the Fossil Bed Member of the Hiwegi Formation (18 Ma; Retallack *et al.*, 1995) indicate drier conditions than those of the underlying Kiahera Formation and Wayondo Beds (19 Ma: Bestland & Retallack, 1993; Bestland & Krull, 1999) or overlying Kibanga Member and Sub-Lunene paleosol (17 Ma: Thackray, 1984). Similarly the basal paleosols in the Fort Ternan quarries (14 Ma) indicate a wetter climate and more wooded vegetation than those higher in the local sequence (Retallack, 1991a), which also include abundant pollen (Bonnefille, 1994) and leaves of open-country grasses (Retallack, 1992b; Dugas & Retallack, 1993). Comparable paleoclimatic swings are

also discernable in the middle to late Miocene Baringo Basin, judging from evidence of fossil plants (Jacobs *et al.*, 1999), carbon isotopic composition of tooth enamel and paleosols (Kingston *et al.*, 1994; Kingston, 1999) and paleolacustrine geochemistry (Renaut *et al.*, 1999). The idea of early Miocene tropical rain forest changing slowly to middle Miocene dry tropical forest (Andrews, 1992, 1996; Andrews & Humphrey, 1999) can be replaced with a dynamic model of climate and vegetation variation on short time scales (Figure 11) and in small areas (Figure 13).

Semiarid to arid paleoclimate for Maboko fossil mammals, more arid than for Fort Ternan, is also supported by evidence from fossil plants (Wynn & Retallack, 2001), fossil snails (Pickford, 1983, 1995) and the size gap in cenogram analyses of mammalian faunas (Cerling *et al.*, 1992; Muhlbacher *et al.*, 1998). Other analyses of the Maboko mammalian fauna interpret its habitat as "tropical forest, albeit a dry seasonal and probably deciduous one" (Andrews, 1992), or "dry to open forest, almost certainly strongly seasonal" (Andrews, 1996). The discrepancy with woodland–grassland–bushland mosaic proposed here may be because the Maboko mammal fauna lacks precise modern analogs, as is evident from principal coordinate and multidimensional scaling of mammalian faunal data (Andrews, 1996), as well as from more general arguments that Miocene faunas were evolving toward, but not strictly analogous to modern faunas (Retallack, 1994c). For example, *Climacoceras* and *Nyanzameri* from the Maboko and Nyakach Formations were among the most hypsodont and cursorial creatures of their time, but short of some modern ungulates in these open grassland adaptations (MacFadden, 2000). Finally there are mistakes, such as Maboko specimens misidentified as flying squirrels, which are forest gliders (Andrews *et al.*, 1981), later identified as mole rats, which are

grassland burrowers (Cifelli *et al.*, 1986; Winkler, 1992, 1994).

Climate aridity interpreted here from the paleosols at Maboko and Majiwa, may have had profound consequences for mammalian evolution. Pickford (1995; Pickford & Morales, 1994) has argued that an arid environment selected for horns and antlers in ruminants (such as *Climacoceras*), lophodonty in suids (*Lopholistriodon*), and cementum and choerodonty in proboscideans (*Choerolophodon*). Several ancient forest lineages became extinct during accumulation of the Maboko Formation: anthracotheres (*Brachyodus*), archaic pigs (*Kenyasus*, *Nguruwe*), and ungulates (*Sivameryx*). At the same time there appeared endemic newly-evolved forms: bush pigs (*Listriodon*, *Lopholistriodon*, *Conohyus*), early giraffelike ungulates (*Climacoceras*) and early bovids (*Nyanzameriyx*; Pickford & Morales, 1994).

Among primates, the fauna of Maboko was a notable turning point toward terrestrial adaptations (McCrossin, 1994; Benefit & McCrossin, 1995; McCrossin *et al.*, 1998). *Victoriapithecus macinnesi* was a small (3.5–4 kg) cursorial terrestrial or semiterrestrial species, with ischial callosities, mobile tail, and cursorial limb and foot proportions, like those of a vervet (*Cercopithecus aethiops*; Strasser, 1988; Harrison, 1989a; McCrossin & Benefit, 1992). The lophodonty of *Victoriapithecus* has been taken as evidence of fresh leaves in its diet, but wear patterns of its molars indicate a diet of mostly (ca. 79%) hard fruits (McCrossin *et al.*, 1998; Benefit, 1999a,b). *Kenyapithecus africanus* was a large (ca. 30 kg) ape, with procumbent incisors and proclined symphyseal axis like those of sclerocarp feeders, as also inferred for the other Miocene apes such as *Afropithecus* (Benefit & McCrossin, 1995; McCrossin & Benefit, 1997). Macaque-like semiterrestrial locomotion is indicated by the low, flat humeral head, elevated greater tuberosity, short intermediate phalanges, dorsal ridge of distal

metacarpal, and adducted hallux of *K. africanus* (McCrossin, 1994; McCrossin & Benefit, 1997). Compared with *Proconsul*, *Afropithecus* and earlier Miocene apes of tropical forest habitats (Retallack, 1991a; Retallack *et al.*, 1995), *Victoriapithecus macinnesi* ranged widely into nonforest vegetation at Maboko, from riparian woodland (Dhero paleosol) into seasonally waterlogged wooded grassland (Yom). *Kenyapithecus* was less abundant than *Victoriapithecus* in these same habitats, but extended also into nyika (Ratong paleosols), where it was virtually the only primate.

Primates unsuited to open vegetation also persisted as rare elements of the Maboko fauna, mainly in gallery woodland (Dhero paleosol) refuges. These include the small oreopithecines (*Mabokopithecus clarki* and *M. pickfordi*, both ca. 10 kg) and proconsulines (cf. *Limnopithecus evansi*, 4–5 kg, and *Simiolus leakeyorum*, 7 kg; Pickford, 1982b, 1985; Benefit *et al.*, 1998). Tooth morphology and microwear is evidence that they ate mostly leaves, and lesser amounts of fruit (Harrison, 1989b; Benefit, 1999a). In accord with this interpretation, *Mabokopithecus* was nearly confined to gallery woodland (Dhero paleosol), where *Simiolus* was most common, but significant numbers of *Simiolus* specimens were in dambo wooded grassland paleosols (Yom).

Bushbabies, *Komba winamensis* and another species of that genus (McCrossin, 1992) are rare at Maboko, in a Swale (bed 3) and a paleosol of dambo grassland (Yom bed 5w), respectively. Although confined to trees, these Miocene bushbabies may also have lived in open grassy woodland and wooded grassland like the modern bushbabies (*Galago senegalensis*) of Kora (Coe, 1985), rather than being restricted to rain forest like living *Galago demidovii*.

Five middle Miocene ape species at Maboko (Table 1) and five at Fort Ternan (Harrison, 1992) are slightly reduced diversities compared with early

Miocene sites such as Songhor and Koru (Andrews, 1981b; Retallack, 1991a), and may be related to the spread of drier climate and more open vegetation than earlier in the Miocene, as indicated by paleosols at these sites. Bushbabies, proconsulines and oreopithecines survived these changes because Miocene vegetation in Kenya remained a mosaic of forested and nonforested habitats (Retallack, 1991a; Kingston *et al.*, 1994; Hill, 1999; Kingston, 1999). *Victoriapithecus* retained some primitive catarrhine features, but also acquired locomotor and other adaptations of vervets and baboons (Benefit & McCrossin, 1997). *Kenyapithecus africanus* also acquired semi-terrestrial adaptations distinct from its arboreal catarrhine ancestors, and may have been ancestral to the subsequent evolutionary radiation of modern African hominoids (McCrossin & Benefit, 1993). Late Miocene cercopithecoids remained well adapted to aridlands, but there was an evolutionary return of colobine and other monkeys to forest habitats (Pickford & Senut, 1988; Benefit, 1999a,b; de Bonis *et al.*, 1999). Evidence from associated paleosols shows that Miocene apes such as *Kenyapithecus wickeri*, and *Samburupithecus*, and early hominids such as *Ardipithecus*, continued to show preference for wooded parts of vegetation mosaics (Retallack, 1991a; White *et al.*, 1994, 1995; Ishida & Pickford, 1997; Sawada *et al.*, 1998; Haile-Selassie, 2001), while avoiding the earliest well-drained C₃ grasslands (Retallack *et al.*, 1990; Retallack, 1991a; Cerling *et al.*, 1997b). Grasslands do not appear to have supported hominids until some 4.2 Ma, with *Australopithecus anamensis* the earliest hominoid fossils actually found in paleosols of sod grasslands (Leakey *et al.*, 1995, 1998; Wynn, 2000). Grasslands have long been considered critical to human evolution (Darwin, 1872), but their role appears to have been limited and late. Nor was African ape and monkey evolution limited to forest and woodland

like those inhabited by modern colobines, chimpanzees and gorillas. Rather, Miocene apes and monkeys evolved in a variety of forests, woodlands, dambo wooded grasslands and nyika shrublands.

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